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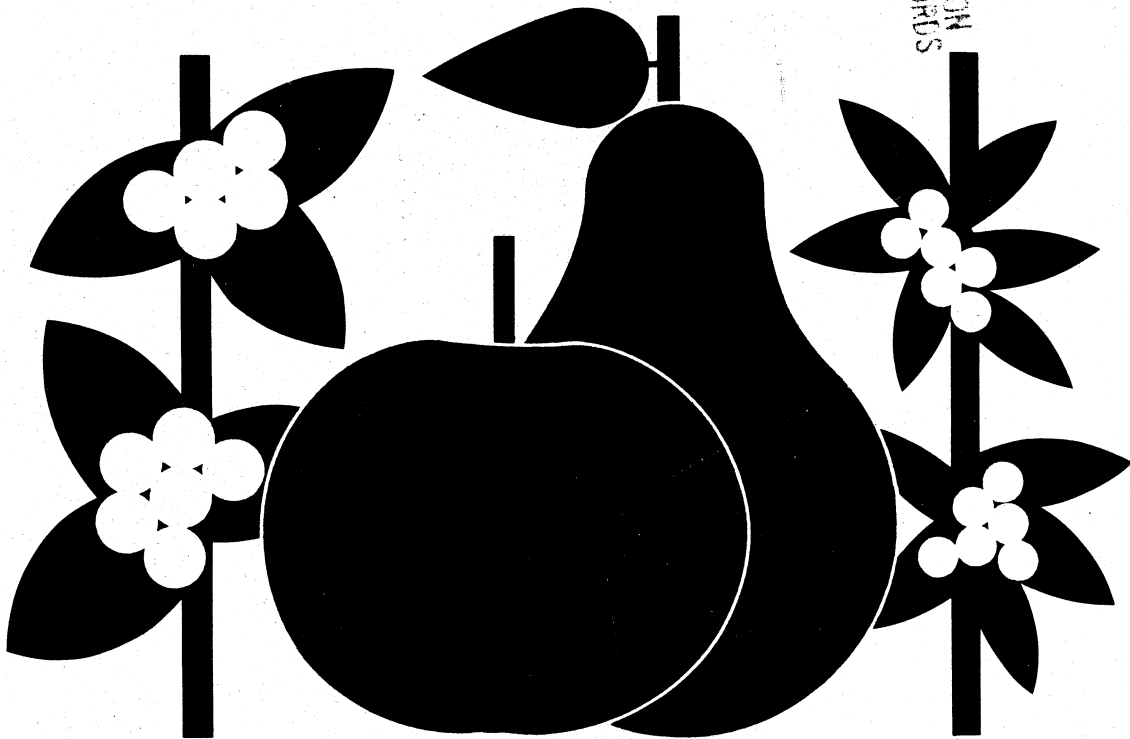
FIRE BLIGHT

A BACTERIAL DISEASE
OF ROSACEOUS PLANTS

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AGRICULTURE
HANDBOOK
NUMBER 510

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FIRE BLIGHT

A BACTERIAL DISEASE OF ROSACEOUS PLANTS

By
TOM VAN DER ZWET and
HARRY L. KEIL
Research Plant Pathologists

Fruit Laboratory
Beltsville Agricultural Research Center
Beltsville, Maryland 20705



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FIRE BLIGHT

A BACTERIAL DISEASE OF ROSACEOUS PLANTS

During 1965–76, an intensive search was made for all available literature on fire blight with the assistance of personnel at the Library of Congress and the Computer Service of the National Agricultural Library. The amount and classification of this literature, published since 1870, are shown in figure 1. Even though the number of publications varied between years, some peaks prior to 1960 were attributed to certain discoveries or other important phases of fire blight research. The increase in publications from 1960 to 1976 was attributed to the follow-

ing factors: (1) First occurrence of fire blight in 1957 and its subsequent spread in Europe, (2) more widespread use of the electron microscope and scanning electron microscope in research, (3) emphasis on studies of internal and epiphytic populations of *Erwinia amylovora* in and on plant tissues, and (4) increased investigations on the nature of fire blight resistance in pear, apple, and ornamental rosaceous plants. Only about 15 percent of the fire blight literature was published outside the United States, principally in Canada, New Zealand, England, Denmark, West Germany, and the Netherlands. The literature search was terminated as of December 31, 1976. Since then we have included several articles that were sent to us or were printed during 1977.

The historical review of fire blight in this publication covers the period 1780–1920 and is followed by a critical analysis of the literature from 1921 to 1976. The section on chemical control is separated into two parts, with the advent of antibiotics in 1950 as the dividing line.

Since 1900 only a few brief reviews on fire blight were published. In 1928, Groves (1104)¹ prepared a master's thesis with 208 reference citations, equaling about 65 percent of the available literature at that time. In 1930 and 1951, Elliott (266, 267) wrote two manuals on bacterial plant pathogens, which included *E. amylovora*. In 1974, three articles appeared in different parts of the world—in California by Schroth et al. (847), in Great Britain by Eden-Green and Billing (257), and in West Germany by Zeller (1046) in German. Our review was prepared to serve as a complete and comprehensive analysis of all available literature in the world. Of approximately 2,000 known references, 63 percent are referred to in the text.

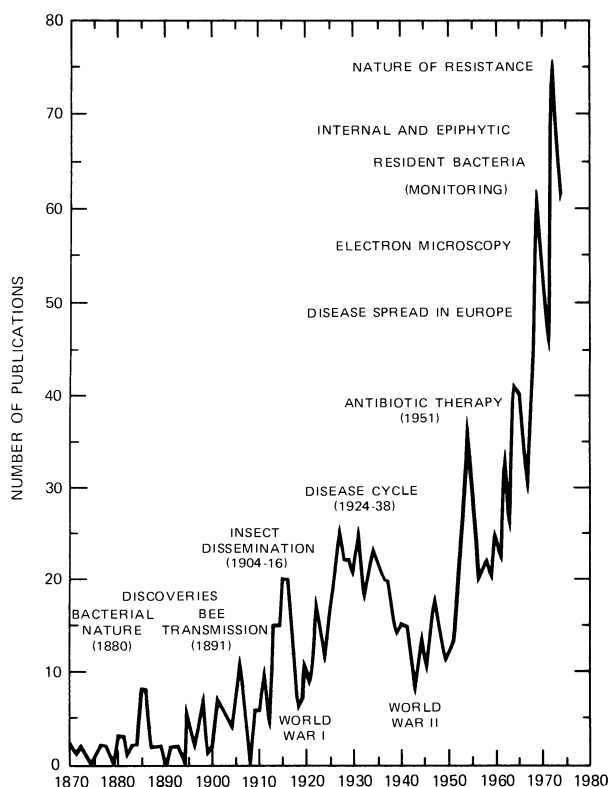


FIGURE 1.—Amount and classification of literature on fire blight, 1870–1976.

¹ Italic numbers in parentheses refer to Literature Cited, p. 154.

CHAPTER 1

HISTORICAL REVIEW

Fire blight, caused by *Erwinia amylovora* (Burr.) Winslow et al., is undoubtedly the oldest, most serious, and perplexing bacterial disease of pomaceous fruit trees. It is very destructive to pear and less so to apple, quince, and several other members of the family Rosaceae. Even though the actual coining of the name cannot be traced, the term "fire blight" was well chosen. Trees with blighted branches and persistent blackened leaves appear scorched. Although its original name is English, the disease is known in many other languages.

Fire blight is apparently indigenous to North America. It was first noticed in the late 18th century in New York and was not reported from any foreign country until over a century later. The disease probably occurred on native American plants, such as crab apple, hawthorn, and mountainash. From these native hosts the bacterium probably spread to the susceptible cultivated pears and apples planted by the early American settlers.

The three principal pome fruits, pear (*Pyrus communis* L.), apple (*Malus sylvestris* Mill.), and quince (*Cydonia oblonga* Mill.), are indigenous to eastern Europe and southwest Asia between Kashmir and the Caspian Sea (625). Many years before the beginning of the Christian Era, cultivated pears and apples were known to the Greeks. According to Magness (624), Theophrastus mentioned wild and cultivated pears and described the art of grafting. Pliny, of ancient Rome, named more than 30 pear and apple cultivars. With the migration of the Romans, the pome fruits were distributed throughout the temperate regions of Europe. During the 18th and 19th centuries, much interest developed in pear breeding in France and Belgium. Van Mons (1765–1842), a physician and pharmacist in Louvain, Belgium, at one time had 80,000 pear seedlings in his gardens and originated over 400 cultivars, 40 of which have proved of lasting value.

The history of pome fruit growing in North America began when the early settlers brought seeds to the New World and possibly grafted trees of European cultivars. George Menifie, who came to Virginia in 1623 and settled along the James River,

had a famous orchard of apple, pear, and cherry trees (307). Taylor (927) mentioned that grafted apple trees were recorded in Virginia as early as 1647. In 1726, Dudley (*in* Fletcher, 307) stated that "our apples are without doubt as good as those of England, and much fairer to look to, and so are the pears." By 1771, the Prince Nursery on Long Island listed 42 pear cultivars in its catalog. Quince never became as popular as pear and apple, and only a few commercial plantings exist in America today.

Early Theories (1780—1880)

The first printed notice on fire blight was a report taken from a letter by William Denning, dated December 22, 1793, which was published in the "Transactions of the New York Society for the Promotion of Agricultural Arts and Manufacturers" (218). Denning saw the "disorder" on apples, pears, and quinces in the Highlands of the Hudson River Valley as early as 1780 and suggested that it was caused by a borer in the tree trunks, which he had found after much labor.

He stated: "In the first I discovered two worm holes, running perpendicular from the tap-root up through the heart; these holes were large enough to admit a common pipe-stem, and reached about fourteen inches above the surface of the ground, and from each hole I screwed out a worm." In the final paragraph he stated: "As I am confident I have discovered it, the next step is to find a remedy; as I have not yet succeeded, I submit it to the consideration of the Agricultural Society, whether a publication of the real cause of the disorder may not lead to a discovery that may tend to stop the ravages of the worm."

Not much was published on fire blight during the next 25 years until 1817, when William Coxe (187) mentioned it in his book "Cultivation of Fruit Trees." He presumably gave it the name "fire blight" and described it as a disease that "frequently destroys trees in the fullest vigor and health, in a few hours turning the leaves suddenly brown, as if they had passed through a hot flame and causing a morbid matter to exude from the pores of the bark,

of a black ferruginous appearance.” He reported the pear cultivar St. Germain as very susceptible and Seckel as quite resistant.

In 1826, Lowell (593) suggested the “insect” theory as the cause for fire blight and stated that *Xyleborus dispar* (F.) (as *Scolytus pyri* Peck) was killing the limbs. He suggested as the most satisfactory control measure the removal and burning of diseased branches 30 cm below the lowest mark of discoloration. A few years later Fessenden (300) mentioned the same insect, followed in 1844 by reports of additional insects (79), as the cause of fire blight. In 1837, the Pennsylvania Horticultural Society offered “a premium of five hundred dollars to be paid to the person who shall discover and make public an effective means of preventing the attack of the disease usually termed pear blight” (306). This offer brought forth many suggestions, such as soaking the ground with soapsuds, wrapping limbs with rags sprinkled with brimstone, and driving rusty nails into the tree to give it “an iron tonic.”

Until this time *X. dispar* (as *S. pyri*) was thought to infest only pear trees, but the same insect was soon also discovered in the limbs of apple trees. Beecher (79), who considered early fall freezes as the cause of pear blight, mentioned an unidentified writer in the “Farmer’s Advocate” in Jamestown, N.C., who had traced the blight to “small, red, pelucid insects, briskly moving from place to place on the branches.” In addition, the ambrosia beetle (*Xyleborus dispar* F.) was also believed to cause fire blight (69).

Even though the insect theory became rather well accepted, there were many who could not believe it, for no other reason than the lack of explanation for the oozing of the branches. With this symptom in mind, thoughts were turning more and more to early freezes in the fall of the year, and thus frozen sap in the branches was suggested.

In 1845, Downing (225) wrote in “Fruits and Fruit Trees of America” that the problem of fire blight should be considered as two distinct diseases. He treated these individually under the headings “insect blight” and “frozen-sap blight.” He described the former as a summer blight caused by the insect *S. pyri* in the young shoot growth. Symptoms of the latter were (1) “the appearance, at the season of winter or spring pruning, of a thick, clammy sap, of a sticky nature, which exudes from the wounds made by the knife,” (2) “the appearance, in the spring, on the bark of the trunk or branches, often a considera-

ble distance from the extremities, of black, shrivelled, dead patches of bark,” and (3) “in early summer months, the disease fully manifests itself by the extremities shrivelling, turning black, and decaying, as if suddenly killed.”

Downing explained his theory at great length by saying that early autumn freezing would change and poison the sap and that the poison, in turn, would be distributed by the movement of the sap in the spring. In support of his theory he also pointed out that those cultivars that ripened their wood early in the fall, like the Seckel, would be the least affected. As preventive measures, he suggested avoiding the use of wet land and unduly enriched soils, late summer pruning, and the culture of pear cultivars that ripen their wood late.

Additional proof for the frozen sap theory was that 1832 and 1844 were serious blight years in Indiana that were preceded by early and severe autumn freezing (79). In addition, an orchard favorably located to ripen its wood early in 1843 had no blight in 1844, whereas all neighboring trees were affected. Spring frosts were not considered to cause blight, for in 1844 they were severe in May, and no blight followed. In Georgia, White (1022) did not accept the frozen sap theory for the simple reason that sap never froze in the warm climate of this State.

In 1846, Eaton (255) published a review of the opinions on pear blight and considered, besides the insect and frozen sap blight theories, the following less publicized theories for the true pear blight: (1) The effect of electricity and atmospheric changes, since diseased trees were often noticed after a thunderstorm, (2) old age or long duration of pear cultivars, and (3) epidemics transmitted by the air, like pneumonia or yellow fever. After careful consideration and examination of his own orchard, Eaton accepted Downing’s frozen-sap theory “in order to give the best accord with facts.”

In 1846, Gookins (355) disagreed with Beecher that freezes change the tree sap to poisonous juices, but he considered the blight a “disease of the circulation.” He had visited Mr. Ragan of Putnam County, Ind., who had obtained fire blight symptoms after introducing a small quantity of diseased sap into an incision in the bark of a young pear tree in the nursery. This was the first known account of the experimental reproduction of fire blight without any knowledge of the actual causal agent.

From 1848 to 1863 the theories as to the cause of fire blight became more confusing. Ernst and

Downing (277) introduced a new “sun scald” theory and ascribed the disease to the heat of the sun, assisted by raindrops acting as lenses. They described the effect as to “scald the sap, burst their vessels, and produce precisely the same results that a scorching fire would.” One of the remedies they suggested was to select cultivars with wood “of a compact texture and slow of growth.” One of the main reasons in favor of the sun scald theory was that summer temperatures were considerably higher in the eastern and central United States as compared with those in the pear-growing countries of northwestern Europe.

In an editorial in the “Horticulturist,” Downing (226) suggested whitewashing the trees during the winter to prevent scalding. In 1848, Wendell and Downing (1013) reported washing trees with lime the previous fall but still losing 15 trees from blight affecting the trunks, although never before had they lost a tree from this disease. In turn, Downing commented that pear blight might not have been due to freezing but to the sun’s rays acting in summer on spots where the lime had been washed off by the showers.

During the next several years the arguments as to the cause of fire blight remained between the insect *S. pyri*, the frozen sap theory, and the sun’s rays, but none seemed sufficiently satisfactory (106, 276, 471, 472). In 1850, Kennicot (519a) reported the disease especially prevalent and severe throughout Illinois, where the general opinion was that the blight was caused by insects. He therefore looked closely for insects and concluded that the insects which killed the twigs did not produce true blight and those which did not kill the twigs had nothing to do with the disease.

By 1860 the knowledge about fungi causing plant diseases was slowly becoming more widespread, in particular that of the potato late blight epidemic in Ireland, a disease with symptoms closely resembling those of fire blight. The first known report suggesting a fungus as the causal organism of fire blight appeared in 1863, when Salisbury and Salisbury (829) described in detail several fungi belonging to the Fungi Imperfecti. They referred all of them to one species, named it *Sphaerotheca pyrus* Salisb., and spoke of it as a “discovery of the cause of fire blight.”

By 1867, Meehan (634) theorized that cells were weakened by frost or other injury and the presence of fungi. He proposed a “fungal” theory as the main

cause of fire blight, even though he also considered insect blight due to *S. pyri* and frozen sap blight. He believed fire blight was caused by the inability of the tree to maintain in a given plant part “heat enough to maintain life.” He commented that the parasitic fungus grew in the bark “causing fermentation,” and that, when it girdled the limb, it prevented the sap from rising and thus killed the portion above the girdled limb “as if cut away or thrown onto the fire.”

In 1868, Hull (455), a physician and fruit grower in Alton, Ill., spoke of seeing small “cells” under a “powerful microscope” and referred to these as fungi. He stated that “blight is induced by an extremely minute fungus” whose spores enter the tree through pores of the bark. Later he grafted small slices of bark with enough wood from diseased apple shoots into succulent pear shoots. After 34 days all were found blighted and the disease had extended up to 5 cm above and 8–36 cm below the wounds. Thus he also proved that fire blight was a transmissible disease and concluded that “the fungi causing pear and apple blight are identical” (457). Hull also practiced root pruning as a remedy for blight control for many years to force early setting of terminal buds (455, 456).

During 1870–80, several investigators reported on fire blight, some favoring the fungal theory but others not (70, 390, 926). In 1875, Kirtland (530) attempted to correlate certain human diseases with this disorder to explain blight epidemics and believed that an atmospheric organism was a more plausible cause for fire blight than any of the previous theories.

Bacterial Origin and Disease Transmission (1881—1900)

Even though bacteria generally have been known since about 1676, when van Leeuwenhoek first described the “very little animalcules,” it was not until the late 1800’s that real emphasis was placed on their importance by such researchers as Pasteur, Koch, and Bijerinck. In April 1870, Thomas J. Burrill (fig. 2) began his lifelong career at the University of Illinois to study the devastating pear blight disease. Six years later in his first report he still accepted the fungal theory as a cause of fire blight (129). He stated that “the cambium of the blighted branch is filled with very minute moving particles, very similar to those known as Spermatia in fungi and other low plants.” At this point Burrill was standing on the



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FIGURE 2. —Thomas J. Burrill (1839–1916).

threshold of discovering the true nature of the causal organism of fire blight.

In 1878, he (129) stated that in “the mucilaginous fluid from the browned tissues under our microscope, the field is seen to be alive with moving atoms known in a general way as bacteria and . . . are discovered in advance of the discolored portions of the tissues.” He concluded that “so far as I know, the idea is an entirely new one – that bacteria cause disease in plants – though abundantly proved in the case of animals.”

In June 1880, Burrill’s attention was again drawn to the blight problem by an unusually destructive outbreak of pear blight in his neighborhood. That summer he inoculated healthy pear and apple trees with material taken from other pear trees affected with blight. Sixty-three percent of the inoculated trees became diseased, and typical characteristic symptoms of fire blight appeared 9 days later. Based on these observations Burrill presented in 1880 his epoch-making contribution in the field of plant pathology to the annual meeting of the American Association for the Advancement of Science (130).

Besides the name fire blight and apple twig blight, he also called the disease “anthrax of fruit trees,” since he considered the organism to resemble the

anthrax bacillus or the “vibron butyrique of Pasteur and the *Bacillus amylobacter* of van Tieghem.” The earliest pictures of the bacterium were published in 1881 (132). It was not until 1882, however, that Burrill (133, 134) published the description of the bacterial species and named the blight pathogen *Micrococcus amylovorus*.

In 1881, Peffer (733) in Wisconsin was the first to report that fire blight started in the flowers, but he did not accept Burrill’s bacteria theory since his inoculation experiments failed to induce the disease without puncturing the shoot. He sent specimens of these blighted blossoms and twigs to Burrill, who accepted Peffer’s theory that blight could start in the blossoms. However, Peffer still believed in the frozen sap theory followed by fermentation of the tissues with the beginning of warm weather.

Even though Burrill discovered the bacterial origin of fire blight, named the causal organism, and performed several inoculation experiments, he never isolated the bacterium in pure culture nor reinoculated it into healthy tissues to prove definitely that *M. amylovorus* was the real causal agent.

In 1884, Arthur (47) at Geneva, N. Y., performed several cross-inoculation experiments with pears, apples, quinces, hawthorns, and juneberries. He isolated and grew the bacteria by means of a succession of artificial cultures in a sterilized infusion of cornmeal. He then separated the bacteria from their juices, filtered a strong infusion of blighted pear through a porous earthenware vessel, and inoculated the bacteria and the filtrate into green Bartlett fruit. After 1 week, fruits inoculated with the bacteria were thoroughly blighted, whereas those treated with the filtrate showed no signs of infection.

Thus in 1885, Arthur (1081) presented the first doctoral dissertation on the blight organism and concluded that the bacteria were the direct cause of the disease (44). During 2 years he published many reports on fire blight, including descriptions of blight symptoms, growth and development of the bacterium in culture media, and the application of control measures through limb removal and the use of lime and sulfur (45, 46, 48–52).

Up to this time the blight organism was known and observations had shown that the disease started in flowers and shoots, but no one had actually observed how the bacteria reached these plant parts. As early as 1884, Forbes (317) observed blight lesions associated with feeding of the tarnished plant bug (*Lygus lineolaris* (Palisot de Beauvois)) (as *L.*

pratensis L.), and with only observational evidence he considered that this insect was acting as a vector of the disease.

In 1890 at the U.S. Department of Agriculture (USDA), Merton B. Waite (fig. 3) was the first to undertake a research project on fire blight. He soon discovered that the blight organism could enter blossom nectaries without punctures and that bees spread the bacterium from infected to healthy pear flowers (986–988). He was able to start a small-scale artificial epidemic by infecting the flowers of a few pear trees on the edge of an orchard and allowing free access of bees. When he protected some flowers with mosquito netting, they remained free from blight. In 1901, Waite (994) stated, “we have scarcely been able to find a direct normal method of introduction of the disease to twigs without the introduction of some mechanical or insect puncture.” He observed up to 40 species of insects visiting pear blossoms, many of which were shown experimentally to be carriers. In 1904, he reported that insects not only distributed the blight organism but that they were active agents injecting the germs into the tissues (995).

In 1895, Waite (989) stated that “after prolonged investigations the complete life history of the microbe, *Bacillus amylovorus* (Burr.) Trevisan, has been worked out” and that the removal of late infections in the fall is “the preventive remedy for pear blight.” In 1898, he published the earliest account of some of the cultural characteristics of the blight pathogen (993). Waite became the first to isolate a “false yellow germ”² from blight-infected tissues, and he was also the first to establish a pear-breeding program for fire blight resistance.

Waite’s (991) chapter on fire blight in the 1895 USDA “Yearbook of Agriculture” was the first detailed account of the disease at that time. He and others during this period agreed that the only satisfactory method of controlling pear blight was to prune the blighted parts of the trees far below visible blight symptoms, followed by burning all diseased branches (190, 896, 910, 992, 999). At this time the succulent watery shoots were generally known to be susceptible to blight infection. Wood ashes and ground bone were being recommended to induce early maturation of the wood.

In New Jersey, Halsted (377) conducted a detailed, long-range experiment to test the effect of

summer or winter pruning on the Kieffer pear cultivar grown in cultivated or sodded rows with or without barnyard manure or commercial fertilizers. He found differences in tree yields not significant and blight incidence inconsistent.

A more detailed description of the new concept of phytobacteriology and the significance of the discoveries by Burrill, Arthur, and Waite was published in 1971 by Baker (61).

Nature, Dissemination, and Disease Control (1901—20)

In 1901, Chester (171) in Delaware was the first to report on a rather detailed inoculation experiment, in which he tried to determine differences in susceptibility between leaves, fruit, buds, succulent shoots, and older wood of pear. He concluded that pears became infected only by direct inoculation if the surface was injured. Only the more tender succulent tree tissues became infected.

In New York, Whetzel (1016, 1017) and Whetzel and Stewart (1018) made detailed studies on the nature and role of blight cankers in apple trees. These were the first and most extensive reports ever published, with numerous photographs of limb, crotch, trunk, and collar cankers.

In Colorado, Sackett (826) determined that 20 percent of blight cankers on small limbs and twigs contained virulent bacteria at the time of tree blossoming.

In 1905, Chisholm (172) used the term “zymotic” pear blight to distinguish the true bacterial blight from insect, frozen sap, and summer blight. Control of the disease was recommended through early maturation of shoots in the growing season and rigorous pruning of blighted branches with emphasis on disinfecting tools.

At the U.S. Department of Agriculture, Erwin F. Smith (fig. 3) was beginning to attract international fame with his extensive research in the newly established field of phytobacteriology (875). In 1905, he was the first to publish detailed accounts of the bacteriological and cultural characteristics of many bacterial plant pathogens, including *B. amylovorus* (876). Of special interest are his detailed studies on flagella stains and the detrimental effect of direct sunlight on the growth of the blight pathogen in vitro. In 1912, Smith (877) reported on a new plating and identification technique to classify bacteria on the basis of their Gram stain. This was the first record of *B. amylovorus* being rod shaped, motile,

² Unpub. data, Fruit Lab., U.S. Dept. Agr., Beltsville, Md.



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FIGURE 3.—Pioneers in pathology and bacteriology of fire blight at the U.S. Department of Agriculture about 1900: *Left*, Merton B. Waite (1865–1945); *right*, Erwin F. Smith (1854–1927).

and a Gram-negative bacterium. His first textbook (878) on bacterial diseases of plants in 1920, in which he devoted 30 pages to fire blight, established the field of phyto bacteriology.

In 1913, Bachmann (55) presented the first definite account with camera lucida drawings that fire blight bacteria travel mainly through the intercellular spaces of the host tissue. In Oregon, McCormick (1116) made the first histological studies of pear tissues and indicated no differences in the cell wall thickness and the size, arrangement, or position of the intercellular spaces between resistant and susceptible pear species or cultivars.

In Washington orchards, Heald (393) observed that blight bacteria were able to enter the leaves of apple and pear without apparent injury to the tissues. He noted all stages of leaf invasion, from slight marginal infections to lesions that had advanced throughout the entire leaf blade and down the petiole. Several years later Heald (394) confirmed his observations through artificial inoculations.

Under Wisconsin conditions, Reinking (1127) confirmed previous observations that *B. amylovorus* is very sensitive to rapid drying conditions. All attempts to isolate the organism from twigs blighted the previous season failed, and he never observed any advance of the disease during the winter or ooze production from cankers in the spring. Fulton (318) also was unable to inoculate healthy apple twigs with pieces of blighted tissues from branches cut several months before. He concluded that the blight organism died rapidly in pruned twigs left on the ground. In Washington,

Hotson (434) observed that blight exudate on branches or fruit remained alive 10–13 days when exposed to direct sunlight. When oozing branches were left on the ground, partly shaded, or in a cover crop, live bacteria were isolated about 30 days after the limbs were cut.

During 1912–20, several interesting observations were made on the epidemiology of fire blight. In New York, Stewart (1135) wrote the second dissertation on fire blight, in which he covered nearly all phases of the nature, life cycle, and control of the disease. He added considerably to the knowledge of bacteriology of *B. amylovorus*, mentioned several additional insects disseminating the disease, and placed considerable emphasis on precautions to prevent disease spread through contaminated pruning tools. In Oregon, O'Gara (704) appears to be the first to mention small bacterial strands (cirri) extending from lenticels of infected pear fruit. He was also among the earliest to prove that certain insects were definite carriers of the blight organism by capturing insects from blighted orchards and allowing them to walk on culture media. Pathogenicity of the resulting cultures was proved by inoculation studies (703).

In 1915, Stewart (904) was the first to mention the effect of hail on severe outbreaks of fire blight. He observed numerous infections on branches and trunks of 2-year-old trees of the Bartlett pear cultivar in a nursery and on 4-year-old trees in an orchard 2 weeks after the trees were struck by a severe hailstorm. The following year, Hotson (433) confirmed similar observations in the Yakima Valley of Washington. On many trees, few twig infections occurred, but 50–60 percent of the fruit was severely blighted.

In 1917, Gossard and Walton (360) reported that rain proved to be an important carrier for fire blight. Branches protected by cheesecloth, located below artificially inoculated blossoms, showed a high percentage of infection. However, check trees, protected from rain drip by oilcloth or from insects by cheesecloth, remained free from blight. The following year, Stevens et al. (898) reported their observations on possible wind dissemination of blight bacteria, but their evidence was inconclusive.

In addition to these meteorological factors, it became evident that rich soils, heavy manuring, use of large quantities of commercial fertilizers containing a great deal of nitrogenous material, irrigation, and severe pruning tended to stimulate the growth of tender, succulent shoots, which in turn increased the

chance and degree of blight development (461, 825, 904, 995, 1023).

Following the pioneer work of Waite on the insect dissemination of fire blight, many investigators reported on different phases of the blight-insect relationship. In 1909, Whetzel and Stewart (1018) concluded on observational evidence that aphids and leafhoppers were largely responsible for introducing the blight germ into the tips of growing shoots. These insects and the curculio were frequently observed inflicting wounds in the fruit.

According to the observations and experimental evidence by Jones (484) in Ontario, a large proportion of the new twig infections, including most of those that occurred after the blooming period, appeared to be due to dissemination and inoculation of the bacterium by aphids, particularly *Aphis mali* F. and the woolly aphid *Eriosoma lanigerum* (Hausmann) (as *Schizoneura lanigera* Hausm.). He also found aphids to be the principal means of spreading the disease in apple nurseries and traced many cases of blight in pear trees to wounds made by the shothole borer (*Scolytus rugulosus* (Ratzeburg)). These beetles were also found in apparently healthy bark that later developed blight near their borings. In 1911, Jones (485) proved experimentally that this beetle carried and injected the blight germ.

In 1913, Stewart (901, 902) observed that fire blight was spread by the apple aphid (*Aphis pomi* De Geer) in quince nurseries. However, he found the tarnished plant bug much more important in the dissemination of the blight organism in nursery stock. Stewart showed that these insects visited blighted tissues, became smeared with the gummy exudate, carried the bacteria to the tender succulent shoot tips, and inadvertently inoculated the tissues while sucking the sap, with the result that the twigs soon developed typical fire blight.

Referring to the collar blight form of fire blight on apple trees, Orton and Adams (714) stated that apple tree borers were probably the most active agents in spreading blight. They found in 90 percent of the observations that these borers had been associated with the disease at the collar. They did not determine whether these insects were direct carriers or only provided points of entry for the blight germ. On account of the almost universal presence of the woolly aphid in collar blight cases in Pennsylvania, this aphid was thought possibly to be the carrier of the organism to the wounds made by the borers.

In 1914, Reed (770) attributed large numbers of

insects, particularly honey bees (*Apis mellifera* L.), to an unusual outbreak of apple blossom blight. He considered that this epidemic was due to the concomitant presence of large numbers of blossoms, insects, and holdover cankers. In New York, Stewart and Leonard (905, 906) proved by direct experimentation in apple seedlings that the following insects could disseminate and inoculate the blight pathogen: A leafhopper (*Empoasca fabae* (Harris) (as *E. mali* (Le Baron))), a capsid (*Plagiognathus politus* Uhler), and four sucking insects (*Campylomma verbasici* (Meyer), *Orthotylus flavosparus* (Sahlberg), *Polymerus basalis* (Reuter) (as *Poeciloscytus basalis* Reuter), and *Adelphocoris rapidus* (Say)). They considered the tarnished plant bug and *C. verbasici* particularly important because of their abundance in nurseries and preference for succulent shoot tips. The pear psylla (*Psylla pyricola* Foerster) and two species of fly (*Pollenia rudis* (F.) and *Homoneura bispina* (Loew) (as *Sapromyza bispina* Loew)) gave negative results.

In Wisconsin, Burrill (128) demonstrated experimentally that the aphid *Macrosiphum avenae* (F.) (as *Aphis avenae* (F.)) and leafhoppers carried the blight organism and inoculated it into the wild crab apple (*Pyrus coronaria* L.). In Kansas, Merrill (641-643) observed a direct relationship between aphid infestation and the amount of blight infection and demonstrated that aphids deposited their eggs in blight cankers and other rough places in the bark. Soon after hatching from the eggs in the spring, the young crawled through the blight exudate.

By 1916, Gossard (357, 358) in Ohio reported on the role of beehives in the spread of fire blight. He found that the blight organisms remained alive and sufficiently virulent after 47 hours' incubation in sterilized honey and 71 hours in aphid honeydew. A few years later, Gossard and Walton (361) summarized their extensive work on bees, beehives, and honey in relation to blight dissemination. They obtained blight infection by inoculation of tender twigs with (1) apple pollen from the baskets of bees, (2) mouth parts of bees, and (3) honey from different beehives. They also found that the organism survived up to 72 hours in honey, up to 7 days in aphid honeydew, and up to 5 days in peach, plum, and cherry nectar.

The earliest methods of controlling fire blight included eliminating or pruning out diseased twigs, branches, and water sprouts (20, 21, 172, 463, 469,

560, 702–704, 928, 1012, 1022). In the larger limbs and tree trunks, cankers were removed with cutting and scraping tools (1012, 1018).

In 1918, Reimer (778) reported a new disinfectant for wound dressings. Cyanide of mercury proved very effective by inactivating all cankers treated. However, cankers treated with bordeaux paste, bichloride of mercury, cresol, lime sulfur, nicotine sulfate (Black Leaf 40), and chlorozene remained active. Cyanide of mercury was not effective for disinfecting metal tools.

Chester (171) also made a rather extensive study of the nature and control of blight cankers in trees. After experimenting with a formaldehyde-glycerin mixture, a copper-whale oil-soap mixture, and a bordeaux-rosin-soap mixture for application to scraped cankers, he found the formaldehyde mixture the most promising for wound treatment and tree recovery. Formaldehyde and corrosive sublimate (bichloride of mercury) were the most extensively used disinfectants for canker blight control for many years.

During the early years of blight control, considerable emphasis was placed on collar blight. With the confusion that some collar blight was due to winter injury, this form of fire blight started receiving attention about 1905 (470, 714, 1016, 1017). At first the disease appeared to be most prevalent and more serious on apples but soon after was also observed on pears. Recommendations for the control of collar blight were similar to those mentioned for cankers in large limbs (460, 713, 714, 997). If tree trunks were more than half girdled and beyond surgical treatment, trees were removed at once.

An interesting attempt to control fire blight was tried by Bolley (100) in North Dakota. He strapped a large bottle to a pear tree to feed it internally with formalin and various nutrient solutions, but the effects on blight control were inconclusive and the treatment required too much manipulation for the average grower.

The earliest attempts to control fire blight by spraying were started with lead arsenate and lime sulfur, which were used to control fungus diseases, the San Jose scale (*Quadraspidiotus perniciosus* (Comstock)), and many other insect problems (323, 704, 851). These chemicals were soon followed by sprays of bordeaux mixture, which were also being used to control apple scab (*Venturia inaequalis* (Cke.) Wint.) (20, 606, 746, 781). Stronger bordeaux was used successfully in a late dormant spray in the spring to kill oozing bacteria on apple and pear.

Soon after 1900 the emphasis was also on varietal resistance as a means of controlling fire blight. With the introduction of many pear and apple cultivars from Europe, differences in degree of blight resistance were observed among cultivars and within seedling populations (20, 396, 850, 918). In 1908, Waite established the earliest pear-breeding program at the U.S. Department of Agriculture (990). Soon after, Hansen (381) and Reimer (777, 780) traveled to the Orient to collect blight-resistant pear material. Cox (186) published an excellent early account of the oriental pears and their hybrids. By 1920, small breeding programs were underway at several locations throughout the United States (54, 63, 381, 731, 1035).

CHAPTER 2

GEOGRAPHIC DISTRIBUTION

In many reports and popular bulletins the presence of fire blight in certain countries has been erroneously mentioned. Based on published records and detailed correspondence, we have attempted to determine accurately the present distribution of fire blight in the world, including North America, Central and South America, Europe, and Oceania and Africa.

If our knowledge and survey are complete, fire blight has been officially recorded in 14 countries—8 in Europe including Egypt and 6 bordering the Pacific Ocean including the United States (fig. 4). This is the extent of the distribution according to published records of the disease. Unavailable records or unpublished observations of fire blight in other countries cannot be ruled out.

North America

United States

Since the earliest known observations in 1780 of fire blight in New York (218), and as orchards became numerous and more contiguous, fire blight gradually spread westward over the Allegheny Mountains into the Mississippi River Valley. By 1817, it was recognized by Coxe (187) in the oldest American book on fruit tree culture as one of the important disease problems in fruit production. Severe blight epidemics were experienced in the Eastern States in 1826 and 1832. About 1840, fire blight reached Ohio, Indiana, and Illinois. Beecher (79) reported that one of the most widespread and destructive epidemics occurred in 1844. Many orchards were completely ruined. During 1876–80, fire blight

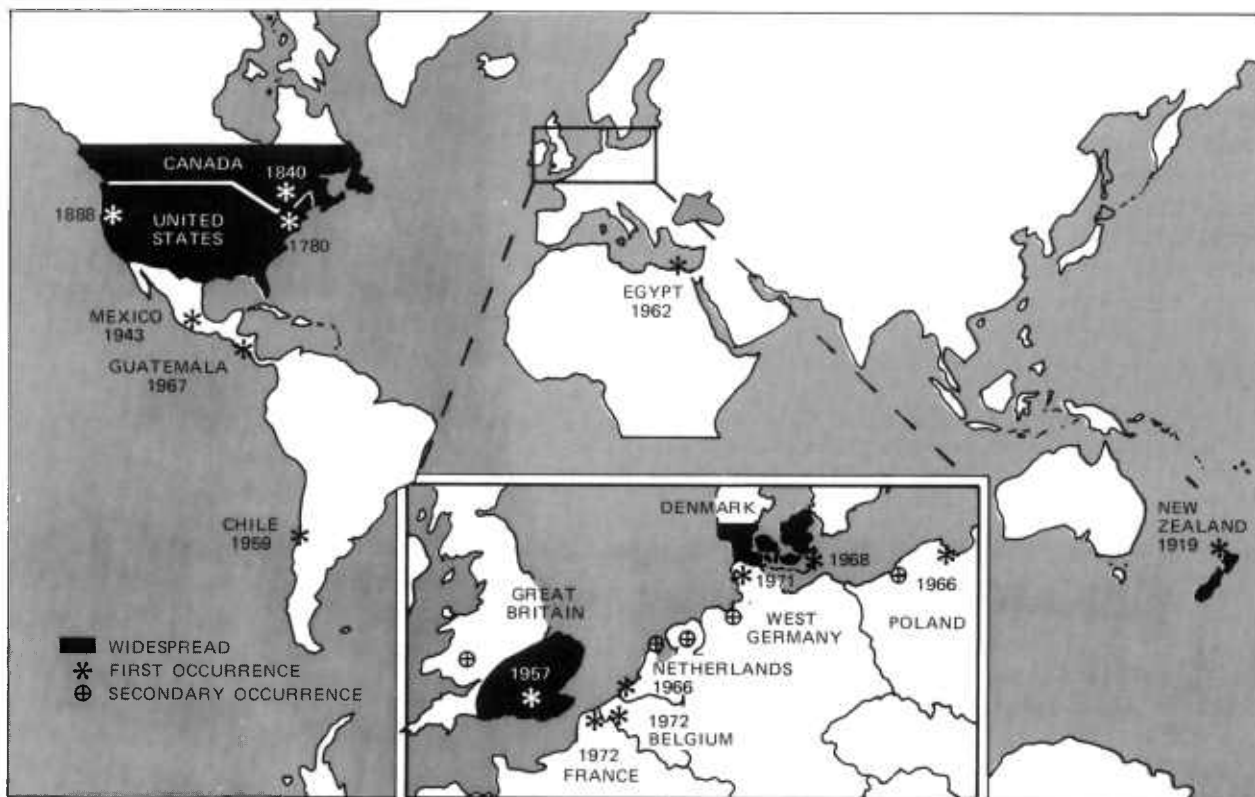


FIGURE 4.— Worldwide distribution of fire blight.

had become so destructive in the orchards of Illinois and adjacent States that it became one of the chief topics of discussion at the State and county horticultural meetings of that period.

Fire blight moved steadily westward with the settlement of the country. For many years the vast expanse of the Great Plains, as well as the Rocky Mountains, provided effective barriers for movement of the bacterium and prevented spread of fire blight to the Pacific Coast States. After reaching the west coast and where there were no plains and mountains as barriers, fire blight rapidly moved into all the Southern and Gulf Coast States.

Despite claims by growers in the fruit regions of California that the blight could not thrive there, it suddenly appeared in the pear orchards about 1888 near Chico, Calif. By 1902, Pierce (740, 741) first confirmed the identity of the disease throughout the State. Fresno and Kings Counties appeared to be the center of the disease. Detailed accounts of the early history of fire blight in California have been published (61, 322).

After blight was found in California, it spread rapidly northward and caused disastrous epidemics in Oregon and Washington. Certain parts of the Rocky Mountain region were the last to be invaded by the disease. Fire blight was not reported in Montana until about 1905, when it first appeared near the town of Hamilton (918). During the following few years it spread to all parts of this State. By 1908, fire blight had appeared in the Rogue River Valley of Oregon and within the next few years it reached the Umpqua and Hood River Valleys (702). It was not until 1915, after the disease had been reported from sections of Washington State and the Province of British Columbia in Canada, that fire blight was discovered in the Willamette Valley of Oregon. About 135 years after it was first observed in New York, fire blight had moved several thousand kilometers across the North American continent and to every corner of the United States.

Canada

Fire blight was first observed outside the United States in the Niagara peninsula of Ontario, Canada. When the disease reached this area is not precisely known; it may well have been before fire blight reached California. In 1904, Harrison (388) mentioned its presence in many counties of Ontario and quoted several fruit growers who had seen the disease as early as 1840. After many years of comparative freedom from blight, an outbreak in 1943 in the

Niagara peninsula brought fire blight into prominence again (159).

On the west coast of Canada, Eastham (253) reported that the disease attracted attention in British Columbia about 1911, but it undoubtedly had been there for some time. By 1924, fire blight was still confined to the interior of British Columbia, but a few sporadic cases of twig blight had been observed along the coast. Since 1924, fire blight has spread to all pear and apple growing areas of Canada. In the French-speaking Province of Quebec the disease is known as "Brulure bacterienne." In the early 1940's, fire blight was very severe in several Quebec apple orchards (766). Thatcher (930, 931) mentioned that the disease was also catastrophic 10–12 years earlier and referred to a "blitzkrieg" by the causal organism.

For many years the Annapolis Valley in the isolated maritime Province of Nova Scotia was known for the absence of fire blight. A report in 1914 mentioned the presence of blossom blight near Wolfville, but the description may have inferred pear blast (113). A survey in 1950 by the Canada Department of Agriculture (142) reported the presence of the disease in New Brunswick on apple and pear and in Prince Edward Island on apple, pear, *Crataegus*, and *Sorbus*. At that time, fire blight was not found in Nova Scotia. In 1966, however, Gourley et al. (362) and Lockhart and Gourley (587) reported the first confirmed identification of fire blight in 17 pear orchards in the Annapolis Valley. The finding of some old cankers indicated the presence of the blight prior to 1966. The disease was also observed on apples and hawthorns adjacent to the pear orchards. Analysis of weather records indicated that in 1966 the number of days of consecutive temperatures exceeding the minimum and optimum for blight development was about double that of the preceding 4 years. This condition, combined with heavy rains during late May and early June, apparently provided ideal conditions for the spread and growth of the bacterium.

For a detailed account of the occurrence of fire blight in each Province since the 1920's, refer to the annual reports of the Canadian Plant Disease Survey (142). A survey in 1972 in southern Ontario revealed that damage of economic significance occurred in one-third of the orchards visited (239).

Central and South America

In 1921, Ramirez (768) included fire blight in a list of plant diseases observed around Mexico City,

Mexico, but this observation was not confirmed at that time. In 1943, fire blight (tizón de fuego) was seen on apples and pears in the Canatlán region of Durango (797). In the fall of 1967, Ridley ³ observed fire blight on Bartlett pear trees in Guanajuato, Mexico.

In 1968, Schieber and Sanchez (842) included fire blight in a preliminary list of plant diseases in Guatemala. They reported finding the disease on the pear cultivars Bosc and Bartlett in Cantel, Departamento de Quezaltenango, and in San Bartolomé Milpas Altas, Departamento de Sacatepéquez. In Guatemala, pear plantings are rather recent and also somewhat isolated at high elevations. Fire blight was most likely introduced with the original plant material.

In South America, fire blight has only been reported from Chile by the U.S. Foreign Agricultural Service. The disease was apparently first observed on apples during the 1959–60 growing season in the locality of Padre Hurtado near Santiago in the Province of Santiago. Identification of the bacterium through reinoculation was confirmed by Mrs. Romoli ⁴ at the Ministry of Agriculture. Fire blight was apparently confined to the Padre Hurtado area and occurred only when climatic conditions were favorable for disease development. In all three Latin American countries the disease is considered of little economic importance.

Europe

Great Britain

The most recent wide-range spread of fire blight occurred with its introduction to England, probably sometime during the late 1940's or early 1950's. Outbreaks were first reported in 1958 by Crosse et al. (192, 193) on pear trees near Maidstone, Kent, in southeastern England. Immediately the disease became very severe on the cultivar Laxton's Superb because of its late blooming characteristic (796). According to the best available information, the bacterium was probably brought into the country either on infected plant material or on contaminated fruit boxes from overseas shipments. Fruit boxes were used in these orchards in Kent where initial blight was found about 1956–57 (570). By 1959, fire blight was observed on pears, hawthorns, and whitebeams (*Sorbus aria* (L.) Crantz) in the southern suburbs of

London as well as in the borough of Southend-on-Sea, located across the Thames River from Kent (429). These areas are both within 16 to 32 km of the infected orchards in Kent.

By 1966, fire blight had spread east to Canterbury and north and westward to Suffolk and Berkshire Counties. This was considered the worst blight year in England, with new infections observed in several thousand pear trees and pyracantha and cotoneaster plants (366). In addition to the Kent area, isolated outbreaks were reported in 1958 from Worcestershire on pear, in 1960 from Wisbech on pear, and in 1967 from the Merthyr Tydfil area in South Wales on hawthorn (367).

Lelliott (571) and Glasscock (329) published detailed accounts of the history, present distribution, and attempted eradication of fire blight in the United Kingdom. Because of its presence in many rosaceous hosts growing in parks and private gardens throughout London and its suburbs, attempts at complete eradication of fire blight have failed. In 1965, Lelliott and Hayward (576) reported several hosts of *Erwinia amylovora*, many of which had not previously been observed with symptoms of blight in the United States or elsewhere. Of interest was their observation that Swedish whitebeam (*Sorbus intermedia* (Ehrh.) Pers.) and *Cotoneaster horizontalis* Decne. appeared to be immune under English conditions, whereas *Sorbus aria* and other cotoneasters were severely infected. In 1971, however, Lelliott (574) and the European and Mediterranean Plant Protection Organization (290) reported moderately severe natural shoot infection in container-grown plants of *C. horizontalis* in a nursery in Bucks.

The first occurrence of apple blight was recorded in 1967 in two commercial apple orchards in Kent (329, 573). The following year it appeared in more trees there and elsewhere. In August 1969, the Ministry of Agriculture (368) announced that severe outbreaks of fire blight had occurred in 37 apple orchards throughout Kent. By September 1969, the number of blighted orchards had risen to 45, with more than 1,700 infected trees. The outbreaks occurred mainly in the Teynham, Faversham, and Canterbury areas but also in fruit-growing areas of Essex and Suffolk. Fire blight was most severe on the 9- to 10-year-old Cox's Orange Pippin cultivar trees on Malling 2 and 9 rootstocks. Many infections were also noticed on the cultivars Egremont Russet, Crawley Beauty, and Miller's Seedling.

³ Pers. commun., Gerber Prod. Co., Fremont, Mich.

⁴ Pers. commun., U.S. Foreign Agr. Serv., Santiago, Chile.

In September 1971, fire blight was found on hawthorn in and around the city of Bristol (283). Apart from this and other outlying occurrences in Somerset, Worcestershire, and Wales, the disease is generally present in the entire area east of a line from Southampton over Oxford to The Wash. Although present knowledge of the distribution of fire blight is restricted to the areas indicated here, infection possibly, if not likely, has occurred in other areas of England and Wales.

Poland

Following a questioning note in 1959 by Pieniazek (739), fire blight was first observed in continental Europe in July 1966 (103). The disease, known as 'zaraza ogniowa,' was seen in experimental orchards of the Research Institute of Pomology at Milobadz, about 25 km south of the port of Gdansk (104). The disease occurred in an orchard of 8-year-old pear cultivars and later spread to two other sections of the orchard. By the end of the summer, fire blight was also observed on 8-year-old apple trees growing near the infected pears. Some apple trees and more than 50 percent of the pear trees were destroyed by the disease in one season. Borecki and Lyskanowska (104) made many isolations and positive identification of the causal organism.

In June 1968, Burkowicz (124) observed a mild case of fire blight in the pear cultivar collection of the main Research Institute of Pomology at Skiernewice. The disease was seen in the current season's growth of a single tree, which had been propagated in the spring of 1968 with grafts of the cultivar Conference obtained from abroad. Careful examination of the other trees in this pear collection revealed no other cases of fire blight, and the infected tree was removed and destroyed. In spite of many surveys, the disease was not observed in Poland in 1969.

In September 1970, new outbreaks were recorded in young apple trees and some old hawthorn bushes in a nursery in Dworek in northwestern Poland (124). In September 1971, fire blight was detected in two pear orchards, 6 km apart and about 40 km south of Gdansk (287). In one orchard only one tree showed disease symptoms, and in the second orchard six trees were infected. Since that time, surveys have been conducted throughout the country, and the northern coastal region has been strictly quarantined to prevent spread of blight to central Poland (124).

The Netherlands

In August 1966, fire blight (perevuur, bacterievuur) was observed for the first time in the Netherlands in a few pear trees and several hawthorn shrubs on the island of Noord Beveland in the Province of Zeeland (679). The following spring, Roosje (800) and Roosje and Meijneke (801) prepared warning articles for Dutch fruit growers to acquaint them with the symptoms of this dangerous disease. This blight, recorded in the far southwest corner of the Netherlands, was not near a seaport but occurred in the Dutch pear-growing area 100 km from the orchards in Kent, England. This suggested the possible dissemination of the bacteria through air currents by long-range flying insects or migratory birds. Severe eradication procedures were started during 1967, including the destruction of 10 km of hawthorn hedges and nearly 175,000 individual bushes and also the strict enforcement of the removal of beehives and secondary blooms from the remaining orchards (635). No recurrences of fire blight were observed in 1967 or during the following 3 years (313, 678).

In 1971, however, new occurrences of fire blight were discovered on the neighboring island of Schouwen-Duiveland and in a second region, 100 km to the north, near the towns of Den Helder and Wieringen in the Province of North Holland (287, 635a, 636, 637). Infection was found in several pear orchards, but primarily on hawthorns along dikes and roads, on farms, and in dunes and private gardens. In 1972 and 1973, infected *Cotoneaster salicifolius* Franch., *Sorbus aria*, and one *pyracantha* were also found (635a, 639, 680). All infected plant material was destroyed by fire and the trunks were covered with a mixture of soluble 2,4,5-T ester and oil.

In 1974, an intensive survey resulted in the discovery of three new foci of fire blight in addition to the two existing ones (635a). They were observed in and around the towns of Castricum (North Holland), Rolde (Drente), and Apeldoorn (Gelderland). The last two were the first areas located away from previous recordings along the coast of the Netherlands. Except for a few infected hawthorns, all blight recordings were made on *cotoneaster*, mainly as blossom blight. In 1975, Meijneke⁵ mentioned additional blight observations on *cotoneaster* in the cen-

⁵ Pers. commun., Plant Protect. Serv., Wageningen, the Netherlands.

tral and northeastern regions of the country. *C. dammeri* Schneid., *C. salicifolius*, and *C. watereri* Exell and their cultivars proved to be very susceptible. In all nurseries, parks, and garden centers combined, more than 2 million cotoneasters were destroyed (635a). Since 1975, the name of the disease has been changed to 'bacterievuur' in order to cover all rosaceous host plants (680a).

Cooperative work is in progress among investigators from Denmark, West Germany, and the Netherlands to establish field plots with various species, cultivars, and clonal selections of rosaceous host plants in a search for resistant germplasm. In the meantime, intensive surveys are continuing in the Netherlands to detect new outbreaks, and a policy of rapid, thorough blight eradication is in effect.

Denmark

In late August 1968, fire blight was reported for the first time in Denmark (217, 488). The disease, known as 'ildsot,' was noticed on approximately 100 fruit trees in 8 orchards within an area of 40 hectares between the towns of Norre-Alslev and Stubbekobing in the northern part of the island of Falster. During a survey by the State Plant Protection Institute, fire blight was found on several pear and apple cultivars, a single bush of *Cotoneaster watereri*, and many hawthorns. The pear cultivar Conference seemed the most seriously infected.

Klarup (531) published a detailed account of the initial outbreaks in Denmark, including eradication measures. These followed the strict procedures used in the Netherlands in 1966, including complete eradication of all host plants in the infected area, strict enforcement of the removal of beehives and secondary blossoms from the fruit orchards, and intensive inspection of nurseries and orchards to locate new outbreaks. Despite the enforcement of these intensive eradication procedures, fire blight recurred in Denmark in 1969.

Nilsson (690) reported that the disease was not observed until early August 1969, but then at 80 locations in the northern part of the islands of Falster and Lolland, as well as on the small islands of Femo, Fejo, and Asko between these two larger islands. By the middle of November, fire blight had been recorded in more than 300 locations, but predominantly in hawthorn hedges surrounding the orchards (56). The disease was reported in an area of about 260 km², restricted to a narrow band 25 km

wide and 130 km in length. Migratory starlings have been suspected of having a role in disseminating the blight pathogen from England or northern Poland (690). Bech-Andersen (77, 77a) stated that the oldest infections were on hawthorns located on migration routes of starlings (*Sturnus vulgaris* L.) and willow warblers (*Phylloscopus trochilus* (L.)).

In 1970, fire blight was observed in new areas on Falster and Lolland and during that summer also on the neighboring islands of Langeland and Sjaelland (282, 488). Infections were observed primarily on hawthorn (74) but also on pears and apples. Klarup (532) reported that the first symptoms in 1970 were noticed in early June with definite evidence of blossom infection in pear. All infected and suspicious plant material was destroyed and additional emphasis was placed on insect control programs in pear and apple orchards. Hellmers (397) and Nilsson (691, 692) reported in more detail on the Danish hosts infected with fire blight and methods of control. Bech-Andersen (75) listed 16 pear cultivars and 25 apple cultivars with their degree of blight resistance.

In 1971, fire blight recurred again on all four islands and again mainly on hawthorn but also on pears and apples (282). After more extensive surveys, many infected hawthorn hedges were also discovered along the west coast of southern Jutland between the towns of Tonder and Ribe. According to the amount of damage caused by blight, the original infections were considered to be 4–5 years old. Following eradication of infected hawthorns surrounding fruit orchards, the amount of fire blight was significantly reduced when hawthorns were kept at least 25 meters away from the fruit trees (76).

In 1976, the Plant Protection Service (216a) reported the presence of fire blight in 72 localities throughout southern Denmark, principally on hawthorn and cotoneaster. Currently about 2,500 plants belonging to 40 species in the Rosaceae are being tested for their degree of blight resistance in 2 localities in Denmark where natural infection on hawthorn is extensive (489).

West Germany

More than 10 years before fire blight (feuerbrand) was first observed in West Germany, several lengthy reports appeared in various journals emphasizing the danger of this disease to the German pome fruit industry (101, 107, 127, 308, 544, 888–890). Since the discovery of fire blight in Denmark in

1968 just north of the Danish-German frontier (south Jutland), the Government of West Germany undertook blight inspection surveys in northern Schleswig-Holstein, particularly on islands in the North and Baltic Seas. In August 1971, fire blight was discovered in hawthorns on the islands of Sylt, Föhr, and Nordstrand, located nearest to Denmark along the upper North Sea coast of West Germany (282, 302, 646). Immediate action by the Plant Protection Service resulted in the uprooting and destruction of 18,000 plants. Of these, 11,349 were infected (88 percent hawthorn and 11 percent pears) (302).

In late May 1972, numerous new infections were noted, many of which were approximately 100 meters from infected shrubs in the previous year (647). In that year, 19,000 plants were destroyed, 50 percent of which were infected (97 percent hawthorn and 3 percent pear). Besides these two hosts, fire blight was also observed on 20 quince trees and 2 *Sorbus aucuparia* L. plants (92, 309, 645, 647). The careful survey of this area of West Germany and the detection and destruction of host plants have been extremely intensive. No consistent spreading of fire blight was found during 1973 except a few infected *Cotoneaster salicifolius* plants in nurseries northwest of Hamburg (293). More inspections in this area did not reveal any other foci. Additional surveys are being continued throughout northern Germany every year to detect blight outbreaks farther south.

In 1974, Zeller (1046) published the first German review on fire blight. Since then, he has established large test plots in Schleswig-Holstein to study the possible existence of resistant plant material among numerous ornamental host plants in the rosaceous family (1046b, 1046c).

Symptoms of fire blight reportedly were observed by Müller⁶ on pear and hawthorn in East Germany, but detailed information on location and degree of damage was not available.

France

In August 1972, fire blight was detected in the northernmost part of France (291, 832). The disease, known as 'feu bacterien,' was found mainly in hawthorn hedges near the Belgian border in an area 20 km long and 10–15 km from the coast, including the city of Dunkirk. This region, which is located on the routes of migratory birds, has no fruit orchards or ornamental nurseries (831). The blight organism

was isolated, identified, and its pathogenicity proved on pear fruit (834).

During 1973, only a few additional blighted hawthorns in the same focal area were found, and all infected and suspected hedges were uprooted and destroyed (291, 294, 831). A study of several cultures of *E. amylovora* recovered from the Franco-Belgian region revealed a close similarity to isolates from Great Britain, Canada, and the United States (732).

Belgium

Within 1 month of the discovery of fire blight in France, the disease was also reported immediately across the Franco-Belgian frontier around the city of Adinkerke (292, 976). In addition, blight symptoms were also observed 5–10 km farther north along the Belgian coast near the towns of Wulpen and Nieuwpoort and 20 km farther south along the French frontier near the town of Haringe. Findings mainly concerned hawthorn hedges, but blight was also detected in two pear trees and one bush of *Cotoneaster salicifolius*. Veldeman and Porreye (977) positively identified the blight organism and reported that a blight detection and destruction program was being followed similar to the one undertaken earlier in France and the Netherlands.

Gautier (325), Ghio (326a), Melckebeke (640), Ride (787), Ride et al. (788), and Veldeman (976a) published brief reviews of fire blight in French.

During 1958–70, fire blight was reported in Europe on about 24 pear and 35 apple cultivars (1055). Several other cultivars have been added since. In addition, the disease has been observed on at least 14 species of *Cotoneaster* and on several species of *Crataegus*, *Sorbus*, *Pyracantha*, and other genera in the Rosaceae (329, 369, 571, 576). Hawthorns in particular seem to have a very important role in the spread of fire blight. In all seven European countries mentioned here, hawthorns either became infected first or were directly responsible for spreading blight to nearby apple or pear orchards (330, 488, 635).

The initial outbreaks of fire blight in Great Britain and in Poland most likely resulted from shipments of infected fruit, contaminated propagating wood, or infected nursery stock through the respective sea-ports of London and Gdansk. Once blight was established on pears, secondary infections were easily transmitted by wind, rain, birds, or insects to other

⁶ Pers. commun., Inst. f. Phytopath., Aschersleben, East Germany.

hosts. The blight observed in 1968 at Skierniewice, Poland, apparently resulted from the introduction of infected propagating wood (124).

The numerous occurrences of blight in hawthorns along the coastline from England and France to northern Poland, particularly on the clusters of islands in Denmark and on those along the coast of West Germany and the Netherlands, are very strong evidence that migratory birds were responsible for spreading the bacterium. For more information, see chapter 8.

The introduction of fire blight to northern Europe has caused increased concern among the central and southern countries. Articles concerning the threatening danger of the disease to apple and pear industries have appeared in Austria (983), Czechoslovakia (545a), East Germany (669, 1036), France (462, 786), Italy (143a), Portugal (221, 222), South Africa (280a), Sweden (289, 710, 710a), and Switzerland (99, 99a, 123, 747, 848, 921). Considering the extensive list of hosts and the fact that in Europe the disease has spread and maintained itself considerably well under less favorable environmental conditions than in the United States, it may only be a matter of time before fire blight will be present throughout the European continent.

It is not possible to predict precisely how the disease would develop in the various European regions. When comparing the experience gained in America with that in England and northwestern Europe, it is apparent that climatic conditions have a decisive effect on the time at which the disease becomes active and on the general way in which infection occurs. In turn, these factors largely determine which host plants will be attacked first as well as the rate of infection by the pathogen. Environmental conditions vary greatly throughout Europe, but average summer temperatures in Bavaria, southern France, and northern Italy are at least at minimum levels for blight development (1064). For several hours during the day they should be well within the optimum range. In addition, unusually high spring or summer temperatures with sufficient moisture could provide optimum conditions for serious outbreaks of fire blight in any country.

For those European countries where fire blight has not yet been observed, the most important control measure is to make all possible attempts to keep the disease out of the country. Rigid quarantine of plant material from areas where the disease is known may prevent or at least delay introduction of

fire blight. Many countries do not enforce such quarantine restrictions, but Norway (288), Sweden (286, 289), and Switzerland (285) have adopted very strict regulations against importation of plant material from the 10 most widespread genera in the family Rosaceae.

Oceania and Africa

New Zealand

In 1919, fire blight first appeared in New Zealand. Cockayne (178) and Campbell (141) reported the initial outbreaks on apple, pear, quince, and hawthorn in Auckland Province on the North Island. Waters (1003, 1004) was the first to isolate and identify the causal organism. Fire blight is believed to have been imported on infected nursery stock. Apparently hawthorn was very important in the spread and overwintering of blight (179, 681). In the early years the disease destroyed many hectares of pear trees in a single season, but within 2 or 3 years damage was limited to the death of a few branches and a small proportion of spurs (53, 205). Eight years after its introduction, the disease caused severe losses to most of the apple cultivars in the Hawke's Bay area (6). Curtis (206) reported that rootstocks of *Pyrus calleryana* Decne. and *P. ussuriensis* Maxim. were distinctly resistant to root and body blight.

Despite several quarantine regulations concerning shipments of bees or plant material from the infected area, fire blight reached the South Island in 1929 (772). It was not detected in the Otago region until 1936. Within a few years, however, after several outbreaks of the disease in other new areas, fire blight seemed to become less serious (205). In 1963, the disease appeared to be increasing in incidence, but excellent control was obtained with streptomycin (682).

Phillips (737) pointed out that considerable daily variations in temperature and humidity might partially account for fluctuations in disease appearance. Even though the use of streptomycin is not allowed in New Zealand, recent work has indicated that excellent control can be obtained by applying bordeaux-streptomycin sprays (250, 1026).

Australia has managed to remain free of fire blight. As early as 1924, a quarantine proclamation prohibited the importation of all deciduous fruit trees and other plants in the Rosaceae family, including fruits and seeds, that were grown in any country

in which fire blight existed (181). That same year, Noble (697) mentioned an additional restriction that honey produced in New Zealand should be held in containers for 14 days prior to export. This strict quarantine enforcement is adhered to today (1).

Egypt

In 1964, El Helaly et al. (264) reported the first localized occurrence of fire blight (el-lafha el-naryah) in northern Egypt near the port city of Alexandria. Blight had been observed during 1962 and 1963 in several localities of Alexandria, Behera, Sharkia, and Dakahlia Provinces. Bacterial isolates were tested for pathogenicity by artificial inoculation of potted 3-year-old Le Conte cultivar pear trees and young, green fruit. A 1966–72 survey of pear orchards and laboratory examination of suspected tree tissues indicated that trees in Egypt are free of the disease (263).

Unconfirmed Reports

During this literature survey we found many unconfirmed reports of fire blight on pear, apple, and other rosaceous hosts (table 1). The causal organisms were reported as *Bacillus amylovorus*, *Bacterium amylovorum*, or *Erwinia amylovora*.

For nearly three-quarters of a century fire blight has been assumed to occur in Japan (1049). As early as 1903 the disease was reported by Uyeda (974) and was believed to have been brought over on nursery stock from America. Fire blight was observed in both apple and pear orchards in Akita prefecture on the island of Honshu and in Ehime prefecture on Shikoku island. The disease was apparently rather prevalent during the 1920's and 1930's (497, 864). In 1955, Okabe and Goto (708) published a list of bacterial diseases and their pathogens in Japan. Even though fire blight was included in the list, the authors also listed it and a pear bacteriosis (*Erwinia* sp.) in a separate list with 13 other bacterial diseases because of unconvincing proof of pathogenesis. In 1974, these investigators reported that all previous reports on fire blight in Japan appear to have been based on misidentification and that the country has never been infected with the blight pathogen (295).

Several articles have been published in the U.S.S.R. and Italy concerning the possible presence of fire blight in these countries. In 1960, Verderevskii (978) described the general fire blight (ozhog plodovykh derer'ev) symptoms, but he did not consider the disease to be present in the U.S.S.R. Izrailskii et al. (467, 468), Shklyar (865),

and Shklyar and Orlova (866) compared many *E. amylovora*-like isolates with Canadian and English isolates of *E. amylovora* in agglutination and fruit inoculation tests. They found *E. amylovora* to be absent in all fruit tree specimens and concluded that previous reports of fire blight in the U.S.S.R. were unfounded.

Additional reports for the U.S.S.R. indicated that several blights, resulting in dieback of twigs on apple, pear, peach, and other fruit trees bearing symptoms similar to fire blight, also were proved not to be fire blight (373, 466, 523, 630a). Studies of biochemical and serological properties of the pathogens reportedly show similarities to *Pseudomonas* species (490, 711a, 712).

In 1963, Luchetti (594) isolated a yellow and white bacterium from cankers of 2-year-old apple trees of the cultivar delicious in the Province of Ferrara, Italy. Based on bacteriological tests and comparative morphology studies, he identified the white bacterium as *E. amylovora*. The following year, Ercolani (275) studied similar cankers on the same apple cultivar in several locations of the Province and concluded that the organism was a species of *Pseudomonas*. Mazzucchi (632) surveyed pear orchards in the Provinces of Ferrara, Modena, and Rovigo and found that blossom blight was most frequently caused by *Pseudomonas syringae* Van Hall. However, he reportedly isolated *Erwinia*-like bacteria from large cankers on branches and trunks of Bartlett and Conference pear.

In 1972, the Ministry of Agriculture in Turkey reported through the European Plant Protection Organization the occurrence of fire blight on pear from several locations along the coasts of the Black Sea and Aegean Sea, i.e., in the Province of Zonguldak near the towns of Zobran and Karabuk and in the Province of Amasya near the town of Caferli and Vakfikebir (284). To date no other reports of its distribution or confirmation of the causal organism have been made.

Without any additional proof or further confirmation, we consider all records of fire blight in table 1 synonymous with those of the well-known blossom blast of pears caused by *P. syringae* (1105). In America, pear blast was first observed about 1932 and has since been found in all fruit-growing regions. Today blossom blast has been reported from many other countries (324, 477, 617, 719, 1040). The symptoms of blast and other diseases resembling fire blight are described in chapter 5.

TABLE 1.—*Unconfirmed reports of bacterial diseases in fruit trees attributed to fire blight organism*

Location	Year	Causal organism	Host	Reference
Bermuda -----	1938	<i>Bacillus amylovorus</i> -----	Loquat-----	Waterston (1005).
China:				
Eastern China -----	1926	<i>Bacillus amylovorus</i> -----	Pear-----	Porter (751).
Southern China-----	1933	<i>Bacillus amylovorus</i> -----	Sand pear-----	Tu (957).
Hopeh, Sikang-----	1952	<i>Bacillus amylovorus</i> -----	Pear-----	Siang (868).
Kwangtung -----	1955	<i>Erwinia amylovora</i> -----	-----do -----	Ciferri (173).
Northwestern China-----	1959	<i>Erwinia amylovora</i> -----	Apple -----	Sun (913).
France: Toulouse -----	1932	<i>Bacillus amylovorus</i> -----	Loquat-----	Nicholas and Aggerly (683, 684).
Germany:				
Baden -----	1919	<i>Bacillus amylovorus</i> -----	Pear-----	Muller (670).
East Prussia -----	1926	<i>Bacillus amylovorus</i> -----	-----do -----	Pape (721).
Italy:				
Catania -----	1912	<i>Bacillus amylovorus</i> -----	-----do -----	Savastano (838).
Torino -----	1922	<i>Bacillus amylovorus</i> -----	-----do -----	Ferraris and Ciferri (299).
Naples-----	1923	<i>Bacterium amylovorum</i> --	Apricot -----	Savastano (839).
Sicily-----	1925	<i>Bacillus amylovorus</i> -----	Loquat-----	Passalacqua (729).
Po Valley-----	1931	<i>Bacillus amylovorus</i> -----	Pear, apple-----	Montemartini (659).
	1963	<i>Erwinia amylovora</i> -----	Apple -----	Luchetti (594).
	1969	<i>Erwinia</i> spp. -----	Pear-----	Mazzucchi (632).
Japan: Honshu, Shikoku -----	1903-30	<i>Erwinia amylovora</i> -----	Pear, apple-----	Kazui (497), Shiraishi (864), Uyeda (974).
Jordan-----	1954	<i>Erwinia amylovora</i> -----	Apple -----	Vestal (980).
Rumania:				
Bessarabia -----	1938	<i>Erwinia amylovora</i> -----	Pear, apple-----	Savulescu et al. (840).
Bukovina -----	1940	<i>Erwinia amylovora</i> -----	-----do -----	Veresciaghin (979).
Southern Rhodesia: Fort Victoria-----	1927	<i>Bacillus amylovorus</i> -----	Apple -----	Hopkins (430).
South Vietnam -----	1965	<i>Erwinia amylovora</i> -----	Plum -----	My (676).
	1967	<i>Erwinia amylovora</i> -----	Apple -----	USAID (962).
Switzerland-----	1939	-----	Pear-----	Osterwalder (715).
Turkey: Black Sea coast-----	1972	<i>Erwinia amylovora</i> -----	-----do -----	EPPO (284).
U.S.S.R.: Kursk, Crimea, Transcaucasia-----	1915	<i>Bacterium amylovorum</i> --	Pear, apple-----	Serbinov (852).

CHAPTER 3

ECONOMIC IMPORTANCE

The injuries caused by the blight pathogen make fire blight not only destructive to the current year's crops but extremely dangerous to the pear or apple industry in a region or country. Blossom infection means a certain reduction in the current crop and that of the next year through the killing of fruit spurs. Twig blight destroys wood that would often bear fruit spurs the following season. In pears and quinces as well as in certain cultivars of apples, twig blight and the blighting of suckers often result in the death of large limbs or even the entire tree. Blighted nursery trees are usually rendered unsalable, even if not completely killed. Trunk, collar, and root blight strike the tree in its most vital parts and their destruction constitutes a heavy drain on orchard stands. The blighting of fruit after it is partly grown or its death from girdling of the branches on which it is produced often causes severe losses, especially in pears.

Accurate estimates are difficult to obtain of the annual losses from fire blight for given localities or for the country as a whole. Fire blight is an epiphytotic disease and occurs very erratically. Moreover its destructiveness varies with the seasons. With no specific methods to measure its devastation, only the most gross losses can be approximated. Some conception of its destruction may be obtained from the following facts and observations.

During 1860–85, thousands of pear trees, mostly the cultivars Duchess and Bartlett, were grown in the Tidewater area between Richmond and Norfolk, Va. (307). Fruit shipped by steamer to New York brought \$12 per bushel (ca. 35 kg), and net profits of \$600–\$1,000 per acre (about \$2,000 per hectare) were realized for several years. In 1873, the Old Dominion Fruit Growing Company planted 20,000 Bartlett trees and paid 20 percent dividend on capital stock in 1880 and 60 percent in 1881. However, the pear boom was soon snuffed out by fire blight, resulting in a great loss to the stockholders.

At the 1860 meeting of the Fruit Growers Association of Eastern Pennsylvania, the undisputed statement was made that “pears do better

everywhere in Pennsylvania than apples” (306). One grower in Jenkintown, Pa., had 7,000 trees of about 500 pear cultivars and obtained \$8–\$12 per barrel (ca. 116 kg) at markets in Philadelphia. The inevitable reaction from 25 years of horticultural inflation came in 1872. One of the four main causes for the depression at that time was the heavy loss in pear trees infected by fire blight.

Soon after fire blight had reached the west coast, the disease wrought such havoc in California between 1901 and 1910 as has seldom been known in a fruit-growing country. In 1902, the State Board of Horticulture reported that Fresno County had 125,000 pear trees and Kings County 43,700 trees. By 1904, fire blight had reduced these numbers to 1,500 and 0, respectively (702). By 1906, considerable blight was observed in the Hollister and Santa Clara Valley areas, and by 1908, two-thirds of the Bartlett trees in the State had been destroyed by blight. One estimate claimed a loss of more than \$5 million worth of Bartlett pear orchards during 1903–8 (1038). In four counties of the southern San Joaquin Valley 95 percent of the pear trees were wiped out and a major pear industry has never been reestablished there.

In 1930, Milbrath (648) reported a loss of 1–35 percent of the pear acreage in 33 counties of California from the previous year. The total expenditures for labor and materials to control blight in 19 of these counties amounted to \$825,000. Figure 5 shows the losses to the California pear industry for 1890–1960. Between 1900 and 1910 there was a 28-percent decline in the total number of pear trees. The small decline in production in 1920–24 as well as the severe decline in 1930–35 was almost entirely due to blight epidemics in the Sacramento area (61).

Except for a few areas near the Great Lakes in New York and Michigan, fire blight has also been very destructive throughout the Eastern, Southern, and Midwestern States. In 1914 there was an estimated loss of \$1,500,000 to the apple and pear crop in Illinois (738). In 1930, blight was also so severe on the apple cultivar Yellow Transparent in southern

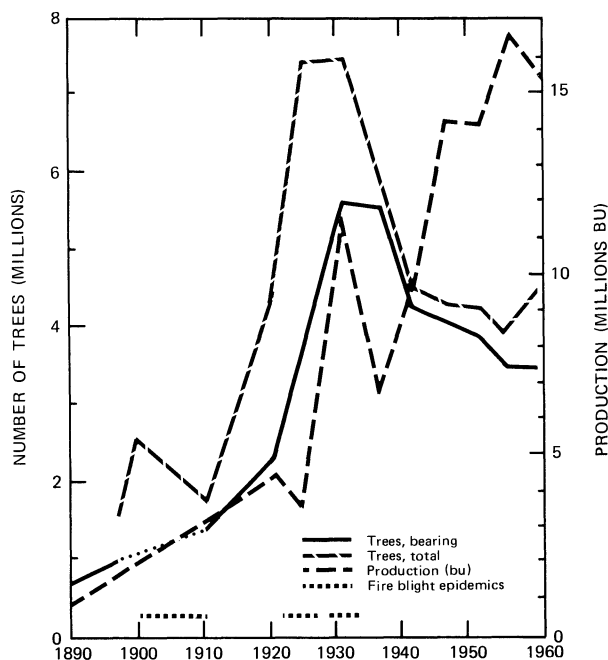


FIGURE 5. — Estimated loss of pear production and orchard trees caused by fire blight in California during 1890–1960 (after Baker, 61).

Illinois that it reduced the crop at least 30 percent and caused a direct loss of \$50,000 (22). Tullis (961) mentioned an average annual loss of 4.6 percent to the apple crop in Michigan due to fire blight during 1921–25. In Pennsylvania this loss amounted to 2.5 percent in 1958 and an average 73 percent of the blossoms blighted in 1944 in nine orchards in the central part of the State (529, 1047).

In the United States alone in 1936 the total production of pears was reduced 14 percent by fire blight, representing an approximate reduction in yield of 2,890,000 bushels (ca. 23,000 tons) or a loss of more than \$4 million (443). In 1938, fire blight was very severe in young apple trees in Pennsylvania and northern Illinois (23, 24, 529) and in 1942 as blossom blight in southern Ohio (18). In 1944 an orchardist near Greenwich, Conn., experienced his third severe outbreak (first in 1922 and second in 1934) in 14 of 65 acres (6 of 28 ha) of pears (149). Many of the trees were reduced to mere stumps. Based on pruning cost and crop loss the operator estimated that the disease cost him at least \$1,000 per week since early June.

For additional estimates of crop losses in America due to fire blight during 1920–40, refer to the data collected by the USDA Plant Disease Survey (965). During 1951–60 the overall average annual loss was estimated at \$1½ million for the pear crop and nearly \$2½ million for the apple crop (970). In the California pear industry with an income of \$20 million, the estimated loss for 1963 due to fire blight was about 14 percent (971). For the apple crop with an income of \$13 million, the loss was estimated at 5 percent. For more information on fire blight in many States during 1915–40, see the Plant Disease Reporter (963, 964, 966–968). In the nursery business, Boyd (1085) reported a 1955 loss to fire blight of about 200,000 apple and pear trees for one nursery in southeast Iowa.

Losses due to fire blight were not limited to North America. Soon after the disease appeared in New Zealand and Great Britain, orchardists were perplexed at the damage it caused. In New Zealand, fire blight destroyed in a single season many hectares of pear trees, but within 2 or 3 years after the initial outbreaks it ceased to cause more damage than the death of occasional branches (205). During 1927–28, bud infection was so severe in apples that the Sturmer and Ballarat cultivars suffered almost 100-percent loss (6).

Once fire blight became established throughout southeast England, the disease caused severe infection and serious losses. In 1966, considered the worst blight year in England, nearly 12,000 infected trees were found from April 1 to November 5, most of which were on farms and in nurseries (366). Of this total, 5,800 were Laxton Superb and 1,600 Bartlett pear trees. During 1958–69, total losses in England amounted to 20,000 pear trees, or about 100 acres (45 ha), and approximately 20,000 hawthorn, 15,000 cotoneaster, and 2,000 pyracantha shrubs (369).

Not until the 1970's, when fire blight became really prevalent on the most popular ornamental host plants, especially cotoneaster, did the disease affect the ornamental nursery business. In 1975, for example, more than 2 million cotoneaster, 13,000 pyracantha, 8,700 stranvaesia, and 4,500 mountainash were destroyed in nurseries and garden centers in the Netherlands (635a). Export trade of these plants to other countries was reduced, and losses to the nursery industry were tremendous.

CHAPTER 4

SYMPTOMATOLOGY

The original name 'fire blight' is descriptive of the most characteristic symptom of this disease—a blackening of twigs, flowers, and foliage as though they had been swept by fire. Depending on the plant part affected, many names, such as blossom, twig, fruit, trunk, and collar blight, have frequently been used.

Pear and Apple

Blossom Blight

This is usually the first symptom of blight and is found in early spring. A single flower or an entire cluster may be affected (pl. 1, *A*). Blossoms first appear water-soaked, then wilt, shrivel, and turn brownish to black. The blight progresses into the peduncle, which also may appear water-soaked, become dark green, and finally turn dark. During warm humid weather, ooze droplets sometimes exude from the peduncle. Young fruitlets often become infected. They turn black, appear dried and shriveled, and usually remain attached to the tree. The disease spreads rapidly and the bacteria invade the neighboring spur leaves through the midrib and main veins. A small canker is frequently seen on the supporting branch. The leaves wilt and the entire spur turns brown in apples or dark brown to black in pears. Infected blossoms may fall or remain attached to the tree, a symptom useful in detecting blighted trees from a distance. Not uncommonly some of the fruitlets of a diseased cluster may at first escape infection but later become invaded through the pedicel from the affected cluster base (pl. 1, *B*).

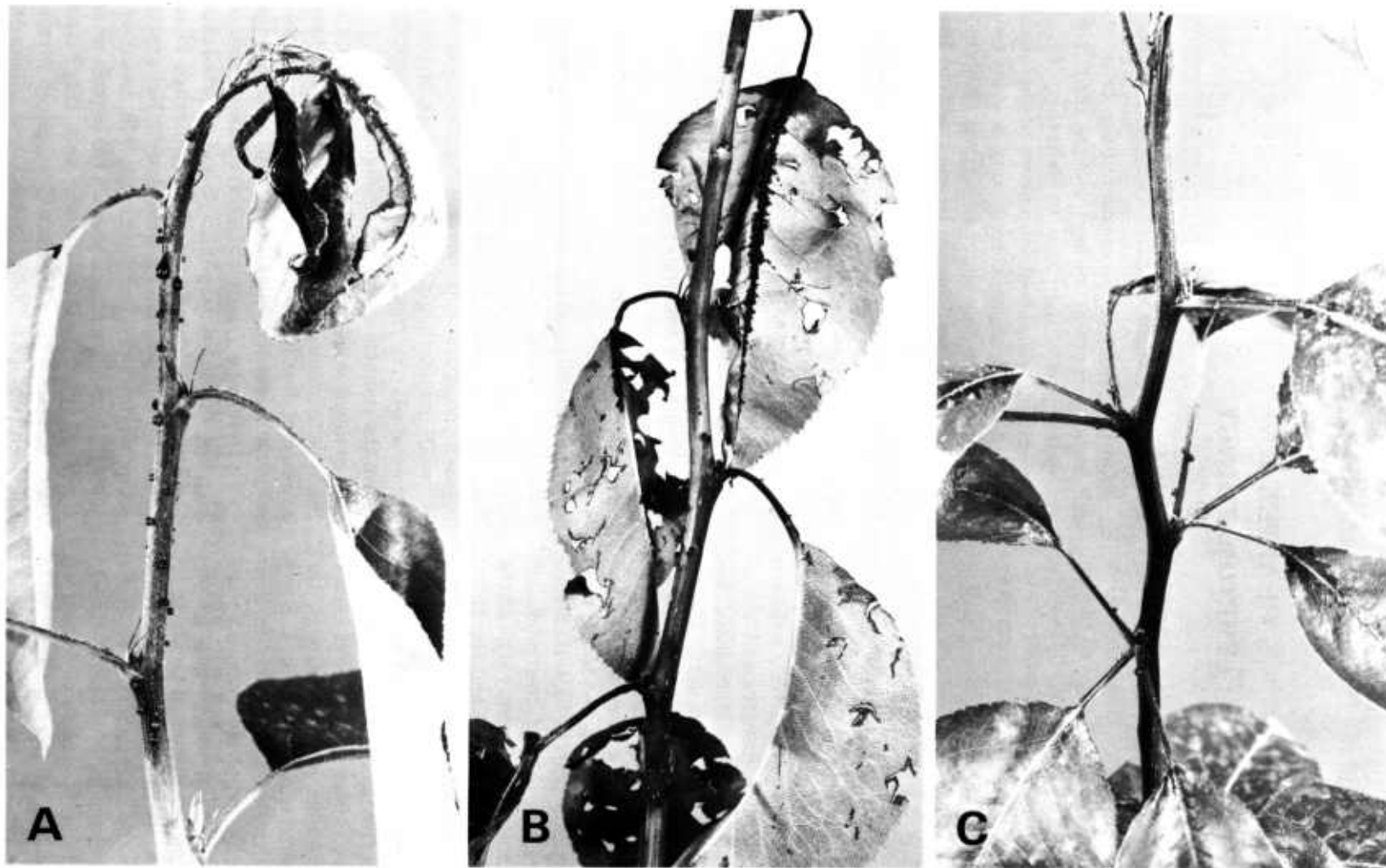
Pear and apple cultivars differ widely in their susceptibility to blossom blight (1057). In England the pear cultivar Laxton's Superb is especially susceptible to blossom blight, attributed partly to its tendency to produce abundant secondary blossoms (194). In Denmark, on the other hand, primary blossom infection is more common, whereas infection in secondary blossoms is only sporadically observed (254). Differences in climatic factors are assumed to be responsible.

Twig and Leaf Blight

After the blossoms, the succulent twigs or shoots and water sprouts or suckers are the next most susceptible part of the plant. In Beltsville, Md., a severe blight area, about 50 percent of the blight observed is twig blight. During some seasons twig blight may be the only blight seen. Twig symptoms are similar to those found in blossoms except that infection usually progresses more rapidly, especially under optimum weather conditions for blight development. In a few days, infection can move 15–30 cm or more into the twig. Infected shoots, bark, and leaves usually appear light to dark brown in apples and dark brown to black in pears (pl. 2, *A* and *D*). Symptom expression in apple shoots inoculated with *E. amylovora* has been due to production of ammonia (592).

Blighted twigs and water sprouts often form a canelike or shepherd's crook at their tips, a characteristic symptom of the disease (pl. 1, *D*). During wet conditions, drops of bacterial ooze frequently appear on the blighted shoots (fig. 6, *A*). The border tissue between healthy and diseased parts of twigs is filled with gum (407). Twig blight may also result from girdling below the shoot tip after invasion through the spurs or previously blighted twigs or leaves. Numerous blighted twigs with attached dead leaves appear as though scorched by fire (pl. 2), hence the common name of fire blight.

A common practice in some parts of the United States is to break or prune water sprouts or suckers to prevent fire blight infection. However, sucker removal increased blight infection in California (973). In Illinois, Tehon et al. (929) studied trends of blight occurrence during 1922–28 and reported that the intensity of blight attack varied much more proportionately than its prevalence. Failure to prune blighted twigs and branches will, however, subject the fruit to attack by such rot organisms as *Botryosphaeria ribis* Gross. and Dug. and *Phyalospora obtusa* (Schw.) Cke., which invade the dead twigs.



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FIGURE 6. — Characteristic symptoms of fire blight in Bartlett pear shoots: *A*, Severe oozing of succulent terminal shoot; *B*, spread of blight infection from petioles into leaf midribs and shoot; injury caused by simulated hail; *C*, infection of leaf spurs, accompanied by ooze production of petioles, originating from blighted stem; note necrosis at base of leaves.

Leaves may become infected after bacteria enter directly through stomata, trichomes, and hydathodes but more frequently through wounds caused by hail and wind whipping. If infection occurs in the blade, a necrotic section appears. This part of the leaf may dry out, but infection frequently spreads through the secondary veins into the midrib, then into the petiole and the stem. Petioles appear to be very susceptible to infection, and characteristic blackening of the petiole and leaf midrib often occurs (fig. 6, *B*). Ooze droplets frequently are observed (fig. 6, *C*). In some infected leaves only a small necrotic part extends inward from the margin 0.6 to 1.2 cm ($\frac{1}{4}$ – $\frac{1}{2}$ in), whereas in others the affected area includes the midrib, and in still others the affected area spreads nearly or completely over the entire leaf. Under certain weather conditions bacterial strands are sometimes produced on the blighted plant tissues but most commonly on petioles (pl. 1, *C*).

Fruit Blight

Fruit blight generally is found in immature fruit, although symptoms in fruit after harvesting and packing for shipment occur occasionally (102, 183). Infection spreads directly through lenticels in the skin, through wounds, or from an infected spur into the fruit. The infected part of the fruit may at first appear oily or water-soaked, with the diseased part becoming brown to black. Pears often show a premature, dark-green, water-soaked edge along the necrotic area, whereas apples commonly produce a premature redness in advance of the rotted area (pl. 3, *C* and *D*). A sticky, milky to amber-colored fluid collects at the core and sometimes oozes from the lenticels (603). Masses of bacterial tendrils or strands have been observed on pear fruit in Washington State (fig. 7, *A* and *B*). Infected apple and pear fruits turn brown and black, respectively, shrivel, and remain attached to the spur, taking on a mummified appearance. Fruit blight is most common following a severe summer hailstorm (596a, 1062, 1070).

Limb and Trunk Blight

In blight-susceptible hosts the disease may advance downward from the blossoms, shoots, or fruit through the larger twigs to older branches causing localized stem cankers. It may continue into the scaffold limbs and main body of the tree, often ac-

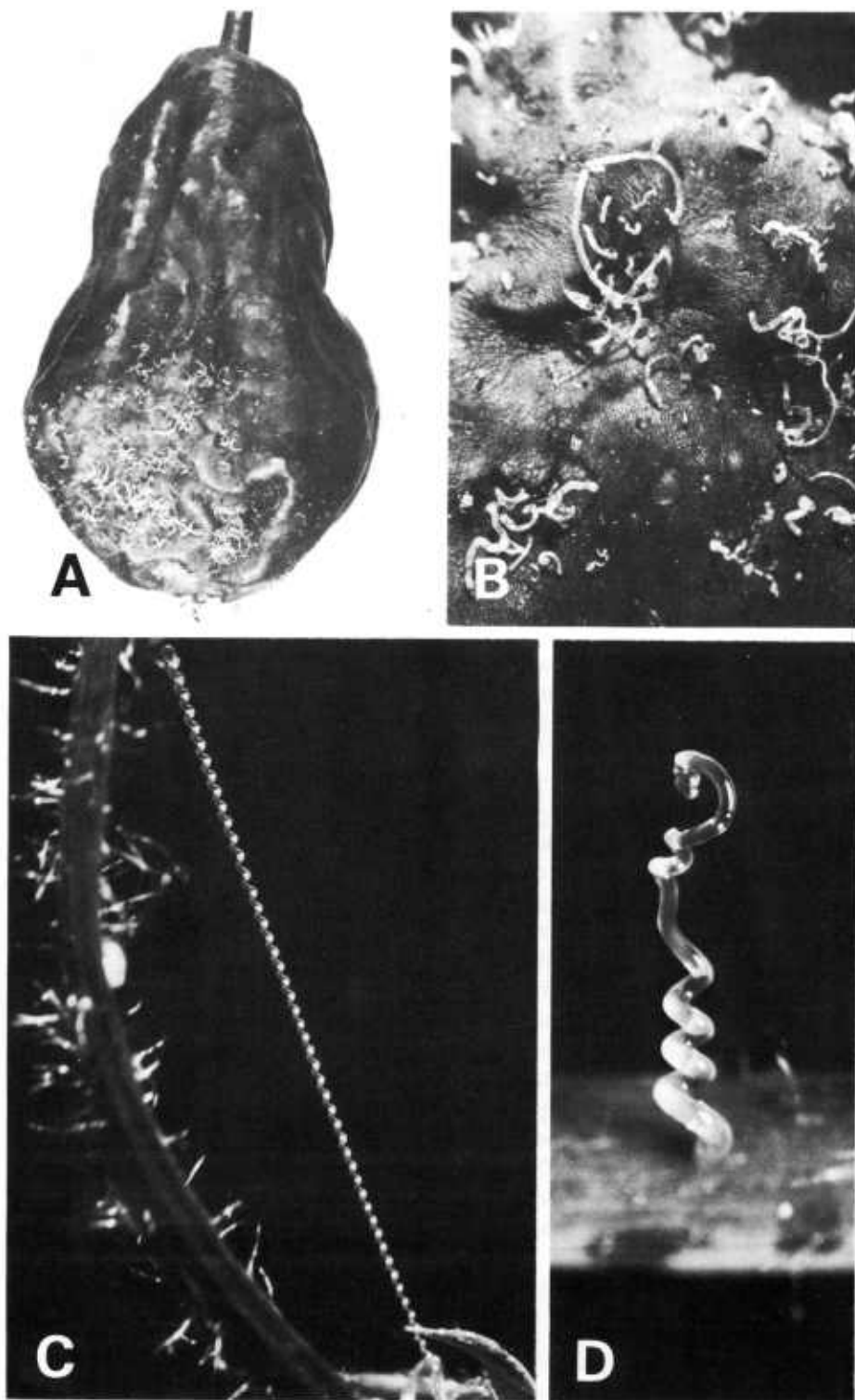
companied by ooze running along the bark (pl. 4, *A* and *B*).

Cankers formed at the base of blighted fruit spurs, water sprouts, or small limbs serve as sites where the bacteria may live over the winter. Cankers develop in the bark when progress of the infection is slowing down. They may be slightly sunken, varying in size and surrounded by irregular cracks in the bark (pl. 3, *A* and *B*). Active fire blight cankers have a dark, water-soaked appearance. The margin is indefinite, raised, or blistered. Later it may become marked by a definite crevice or crack (pl. 3, *A*).

The surface of the affected bark becomes sunken and remains smooth. Sometimes cankers, not identified by cracks or blisters, can be recognized by an outward discoloration of the bark, often purplish. Cankers formed early in the season, especially the small ones, usually are surrounded by a callus. They may girdle entire limbs and thus kill that part of the limb above the girdle; if in the trunk, they may kill the entire tree. Characteristic reddish-brown streaks are often found in the sapwood when the bark is peeled or cut away from the infected limb or twig. In England the overwintered cankers are distinguished from newly established summer cankers in that "the tissues become 'foxy-red,' merging through a diffuse mottled red-green area into the healthy bark" (194).

Fire blight in the main part of a tree trunk is referred to as trunk or body blight. One of its earliest symptoms is usually the presence of ooze running along the bark, sometimes accompanied by small cracks visible in the bark tissue (pl. 4, *C*). In trees with trunks susceptible to fire blight, such as the Magness pear cultivar, infection usually spreads rapidly from the trunk into scaffold limbs within a few months, frequently resulting in death of the tree. In this cultivar a distinct purplish coloration of the diseased bark tissue aids in identifying the disease (pl. 4, *D*).

Active fire blight cankers in the trunk have a dark water-soaked appearance. Their margins are indefinite or raised and blistered at first but later become definite and marked by a crack or crevice. The surface of the affected bark finally becomes sunken and usually remains smooth. The affected area may show streaking caused by an amber-colored exudate running down the trunk (pl. 4, *A*). Trunk blight may occur in trees that show no other evidence of blight



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FIGURE 7. — Bacterial strands on pear fruit and hawthorn shoots: A, Numerous cirri-like strands on blighted Bartlett fruit (natural size); B, section of fruit in A magnified five times; C, thin, uniformly coiled strand on hawthorn shoot; D, short, unevenly coiled strand originating from hawthorn shoot. (A and B, Courtesy Tree Fruit Res. Cent., Wenatchee, Wash.; C and D, courtesy East Malling Res. Sta., Maidstone, Kent, England.)

infection. This has been particularly evident in Magness trees at Beltsville (1060, 1063).

Collar and Root Blight

These two types of fire blight can be most destructive and frequently cause the immediate death of the tree. Fire blight cankers at the base (collar or crown) of the tree trunk or at ground level usually are referred to as collar blight. It may spread from the collar into the roots or sometimes from the roots into the collar. Detailed descriptions of symptoms and pictures of collar and rootstock blight have been published (694, 714, 1016).

Bark on the roots is killed in much the same manner as that on the trunk. Invasion of the crown and roots may occur in one of several ways: (1) Through infected suckers or water sprouts, (2) washing of bacteria from infected twigs and fruit down the trunk into the soil containing the roots, and (3) internal translocation of the fire blight bacteria from infected plant parts above ground to the roots. In recent years considerable collar and root blight have been found in apple rootstocks used for dwarfing purposes (513).

In Oregon, Coyier (188) frequently observed poor growth of apple and pear trees associated with fire blight infection in their root system. In preliminary experiments, apple seedlings were root pruned and either dipped in a suspension of *E. amylovora* or planted in soil infested with the blight pathogen. He⁷ found a marked difference in growth between the inoculated and noninoculated plants. He concluded that in commercial nursery plantings the trees may be accidentally inoculated by fire blight bacteria during planting from using contaminated pruning tools.

Quince and Crab Apple

Symptoms of fire blight in quince and crab apple are similar to those described for apple. Succulent shoots often produce ooze. In early summer the leaves turn light to dark brown and remain attached to the branches. The fruit of crab apple oozes as much as that of regular apples; however, oozing has not been observed as frequently on quince fruit.

Pyracantha and Hawthorn

With few exceptions, blight symptoms on pyracantha or firethorn (*Pyracantha* sp.), hawthorn

(*Crataegus* sp.), and cotoneaster (*Cotoneaster* sp.) are generally similar to those described on other hosts.

In pyracantha the blossom clusters are generally infected first. They turn brown and die. Although infection of soft shoots is reported infrequently and infection of branches is rare in England (369), the reverse is usually true in the United States.

Characteristic symptoms of fire blight on soft pyracantha shoots are reddish-brown leaves, whereas the shoot tip often shows the typical shepherd's crook (pl. 5, A). Infection frequently penetrates from the infected blossoms and the young shoots into the larger branches, sometimes killing a large part of the plant (pl. 5, B). In a later stage of infection, the leaf turns a characteristic light brown. Ooze droplets are rarely observed on young succulent shoots but more frequently on older branches.

In susceptible hawthorn shrubs the disease produces many infected shoots with light- to dark-brown clinging leaves (pl. 5, C). However, a closer observation may reveal that these branches are dead from winter damage, Monilinia canker, or salt-wind injury when plants are growing near the ocean. More positive identification can be obtained, however, if cankers can be located on the larger limbs. Meijneke (635) reported a characteristic purplish discoloration without cracks along the edge of the canker (pl. 5, D). Upon slicing the bark in this discolored area and immediately below, the typical watery, red-brown discoloration of the inner bark appears (87a, 462, 680). With slight pressure, droplets of bacterial exudate may be produced. Usually they are first milky white, later changing to orange and brown. In addition to ooze, bacterial strands have also been observed on hawthorn (fig. 7, C and D) (256, 635).

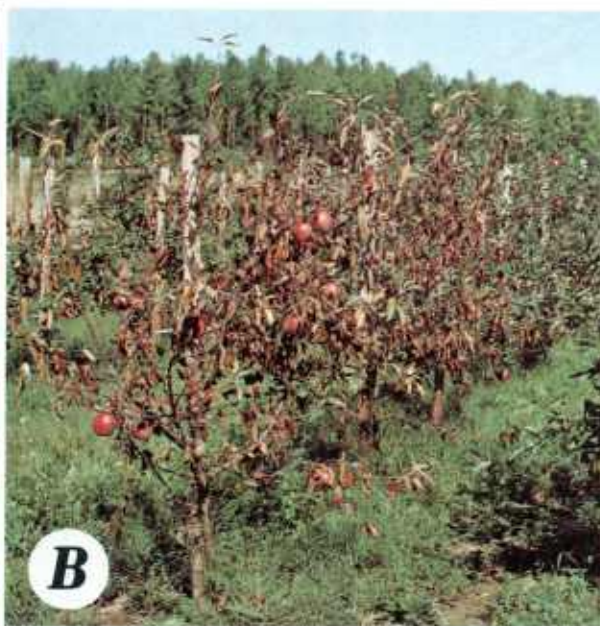
Meijneke (639) described an interesting blight symptom on hawthorn during field inspection in the Netherlands in 1972. He noticed bacterial ooze in the form of many tiny glistening droplets on petioles of leaves and fruit as well as shoot tips. The droplets did not become discolored but dried out and remained as a silvery film on the plant surface. These symptoms reportedly occurred only under special, yet unknown weather conditions.

Clusters of black shriveled blossoms have been reported on hawthorn, but opinions vary as to whether the flowers became infected directly or indirectly from nearby shoots (74, 76, 788). Meijneke (636, 638) reported from the Netherlands that twig

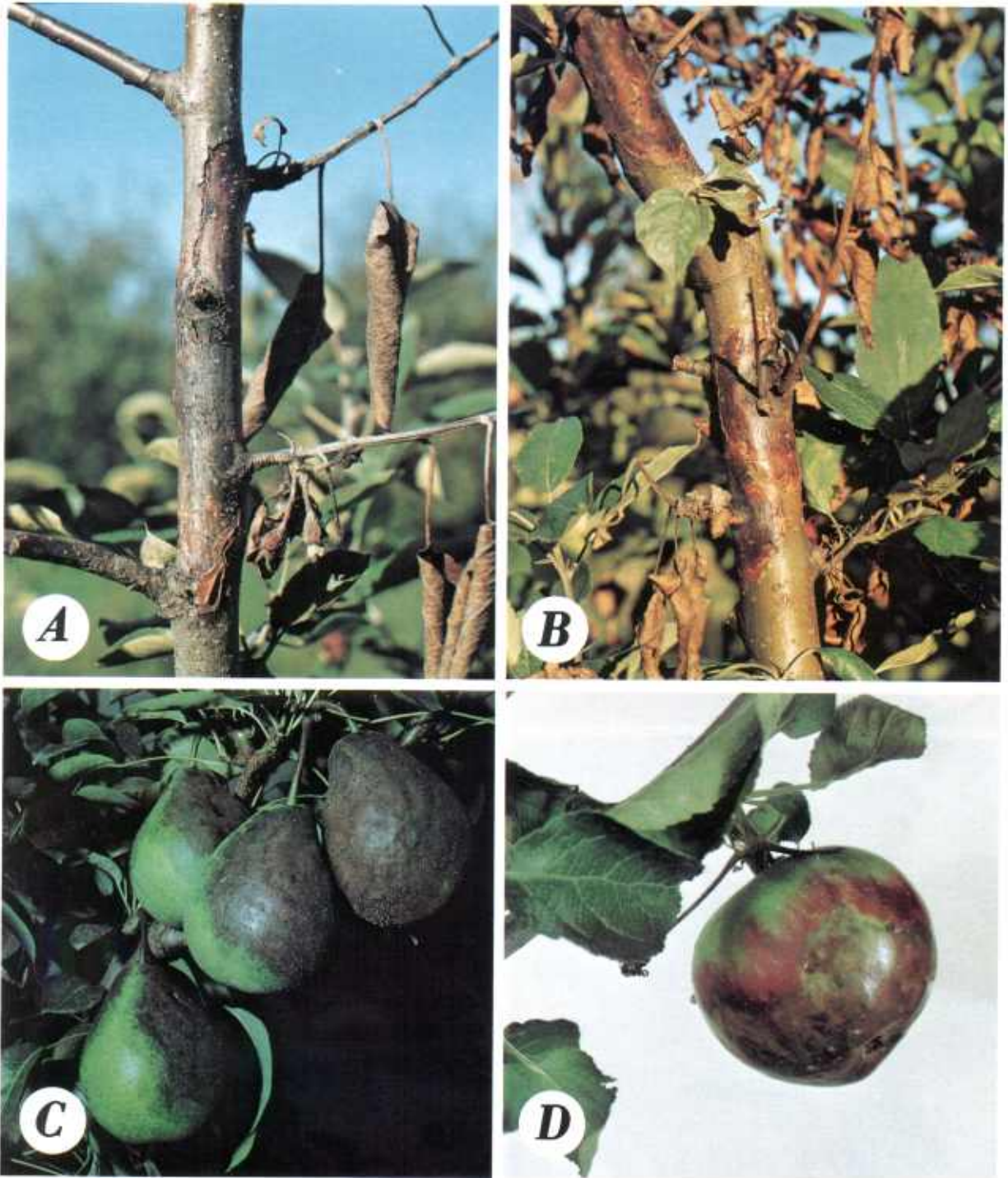
⁷ Unpub. data, Ornamental Plants Res. Lab., U.S. Dept. Agr., Corvallis, Oreg.



A, Severe blossom blight of pear, showing light- to dark-brown flower clusters; B, closeup of blighted pear blossoms and young fruitlets, with characteristic water-soaking and light-brown to black discoloration of stem tissues; C, aerial bacterial strands of *Erwinia amylovora*, forming a cottony mass around leaf petiole; note pale-yellowish ooze exudate on infected stem; D, blighted pear shoots, originating in terminal blossoms, forming characteristic shepherd's crook and clinging brown leaves.



A, Twig blight in apple tree, showing typical brown leaves adhering to branches; *B*, severe blight in apple trees on dwarf rootstock; *C*, pear orchard showing many dead trees due to fire blight; *D*, severe twig blight in Bartlett pear tree, with characteristic necrotic, dark-brown to black leaves attached to branches.



A, Advanced blight canker in main leader of young pear tree, showing typical cracking along upper margin of cankered area; note characteristic blackening toward base of canker and brown clinging leaves; B, several young blight cankers on branch of Golden Delicious apple tree, with characteristic orange-brown discoloration within cankered area; infection apparently started in young shoots and spread into main limb; C, advanced symptom of blight in Moonglow pear fruit, exhibiting typical water-soaked margin and green ring along border of blackened necrotic area; note numerous droplets of bacterial ooze clinging to blighted fruit; D, advanced blight in Jonathan apple fruit, showing characteristic reddish margin along blotchy necrotic area; note ooze droplet on left of fruit.



A, Characteristic brown streaking on central leader of pear tree resulting from profuse production of bacterial ooze; note typical orange color of dried ooze and brown leaves on recently infected branch; *B*, closeup of bacterial ooze on tree trunk of pear tree, exhibiting white to light-brown exudate starting to flow; *C*, first sign of blight in Magness pear tree trunk, manifested as cracking of bark and yellowish ooze running on surface; *D*, canker in trunk and base of scaffold limbs in Magness pear tree due to blight infection originating in trunk; note characteristic purplish to black discoloration of bark in this cultivar.



A, Twig blight in young pyracantha shoot, showing characteristic reddish-brown leaves and typical curving of shoot tip; B, advanced blight in pyracantha; note retention of dark-brown leaves on shoots invaded by blight organism and light-brown leaves on limbs apparently girdled at their base; C, numerous blighted shoots on large hawthorn bush in background, with brown discolored clinging leaves; D, closeup of blighted spur on hawthorn, showing darkened necrotic canker in main limb. (A and B, Courtesy U.S. Natl. Arboretum, Washington, D.C.; C and D, courtesy Plant Protect. Serv., Wageningen, the Netherlands.)



A, Severely infected cotoneaster shrub, showing characteristic brown-black leaves clinging to shoots; *B*, typical shepherd's crooks on cotoneaster twigs with light-brown leaves and dark midribs; note constriction at base of necrotic portion on two shoots at left; *C*, blighted blossom cluster and light-brown leaves on stranvaesia shrub; *D*, masses of clinging brown leaves on blighted mountainash tree. (*A*, Courtesy Biol. Bundesanstalt, Kitzberg, West Germany; *B*, *C*, and *D*, courtesy Plant Protect. Serv., Wageningen, the Netherlands.)

blight is much more important than blossom blight and that hawthorn fruit blight has not been observed. Twig blight of hawthorn can best be recognized at first by the yellowing of the leaves, which later turn brown and remain attached to the tree, but some investigators report infected branches without clinging leaves (77, 369). This phenomenon has also been observed on pear and may be a result of the blight organism moving slowly through its host tissue and thus enabling the plant to produce abscission substances.

Cotoneaster, Stranvaesia, and Mountainash

Symptoms of fire blight in cotoneaster are usually similar to those in pyracantha, but the affected internal tissue is often a lighter brown and the reddish-brown discoloration of soft shoots is less apparent. On larger shrubs with older woody branches the leaves turn dark brown following infection and usu-

ally cling to the shoots (pl. 6, A). Meijneke⁸ reported a remarkable symptom on cotoneaster in the Netherlands, i.e., the rapid girdling around the infection in blossom trusses and in shoots and twigs (pl. 6, B). As a result, these trusses partially contained healthy flowers and the shoots often showed the well-known shepherd's crook.

On stranvaesia, the drooping of large brown terminal blossom clusters with light-brown leaves underneath is the most characteristic symptom of fireblight on this shrub (pl. 6, C). On infected cotoneaster and stranvaesia leaves, Meijneke⁸ also observed ooze droplets in rows on both sides of the midrib on the undersurface of the brown-black leaves. These droplets were grayish white and later changed to light brown.

On mountainash (*Sorbus*), fire blight is characterized by masses of light-brown leaves clinging to the branches (pl. 6, D).

Symptoms of fire blight on other rosaceous hosts generally agree with one or more of the symptoms described here (90, 311, 823, 934, 938).

⁸Pers. commun., Plant Protect. Inst., Wageningen, the Netherlands.

CHAPTER 5

DISEASES RESEMBLING FIRE BLIGHT

Blight or blast, similar to fire blight, especially in buds and blossoms, sometimes is caused by organisms other than *E. amylovora*. The following causal agents of blossom blast have been reported: *Pseudomonas nectarophila* (Doidge) Burkholder (as *Bacterium nectarophilum* Doidge) (220, 244), *Pseudomonas barkeri* (Berridge) Clara (64, 65, 267), *P. prunicola* Wormald (810, 1040), *P. utiformica* Clara (175), and *P. syringae* Van Hall (91, 324, 477, 617, 633, 711, 719, 789, 835, 837, 1027). The symptoms described under these organisms, and the records of the unconfirmed reports of fire blight from various European and other countries since about 1910, are thought to be similar to those of one single disease known as blossom blast, caused by *P. syringae* (138, 331, 719, 1105).

To diagnose the cause of blast symptoms is often very difficult. During the bloom period the blossom and bud blast may be the only symptom seen. Discolored water-soaked spots first appear and sometimes increase in size. They may spread until the flower receptacle becomes diseased. In some cases the peduncle becomes infected and the entire flower blackens and withers. The infection may stop in the flower or it may extend 2–5 cm into the stem and cause darkening and cracking of the bark, and it produces definite cankers. Blast cankers are usually light brown to tan and when older the outer bark becomes scaly. Leaf infections appear as dry, localized lesions.

Confusion between fire blight and blossom blast is most likely to occur with blossom infection because at this time the two diseases cannot be separated based on symptoms alone. Usually fire blight infection in blossoms, unlike that caused by *P. syringae*, originates through nectariferous tissues in the calyx cup and spreads rapidly into the receptacle and then through the peduncle into the branches. Such differentiation is rarely possible in the field because origins of infection are quickly obscured by their extension. Even though blossom blast rarely progresses beyond the base of the peduncles or distal parts of the spurs, there are exceptions where extensive

cankering into branches may occur (572, 1027). It is these exceptions that require accurate diagnostic methods to separate the two diseases.

Brief but detailed descriptions of the comparative symptoms of fire blight and blossom blast and their respective causal organisms have been published (391, 392). The first and simplest method to identify the respective causal organisms is to use the potato and pear test (88, 572). From 48 to 72 hours after placing the suspected organisms on a surface-sterilized potato slice or injured pear fruitlet, *P. syringae* should cause a rotting of the entire potato slice but should only produce localized, dry, black lesions on the fruitlets. In contrast, *E. amylovora* should not cause a potato rot but should produce typical drops of milky bacterial exudate on the pear surface. About 1970, Kleinhempel et al. (532a) modified the pear fruitlet test by implanting infected tissue directly into the fruit.

Confirmatory diagnosis of *P. syringae* and *E. amylovora* can be made with serological tests (268, 712, 822, 828, 1046a, 1128a), phage sensitivity tests (195, 340, 353, 718), and slide or tube agglutination tests (88, 326, 467, 468, 533, 572).

There seems to be no doubt that bud or blossom blast (*P. syringae*) usually occurs when trees are predisposed to frost or cold periods during the spring (719). Several investigators mentioned serious outbreaks of blast following such weather conditions (65, 1040). Panagopoulos and Crosse (720) found that pear blossoms exposed immediately before inoculation to temperatures from -1° to -2° C (30° – 28.5° F) increased their susceptibility to blast infection. They furthermore showed that the causal organism (*P. syringae*) in the surface microflora can induce infection when conditions are provided, i.e., sprayed with water after frost treatment (719). There are, however, records where blossom blast has occurred without mention of frost or after wet cold periods in the spring (65, 477, 1040).

Until recently, bacterial ooze on blasted pear buds was associated only with infection caused by *E. amylovora*. In fact, the absence of ooze was one of

the features used to separate the two diseases. In the spring of 1968, however, we observed ooze produced by an unidentified *Pseudomonas* species in or on pear blossom and leaf buds (fig. 8). This organism caused a severe loss of flower buds in Magness pear, and temperatures preceding the first observations were higher than those normally recorded for infection by *P. syringae* (506).

In the U.S.S.R., D'yakova (*in* Gorlenko, 356, 1096) described a bacterial blight on pear caused by *P. pyri* (Djakowa) Gorl. This disease is also characterized by a twisted shoot tip but differs from fire blight and blast in that the bark cracks and peels off and no infection of unripe fruit occurs. This organism reportedly is a nonspore-forming, lophotrichous rod, which does not produce ooze.

Certain fungus diseases have been reported associated with fire blight. Black rot (*Phylospora obtusa*) and bitter rot (*Glomerella cingulata* (Ston.) Spauld. and Schrenk) usually follow infection by *E. amylovora* (235, 555, 713, 924). Both of these diseases may cause difficulty in identifying fire blight the following season because of holdover cankers.

Fire blight damage sometimes may be confused with the periodic cicada (*Magicicada septendecim* (L.)) and winter injury. Soon after the cicada or 17-year locust lays its eggs, the leaves on infested apple and pear branches start to wilt. The leaves become shriveled and dry and many remain attached to the branches, but ooze is not produced as it sometimes is in branches showing fire blight. Fire blight-like symptoms have also been observed on hawthorn in Denmark caused by larvae of the gall midge *Resseliella crataegi* (Barnes) (as *Thomasiniana crataegi* (Barnes)) (952).

Limbs showing winter damage usually shrivel and dry without the presence of attached leaves, which may occur on blighted limbs during the final stages of the disease. On the other hand, dead branches with attached leaves have been observed on hawthorn near the ocean, caused by salt in the air blown by severe winds. In all cases regardless of the cause,



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FIGURE 8.—Cluster of flower buds from Magness pear, showing ooze drops produced by unidentified *Pseudomonas* species.

such damaged limbs should be pruned for they serve only as a haven for secondary organisms.

Two bacterial diseases should be mentioned that are unrelated to fire blight of apple and pear. They are referred to by the same name but caused by different species of *Erwinia*. They are fire blight of cosmos (*Cosmos bipinatus* Cav.) caused by *E. cosmovora* Prasad (763) and fire blight (vlamsiekte) of grape (*Vitis* sp.) caused by *E. vitivora* (Baccarini) du Plessis (272). Both diseases are characterized by necrotic lesions on the leaves and by cankers on the shoots and woody twigs.

CHAPTER 6

HOST RANGE

To determine the types and numbers of host plants susceptible to fire blight, many natural blight observations and artificial inoculations of plants were made during 1925-35 (726, 742, 804, 823, 934, 937, 938). Table 2 is a listing of the genera and species reported susceptible to fire blight except *Malus* and *Pyrus*, which are included in chapter 13. Besides these 2 genera, 129 species in 37 genera of the family Rosaceae have been reported susceptible to fire blight. Of these genera, those that are most

important economically and show the most severe blight are *Cotoneaster*, *Crataegus*, *Cydonia*, *Pyracantha*, and *Sorbus*. The genera and species in the rosaceous family that reportedly showed no infection following artificial inoculation are listed after table 2. Among this group are 21 genera containing 39 species (859, 934, 938). One wonders if additional investigations might find many or all of these plants susceptible to fire blight.

TABLE 2.—*Genera and species in family Rosaceae susceptible to fire blight* ¹

Scientific name	Common name	Blight index ²	Location	Reference ³
<i>Amelanchier</i> :				
<i>alnifolia</i> (Nutt.) Nutt. -----	Serviceberry-----	1 (s)	Calif., Wash.-----	702, 934
<i>canadensis</i> (L.) Medic. -----	-----do-----	1 (b)	N.Y., Wis., West Germany.	45, 47, 859, 1046b, 1046c
<i>laevis</i> Wieg.-----	Juneberry -----	1 (b)	Ark., Wis., Denmark----	804, 859, PC
<i>Aronia</i> :				
<i>arbutifolia</i> (L.) Pers.-----	Red chokeberry-----	1	Calif., Wis. -----	859, 934
<i>melanocarpa</i> (Michx.) Ell.-----	-----	1	Denmark -----	PC
<i>Aruncus sylvestris</i> Kostel. -----	Goatsbeard-----	2	Calif. -----	934
<i>Chaenomeles</i> :				
<i>japonica</i> (Thunb.) Lindl. ex Spach.	Flowering Japanese quince.	2-3 (b)	Calif., D.C., N.J., West Germany.	934, 1046b, 1046c, PC
<i>lagenaria</i> (Loisel.) Koidz.-----	-----do-----	1-2	Ark., Calif., N.Y. -----	742, 823, 934
<i>Cotoneaster</i> :				
<i>acuminatus</i> Lindl. -----	Sharpleaf cotoneaster-----	1-4	D.C., N.J. -----	207a, 261, 1021
<i>adpressus</i> Bois -----	Creeping cotoneaster-----	1-4	Calif., D.C., N.J., West Germany.	207a, 261, 934, 938, 1021, 1046b, 1046c
<i>affinis</i> Lindl.-----	-----	1-4 (s)	D.C., Gt. Brit. -----	261, 576
<i>ambiguus</i> Rehd. and Wils. -----	-----	1-4	Calif., D.C. -----	261, 934
<i>apiculatus</i> Rehd. and Wils. -----	Cranberry cotoneaster-----	1-2	Calif., D.C., N.J. -----	207a, 261, 934
<i>ascendens</i> Flinck and Hylmö-----	-----	4	D.C. -----	261
<i>bullatus</i> Bois-----	-----	1-4 (b)	D.C., Denmark, West Germany.	261, 1046b, 1046c, PC
<i>bullatus</i> f. <i>floribunda</i> (Stapf) Rehd. and Wils.	-----	1	Calif. -----	934
<i>buxifolius</i> Wall. ex Lindl.-----	-----	4	D.C. -----	261
<i>buxifolius</i> f. <i>vella</i> Franch. -----	-----	2	Calif. -----	934
<i>commixtus</i> (Schneid.) Flinck and Hylmö.	-----	4	D.C. -----	261
<i>congestus</i> Baker-----	-----	3-4	D.C., West Germany----	261, 1046b, 1046c
<i>conspicuus</i> Marquand-----	Necklace cotoneaster-----	1-2	D.C., N.J., West Germany.	207a, 261, 1046b, 1046c
<i>dammeri</i> Schneid.-----	Bearberry cotoneaster-----	2-4	D.C., N.J., West Germany.	261, 1021, 1046b, 1046c

See footnotes at end of table.

TABLE 2.—*Genera and species in family Rosaceae susceptible to fire blight* ¹—Continued

Scientific name	Common name	Blight index ²	Location	Reference ³
<i>dielsianus</i> Pritz.-----	Diels cotoneaster-----	1-2	D.C., N.J., West Germany.	207a, 261, 1021, 1046b, 1046c
<i>divaricatus</i> Rehd. and Wils.-----	Spreading cotoneaster-----	1-3 (b)	D.C., N.J., Denmark, West Germany.	207a, 261, 1046b, 1046c, PC
<i>elegans</i> (Rehd. and Wils.) Flinck and Hylmö (syn. <i>C. dielsiana</i> var. <i>elegans</i>).	-----	1	Calif.-----	934, 938
<i>floccosus</i> (Rehd. and Wils.) Flinck and Hylmö.	-----	2-4	Calif., D.C.-----	261, 938
<i>foveolatus</i> Rehd. and Wils.-----	Glossy cotoneaster-----	1	D.C., N.J.-----	207a, 261
<i>franchetii</i> Bois-----	Franchet cotoneaster-----	1-4	D.C., N.J.-----	207a, 261, 1021
<i>frigidus</i> Wall. ex Lindl.-----	Himalayan cotoneaster-----	1-4 (s)	Calif., D.C., Gt. Brit.---	261, 576, 934, 938
<i>glabratus</i> Rehd. and Wils.-----	-----	1	Calif.-----	934
<i>glaucophyllus</i> Franch.-----	-----	1 (s)	D.C., Gt. Brit.-----	261, 576
<i>harrysmithii</i> Flinck and Hylmö.	-----	4	D.C.-----	261
<i>henryanus</i> (Schneid.) Rehd. and Wils.	-----	3 (s)	Calif., Gt. Brit.-----	576, 938
<i>hissaricus</i> Pojark.-----	-----	1	D.C.-----	261
<i>horizontalis</i> Decne.-----	Rockspray cotoneaster-----	2-4 (b, s)	Calif., D.C., N.J., Denmark, Gt. Brit., West Germany.	207a, 261, 574, 934, 938, 1021, 1046b, 1046c, PC
<i>ignavus</i> Wolf-----	-----	1	D.C.-----	261
<i>insignis</i> Pojark. (syn. <i>C. lindleyana</i>).	-----	1-2	Calif., D.C.-----	261, 934
<i>khasiensis</i> Klotz-----	-----	1	D.C.-----	261
<i>lacteus</i> W. W. Smith-----	-----	1	Calif.-----	934, 938
<i>laxiflorus</i> Jacq. (syn. <i>C. melanocarpa</i> var. <i>laxiflora</i> (Jacq.) Schneid., <i>C. polyanthema</i> E. Wolf.).	-----	1 (s)	Gt. Brit.-----	90
<i>lucidus</i> Schlecht.-----	Hedge cotoneaster-----	2-4 (s)	D.C., N.J., Denmark---	207a, 261, PC
<i>melanocarpus</i> Lodd.-----	-----	1	D.C.-----	261
<i>microphyllus</i> Wall. ex Lindl.-----	Rockspray cotoneaster-----	1-4	Calif., D.C., N.J., West Germany.	207a, 261, 934, 938, 1021, 1046b, 1046c
<i>moupinensis</i> Franch.-----	-----	4	D.C.-----	261
<i>multiflorus</i> Bge.-----	Large flowering cotoneaster	1-4 (b)	D.C., N.J., West Germany.	207a, 261, 1046b, 1046c
<i>nanshan</i> Mottet-----	-----	4	D.C.-----	261
<i>nitens</i> Rehd. and Wils.-----	Ko Ko Nor cotoneaster-----	2-4	Calif., D.C., N.J., Wis.-	207a, 261, 859, 934
<i>obscurus</i> Rehd. and Wils.-----	Bloodberry cotoneaster-----	1-4 (s)	D.C., N.J., Gt. Brit.---	207a, 261, 576
<i>obtusus</i> Wall. ex Lindl.-----	-----	1	D.C.-----	261
<i>pannosus</i> Franch.-----	Silverleaf cotoneaster-----	3-4 (s)	Ark., Calif., D.C., N.J.-	261, 809, 873, 934, 938, 1021
<i>perpusillus</i> (Schneid.) Flinck and Hylmö.	-----	1	D.C.-----	261
<i>polyanthemus</i> E. Wolf.-----	-----	1	Gt. Brit.-----	90
<i>prostratus</i> Baker-----	-----	2	Calif.-----	934, 938
<i>racemiflorus</i> (Desf.) K. Koch-----	Sungari rockspray cotoneaster.	3-4	D.C., N.J.-----	207a, 261
<i>radicans</i> (Dammer ex Schneid.) Klotz (syn. <i>C.</i> <i>dammeri</i> var. <i>radicans</i>).	-----	2-3	Calif., West Germany---	934, 938, 1046b, 1046c
<i>rhytidophyllus</i> Rehd. and Wils.--	-----	(s)	Gt. Brit.-----	576

See footnotes at end of table.

TABLE 2.—*Genera and species in family Rosaceae susceptible to fire blight* ¹—Continued

Scientific name	Common name	Blight index ²	Location	Reference ³
<i>roseus</i> Edgew. -----	-----	4	D.C. -----	261
<i>rotundifolius</i> Wall. ex Lindl. -----	Redbox cotoneaster -----	1-2	Calif., D.C. -----	261, 934
<i>rubens</i> W. W. Smith -----	-----	1	D.C. -----	261
<i>salicifolius</i> Franch. -----	Willowleaf cotoneaster -----	3-4 (b, s)	Calif., D.C., N.J., Belgium, Denmark, Gt. Brit., Netherlands, West Germany.	90, 261, 293, 429, 576, 639, 934, 976, 977, 1021, 1046b, 1046c, PC
<i>simonsii</i> Baker -----	Simons cotoneaster -----	1 (s)	Calif., D.C., N.J., Gt. Brit.	261, 576, 938, 1021
<i>soongoricus</i> (Regel) Popov (syn. <i>C. racemiflora</i>). -----	Redbead cotoneaster -----	4	Calif., D.C. -----	261, 934
<i>splendens</i> Flinck and Hylmö -----	-----	4	D.C. -----	261
<i>sternianus</i> (Turrill) Boom -----	-----	1-4	D.C., West Germany -----	261, 1046b, 1046c
<i>tenuipes</i> Rehd. and Wils. -----	-----	4	D.C. -----	261
<i>tomentosus</i> (Ait.) Lindl. -----	-----	2-4	Calif., D.C. -----	261, 934
<i>veitchii</i> (Rehd. and Wils.) Klotz- Flinck and Hylmö (syn. <i>C. acutifolia</i>). -----	Peking cotoneaster -----	4 1-4 (b)	D.C. ----- Calif., D.C., N.J., Denmark, West Germany.	261 207a, 261, 934, 1046b, 1046c, PC
<i>wardii</i> W. W. Smith -----	-----	4	D.C., Gt. Brit. -----	261, 571, 576
<i>X watereri</i> Exell -----	-----	1-4 (b, s, f)	D.C., Denmark, Gt. Brit., West Germany.	261, 571, 1046b, 1046c, PC
<i>zabelii</i> Schneid. -----	Cherryberry cotoneaster -----	1-4	Calif., D.C., N.J. -----	207a, 261, 934
<i>Cowania stansburiana</i> Torrey (syn. <i>C. mexicana</i>). -----	Cliff rose -----	1	Calif. -----	934
<i>Crataegomespilus dardarii</i> Simon-Louis. -----	-----	1	Gt. Brit. -----	576
<i>Crataegus</i> :				
<i>arnoldiana</i> Sarg. -----	-----	1	N.Y., Wis. -----	859, 937
<i>crusgalli</i> L. -----	Cockspur thorn -----	1-2 (b, s)	Mo., N.Y., Wis., Gt. Brit.	576, 770, 859, 937
<i>douglasii</i> Lindl. -----	Western black hawthorn -----	1	Wash., Netherlands -----	639a, 702
<i>flabellata</i> var. <i>grayana</i> (Egglest.) Palmer (syn. <i>C. grayana</i>). -----	-----	1	Wis. -----	859
<i>mollis</i> (Torrey and Gray) Scheele -----	-----	1	N.Y. -----	937
<i>monogyne</i> Jacq. -----	English hawthorn -----	1-3 (b, s, f)	Calif., N.Y., Wis., Denmark, Gt. Brit., West Germany.	74, 87a, 282, 308, 330, 571, 576, 645, 692, 859, 934, 937, 1046b, 1046c, PC
<i>oryacantha</i> L. -----	-----do-----	1-3 (b, s)	Calif., N.Y., Wis., Denmark, Gt. Brit., West Germany.	45, 47, 74, 87a, 282, 571, 576, 645, 692, 742, 859, 934, 937, PC
<i>pedicellata</i> Sarg. (syn. <i>C. coccinea</i>). -----	-----	1	Wis. -----	859
<i>phaenopyrum</i> (L.) f. Medic. (syn. <i>C. cordata</i>). -----	-----	2	Wis. -----	859
<i>punctata</i> Jacq. -----	-----	2 (s)	N.Y., Wis. -----	859, 937
<i>succulenta</i> Link -----	-----	2 (s)	N.Y. -----	937
<i>uniflora</i> Muenchh. (syn. <i>C. tomentosa</i>). -----	-----	1	Wis. -----	859
sp. -----	Oriental crataegus -----	3 (s)	Ark. -----	804

See footnotes at end of table.

TABLE 2.—*Genera and species in family Rosaceae susceptible to fire blight* ¹—Continued

Scientific name	Common name	Blight index ²	Location	Reference ³
<i>Cydonia</i> :				
<i>oblonga</i> Mill.-----	Quince-----	1-2 (s)	Calif., Ill., N.Y., Gt. Brit., West Germany.	131, 302, 424, 576, 645, 901, 934, 938
<i>sinensis</i> (Dumont de Cour.) Thouin.	Chinese quince-----	4 1 (f)	Denmark----- Calif.-----	PC 934, 938
<i>Dichotomanthes tristaniaecarpa</i> Kurz.	-----	1 (s)	Gt. Brit.-----	576
<i>Docynia delavayi</i> (Franch.) Schneid.	-----	2	Calif.-----	934
<i>Dryas</i> sp.-----	Mountain avens-----	(s)	N.Y.-----	726
<i>Eriobotrya japonica</i> (Thunb.) Lindl.	Loquat-----	1 (s)	Calif., D.C., Fla., Ga., N.Y., New Zeal.	206, 424, 722, 934, 996, 1003
<i>Exochorda</i> sp.-----	Pearlbush-----	(s)	N.Y.-----	726
<i>Fragaria</i> :				
<i>X ananassa</i> Duch. (syn. <i>F. chiloensis</i>). <i>virginiana</i> Duch.-----	Strawberry-----	2 1-2	Calif., N.Y.----- N.Y.-----	671, 742 742
<i>Geum</i> sp.-----	Avens-----	(s)	N.Y.-----	726
<i>Heteromeles arbutifolia</i> M. Roem. (syn. <i>Photinia arbutifolia</i>).	Toyon (Calif. holly) or Christmasberry.	1-2 (s, f)	Calif., D.C., Wash.-----	702, 934, 938, 996
<i>Holodiscus discolor</i> (Pursh.) Maxim.	Creambush-----	1 (s)	Calif., N.Y., Denmark--	726, 934, PC
<i>Kageneckia oblonga</i> Ruiz and Pavon.	-----	1	Calif.-----	934
<i>Kerria japonica</i> (L.) DC.-----	Kerria-----	(s)	N.Y.-----	726
<i>Mespilus germanica</i> L.-----	Medlar (<i>Mespil</i>)-----	(s)	N.Y., New Zeal.-----	206, 424, 726, 1003
<i>Osteomeles anthyllidifolia</i> Lind.-----	-----	2	Calif.-----	934
<i>Peraphyllum ramossissimum</i> Nutt. -	-----	1	Calif.-----	934
<i>Photinia</i> :				
<i>deflexa</i> Hemsl.-----	-----	1	Calif.-----	934
<i>glabra</i> (Thunb.) Maxim.-----	-----	2	Calif.-----	934
<i>villosa</i> (Thunb.) DC.-----	-----	3	Calif., N.Y.-----	742, 1021
<i>Physocarpus</i> sp.-----	Ninebark-----	(s)	N.Y.-----	726
<i>Potentilla</i> sp.-----	Cinquefoil-----	(s)	N.Y.-----	726
<i>Prinsepia</i> sp.-----	-----	(s)	N.Y.-----	726
<i>Prunus</i> :				
<i>alleghaniensis</i> Port.-----	Allegheny plum-----	1	Calif.-----	938
<i>armeniaca</i> L.-----	Apricot-----	1	Calif.-----	938
<i>avium</i> (L.) L.-----	Sweet cherry-----	(f)	Wash.-----	432
<i>besseyi</i> Bailey-----	Western sand cherry-----	1	Calif.-----	938
<i>cerasifera</i> Ehrh.-----	Myrobalan plum-----	1	Calif., Denmark-----	938, PC
<i>dasycarpa</i> Ehrh.-----	Purple apricot-----	1	Calif.-----	938
<i>domestica</i> L.-----	Agen prune, Italian prune, Spaulding plum.	4 (s) 3 (s)	Oreg.----- N.Y., Oreg., Wash.-----	470 432, 470, 1018
<i>fremontii</i> Wats.-----	Native desert apricot-----	1 (s)	Conn.-----	911
<i>ilicifolia</i> (Nutt.) Walp.-----	Hollyleaf cherry-----	1	Calif.-----	934
<i>lusitanica</i> L.-----	Portugal-laurel-----	1 (s)	Calif.-----	934, 938
<i>mume</i> Sieb. and Zucc.-----	Japanese apricot-----	1	Calif.-----	934
<i>nigra</i> Ait. (as <i>P. americana</i>)-----	Cheney plum-----	1 (s)	Vt.-----	938
<i>salicina</i> Lindl.-----	Japanese plum-----	(s)	Ark., Conn.-----	487
<i>simonii</i> Carr.-----	Apricot plum-----	1 (s)	Calif., Colo.-----	823, 911 717, 938

See footnotes at end of table.

TABLE 2.—*Genera and species in family Rosaceae susceptible to fire blight*¹—Continued

Scientific name	Common name	Blight index ²	Location	Reference ³
<i>spinosa</i> L. -----	Sloe plum -----	1	Denmark -----	PC
<i>triloba</i> Lindl. -----	Flowering almond -----	(s)	N.Y., Wis. -----	424, 881
<i>Pyracantha</i> (fire thorn):				
<i>angustifolia</i> Schneid. -----	-----	4 (s)	Calif., D.C., New Zeal. -	206, 262, 772, 934, 938
<i>atalantioides</i> (Hance) Stapf. -----	-----	4	D.C. -----	262
<i>coccinea</i> Roem. -----	-----	1-3 (b, f, s)	Calif., D.C., N.Y., Denmark, Gt. Brit., West Germany.	45, 47, 262, 429, 934, 938, 1046b, 1046c, PC
<i>crenulata</i> (D. Don) Roem. -----	-----	1-3 (s)	Calif., D.C. -----	262, 938
<i>crenulata</i> var. <i>kansuensis</i> Rehd. -----	-----	1	D.C. -----	262
<i>fortuneana</i> (Maxim.) Li (syn. <i>P. gibbsii yunnanensis</i>). -----	-----	1-3	Calif., D.C., N.Y. -----	262, 424, 934, 938
<i>koidzumii</i> (Hayata) Rehd. (syn. <i>P. formosiana</i>). -----	-----	1-3	Calif., D.C. -----	262, 934, 938
<i>rogersiana</i> (A.B. Jacks.) Bean --	-----	1-3 (s)	Calif., D.C., Denmark --	262, 938, PC
<i>Raphiolepis</i> :				
<i>indica</i> (L.) Lindl. -----	Indian hawthorn -----	2	Calif. -----	934, 938
<i>umbellata</i> (Thunb.) Mak. -----	-----	1 (s)	Calif., N.Y. -----	424, 934, 938
<i>Rhodotypos scandens</i> (Thunb.) Mak. -	Jetbead -----	(s)	N.Y. -----	726
<i>Rosa</i> :				
<i>blanda</i> Aiton -----	-----	1	N.Y. -----	742, 998
<i>multiflora</i> Thunb. -----	-----	1	Calif., West Germany --	934, 1046b, 1046c
<i>rubiginosa</i> L. -----	Sweetbriar eglantine -----	1	N.Y., West Germany -----	742, 1046b, 1046c
<i>rubrifolia</i> Vill. -----	-----	1	N.Y. -----	742
sp. -----	Cultivated rose -----	1-3 (b, s)	Ark., D.C., N.Y., Wash.	742, 823, 998
<i>Rubus</i> :				
<i>idaeus</i> L. -----	Red raspberry -----	2 (b, s, f)	Maine, N.C. -----	310, 569, 892
sp. -----	Thornless blackberry -----	1 (s, f)	Ill. -----	789a
<i>Sorbaria</i> sp. -----	False-spirea -----	(s)	N.Y. -----	726
<i>Sorbus</i> :				
<i>americana</i> Marsh -----	American mountainash -----	2	N.Y., Wis. -----	45, 859, 984, 1039
<i>aria</i> (L.) Crantz -----	Whitebeam -----	1-2	Gt. Brit., Netherlands ---	90, 576, 639
<i>aucuparia</i> L. (syn. <i>S. laciniata</i>) --	European mountainash -----	1 (s)	Calif., N.Y., Wis., Denmark, Gt. Brit., West Germany.	90, 302, 645, 859, 867, 934, 937, 1046b, 1046c, PC
<i>mougeotii</i> Soyer-Will. and Godr. --	-----	1	Wis. -----	859
<i>occidentalis</i> (Watson) Greene -----	Western mountainash -----	(s)	Wash. -----	702
<i>tianshanica</i> Rupr. -----	-----	2	Gt. Brit. -----	576
<i>Spiraea</i> :				
<i>cantoniensis</i> Lour. -----	-----	1 (s)	Calif., Va. -----	375, 938
<i>densiflora</i> Nutt. ex Torr. and Gray.	Native spirea -----	1	Calif. -----	934
<i>vanhouttei</i> (Briot.) Zabel -----	Vanhoutte spirea -----	1	Ark., Calif., West Germany.	923, 938, 1046b, 1046c
<i>Stranvaesia davidiana</i> Decne. -----	-----	1-2 (b, s)	Calif., Denmark, Gt. Brit., West Germany.	576, 867, 934, 1021, 1046b, 1046c, PC

¹ Not included are *Malus* and *Pyrus*, which are listed in chapter 13.² Based on artificial inoculation in shoot: 1 = 1–25, 2 = 26–50, 3 = 51–75, and 4 = 76–100 percent of shoot blighted; letter in parenthesis indicates reported natural blossom (b), shoot (s), or fruit (f) infection; single scores indicate most severe blight recording obtained from multiple entries; blanks indicate no mention made of degree of infection.³ PC = pers. commun., Jorgensen, H. A., and Jensen, A., State Plant Path. Inst., Lyngby, Denmark (489).

The following genera and species in the family Rosaceae showed no blight infection after artificial inoculation (859, 934, 938):

Acaena microphylla Hooker f.
Adenostoma sparsifolium Torrey
Cercocarpus betuloides Nutt. ex Torrey and Gray
Chamaebatia foliolosa Benth.
Cotoneaster bacillaris Wall. ex Lindl.
Cotoneaster disticha Lange (as *C. decora*)
Cotoneaster harroviana Wils.
Cotoneaster hebeophylla Diels
Cotoneaster newryensis Lemoine
Cotoneaster silvestri Pamp. (syn. *C. hupehensis*)
Crataegus prunifolia Pers.
Dryas X suendermannii Kell. ex Sundermann
Erochorda racemosa (Lindl.) Rehd.
Fallugia paradoxa (D. Don) Torrey
Fragaria chiloensis (L.) Duch.
Geum chiloense Balbis
Lyonothamnus floribundus Gray
Margyricarpus setosus Ruiz and Pavon
Osmaronia cerasiformis (Torrey and Gray) Greene
Photinia serrulata Lindl.
Physocarpus capitatus (Pursh) Kuntze
Potentilla fruticosa L.
Prinsepia sinensis (Oliv.) Oliv. ex Bean.
Prunus americana Marsh.
Prunus bokhariensis Royle
Prunus cerasus L.
Prunus dulces (Mill.) D. A. Webb (as *P. amygdalus*)
Prunus hortulana Bailey
Prunus insititia L.
Prunus mahaleb L.
Prunus mira Koehne
Prunus persica (L.) Batsch
Prunus tomentosa Thunb.
Rosa californica Cham. and Schlecht.
Rosa gymnocarpa Nutt. ex Torrey
Rosa spithamea Watson
Spirea prunifolia Sieb. and Zucc.

Cotoneaster

The earliest known report of this ornamental genus as a host for fire blight came from California in 1930 (873). During the following 5 years several species of *Cotoneaster* were reported susceptible to the blight organism under natural conditions or following artificial inoculation (809, 859, 938). As observed with other hosts, individual clones of a species may differ in their degree of blight resistance. *C. microphyllus* was reported as only slightly susceptible after artificial inoculation in the field in California (934), whereas the cultivar Emerald Spray of this species proved to be rather susceptible following inoculation under optimum blight conditions in the greenhouse (304). Egolf (261) reported

C. microphyllus very susceptible following artificial inoculation in the greenhouse.

A few years after fire blight was observed in England, *Cotoneaster* was found to be an important host of the blight organism. Lelliott (571) and Lelliott and Hayward (576) found 11 species of *Cotoneaster* susceptible to fire blight that had never been reported previously. At first *C. horizontalis* seemed immune under field conditions, but later severe blight development was observed in a collection of young container-grown plants at a nursery (290, 574). Eight species of *Cotoneaster* reportedly were unaffected following artificial inoculation, as shown in the preceding list.

At the U.S. National Arboretum in Washington, D.C., Egolf (261) has inoculated and screened large numbers of cotoneasters for blight resistance. Of 52 species evaluated, 15 percent did not show blight symptoms after repeated inoculations (table 2). An additional 10 percent of the plants showed no more than 6 percent of the plant blighted. Of all resistant cotoneaster species, *C. glaucophyllus* appeared to be most tolerant to fire blight. In New Jersey, Davis and Peterson (207a) reported 8 of 25 cotoneaster species as fairly resistant to fire blight following a severe blight year.

In West Germany, Zeller (1046b) evaluated 25 species and hybrids of cotoneaster against natural and artificial inoculation of the blight organism. To date, more than half of the plants appear susceptible to the disease.

Hawthorn

The occurrence of fire blight in hawthorn (*Crataegus*) dates back to the early 1900's (770). In 1929, Rosen (804) made the first report of fire blight severely injuring large limbs of an oriental species of hawthorn in a short time. Shaw (859) published detailed records on artificial inoculation of 10 species of *Crataegus* and stated that differences in degree of resistance were very marked, ranging from no blight in *C. prunifolia* to severe in *C. oxyacantha*.

Soon after the introduction of fire blight into Europe about 1957, hawthorn obviously became an important secondary host. This was especially true in England, Denmark, West Germany, and the Netherlands, where the plant is used in hedgerows to serve as windbreaks or property boundaries. A complete issue of the "Netherlands Forestry Journal" was dedicated to the taxonomy of *Crataegus* and to the importance of hawthorn as an essential

and beautifying plant on the Dutch landscape (545). Meijneke (638) published a detailed account of the role of hawthorn in maintaining and disseminating the fire blight organism.

Shortly after the introduction of fire blight in New Zealand, hawthorn proved very instrumental as a host for the overwintering bacterium (6, 179, 205). This, in turn, made satisfactory control very difficult. Since recent occurrences of fire blight in Europe, infested hawthorn hedges have served as a definite source of inoculum in disseminating the bacterium to apple and pear orchards (76, 330, 638, 639).

Quince

Many references can be found regarding natural and artificial infections in the cultivated quince (*Cydonia oblonga* Mill.) (131, 823, 934, 938). Certain quince cultivars are as susceptible to fire blight as the most susceptible pears and apples. Stewart (901) listed six quince cultivars equally susceptible following artificial inoculation of shoots on 2-year-old trees.

The flowering Japanese quince (*Chaenomeles japonica* (Thunb.) Lindl. ex Spach) is a closely related ornamental shrub, commonly planted in the United States. Artificial inoculations of this plant have shown that it is very susceptible to blossom blight and moderately susceptible to twig blight (823).

Pyracantha

One of the earliest records of fire blight on this ornamental host dates back to the late 19th century (47). Since then pyracantha has proved to be an important host for the blight pathogen (934, 938).

Following repeated inoculations, Egolf (262) reported 25 percent of eight pyracantha species tested as highly resistant to fire blight (table 2). Two blight-resistant cultivars — Shawnee and Mojave — are commercially available (259, 260).

Mountainash

Shaw (859) was among the first to perform artificial inoculation on mountainash (*Sorbus* species). Today the important ornamental tree *S. aria* (L.) Crantz. and its cultivars *S. lutescens* Hartw. and *S. majestica* Zab., as well as *S. tianshanica* Rupr., have been severely affected in England (90, 576).

Miscellaneous Plants

In addition to these 5 important genera there are 33 additional genera in the family Rosaceae with plants found susceptible to fire blight. Most of them are ornamental shrubs or trees. Of the few remaining fruit crops, the genera *Fragaria*, *Prunus*, and *Rubus* deserve mention. Records of fire blight on these three fruit crops have been rare, and all those on strawberry and stone fruits were made prior to 1935 (432, 487, 671, 717, 881, 934, 938). Three observations on raspberry have been made since 1947, and the blight organism was reisolated from the infected plant material (310, 569, 892). In 1976, Ries and Otterbacher (789a) reported rather severe fruit blight on thornless blackberries in Illinois.

Crosse ⁹ reported definite isolation and proof of virulence of *E. amylovora* from blighted apricot in Missouri. Ten species of *Prunus* reportedly were unaffected with fire blight following artificial inoculation (p. 34). In addition to these and the 8 *Cotoneaster* species, there were 21 species in 19 other genera reported without blight symptoms following artificial inoculation.

In the spring of 1972 an extensive host plant experiment was conducted in Denmark to evaluate many rosaceous hosts, mainly ornamental shrubs and trees, for fire blight resistance (489). This evaluation planting consisted of more than 2,300 plants in 35 species of 14 genera. Available results are incorporated in table 2.

In addition, two extensive trial plantings were established in Schleswig-Holstein, the northernmost section of West Germany (1046b). Besides several apple and pear cultivars, these plantings contained 59 different ornamental plants belonging to 15 genera in the family Rosaceae. At one location more than 5,000 cotoneaster seedlings comprising 15 cultivars were planted and artificially inoculated. Preliminary data indicated a high percentage of very susceptible seedlings.

Some plants outside the family Rosaceae have been inoculated and tested for susceptibility to the blight organism. Black necrotic lesions were obtained on shoots and nuts of several species of *Juglans* (walnut) in California (874). Inoculations on shoots of *Hicoria pecan* Brit. gave negative results. In Canada, Layne (562) obtained definite sunken

⁹ Pers. commun., East Malling Res. Sta., East Malling, England.

lesions on stems of cowpea (*Vigna sinensis* (Torner) Savi) 3 days after needle inoculation. However, some isolates of *E. amylovora* failed to produce a positive reaction (546). Additional plants producing

negative results following artificial inoculation of the shoots with *E. amylovora* are avocado (*Persea* sp.) (431), persimmon (*Diospyros* sp.) (938), and poplar (*Populus* sp.) (52).

CHAPTER 7

CAUSAL ORGANISM

Taxonomy

In 1882, Burrill (133) published the first technical description of the fire blight pathogen and named it *Micrococcus amylovorus* under the erroneous assumption that the bacterium destroyed starch. In the description published in the "American Naturalist" the following year, the organism was accidentally misspelled as *M. amyliovorus*, which caused some confusion in the literature until 1914, when it was corrected (135, 903).

In 1889, Trevisan (956) published his "I Generi e le Specie delle Batteriacee," in which he changed the generic name of the blight organism from *Micrococcus* to *Bacillus amylovorus*. Eight years later, Chester (170) in Delaware changed the name to *Bacterium amylovorus*. By 1915, Serbinoff (852) described a bacterial necrosis of the bark of fruit trees in several regions of the southern U.S.S.R. He considered the disease synonymous with fire blight but described the causal organism as *Bacterium amylovorum*. In 1920, Winslow et al. (1030) established the genus *Erwinia*, with *E. amylovora* as its type species. Three years later, this name was officially accepted by the Society of American Bacteriologists and has been maintained until today. The changes in the nomenclature of the fire blight bacterium are summarized as follows:

- 1882 *Micrococcus amylovorus* Burrill
- 1889 *Bacillus amylovorus* (Burr.) Trevisan
- 1897 *Bacterium amylovorus* (Burr.) Chester
- 1915 *Bacterium amylovorum* (Burr.) Serbinoff
- 1920 *Erwinia amylovora* (Burr.) Winslow et al.
- 1923 *Erwinia amylovora* (Burr.) Com. Soc. Amer. Bact.

The genus *Erwinia*, named after the famous American bacteriologist Erwin F. Smith (fig. 3.), was established to combine all the peritrichous plant pathogens into one group. *Erwinia amylovora* (Burr.) Winslow et al., the first bacterium proved to cause a plant disease, is today the type species of the genus *Erwinia* (575a).

The tribe Erwineae, containing *Erwinia* as the only genus, was established within the family Bacteriaceae (1030). In 1923, an additional genus, *Phytomonas*, was created to accommodate the phytopathogenic bacteria other than *Erwinia*, and a few years later the family Enterobacteriaceae was established with the genus *Enterobacter* (893). Waldee (1000) and Waldee et al. (1002) proposed three well-defined groups of genera for the phytopathogenic species of *Bacillus*, one of which would contain the type species *E. amylovora*. It was proposed that the genus *Erwinia* be restricted to the nonpectolytic, phytopathogenic enterobacteria, and a new genus *Pectobacterium* be established for the pectolytic ones (893, 1001).

On the basis of phenotypic similarity, Martinec and Kocur (630) proposed that all phytopathogenic enterobacteria be grouped into only two species of the genus *Erwinia*, i.e., *E. amylovora* and *E. carotovora* (L. R. Jones) Bergey et al. They found that 40 strains of *E. amylovora* agreed with the description of the type specimen. They also proposed *E. vitivora* as a synonym of *E. amylovora* and *E. cosmovora* as a synonym of *E. amylovora* var. *salicis* (see chap. 5). In Japan, Komagata (540) and Komagata et al. (542) recognized three species in adding *E. herbicola* to *E. amylovora* and *E. carotovora*. They found *E. amylovora* and *E. herbicola* homogeneous for the tested characteristics, whereas *E. carotovora* was taxonomically heterogeneous.

Phenetic Data

The most detailed taxonomic studies on the genus *Erwinia* were completed in 1968–69 by Dye (246–249) in New Zealand. Based on biochemical characteristics, he recognized four groups within the genus, i.e., *amylovora* (246), *carotovora* (247), *herbicola* (248), and a group consisting of atypical *Erwinia* species (249). In the *amylovora* group, Dye (246) found no main differences in biochemical characters or carbohydrate utilization to suggest species different from *E. amylovora* and proposed

the following five subspecies under *E. amylovora*: Var. *tracheiphila*, var. *salicis*, var. *nigrifluens*, var. *quercina*, and var. *rubrifaciens*.

Lockhart and Koenig (588) made a numerical taxonomic analysis of the genus *Erwinia*, including three isolates of *E. amylovora*. They showed that the blight pathogen was separable from the other *Erwinia* species and that there are apparently no distinctions within the homogeneous group consisting of *E. carotovora*, *E. aroideae* (Town.) Bergey et al., *E. atroseptica* (Van Hall) Jennison, and *E. ananas* Serrano. They obtained similar results when such "key" characters as pathogenicity and pectinase production were omitted from the numerical analysis. In a cross-inoculation study Spalding and Smale (884) observed limited necrosis without ooze production when *E. carotovora* was injected into succulent Bartlett shoot tissue but no symptoms when *E. amylovora* was inoculated into leaves and petioles of potato plants.

Comparative gel-electrophoresis studies by Gardner and Kado (320) and Kado et al. (492) showed that proteins clustered into two major electrophoretic groups of six to nine bands each. They concluded therefore that *Erwinia* is a heterogeneous and somewhat artificial genus whose members should be distributed within the general family of Enterobacteriaceae (320).

In England, Lund (598a) studied the formation of reducing sugars from sucrose as a possible tool to distinguish *Erwinia* species. She found glucose and fructose as the main reducing sugars and an unidentified compound, possibly oligosaccharide. Results were inconclusive and further tests are needed to separate *E. amylovora* from other *Erwinia* species.

Serology

Burkholder (122) discussed in detail the taxonomic position of the genus *Phytomonas* in the order Eubacteriales and its relation to other genera and families. Rosen and Bleecker (822) made a detailed comparative serological and pathological study of *E. amylovora* and several species of *Phytomonas*, especially *P. syringae*. They emphasized the value of serological investigations for determining relationships of bacterial plant pathogens. Elrod (268, 1099) made a detailed serological study of *E. amylovora* and could not detect any antigenic differences among the isolates tested. Four isolates of *E. amylovora* failed to reduce trimethylamine and produced no growth with the Eijkman reaction test

(269). He concluded that serologically *E. amylovora* was an exceedingly homogeneous species (268).

Hildebrand (409) demonstrated the failure of *E. amylovora* to form pits on polypectate gels, whereas all other tested *Erwinia* and *Xanthomonas* species did so. This trait was suggested as a useful taxonomic character. In another study of immunological techniques, Lazar (567) concluded that there was a close serological relationship among the three principal species included in the genus. Slide agglutination tests by Le Minor et al. (577, 578) in France revealed that the species belonging to these three *Erwinia* groups all possessed the common antigen (CA). However, *E. amylovora* agglutinated, whereas *E. carotovora* did not (578). Samson (830) analyzed the antigenic structure of 25 isolates of *E. amylovora* by the agglutination method. Apart from a common antigen in each isolate, three more were detected and the isolates were classified into five serotypes. Immunodiffusion tests also showed that serotypes O are due to different antigens in the lipopolysaccharide of the cell wall (833).

Molecular Genetics

In California, Starr and his associates (166, 168, 548, 672, 893, 895) have made extensive and detailed studies of the taxonomy, biochemistry, metabolism, and genetics of *Erwinia*. Certain groups of *Erwinia* species were found related on the basis of the "GC content" (percentages of guanine + cytosine) of the base ratios of deoxyribonucleic acid (DNA) (895). Of 45 *Erwinia* isolates tested from animals, 16 were as injurious to certain test plants as some *Erwinia* strains that were generally considered as phytopathogens (548). Murata and Starr (672) found that all of Dye's phenotypic groups in the genus *Erwinia* were hardly separable on the basis of DNA segmental homology. In-depth studies on gene transmission of certain factors elucidated some connections of the taxonomic relationship of *Erwinia* species to other enterobacteria (165-169).

Chatterjee and Starr (168) were able to obtain stable donor strains of *E. amylovora* from strain EA178R₁ by selection for clones resistant to curing by acridine orange. They observed integration of plasmids (F' factors) into the *E. amylovora* chromosome, including the fertility plasmid E (169).

In 1972-73 studies of DNA relatedness among *Erwinia* species, Brenner et al. (108-111) confirmed ideas by others that *E. amylovora* and the soft rotting species belong to the same genus in the family of

the enterobacteria. They also supported the view, however, that the phytopathogenic soft rot organisms be placed in the genus *Pectobacterium*, as proposed by Waldee (1000, 1001).

In Canada, Wu and Middleton (1042a) produced phenotypically stable Trp⁺ hybrids between *E. amylovora* and *Salmonella typhimurium* (Loeffler) Castellani and Chalmers. These hybrids had high genetic homology values in the tryptophan region.

In a 1974 review of the overall taxonomic position of *E. amylovora*, Fomesbech (312) concluded that species within *Erwinia* show marked differences and should not belong to the same genus. She proposed that this genus be amended so as to comprise only such organisms that do not reduce nitrate to nitrite but which otherwise behave as enterobacteria with regard to other metabolic characters (1100).

This brief summary on the phenetic, serological, and molecular investigations of the family Enterobacteriaceae and the genus *Erwinia* shows that more research is needed to elucidate the real taxonomic position of the different species as well as

the genetic mechanism controlling virulence among the species to both plants and animals.

Morphology and Cultural Characters

Since the first brief description of the morphological characters of *Micrococcus amylovorus* by Burrill (133, 134) in 1882 and 1883, several investigators have studied the causal organism of fire blight in more detail. The morphological characters of *Erwinia amylovora* are summarized in table 3. The wild- or normal-type cell ranges from 0.6 μ m to 2.5 μ m in length and from 0.5 μ m to 1.2 μ m in width (av. 1.1 μ m–1.6 μ m \times 0.6 μ m–0.9 μ m). These bacterial cells are usually reported as Gram-negative short rods, with rounded ends and motile by many peritrichous flagella. In 1926, Bryan (120) published the earliest good photographs showing clearly the peritrichous flagella of the bacterium (fig. 9, A). Rosen (802), however, disagreed after finding only single polar flagella and believed that the organism should be placed in the genus *Phytomonas*. Several years later, Rosen (819) showed that the bacteria derived from exudate were enveloped in slimy capsules of stainless material, which was nonproteinaceous (fig. 9, B and C). An extreme outer layer of staining matter surrounded the stainless material.

TABLE 3.—*Morphological characters of Erwinia amylovora*

Year	Cell size		Cell shape	Motility and flagella	Staining reaction	Reference
	Length (μ m)	Width (μ m)				
1883-----	1.0–1.4	0.7	Singly or united in pairs, never in elongated chains.	-----	-----	Burrill (134).
1886-----	1.0–1.25	0.5–0.75	-----	Motile; not motile in acid or alkaline media.	Stains well with usual dyes.	Arthur (50).
1898-----	1.0–1.6	.6–.8	Bacillus singly, pairs, chains, or masses.	Actively motile; scattered flagella.	Stains readily with aqueous aniline dyes.	Waite (993).
1901-----	1.5–2.0	.7–1.0	Short rods, rounded ends; singly, in pairs or chains, oval rodlike.	Many cells motile but not all.	-----	Whetzel (1016).
1901-----	1.0–2.5	.8	-----	Cells nonmotile; no flagella.	Stains uniformly with usual dyes.	Chester (170).
1904-----	1.0–1.8	.5–.9	Rounded ends; mostly singly, sometimes in 2's.	Cells motile; 1–3 flagella at 1 pole.	Gram-negative---	Jones (484).
1913-----	1.6–1.8	.7–.9	Rods with rounded ends; singly in pairs, occasional chains of 3 or 4.	Cells motile; 2–3 peritrichous flagella.	-----do-----	Stewart (901).

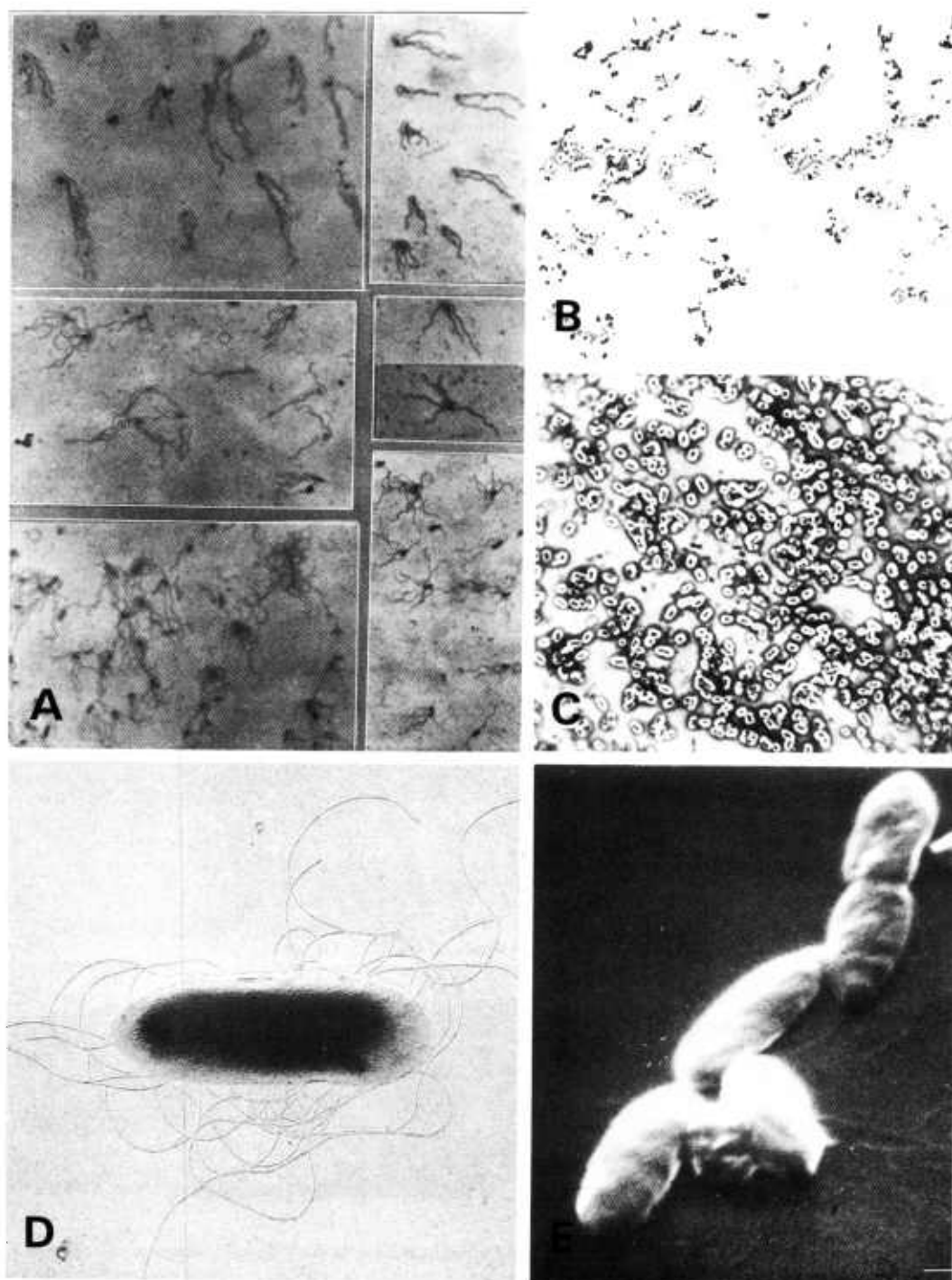
TABLE 3.—*Morphological characters of Erwinia amylovora*—Continued

Year	Cell size		Cell shape	Motility and flagella	Staining reaction	Reference
	Length (μm)	Width (μm)				
1913-----	1.0	0.5-.75	Mostly singly, sometimes short chains (2-4).	-----	-----	Hewitt (404).
1922-----	1.0-1.9	.5-.7	-----	Cells motile.	-----	Snow (881).
1926-----	-----	-----	Rods -----	Single, polar flagella.	Rosen stain -----	Rosen (803).
1927-----	-----	-----	-----do -----	Peritrichous; some cells with single polar flagella.	Casares-Gil stain.	Bryan (120).
1937---	.93-1.40 (strong); 1.50-1.71 (weak).	-----	-----	Cells motile; peritrichous flagella.	-----	Ark (30).
1948-----	Short, 1.5 diameters.	-----	Rods with rounded ends.	Actively motile; peritrichous.	Gram-negative ---	Waldee (1001).
1954-----	1.42-1.61	.67-.72	-----	1-7 flagella; shortest cells with most numerous and longest flagella.	-----	Hildebrand (424).
1961---	1.2-1.8; .8-1.2	.8 (live); .5 (heat fixed).	Ovoid or rod shaped; singly or in pairs or groups; occasional long rods or in filaments.	Motile; 1-5 peritrichous flagella.	Gram-negative ---	Billing et al. (87).
1964 -----	.6-1.2	.6-.9	Rods singly or in clumps; short rods.	Most strains nonmotile; peritrichous flagella.	-----do-----	Martinez and Kocur (630).
1964 -----	.9-1.8	.7-.8	Short rods; singly or in pairs.	-----	-----do-----	El Helaly et al. (264).
1965 -----	1.0-2.0	.8-1.2	Short-----	Motile -----	-----	Voros and Goodman (982).
1965 -----	2.0-7.0	.8-1.2	Intermediate-----	Nonmotile -----	-----	Do.
1965 -----	7.0-35.0	.8-1.2	Filamentous-----	Actively motile---	-----	Do.
1969 -----	1.0-2.5	.8-1.2	Wild type-----	Peritrichous flagella.	-----	Huang and Goodman (451), Huang (1109).
1969 -----	7.0-35.0	.8-1.2	Filamentous-----	-----do-----	-----	Do.

In Great Britain, Billing (83) examined 150 isolates of *E. amylovora* and distinguished between the "typical" dominant type of colony displaying characteristic markings on Yeastrel peptone agar plates incubated at 30° C (86° F) and the "atypical" colonies, which were relatively featureless and less opaque. Phase-contrast microscopy with the use of india ink demonstrated that the cells of typical strains had small capsules, some atypical strains had none, and the remainder had varying proportions.

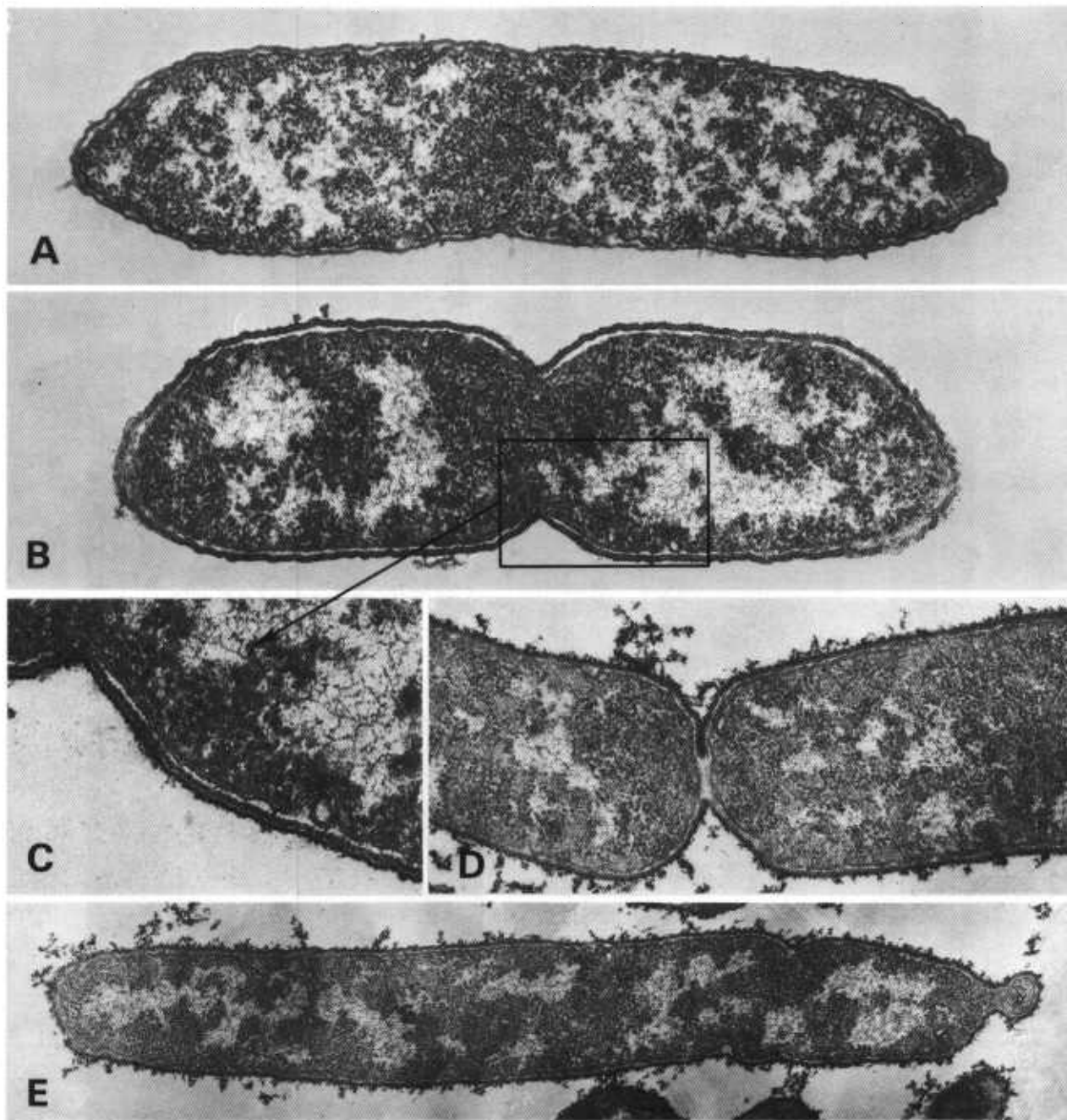
At the University of Missouri, Huang and Goodman (451, 452) and Huang (1109, 1110) studied in

great detail the morphology of *E. amylovora*. By using electron microscopy they showed the characteristic rounded ends and numerous peritrichous flagella of the cells (fig. 9, *D* and *E*). Ultrathin sections of the wild-type virulent *E. amylovora* cells prepared at room temperature revealed two separate, electron-dense layers in their walls (fig. 10, *A-C*). When cells were fixed at 4° C (39° F), three layers were visible. Silva and Sousa (869) found that these cell walls were almost indistinguishable when uranyl acetate and calcium were omitted in their procedure.



PN-6379

FIGURE 9. — Bacterial cells of *Erwinia amylovora*: A, Isolated from pear, apple, and hawthorn and stained by Casares-Gil's flagella stain (after Bryan, 120); B, derived from fresh exudate, dried rapidly, and stained in basic fuchsin ($\times 1,725$) (after Rosen, 819); C, derived from fresh exudate kept at 50 percent relative humidity for 4 months and stained as in B; note unstained envelope around cells followed by extreme outer layer of staining matter ($\times 1,820$) (after Rosen, 819); D, single virulent cell with abundant peritrichous flagella ($\times 18,000$) (after Huang, 1109); E, scanning electron micrograph of wild-type virulent cells ($\times 19,500$) (after Huang, 1109).

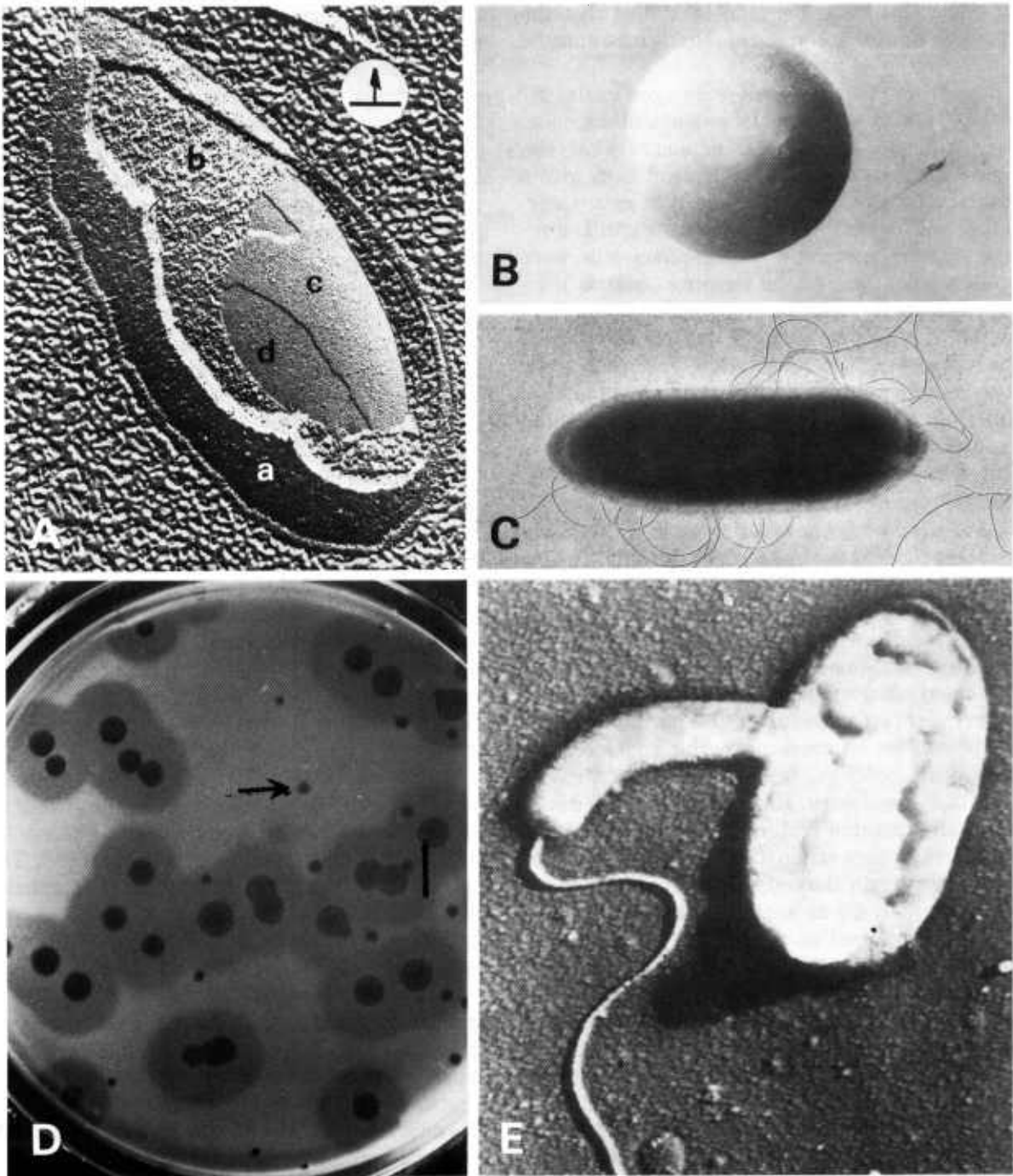


PN-6380

FIGURE 10.—Ultrastructure of *Erwinia amylovora*: *A*, Single virulent cell ($\times 54,000$); *B*, early stage of cell division ($\times 55,900$); *C*, enlarged part of cell wall in *B*, showing double-track structure ($\times 118,250$); *D*, advanced stage of cell division, with cell membranes of daughter cells entirely formed before completion of cell wall constriction ($\times 57,000$); *E*, filamentous cell with minicell attached ($\times 36,000$); (after Huang and Goodman, 451, 452).

In Canada, Gibbins et al. (327a) made a study of the ultrastructure of the cell envelope of *E. amylovora* NCPPB595, using the freeze-fracture tech-

nique. This technique exposed the outer regions of the cell envelope at the level of the plasma membrane (fig. 11, *A*). Thus they were able to expose



PN-6381

FIGURE 11.—A, Freeze-fractured exponential phase cell of *Erwinia amylovora* NCPPB595: a, Convex surface exposed by probable cleavage of outer membrane; b, outer surface of cytoplasmic membrane (particulate); c, outer surface of cytoplasmic membrane (nonparticulate); d, surface revealed by cleavage of cytoplasmic membrane; arrow indicates direction of metal deposition and bar represents 0.1 nm (courtesy L. N. Gibbins, Dept. Microbiol., Univ. Guelph, Canada). B, Colony of avirulent *E. amylovora* on crystal violet medium, showing only few craters (after Huang, 1110). C, Single avirulent cell of *E. amylovora* with few peritrichous flagella ($\times 18,000$) (after Huang, 1110). D, Plaque morphology of phage PEal halo and nonhalo (arrow) after 48 hours' incubation at 27°C (81°F) with *E. amylovora* 110; scale bar equals 1.0 cm (after Ritchie and Klos, 795b). E, *E. amylovora* cell parasitized by *Bdellovibrio bacteriovorus* ($\times 26,200$) (after Stolp and Starr, 907).

four planes in this region and concluded that the plasma membrane at the site of the fracture must be devoid of included particles.

In addition to the small wild-type cells, *E. amylovora* also produces long filamentous cells. Voros and Goodman (982) reported that the filamentous cells were 7.0 μ m–35.0 μ m long with a width similar to that of the wild-type cell. Intermediate cells were 2.0 μ m–7.0 μ m in length and reportedly were nonmotile. Filamentous cells were equally virulent and phage sensitive (982) as wild-type cells, whereas many produced minicells (451) (fig. 10, *E*). Huang (1109) reported the size of minicells as 0.3 μ m–0.8 μ m in diameter, but serial sections showed no evidence of any nuclear material (451). Both types of cells divided similarly (1109) and were preceded by the invagination of cell membranes followed by cell wall constriction (fig. 10, *B* and *D*).

Besides the wild- and filamentous-type cells, *E. amylovora* may also have avirulent cells and thus produce avirulent isolates. They usually appear rather rough in culture and are often referred to as rough isolates (30, 354). In California, Ark (30, 1080) observed the dissociation of *E. amylovora* in culture from the normal smooth (S) colony to the rough (R) forms upon aging of the cultures. He found the R type avirulent on some susceptible shrubs and only slightly virulent on green pear fruit and succulent tips of pear seedlings. In contrast to the virulent strains of *E. amylovora*, Huang (1110) reported only a few well-separated craters on the surface of colonies of an avirulent strain (fig. 11, *B*). Single cells of an avirulent strain showed only a few peritrichous flagella (fig. 11, *C*) as compared with a virulent strain. She observed no remarkable differences in external morphology and ultrastructure between the two types except the precocious flagellar development of the virulent strain. After 26–48 hours' incubation the avirulent strain formed small butyraceous colonies with dark-red centers, whereas the virulent ones formed fluidal white colonies with small bright-pink centers.

When *E. amylovora* is isolated from blighted host tissue, nearly pure cultures may be obtained when the surface is properly sterilized and laboratory conditions are aseptic (511). Bacterial growth from small sections of host tissue is a characteristic smooth creamy white (fig. 12, *A*). When this growth is streaked on standard culture media, single colonies should be small, round, and white, with a typical glistening shine (fig. 12, *B*).

Miller and Schroth (653, 654) developed a selective medium for isolating *E. amylovora* and described the colony morphology as having characteristic dark-orange centers, smooth peripheries, and translucent margins (fig. 12, *D*). Goldberg and Morgan (332) observed lumps in the cytoplasm of *E. amylovora* cells treated with noninhibitory concentrations of streptomycin. These lumps were thought to be any solid constituent of the cytoplasm, including nuclei, lipoids, or chromatin material.

At the University of Missouri, Crosse and Goodman (196) observed characteristic craters when colonies grown on a high sucrose medium were examined under oblique light at maximum 30 magnification. Later, Huang (1110) reported more numerous craters, especially on colonies of virulent isolates (fig. 12, *C*). She observed that several of these craters fused and formed irregular bowl-shaped depressions. In Canada, Dueck and Quamme (239) reported that *E. amylovora* colonies on the high sucrose medium appeared convex and "uniquely striated" when viewed with transmitted incandescent light after 48–72 hours' incubation at 28° C (82.5° F). Some of the colonies from pear reportedly were more cone shaped than convex, had darker striations in the center, and were not striated at the margins (fig. 12, *E*). They observed the cratered appearance only in very young colonies.

Moore and Hildebrand (661) subjected bacterial cells from ooze to electron microscopy and found that they were essentially nonvacuolated, whereas vacuoles were common in cultured cells. They suggested that differences in cellular morphology may be manifestations of physiological changes operating in the survival mechanisms of the blight pathogen.

Besides the morphological characteristics, the principal cultural characteristics of *E. amylovora* are confinement of liquefaction in gelatin stabs to the upper layers, a thin turbidity in nutrient broth, no odor or pigmentation on potato, coagulation of litmus milk after 3–4 days, no production of indole, and no nitrites produced from nitrates. The positive effect of nicotinic acid for optimum growth of *E. amylovora* has been well documented (265, 894). Lewis and Tolbert (581) and Lewis (1113) found that *E. amylovora* readily used aspartic acid, glutamic acid, asparagine, glutamine, beta-alanine, and gamma-amino butyric acid as sources of nitrogen in synthetic culture media.

Standard selective culture media generally used

for *E. amylovora* are mentioned at the end of this section. The effect of temperature, pH, and light, as well as the effect of other micro-organisms, including *E. herbicola*, is discussed later in this chapter.

Generation Time

Naturally the rate of growth and generation time for *E. amylovora* vary with the culture medium and incubation temperature. In 1938, Hildebrand (419) determined a generation time of 71–94 minutes (av. 82 min) for seven strains of *E. amylovora* grown in nutrient broth at 30° C (86° F). Adding glucose to the basic nutrient medium increased the generation time by 13 minutes, whereas the deviation between

the original strain and single-cell isolates amounted to 17 minutes in the extreme. Later he (424) reported an apparent relationship between generation time and degree of pathogenicity. For an apparent avirulent isolate the generation time was 72–77 minutes and for a virulent isolate 80–82 minutes.

In England, Billing et al. (87) determined a generation time of 72–75 minutes for an *E. amylovora* isolate obtained from a canker on a Laxton's Superb pear. In vitro growth experiments with shaken broth cultures indicated that temperatures of 27° C (80.5° F) or more were not much more favorable for bacterial multiplication than those between 21° (70°) and 27° (84a, 85). Below 18° (64.5°) the doubling time

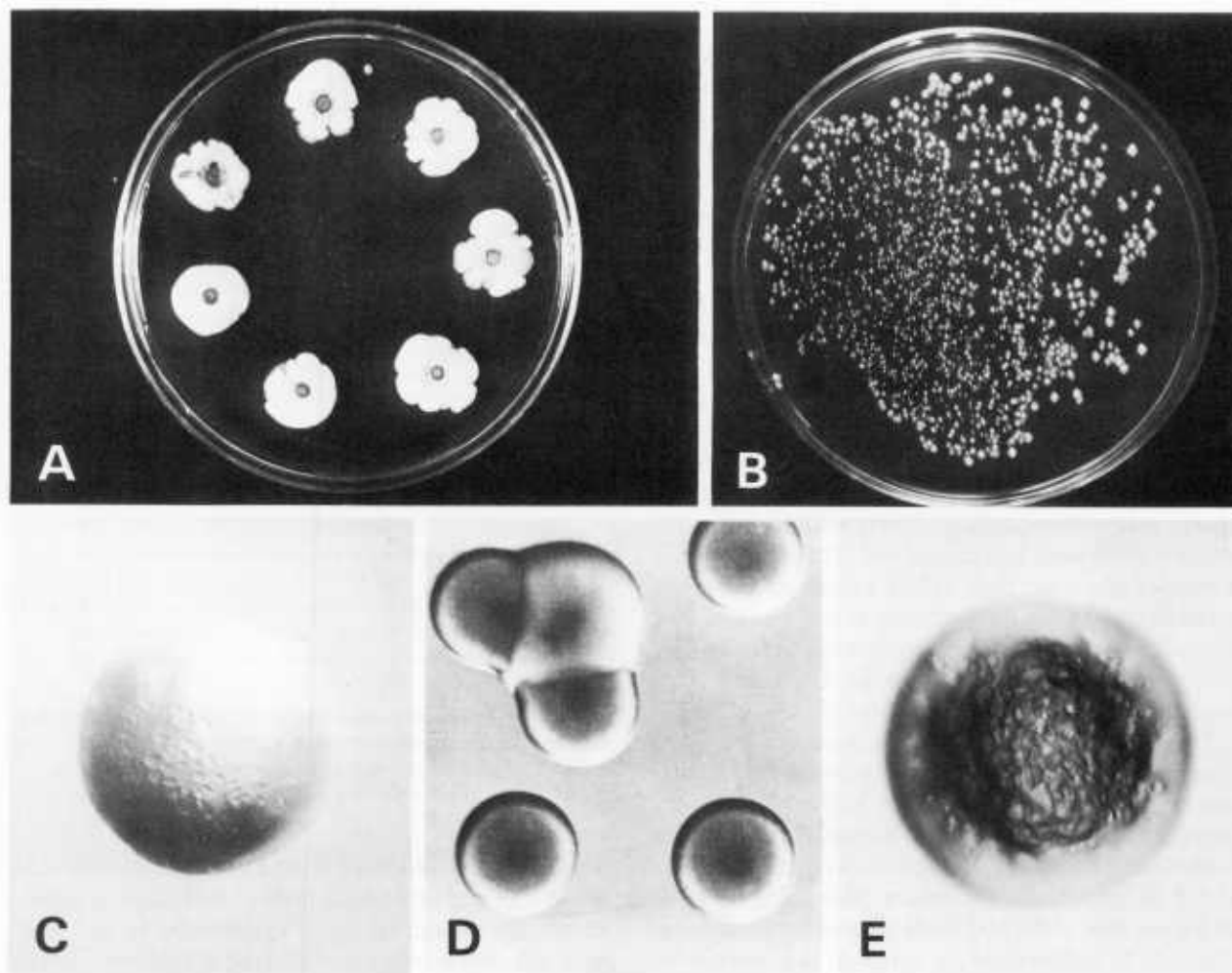


FIGURE 12.—Colony characteristics of virulent isolates of *Erwinia amylovora*: A, Growth surrounding sections from infected pear shoots plated on nutrient-yeast-dextrose agar (NYDA); B, small, round, white, glistening colonies on NYDA isolated from oozing pear canker; C, single colony on crystal violet medium, showing numerous characteristic craters on surface (after Huang, 1110); D, smooth colonies with dark-orange centers and translucent margins on selective medium (after Miller and Schroth, 654); E, colony isolated from pear, with dark striations in center and smooth margin (after Dueck and Quamme, 239).

increased rapidly, requiring more than 36 hours at 3° (37.5°) (84a). Doubling times of streptomycin-resistant cultures were greater than those of the parent culture both in shake broth culture and in apple seedlings (81g). In a study of virulent and avirulent isolates of *E. amylovora* in Missouri, Burkowicz (1088) determined mean generation times at 28° C (82.5° F) of 3.7 hours for the avirulent isolate and 4 hours for the virulent one. For a saprophytic yellow bacterium (*Erwinia* sp.), the generation time was about 10 hours.

Standard and Selective Media

The following standard media have generally been used by many investigators for culturing *E. amylovora* in fire blight research: Nutrient agar (NA), containing 23 g of nutrient agar per liter of distilled water; nutrient yeast dextrose agar (NYDA or NYGA), containing, in addition to the nutrient agar, 10 g of dextrose (glucose) and 5 g of yeast extract per liter of distilled water; and nutrient yeast dextrose (glucose) broth (NYDB or NYGB), in which 8 g of nutrient broth is substituted for the nutrient agar in NYDA.

In addition to these media, some workers have used a partial or completely synthetic medium for special studies of *E. amylovora* (30, 265, 427, 572, 581, 894, 1080, 1113). This synthetic medium usually contains per liter of distilled water varying quantities of the following ingredients: Ammonium chloride, monobasic and dibasic potassium phosphate, magnesium sulfate, ferric sulfate, zinc sulfate, nicotinic acid, and phenol red. The nicotinic acid is usually dissolved first before adding all the other ingredients and the final mixture is well shaken. For special studies of amino acid utilization by *E. amylovora*, Lewis (1113) used several liquid and solid media for growth of the organism.

The phosphate buffer solution sometimes is used to prepare a suspension of *E. amylovora* for inoculation experiments (353a). This buffer supposedly prevents inactivation of the bacterial cells and is made from two stock solutions—(A) 27.2 g per liter of 0.2 M monobasic potassium phosphate and (B) 34.8 g per liter of 0.2 M dibasic potassium phosphate. The 0.05 M buffer solution (pH 6.5) is prepared by adding 70 ml of stock A and 30 ml of stock B to 300 ml of distilled water.

Certain media have been prepared for the selective isolation of *E. amylovora*. In 1970, Kado and Heskett (491) reported five selective plating media

for plant pathogenic bacteria. They obtained a plating efficiency of 77.7 percent for *E. amylovora* on medium D3. This medium contains the following ingredients per liter:

	G
Agar-----	15.0
Sucrose-----	10.0
Arabinose-----	10.0
Lithium chloride-----	7.0
Casein hydrolysate-----	5.0
Sodium chloride-----	5.0
Glycine-----	3.0
Magnesium sulfate-----	.3
Acid fuchsin-----	.1
Bromothymol blue-----	.06
Sodium dodecyl sulfate-----	.05

It is adjusted to pH 8.2 with sodium hydroxide before autoclaving at 121° C (250° F) for 15 minutes and has a pH of 6.9–7.1 after autoclaving. Following plating, the medium produces a characteristic red, the intensity depending on the species. The amylovora group produces a lighter tint of red than the group that causes soft rots.

Another selective medium, developed by Miller and Schroth (652–654), contains the following ingredients in 970 ml of distilled water:

	G
Agar-----	20.0
Mannitol-----	10.0
L-Asparagine-----	3.0
Sodium taurocholate-----	2.5
Dibasic potassium phosphate-----	2.0
Nicotinic acid-----	.5
Magnesium sulfate-----	.2
Nitrilotriacetic acid ¹ -----	.2
Sodium heptadecyl sulfate-----	.1 (ml)
Bromothymol blue ² -----	.04
Neutral red ³ -----	.01

¹As 10 ml of 2 percent aqueous solution neutralized with 0.73 g of potassium hydroxide per gram of NTA.

²As 9 ml of a 0.5 percent aqueous solution.

³As 2.5 ml of a 0.5 percent solution.

The pH is adjusted to 7.3 with N sodium hydroxide (ca. 5 ml), and after autoclaving the following ingredients are added: 50 mg of cycloheximide as 1 percent aqueous solution and 17.5 mg of thallium nitrate as 1.75 ml of a 1 percent aqueous solution. Reddish-orange colonies were indicative of the *Erwinia* genus. These authors also found that substitution of 10 g of sorbitol for mannitol restricted the growth of *E. herbicola*.

Crosse and Goodman (196) developed a high sucrose medium to isolate *E. amylovora* living epiphytically on apple leaf surfaces. This medium contains in 380 ml of distilled water 160 g of sucrose, 0.8 ml of crystal violet (0.1 percent in absolute alcohol), 20 ml of 0.1 percent cycloheximide, and 12 g of agar. The medium had a high plating efficiency and colonies examined under oblique light at 15–30 magnification showed characteristic craters for *E. amylovora*, as reported by Huang (1109).

In 1976, Ritchie and Klos (795c) reported a less complex selective medium containing some of the same ingredients as the Miller-Schroth medium. This medium produced moist, chalky-white colonies with a cleared center and gave the colony an “eye” appearance. It was used successfully for 3 years in detecting *E. amylovora* in cankers, blossoms, and other apple and pear tissues.

In West Germany, Zeller (1046a) used Lelliott's (572) sucrose nutrient agar (SNA) and observed

raised, hemispherelike colonies of *E. amylovora* after 2–3 days' incubation at 27° C (81° F).

These are not the only media used by fire blight investigators. Special media are required for specific studies on isolation and identification of *E. amylovora* (88, 264, 617, 649, 783, 877, 887, 1046a), growth and metabolism (3, 29, 30, 265, 354, 421, 424, 458, 521, 581, 585, 836, 855, 894), and detection of streptomycin resistance (853, 949).

Growth and Metabolism

In addition to the cultural characteristics of *E. amylovora* mentioned previously, the more complex phases of its growth are covered under metabolism. The principal references on amino acid, carbohydrate, and organic acid utilization as well as enzyme production have been summarized in tables 4 and 5 according to positive, negative, or variable results in utilization of the compounds by *E. amylovora*.

TABLE 4.—*Amino acid, carbohydrate, and organic acid utilization by Erwinia amylovora based on literature cited*

Compound	Utilization		
	Positive	Negative	Variable
AMINO ACID			
Acetamide -----	-----	581, 1113	-----
Alanine -----	-----	-----	30, 424
alpha-Alanine -----	-----	581, 1113	-----
beta-Alanine -----	1113	581	-----
alpha-Amino butyric acid -----	-----	581, 1113	-----
gamma-Amino butyric acid -----	1113	581	-----
Arginine -----	-----	1113	-----
Asparagine -----	30, 424, 1027	-----	-----
D-Asparagine -----	581, 1113	-----	-----
DL-Asparagine -----	581, 1113	-----	-----
L-Asparagine -----	581, 1113	-----	-----
Alanylasparagine -----	581, 1113	-----	-----
D-Aspartic acid -----	581, 1113	-----	-----
DL-Aspartic acid -----	581, 1113	-----	-----
L-Aspartic acid -----	581, 1113	-----	-----
Chloracetamide -----	-----	581, 1113	-----
DL-Citrulline -----	-----	581	-----
Cysteine -----	-----	30, 424, 1113	-----
L-Cysteine -----	-----	581	-----
Cystine -----	424	30	-----
DL-Glutamic acid -----	581, 1113	-----	-----
L-Glutamic acid -----	581, 1113	-----	-----
DL-Glutamine -----	581, 1113	-----	-----
L-Glutamine -----	581, 1113	-----	-----
Glycine -----	-----	30, 581, 1113	424
Glycineamide -----	1113	581	-----
Glycylglycineamide -----	-----	581, 1113	-----

TABLE 4.—*Amino acid, carbohydrate, and organic acid utilization by Erwinia amylovora based on literature cited*—Continued

Compound	Utilization		
	Positive	Negative	Variable
AMINO ACID—continued			
Histidine -----		1113	-----
L-Histidine -----	581	-----	-----
L-Homoserine -----	581	-----	-----
Isoleucine -----	-----	30	-----
Leucine -----	-----	1113	30, 424
L-Leucine -----	-----	581	-----
L-Lysine -----	-----	581	-----
Nicotinamide -----	-----	581, 1113	-----
DL-Ornithine -----	-----	581	-----
Phenylalanine -----	-----	1113	-----
DL-Phenylalanine -----	-----	581	-----
Proline -----	-----	-----	30, 424
L-Proline -----	-----	581	-----
Serine -----	-----	1113	-----
DL-Serine -----	-----	581	-----
DL-Threonine -----	-----	581	-----
Tryptophane -----	-----	30, 424, 1113	-----
DL-Tryptophane -----	-----	581	-----
Tyrosine -----	-----	30	424
Valine -----	-----	30, 424, 1113	-----
DL-Valine -----	-----	581	-----
CARBOHYDRATE			
Amygdalin -----	30, 424	-----	-----
Arabinose -----	30, 87, 267, 424, 1027	630	-----
Arbutin -----	30, 424	-----	-----
Cellobiose -----	30	630, 1001	87, 424
Cellulose -----	-----	424, 630, 1001	-----
Dextrin -----	30, 424	87, 1001	-----
Dextrose -----	30, 87, 265, 424, 438, 484, 630, 1001, 1027	-----	-----
Erythritol -----	-----	424, 1001	-----
Fructose -----	30, 87, 265, 424, 438, 630, 1001, 1027	-----	-----
Galactitol (as dulcitol) -----	-----	30, 424, 630, 1001	-----
Galactose -----	87, 265, 424, 630, 1027	-----	30
Glycerol -----	265	87, 630, 1027	30, 424
Glycogen -----	-----	87	424
Inositol -----	87	630, 1001	424
Inulin -----	30	87, 630, 1001	424
Lactose -----	-----	87, 265, 630, 1001, 1027	30, 424, 438
Maltose -----	30, 484, 1027	265, 630, 1001	87, 424, 438
Mannitol -----	87, 424, 630	1001, 1027	30
Mannose -----	30, 87, 265	1001	424, 630
Melezitose -----	-----	-----	424
Phloridzin -----	30, 424	-----	-----
Raffinose -----	30, 265, 1027	1001	424, 630
Rhamnose -----	-----	30, 630, 1027	87, 424
Ribitol (as adonitol) -----	-----	630	-----
Salicin -----	30, 265, 424	87, 1001	630
Sorbitol -----	87, 630	1001	424
Sorbose -----	-----	87, 1001	-----

TABLE 4.—*Amino acid, carbohydrate, and organic acid utilization by Erwinia amylovora based on literature cited—Continued*

Compound	Utilization		
	Positive	Negative	Variable
CARBOHYDRATE—continued			
Starch-----	-----	30, 87, 265, 424, 630, 1001	-----
Sucrose-----	30, 87, 265, 424, 438, 484, 630, 1001, 1027	-----	-----
Trehalose-----	87, 630, 1027	-----	424
Xylose-----	-----	30, 424, 1027	87, 630
ORGANIC ACID			
Acetic-----	-----	87, 424, 1027	630
Benzoic-----	-----	30, 424, 630	-----
Citric-----	30, 87, 424	1027	630
Formic-----	630	87, 1027	424
Glycolic-----	-----	-----	424
Hippuric-----	30, 424	-----	-----
Lactic-----	-----	87, 1027	30, 424, 630
Maleic-----	-----	30, 87, 424	-----
Malic-----	30, 87, 424	1027	-----
Malonic-----	-----	30, 87, 424, 630	-----
N-Methylglycine (as sarcosine).	30	-----	-----
Oxalic-----	-----	30, 87, 424, 1027	-----
Propionic-----	-----	87, 424	-----
Salicylic-----	-----	30, 424	-----
Succinic-----	87, 424, 630	1027	30
Tartaric-----	-----	30, 87, 630, 1027	424
Valeric-----	-----	30	-----

TABLE 5.—*Enzyme production by Erwinia amylovora based on literature cited*

Enzyme	Production		
	Positive	Negative	Variable
Amylase-----	-----	742, 1001	-----
Arginine dihydrolase---	-----	630	-----
Catalase-----	87, 630	-----	-----
Cytochrome oxidase----	-----	87, 630	-----
beta-Glucosidase-----	-----	-----	413, 846
Glutamic acid decarboxylase.	-----	-----	630
Lecithinase C-----	-----	630	-----
Lipase-----	-----	87, 630	-----
Lysine decarboxylase---	-----	630	-----
Ornithine decarboxylase	-----	630	-----
Pectase-----	-----	742	-----
Pectinase-----	-----	742	-----
Phenylalanine deaminase.	-----	87, 630	-----
Protopectinase-----	-----	424	-----
Tyrosinase-----	-----	87, 630	-----
Urease-----	-----	87, 630	-----

The nutritional requirements of the phytopathogenic *Erwinia* species, including *E. amylovora*, were determined by Starr and Mandel (894). They reported that with few exceptions *Erwinia* species grew in the glucose-salts basal medium and that *E. amylovora* required nicotinic acid obligately for its growth. This has been confirmed by El-Helaly et al. (265) in Egyptian isolates of *E. amylovora*.

In 1940, Kent (520) and Kent and Melhus (521) showed that *E. amylovora* could utilize only complex organic forms of nitrogen after successive transfers in liquid synthetic media at 48-hour intervals. In comparison, various soft rot bacteria were capable of using nitrates or ammonium salts as well as simple amino or amide forms.

Sutton and Starr (914) determined that the major products of glucose dissimilation by *E. amylovora* were lactic acid, ethanol, and carbon dioxide and that lactic acid and ethanol were produced in greater quantities than reported for other enterobacteria. They suggested that the high yield of ethanol may be the result of a possibly unique enzyme reduction of pyruvate in *E. amylovora*. This idea has since been substantiated by Haq and Dawes (385) based on the thiamine pyrophosphate-dependent pyruvate decarboxylase of *E. amylovora*. Later Sutton and Starr (915) showed that some extract of *E. amylovora* contained the enzymes necessary for cyclic operation of the hexose monophosphate shunt in aerobic metabolism of glucose. Tracer evidence substantiated the effective operation of the Embden-Meyerhof pathway of glycolysis in anaerobic metabolism of glucose by cells of the blight organism.

White and Starr (1020) studied the glucose fermentation end products by *Erwinia* species and other enterobacteria. They observed five different fermentation patterns in eight isolates of *E. amylovora* and concluded that members of this and several other genera were heterogeneous in fermentation end product patterns, and this may account for the very slow fermentation. The production of acetoin (3-hydroxy-2-butanone), a product related to the production of 2,3-butanediol, has been reported as variable in this species (630).

Nitrate reduction, as shown in *E. carotovora* and *E. herbicola* (540), has not been detected in *E. amylovora*. In the conventional peptone-nitrate media, *E. amylovora* and related *Erwinia* species do not form detectable nitrite (893). This inability to

reduce nitrate in a complex medium, but to do so readily in a minimal medium supplemented with nicotinic acid and nitrate as the sole source of nitrogen, might result from regulation of enzyme activity, enzyme synthesis, or both in the presence of a readily utilizable source of organic nitrogen (893).

In Canada, Katznelson (493-495) found that *E. amylovora* utilized 2-oxogluconate (ketogluconate) in the oxidation of glucose and produced carbon dioxide anaerobically from glucose. Studies with sonic preparations of the organism demonstrated the presence of certain key enzymes involved in the glycolytic and shunt pathways of glucose metabolism. He suggested that species of *Erwinia* may use either the glycolytic or the oxidative route (495). The latter route was confirmed by Suzuki and Uchida (916, 917). Farago and Gibbins (296a, 297) found that dissolved oxygen tension and rate of growth affected the metabolism of glucose-limited chemostat cultures of *E. amylovora*.

Lewis and Tolbert (581) and Lewis (1113) determined the nitrogenous compounds used by *E. amylovora* in synthetic media. They found that the bacterium grew when aspartic acid, asparagine, alanyl asparagine, glutamic acid, glutamine, or ammonia was the only source of nitrogen available to the bacterium (table 4). *E. amylovora* did not grow well on 24 other amino acids. Grou (374) made a comparative study on the changes in amino acids and electrophoretic characters of cytoplasmic components by species of *Erwinia* belonging to the amylovora, carotovora, and herbicola groups.

Casida (148) found that *E. amylovora* (strain P-182) utilized phosphite phosphorus (orthophosphite) for heterotrophic growth but did not accumulate phosphate in the oxidation product.

The enzyme production by *E. amylovora* reportedly has been entirely negative for the production of catalase (table 5). Martinec and Kocur (630) observed that 49 strains of the bacterium reacted positively.

Negative results are recorded in the literature for the following miscellaneous biochemical tests: Acetylmethylcarbinol (3-hydroxy-2-butanone), ammonia production, Braun's test, casein hydrolysis, hemolysis, hydrogen sulfide production, indole, methyl red, methylene blue reduction, sodium chloride tolerance (5 percent), and nitrate and nitrite reduction (30, 87, 484, 630, 1001, 1095). The only reported positive test is that for gelatin hydrolysis (87, 484, 1001).

There are some reports of the detrimental effect of certain conditions on the growth of *E. amylovora*. Perry and Weinberg (735) showed that rate of death of many bacterial strains, including the blight organism, was accelerated by iron deprivation and slowed by storage at low temperatures. Stewart (900) found growth of *E. amylovora* retarded by tributyl (2,4-dichlorobenzyl)phosphonium chloride (Phosfon) at concentrations from 10^{-2} to 10^{-5} M. Chantano (1093) reported a significant reduction in the number of colonies and viable cells of *E. amylovora* following 15- to 25-minute exposure to 1.3–2.0 ppm of chlorine.

Basic studies on growth and metabolism of *E. amylovora* should be expanded and the results correlated with research on the infection process between host and pathogen.

Details on *E. herbicola* and its morphology, metabolism, and possible relation to *E. amylovora* are discussed at the end of this chapter under Effect of Micro-Organisms.

Bacterial Exudate and Toxin

Ooze Formation

The nature of the bacterial exudate or ooze of *E. amylovora* has been studied through the years (114, 416, 421, 629, 651, 742, 813, 819). Ooze is most commonly known in the liquid form as single droplets on succulent shoots or blighted fruit (fig. 6, A; pl. 3, C and D) or running along the bark of a severely blighted tree (pl. 4, A and B). Bacteria in such ooze are generally virulent. However, Rosen (804) reported that cultures obtained from ooze in Arkansas failed to produce infections in vigorous Bartlett shoots inoculated in the greenhouse. Bacteria in dried ooze stored at room temperature as long as 2 years or more reportedly have retained their viability and pathogenicity (27, 742, 819, 1123).

When Rosen (819) subjected natural exudate to a controlled temperature of 16° C (61° F) in Arkansas, the bacteria remained viable and infectious for over a year at relative humidities of 0–45 percent. At controlled temperatures of 25°, 30°, 35°, and 40° (77°–104°), the bacteria remained viable for long periods when the relative humidity was low, but they died when it reached 45 percent. When exudate was exposed to fluctuating outdoor temperatures, the bacteria remained viable for almost a year at 0 percent relative humidity and for over 9 months at 50 percent, but they died rapidly at relative humidities of 45–90 percent. Bacteria within blight-

ed host tissue lived for approximately the same length of time as those in the natural exudate at low relative humidities, whereas bacteria in artificial cultures were very short lived under similar conditions. Morphological studies of the bacteria obtained from exudate indicated that they were enveloped in slimy capsules, which were mainly nonproteinaceous (fig. 9, B and C).

The most detailed study of the nature of ooze was made by Hildebrand (421) in New York. He actually tasted blight exudate and considered it relatively free from sugar but with a flat, starchy, acid taste. Chemical analysis, however, indicated that ooze contained 31 percent dextrose. The thermal death point of the bacteria in ooze was 5° C (9° F) lower than when grown on agar or in broth. In its natural matrix *E. amylovora* was also more sensitive to the action of bactericides than on culture media. Cultures of the organism on the synthetic carbohydrate medium could utilize the dilute sterile exudate as a source of carbon.

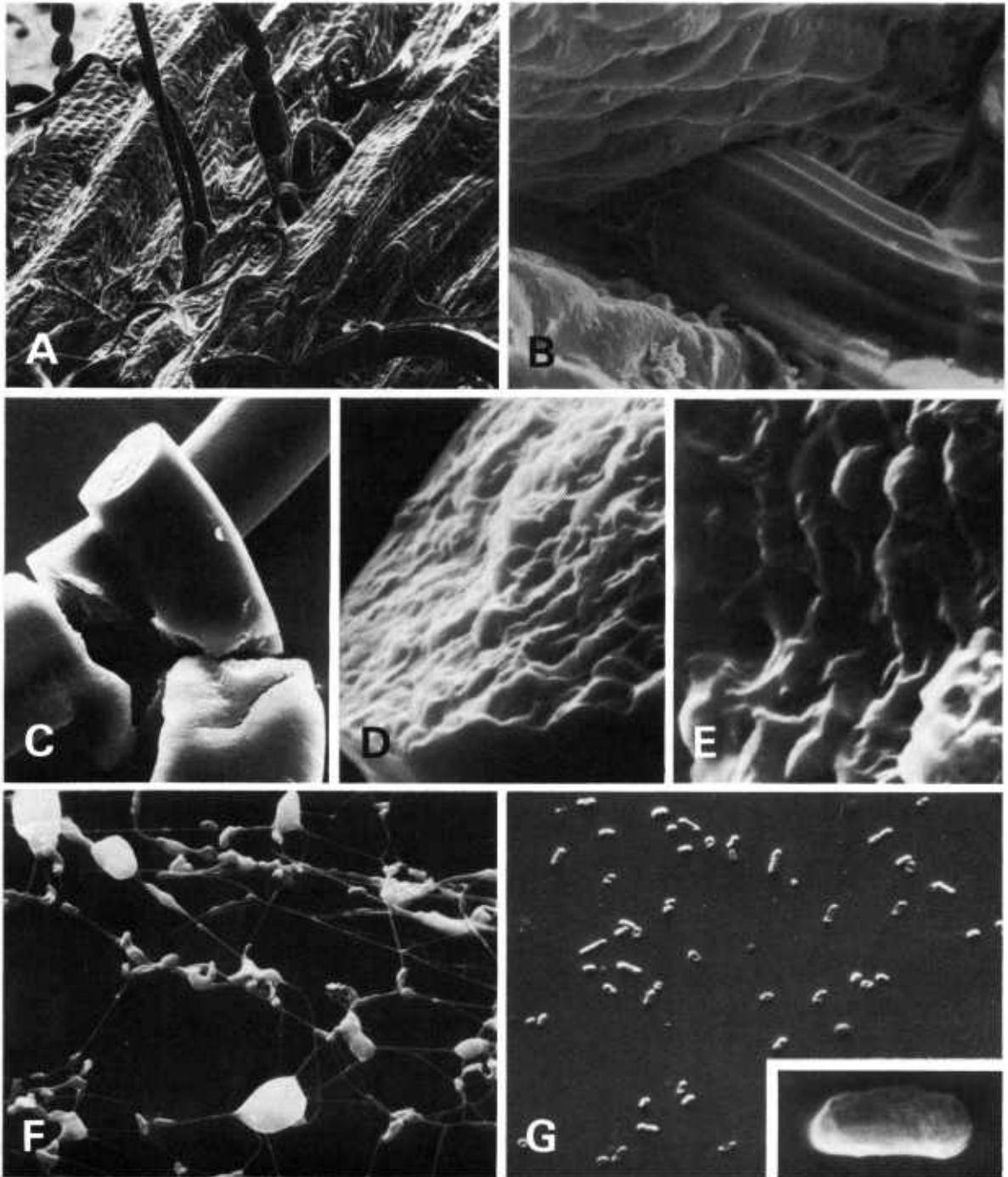
Ooze can vary from pure white to deep red, with various shades of brown, yellow, and orange in between (421, 1051). Martin (629) reported the production of a dark-green ooze on the twig of a loquat tree (*Eriobotrya japonica* (Thunb.) Lindl.) artificially inoculated with a pure culture of *E. amylovora*.

Strand Development

In 1937, Ivanoff and Keitt (464) reported the first observations of abundant aerial bacterial strands of *E. amylovora* on potted pear trees inoculated in the greenhouse. Since that time strands have been reported from Maryland (509, 512), Iowa (72), Washington (885), and Great Britain (89, 256) (fig. 7; pl. 1, C).

The length of bacterial strands reportedly varies from a fraction of a millimeter to several centimeters and the width from 6 μ m to 300 μ m (256, 464, 512). All investigators have reported that strands could easily blow in the wind, were instantly dispersible in water, and could thus have a significant role in the dissemination of fire blight (chap. 8). One wonders if the appearance in certain orchards of blight infection attributed to streptomycin-resistant *E. amylovora* may be due to strands blown by wind into these orchards from long distances.

In 1971 we made a detailed study of bacterial strands by means of a scanning electron microscope (510, 512). Two principal types of strands were observed—smooth and beaded (fig. 13, A). Smooth



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FIGURE 13. —Scanning electron micrographs of aerial strands of *Erwinia amylovora*: *A*, Smooth and beaded strands among trichomes on petiole surface ($\times 120$); *B*, ridged strand extruded from lenticel ($\times 1,000$); *C*, pieces of broken smooth strands, showing irregular breaks and cracks ($\times 1,300$); *D*, enlarged portion of strand end shown in upper center of *C*, ($\times 13,000$); *E*, magnified part of cross section in *D*, showing bacterial cells (rounded structures) and cavities (depressions) in cementing material ($\times 26,000$); *F*, clumps and single cells connected by cobweblike network resulting from strands dissolved in water and liquid evaporated under vacuum ($\times 2,600$); *G*, individual bacterial cells resulting from strands dissolved in water and resuspended in ethyl alcohol ($\times 2,600$); insert shows single cell of *E. amylovora* ($\times 26,000$).

strands appeared to be formed by a uniform quantity of matrix extruded through natural openings of the epidermis. Beaded strands, however, seemed to be formed by extrusion of matrix in spurts. Figure 13, *B*, shows a ridged strand originating from a lenticel. Time-lapse photography in England showed that fine strands were produced gradually over periods of several hours (254).

Strands are very firm and rigid, become brittle with age, and when crushed they break or shatter like glass into many fragments with irregular ends (fig. 13, *C* and *D*). Broken ends of strands suggested that they are composed largely of matrix rather than bacteria. A magnified part of a broken strand clearly showed rounded ends of bacterial cells and pockets where cells were missing (fig. 13, *E*). Preliminary analyses indicated a composition of 80 percent matrix and 20 percent bacterial cells, which recently has been confirmed by Eden-Green and Knee (258). Their studies showed that material similar to sorbitol accounted for 28 percent of the dry weight of the exudate.

When strands were dissolved in water and later evaporated under vacuum, the bacterial cells remained connected by a thin cobweblike network (fig. 13, *F*). When strands were dissolved in water, the suspension was diluted with 95 percent ethyl alcohol or acetone, and the liquid was then evaporated under vacuum; the network disappeared and the bacteria were observed as individual cells (fig. 13, *G*). Collapsed sections of the cell wall were observed due to prolonged exposure to the electron beam. Flagella were not observed and may have been detached during preparation of the samples (fig. 13, *G*, insert).

Toxin Production

With the presence of the bacteria in the intercellular spaces, some toxic action seemed necessary to cause plasmolysis of the protoplasts in the host cells. In 1886, Arthur (49) performed repeated tests to find the poisons or "ptomaines" produced by *E. amylovora*. Sterilized, filtered solutions in which the bacteria were grown did not cause rotting of green pear fruit, however. In Canada, Jones (484) made extensive cultural studies of the organism, but found no toxin produced in culture. By 1913, Bachmann (55) stated that "all of the first changes in the cells which result from infection may be attributed wholly to a loss of water." Stewart (901) disagreed with her and thought that a toxic or en-

zymic substance caused the killing of the host cells. All his extractions to produce diastase or the cell wall dissolving enzymes, pectinase and cellulase, from bouillon cultures proved negative, however. By 1927, Nixon (695) observed an apparent toxic plasmolysis followed by a complete collapse of the protoplast and the formation of schizogenous cavities. However, he never observed a complete dissolution of the cell walls or cell contents.

In 1931, Pierstorff (742, 1123) made the earliest recording of the presence of a toxic substance in the bacterial exudate of *E. amylovora* on green pear fruit. He reported that this substance contained many of the characteristics of a true bacterial toxin but that it was not thermolabile and was not inactivated when exposed to air for 14 hours. He concluded it to be an endotoxin or a decomposition product of the host cells. Eight years later Hildebrand (421) observed wilting in cut pear shoots immersed in sterile exudate matrix and thus pointed to the presence of a true toxin. The wilting was accompanied by necrosis of the cut ends and plasmolysis of the cells in the lower parts of the stem. The toxic substance was thermostable, withstanding steam heat for several hours and a dry air oven at 100° C (212° F) for 3 months.

In Missouri, Shaffer (1129) observed that one of the rough isolates of *E. amylovora* grown on solid medium produced an endotoxic substance, whereas a smooth isolate evoked a response in test shoots indicative of an exotoxic principle. It was not until 1974 that Goodman and his coworkers (347, 348) announced the isolation of a true host-specific toxin and named it amylovorin. This toxin, isolated from previously inoculated green apple fruit, consisted of 98 percent galactose in polymeric form and 0.375 percent protein, and it had an average molecular weight of about 165,000. Tip cuttings from susceptible pear and apple cultivars showed wilting within 1–3 hours, whereas those from resistant cultivars showed no visible symptoms until 12–24 hours after they were placed in the toxin solution at a concentration of 100 µg per milliliter. The polysaccharide was found to resist the enzymatic degradation of beta-galactosidase but was partially hydrolyzed by this enzyme prepared from a fungus (448). Later, Stoffl et al. (906a) separated amylovorin into three fractions on a Dow 1-X8 column in the carbohydrate form. Each fraction contained a carbohydrate and a protein component. Tests with apple shoots revealed that only the carbohydrate induced wilt. No

toxin activity was detected at pH 4.0–5.0, but a maximum was noted at pH 7.0–8.0.

In 1976, Hsu and Goodman (444a) reported that the host-specific toxin could not be produced in an artificial culture medium, in the filtrate from control suspension culture, nor in such a filtrate inoculated with an avirulent strain of *E. amylovora*. In host ultrastructural studies with amylovorin, Goodman and White (354a) found that some xylem parenchyma cells appeared plasmolyzed and neighboring vessels became occluded with a loose gellike substance. Under high magnification this substance appeared to be composed of a network of fibrils and granules.

In New York, Sjulín (1132) studied the effect of a wilt-inducing polysaccharide (PS) from oozing, immature pear fruit on succulent shoots of *Cotoneaster pannosus* Franch. He found the mean water potential of PS-wilted shoots to be significantly lower than that of nonwilted control shoots but not from that of shoots wilted to a similar degree by sealing shoot bases with wax. Sjulín and Beer (871a) concluded that PS induced wilting by water stress resulting from occlusion of vascular elements. They (871b, 871c) also indicated that infection altered cell permeability, whereas amylovorin caused wilt by nonspecific restriction of water movement in the xylem. Thus their results did not agree with the host-specific toxin theory.

The production of large amounts of toxin may have a significant impact on future studies of fire blight, especially in attempts to understand the nature of resistance. Preliminary studies by Beer and Aldwinckle (81) indicated no significant relationship in several apple cultivars between blight susceptibility and sensitivity to amylovorin.

McIntyre et al. (613, 614) protected etiolated pear seedlings with cell-free sonicates of virulent and avirulent *E. amylovora*. These sonicates, however, did not inhibit reproduction or affect the virulence of *E. amylovora* in vitro, and this finding suggested that induced resistance occurred in Bartlett pear. Samples of these extracts, supplied by the Indiana investigators, failed in tests conducted at Beltsville to produce any significant practical change in the resistance of Bartlett pear trees grown under either field or greenhouse conditions.

Strains

Arthur (50) was among the earliest fire blight investigators who attempted to prove the existence

of different strains of *E. amylovora*. He observed some differences in blight infections when Bartlett and Seckel trees were inoculated with the bacterium. Variations in cultures of the blight organism were also noticed by Stewart (901). He used the term "strain" to indicate different isolations and stated that an isolate from Colorado always grew more slowly than other isolates, whereas an apple isolate from New York was usually the most rapid grower. Pierstorff (742) noted extreme variations in the ability of different cultures to cause blight infections. His use of pear seedling material probably accounted for some of the differences. Howard (438) studied in detail *E. amylovora* cultures collected from various parts of the United States and New Zealand. He subjected the isolates to several pathogenicity and cultural tests and concluded that the slight differences between the cultures were insufficient to justify establishing distinct strains. He considered *E. amylovora* an exceptionally constant species.

In California, Ark (28, 30) studied 10 different isolates of *E. amylovora* from 6 localities and 8 suspects. Morphological studies showed the isolates varied in cell size and in size and form of the colony. Marked variability in virulence was also noted and correlated with some morphological and physiological characters (1080). Variation was found among the isolates in utilizing sugars, alcohols, glucosides, amino acids, proteins, fatty acids, and amides. It is doubted that the differences he found are stable enough to separate the isolates into strains.

Hildebrand (422, 424) made a 5-year study of 136 isolates from Canada, New Zealand, and the United States, including numerous morphological, physiological, and pathogenicity tests. The effect on virulence of successive biweekly transfers to nutrient broth demonstrated more variability than stability. The physiological experiments failed to find a more reliable criterion for evaluating strains of the organism than pathogenicity. Although numerous small differences were obtained between individual strains or isolates, he concluded that no strain was outstanding enough to be used in any breeding program for disease resistance.

At Beltsville, 15 different cultures of *E. amylovora* were isolated from as many different pear cultivars. They were compared morphologically in the laboratory and inoculated into succulent shoots of clonal Bartlett trees in the greenhouse. All isolates appeared morphologically similar and typical of the

type. Aqueous cell suspensions were equally pathogenic on immature pear fruit slices and nearly so in the Bartlett shoots. We concluded that the small differences in virulence were inadequate to consider any strains among these 15 isolates (1056, 1057). Additional unpublished data¹⁰ failed to show any significant difference in pathogenicity or degree of virulence in *E. amylovora* isolates from Magness and Bartlett pear when cross-inoculated into pear and apple.

Studies in Great Britain using phage sensitivity, interactivity with common epiphytes, and virulence in pear slices have all failed to demonstrate differences between isolates of *E. amylovora* from different hosts (254). In general, therefore, all these studies on various isolates of *E. amylovora* have failed to show any good evidence that might be used to separate the isolates into true strains.

As far as we know, the only record of a form species of *E. amylovora* was published in 1951, when Starr et al. (892) suggested the name *E. amylovora* f. sp. *rubi* for a bacterial isolate obtained from red raspberry in Maine. Upon artificial inoculation, this pathogen produced no infection in McIntosh apple shoots in the greenhouse but did so in raspberry. On the other hand, an apple isolate produced infection in apples but not in raspberry.

Virulence and Pathogenicity

Even though there is no definite indication for the existence of strains, isolates of *E. amylovora* have been known for a long time to differ in their degree of virulence and pathogenicity. Jackson (470) found cultures of *E. amylovora* from prune to be more virulent than pear cultures. In New Zealand, Waters (1003) repeatedly isolated fire blight cultures from medlar (*Mespilus germanica* L.), which showed "wavy radiations" in the colonies in addition to being very virulent. Ark (28, 30, 1080) observed smooth, virulent, and rough avirulent isolates of *E. amylovora* and found a reversion of the rough to the smooth form. He also found life of the blight pathogen prolonged and degree of virulence diminished after adding different reducing substances to the culture medium (31). Virulence returned to normal, however, even after the first transfer to a medium without any reducing agent. Dalzell (1095) distinguished between smooth and mucoid phases of *E. amylovora* and their degree of resistance to ultraviolet radiation.

In Illinois, Powell (756) and Reinhardt (1126) did not observe any noticeable changes in pathogenicity of *E. amylovora* due to storage at subfreezing temperatures but found a direct relationship between survival and concentration of the bacterial cells. Frampton and Hildebrand (315) were unable to find a correlation between pathogenicity or virulence and electrophoretic velocity of the bacterial cells. In New York, Hildebrand (422, 424) observed the following relationship between degree of virulence in 63 cultures and the mean length of the bacterial cells: Very virulent (1.42 μ m), moderately virulent (1.57 μ m), slightly virulent (1.61 μ m), and nonvirulent (1.59 μ m). Length of the flagella also seemed to be related in some way to virulence; the proportion of cells with short flagella increased directly with a decrease in pathogenicity. However, there was no correlation between virulence and the physiological behavior of cultures.

At the University of Missouri, Shaffer (1129) and Shaffer and Goodman (853, 855) studied in detail virulent and avirulent isolates of *E. amylovora*. They confirmed Ark's observation of the avirulent growth pattern in vitro of the rough colony form and the virulent pattern of the smooth type. Avirulent isolates reached maximum growth after 11 hours and the virulent isolates in 50 hours. They also obtained some avirulent isolates resistant to 1,000 ppm of streptomycin after three to four transfers when exposed to increasing concentrations of the antibiotic (853). At first, however, virulent forms could not be made resistant to concentrations of more than 5 ppm, but later studies indicated the use of virulent *E. amylovora* resistant to 1,000 ppm (582, 1114).

Similar results were obtained by Bennett and Billing (819) in England in 3 out of 16 virulent strains of *E. amylovora*. They also demonstrated that streptomycin resistance was more readily developed in strains of *E. herbicola* than *E. amylovora*. In one case, resistance was associated with a complete loss of virulence.

The occurrence of streptomycin resistance in fruit orchards in the United States and its implication in the fire blight control program are discussed under Chemical Control in chapter 12.

Goodman and Shaffer (353) obtained more than 1,300 bacterial isolates, 80 percent of which were avirulent, yellowish mucoid, and phage sensitive. They also isolated phage-negative virulent and avirulent cultures (855). Rough avirulent isolates from apparently healthy apple buds or from known

¹⁰ Fruit Lab., U.S. Dept. Agr., Beltsville, Md.

virulent cultures of *E. amylovora* reverted repeatedly to the smooth virulent form in a minimal broth containing a water extract of homogenized aphids (354, 1082). Goodman (342, 344) studied 240 isolates of *E. amylovora* obtained from several rosaceous hosts around the world and concluded that differences in degree of virulence occurred. Computer analysis of data on 196 responses to biochemical and cultural tests revealed no clear "clustering" of isolates to permit associating specific responses with virulence. A study of population trends of selected virulent and avirulent isolates in susceptible host tissue suggested virulence to be "an all or nothing phenomenon for this pathogen" (344).

In California, Pugashetti and Starr (764) demonstrated that the genes which determined plant virulence in *E. amylovora* appear to be transferred readily and completely from the donor strain (Hfr 99) to avirulent recipient strains (EA 178-M64S and EA 178-M173-M173S) during the first 15 minutes of a 3-hour mating period. This appears to be the first report showing that such genetic determinants of *E. amylovora* virulence can thus be transferred to avirulent recipient strains. Chatterjee and Starr (165) found that the episomic element F'lac⁺ (lactose) was transferred, probably by conjugation, from *Escherichia coli* to Lac⁻ strains of *Erwinia herbicola* (Geilinger) Dye, *E. amylovora*, and *E. chrysanthemi* Burkholder et al. In further studies they demonstrated that antibiotic resistance carried on R factors was transferred by conjugation from *E. coli* and *Shigella flexneri* Castellani and Chalmers to *E. amylovora* as well as to other *Erwinia* species (166). Transfer of multiple antibiotic resistance from *Erwinia* exconjugants harboring a repressed plasmid, SR1, was not obtained in preliminary trials with an *E. coli* F⁻ strain as the recipient culture.

In England, Bennett and Billing (81g) reported in 1975 that streptomycin resistance carried on an R factor was transferred by conjugation from *E. coli* to *E. amylovora* and *E. herbicola*. They suggested that avirulent cells of *E. amylovora* might persist or even progress together with virulent ones in natural infections. These findings could have serious implications in the nature of resistance and control of fire blight.

Effect of Temperature, pH, and Light

The principal references on the temperatures and hydrogen ion concentrations (pH) needed for growth of *E. amylovora* are summarized in table 6. With

few exceptions nearly all investigators agreed that the optimum temperature for growth in vitro occurs between 21° and 28° C (70°–82.5° F) (30, 85, 87, 484, 742, 901). Minimum temperatures vary from 3° to 12° (38°–54°) (30, 87, 630, 1115) and maximum temperatures from 35° to 37° (95°–99°) (30, 87, 630, 901). Lipman (586) reported high resistance to low temperatures of liquid air. The thermal death points reportedly range from 45° to 50° (113°–122°).

These summary data, however, are very brief. Each bacteriologist conducted many additional experiments in which *E. amylovora* was tested in different solid and liquid media and was incubated under various conditions. Pierstorff (742) determined that the blight organism withstood -183° C (-297° F) for 10 minutes and that heating to 48° (118.5°) did not always inhibit its growth. Stewart (901) observed growth of *E. amylovora* in bouillon at 23° (73.5°) following previous exposures of -14° to -28° (7° to -18.5°). Jones (484) reported that bacteria in freshly inoculated bouillon cultures were not killed after 10 minutes' exposure at 45° (113°) but were killed after similar exposure at 50° (122°). Bacterial growth also occurred when freshly seeded agar plates were placed for 30 minutes to 20 hours in an ice and salt freezing mixture at 0° to -10° (32°–14°) and then incubated at 25° (77°).

In Illinois, Reinhardt and Powell (783) and Reinhardt (1126) found that anaerobically grown *E. amylovora* was more sensitive to freezing and that bacterial ooze protected the cells from death by freezing. The organism could not stand suspension in phosphate buffer or Emerson broth at -4.5° C (24° F) in a supercooled state. Reinhardt also found repeated freezings more lethal than a single freezing. In 1976, Ritchie and Klos (795b) kept excised Jonathan apple cankers, 1.6–3.0 cm in diameter, at four temperatures from 20° to -28° (68° to -18.5°) for 3 months. *E. amylovora* was detected only in the cankers kept at -28° (-18.5°).

E. amylovora has little resistance to drying. The organism reportedly survived on cover glasses for 24–36 hours irrespective of the presence or absence of moisture and from 4 to 10 days in gauze strips (30). Jones (484) observed growth of a glass smear culture from broth dried in the dark at room temperature for 5 days and then resuspended in bouillon. Similar smears exposed to sunlight for 30 minutes and kept dry in the laboratory for 6 days showed no growth in bouillon. However, Stewart (901) did observe growth after 9 days. In Egypt, El-Helaly et al. (264)

TABLE 6.—*Temperatures and pH needed for growth of Erwinia amylovora*

Year	Temperature (°C) ¹			Thermal death point (°C) ¹	pH			Reference
	Minimum	Optimum	Maximum		Minimum	Optimum	Maximum	
1911---	-----	23-25 (73.5-77)	37 (99)	45-50 (113-122)	6.6	7.0	7.6	Jones (484).
1913---	-----	22-25 (71.5-77)	37 (99)	47 (117)	5.9	6.6-7.5	7.6	Stewart (901).
1929---	-----	25 (77)	-----	-----	4.6	-----	8.7	Howard (438).
1931---	-----	-----	-----	49 (120)	4.6	-----	-----	Pierstorff (742).
1937---	3-8 (37.5-46.5)	28 (82.5)	37 (99)	45.1-48.3 (113-118.5) 48.3-49.5 (118.5-121)	4.0-4.4	6.8	8.8	Ark (30).
1960---	12 (54)	21-27 (70-81)	35 (95)	-----	-----	-----	-----	Luepschen (1115).
1961---	3-5 (37.5-41)	25-27.5 (77-81.5)	37 (99)	47.5-50.0 (117.5-122)	5.2	6.0	8.1	Billing et al. (87).
1964---	10 (50)	30 (86)	35 (95)	-----	4.3	6.6-7.5	8.5	El-Helaly et al. (264).
1964---	3-8 (37.5-46.5)	30 (86)	37 (99)	-----	4.0-4.4	6.8	8.8	Martinec and Kocur (630).
1972---	-----	21-30 (70-86)	-----	-----	-----	-----	-----	Eden-Green (1097).
1974---	-----	18-28 (64.5-82.5)	-----	-----	-----	-----	-----	Billing (85).

¹Approximate °F in parentheses.

found that *E. amylovora* did not survive more than 48 hours when it was exposed to 27°–29° C (81°–84° F) on glass rods dipped in a concentrated saline suspension and transferred to tubes of sterile saline solution at various intervals.

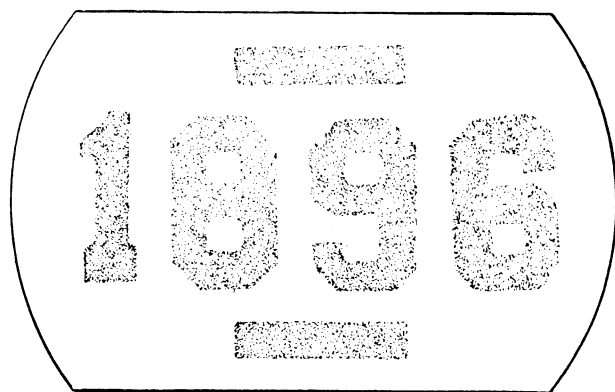
The most recent temperature studies were performed by Billing (85) and Eden-Green (1097) at East Malling. They showed a linear relationship between the doubling rate of the bacterium and temperatures from 9° to 18° C (48°–64.5° F). The doubling time decreased sharply at 18°–28° (64.5°–82.5°). They found this change at 18° of special interest, because this temperature has been cited by many as the minimum for the occurrence of blossom blight (598, 656, 758).

The optimum hydrogen ion concentration (pH) on the growth of *E. amylovora* varies from 6.0 to 7.5 (30, 87, 264, 484, 630, 901). These and other investigators reported the minimum range at pH 4.0–5.9 and a maximum at 7.6–8.8. Again the differences were based on such factors as variation in culture media and incubation temperatures. Reinhardt (1126) observed that *E. amylovora* was killed when

suspended in juice of pH 2.8 obtained from green apples. The organism was able to grow in this juice, however, when the pH was raised to between 4.0 and 4.4.

The earliest evidence of the detrimental effect of direct sunlight on the growth of *E. amylovora* in culture was published in 1905 by Smith (876). He exposed a gelatin culture of the bacterium in a petri dish for 4 hours to direct sunlight after covering parts of the plate with pasteboard numbers of the year 1896 (fig. 14). The culture was then incubated for 5 days at about 24° C (75° F). The bacteria grew exclusively under the protected parts. In similar tests Stewart (901) confirmed these observations, whereas Jones (484) in Canada reported 15-percent loss of colonies after 30 minutes' exposure of plates to sunlight.

In field observations, Hotson (434) determined that *E. amylovora* bacteria on pruned blighted branches survived for 10–13 days when they were exposed to direct sunlight. When left in part sunlight and part shade the bacteria remained alive for 27 days, and when left under a cover crop providing



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FIGURE 14. — Inhibitory effect of sunlight on growth of *Erwinia amylovora*; bacteria grew only under protected parts of petri dish covered with pasteboard numbers (after Smith, 876).

protection they lived for 29 days. Luepschen (596a) reported survival of the blight pathogen in the orchard under high light intensity conditions (1,650-meter elevation) in western Colorado following artificial inoculation and exposure for 47 days to high temperature and low humidity. In Michigan, Sobiczewski and Klos (881b) exposed inoculated apple leaves to ultraviolet light and observed that most bacteria were killed after a 5-minute exposure. However, some cells survived even after 120 minutes.

From Wisconsin, Brooks (114) reported that exposure of small drops of exudate to direct sunlight killed the bacteria after 22 hours. In drops of exudate kept in the laboratory in wax paper bags open to the air but protected from direct sunlight, they remained viable for 2-9 months. In small twigs cut from the trees and exposed to sunlight for 2 hours each day during June and July, the organism remained viable for 15 days but was dead after 25 days.

Longevity

The longevity of *Erwinia amylovora* may be different in various media and may be affected by different circumstances. Apart from such conditions as culture media, temperature, pH, light, and drought previously mentioned, additional factors that have been studied are nectar, honey, soil, and age of tree branches as they affect survival of the organism.

In 1935, Thomas and Ark (935) reported that the nectar of fruit tree blossoms grown in a dry atmosphere contained sugars in concentrations greater than those permitting growth of the blight organism in culture solutions. In Wisconsin, Ivanoff and Keitt

(465, 515) concluded beyond any doubt that nectar concentration could limit blossom blight infection. Growth of *E. amylovora* rapidly decreased with increased sugar concentration, and none occurred at 30 percent. The bacteria survived for 48 hours in nectar drops containing 20 percent sugar, 24 hours in 30 percent, and less than 24 hours in 40-50 percent sugar. However, when tubes of artificial nectar containing 40 percent sugar were heavily seeded, the bacteria survived for 72 hours and incited infection when placed in pear blossoms. Infection of unwounded pear or apple blossoms, inoculated by placing small droplets of bacterial suspension in the nectar, occurred freely only when sugar concentrations were lower than those in natural nectar.

In detailed experiments and observations in Ohio, Gossard (357) and Gossard and Walton (359, 361) found that *E. amylovora* survived in honey for a maximum of 72 hours. When contaminated honey, incubated for 4, 28, and 47 hours, was inoculated into succulent apple shoots, it resulted in 84, 64, and 52 percent infection, respectively. When drops of aphid honeydew were contaminated with the blight pathogen and then inoculated after incubation of 20, 43, or 71 hours, 67, 83, and 100 percent of the shoots became blighted, respectively. They also found the bacterium to be infectious following survival for 5 days in peach, plum, and cherry nectar. Pierstorff and Lamb (745) showed that the longevity of *E. amylovora* in pure honey varied from 5 to 11 days, and McLarty (618) found live bacteria after 6 weeks. Thomas (933) reported isolation of the bacterium from artificially contaminated honeycomb cells, wood of the frame, and waxy surface of the comb up to 15, 20, and 55 days, respectively.

In East Germany, however, Beyme et al. (82a) did not detect the bacterium on wooden frames after 3 days or on combs after 21 days. On the other hand, they isolated *E. amylovora* from the digestive tract of the bee up to 24 hours after feeding the insect a 50 percent sugar solution containing 1×10^8 cells per milliliter of the pathogen.

In New York, Hildebrand and Phillips (427) made the most extensive study of the longevity of *E. amylovora* in various sugar-containing media (fig. 15). When they used a synthetic culture solution as a base, the maximum sugar concentrations at which the blight pathogen grew in dextrose, levulose, artificial nectar, and sucrose were 30, 30, 35, and 58 percent, respectively. When introduced through the food of the bees, *E. amylovora* was not reisolated

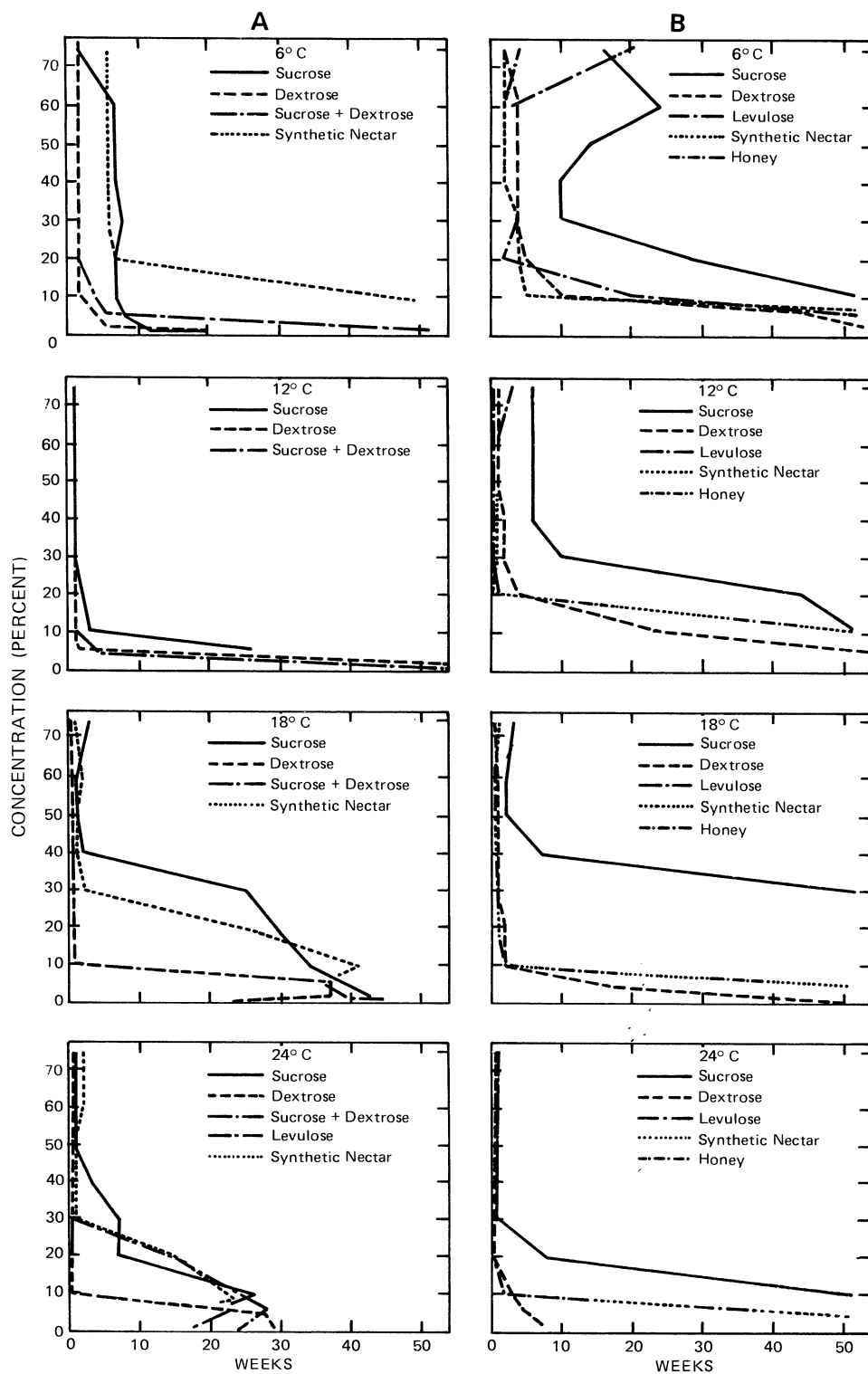


FIGURE 15.— Effect of several sugar solutions, nectar, and honey at various temperatures on longevity of *Erwinia amylovora*: A, Single culture; B, mixture of 30 cultures. (After Hildebrand and Phillips, 427.)

after 3 days from honey, comb, frame, and bees. The only exceptions were from pollen after 13 days and from frame scrapings after 12 days. Because the longevity of the fire blight bacterium varied with the incubation temperatures, the sugar concentration, and the various sugars used, they concluded that survival of the organism in beehives was highly improbable at the temperatures and sugar concentrations normally found in the apiary.

In California, Ark (30, 1080) studied numerous isolates of *E. amylovora* and found all grew in 50 percent sucrose. Two cultures from *Crataegus crus-galli* L. and one from pear tolerated 60 percent sucrose. However, the pear strain failed to grow in 14 percent glucose, whereas an isolate from *C. crus-galli* in a California collection developed in 20 percent glucose.

Using the insect *Aphis pomi* DeGeer, usually associated with blight dissemination, Plurad (1124) and Plurad et al. (749, 750) showed that *E. amylovora* persisted for at least 72 hours in the body of the insect. However, aphids feeding on plants were unable regularly to introduce 70 or more bacterial cells into apple leaves. Blight infection did not occur even though the aphids were maintained for 72 hours on the host plants.

Ark (30) obtained *E. amylovora* from orchard soils and found that the organism persisted for 54 days in sterilized soil and for 38 days in unsterilized soil in the laboratory. He used a simple technique of immersing green, immature pear fruit in a water suspension of soil collected from beneath a blighted tree. The blight organism appeared in the form of characteristic droplets of bacterial exudate. Rosen (818), however, was unable to isolate the organism from 67 soil samples collected from beneath severely blighted pear and apple trees.

The blight organism is also reported to survive on the surface of tree branches for a certain length of time. Hotson (434) reported a longevity of 10–29 days on pruned branches depending on their sunny or shady exposure in the orchard. In Arkansas, Rosen (815, 818) found that *E. amylovora* in ooze attached to blighted pear twigs and kept in the laboratory for varying periods was dead after 1 year. On the other hand, cells were still viable and infectious after that length of time after being placed over concentrated sulfuric acid in an atmosphere approaching 0 percent relative humidity. Fire blight exudate kept in corked vials suspended from an apple limb in an orchard yielded no viable bacteria after less than 3 months.

In our longevity studies of the blight pathogen at Beltsville, young Bartlett trees in the greenhouse were sprayed with a bacterial suspension and allowed to dry. When these trees were sandblasted 4 weeks later to simulate a severe hailstorm, 67 percent became infected, indicating that the bacterium could survive in this dry state for at least 1 month (500, 501). In followup experiments, Bartlett trees were spray-inoculated with a different isolate of *E. amylovora* and sandblasted 4 weeks after storage at 32° C (90° F). One isolate caused infection, whereas the other did not, thus indicating differences in ability of *E. amylovora* to survive on tissue surface (1052, 1062).

Bacteriophagy

Several reports have described the isolation of bacteria other than *E. amylovora* from hosts infected with fire blight and their separation through using bacteriophagy. Coons and Kotila (182) in 1925 isolated a lytic principle (phage) from soil, river water, and diseased tissue showing fire blight symptoms. Phage titer was increased by repeated association with susceptible bacteria. Its activity varied according to the strains of the organism tested. These investigators pointed out that phages may be important in the infection phenomena as well as in plant disease control.

It was not until 1947, when Thomas (942, 943) showed that phages could be used to identify and differentiate *E. amylovora* isolates from pear, apple, mountainash, cotoneaster, and hawthorn. Since then several articles have been published on bacteriophagy. In Missouri, Baldwin and Goodman (62) and Goodman and Shaffer (353) obtained 1,324 avirulent bacterial isolates from 758 dormant apple buds in orchards with fire blight. Forty-eight percent of the buds harbored bacteria sensitive to one or more *E. amylovora* phages and thus accounted for 40 percent of the isolates. Yellowish-white mucoid isolates were the most frequent of six colony types identified. Later two yellowish-white mucoid isolates were shown to be mixtures of a virulent white *E. amylovora* and a nonvirulent yellow bacterium (340). The component cultures were considered related because they were lysed by some of the same phages.

In England, Billing (83) used phages to identify and separate bacterial isolates of *E. amylovora* from saprophytic *Erwina*-like organisms and *Pseudomonas* species. Billing et al. (88) also used phages to

show the relationship of typical *E. amylovora* strains with capsules and atypical strains without capsules when grown on Yeastrel peptone agar.

Hendry et al. (401) studied 616 Gram-negative bacterial isolates from trees and orchards with fire blight. Serologically 194 *E. amylovora* isolates were distinguished from 57 nonpigmented isolates of miscellaneous colonial types (1106). All the *E. amylovora* isolates, 26 miscellaneous white isolates, and 94 yellow isolates were lysed by 1 or more of 7 phages. Two phages lysed many isolates from all three groups indicating a relationship.

Neal et al. (677) attempted to determine whether aphid eggs are possible overwintering sites of *E. amylovora* by challenging bacterial isolates from the eggs with phages specific for the fire blight organism. Of 156 isolates, 14 of 46 white rough isolates were sensitive to the phage but avirulent. None of the yellow mucoids were sensitive, although one proved virulent in apple tissue and one white smooth isolate was sensitive and virulent.

Erskine (279) went a step farther than other investigators to show the possible role of *E. amylovora* phage in the epidemiology of fire blight. Bacteriophage isolated from soil beneath pear trees with fire blight lysogenized yellow saprophytic bacterial isolates associated with *E. amylovora* but did not lysogenize a virulent strain (PR 1) of *E. amylovora*. These studies suggested that the yellow saprophyte, which is invariably isolated from fruit trees with *E. amylovora*, may frequently occur in its lysogenic form in nature and serve as a reservoir of phage, which may affect the occurrence and severity of fire blight.

Erskine (278, 280) demonstrated indirectly the possible role of toxin in the etiology of fire blight. He found that phage lysis of highly virulent forms of *E. amylovora* led to the release of a highly toxic agent when injected into rabbits. The toxic factor was liberated to a less extent from less virulent forms of the pathogen but not from related nonpathogenic saprophytes. These results suggested that toxin production by the pathogen may be determined by the activity of the phage and the possible association of the toxin with virulence characteristics of the bacterium in plant tissues.

In Canada, Harrison and Gibbins (387a) studied the morphology and activity of a temperate phage isolated from *E. herbicola* Y46. They found that the range of bacterial strains to this phage was limited to two isolates of *E. herbicola* and none of *E. amylovora*.

In Michigan, Ritchie and Klos (795b) demonstrated the presence of high titers of *E. amylovora* bacteriophage (10^6 plaque forming units per terminal) from diseased and symptomless aerial parts of apple and pear trees. Plaque morphology of phage PEal halo and nonhalo types occurred after 48 hours' incubation at 27° C (81° F) (fig. 11, D). Three phage isolates were found specific to *E. amylovora* and did not lyse *E. herbicola*, *Agrobacterium tumefaciens* (Smith and Townsend) Conn, or *Pseudomonas syringae*.

When the scientist learns how to manipulate and maintain high titers of *E. amylovora* bacteriophage on plants in the field, this bacteriophage may become potentially useful in biological control.

Effect of Micro-Organisms

Some investigators have referred to the effect of certain saprophytes on *E. amylovora*. Other organisms in the soil and plant microflora also seem to affect the etiology and epidemiology of *E. amylovora*.

Bacillus and Bdellovibrio

In California, Ark and Hunt (38) studied two soil bacteria that showed a strong antagonism to *E. amylovora* as well as certain other bacteria. The bactericide produced by these two organisms withstood boiling for 60 minutes. However, when the bactericide-containing medium of the yellow species was autoclaved, the bactericide was inactivated after 15 minutes at a pressure of 10 pounds per square inch (0.7 g/cm²), whereas that of *Bacillus vulgatus* Trevisan was still active after 10 minutes' sterilization at 20 pounds per square inch (1.4 kg/cm²).

In Egypt, Abo-El-Dahab and El-Goorani (2) showed that *Bacillus subtilis* (Ehrenberg) Cohn produced an antibacterial substance in sucrose nutrient broth in sufficient concentration to inhibit the growth of *E. amylovora*. They found the inhibitory effect of the *Bacillus* equivalent and sometimes superior to that of certain antibiotics, particularly streptomycin.

In 1963, Stolp and Starr (907) isolated from soil and sewage an interesting new group of bacteria (*Bdellovibrio bacteriovorus* Stolp and Starr) that was parasitic on other bacteria (fig. 11, E). These bacteria caused reactions similar in their outward manifestations to bacteriophage-induced lysis. All isolates studied possessed lytic activity only against Gram-negative bacteria, including *E. amylovora*.

Further studies by Starr and Baigent (891) showed that *B. bacteriovorus*, after attaching to the host cell, formed a pore in the cell wall followed by disorganization of the host nucleus and of the murein layer of the wall. The parasite completely invaded the host cell, and the cell contents were digested. When the host protoplast was entirely lysed, the parasites left the disintegrated 'ghosted' cell envelope and were ready to reinitiate the parasitic cycle.

Erwinia herbicola

Since the earliest available report of a "yellow, non-parasitic schizomycete" by Waite (chap. 1) in relation to fire blight, many investigators mentioned such a saprophyte association with *E. amylovora* after conducting isolation studies from cankers and other blighted host tissues (62, 280, 281, 296, 340, 353, 790, 791, 879, 1051, 1130). Other yellow-pigmented bacteria, possibly similar to those described here, have been isolated from plants, animals, and miscellaneous sources (86, 364, 541). In 1920, Smith (878) referred to Waite's observation and added that "Dr. Arthur must also have had it in some of his cultures for in one place he described the growth of *Bacillus amylovorus* as 'yellowish.'"

By 1929, Shaw (1130) made the first detailed study at the University of Arkansas relative to the identity of a yellow organism associated with fire blight. He described it as a Gram-negative rod, usually occurring singly, motile by means of peritrichous flagella, not acid fast, and producing a yellow color on most ordinary culture media. After 48 hours on potato dextrose agar plates at pH 6.8, colonies were described as "circular, smooth, raised entire to very finely lobed, amorphous, yellow in center and averaging 2.5 mm. in diameter." As the colonies grew, Shaw mentioned a slightly irregular colony margin, a distinct buff yellow to apricot yellow in the center, and a very thin (1–4 mm width) grayish precipitate developed around the colonies. He concluded that the organism was a species of *Flavobacterium*, possibly *F. aquatilis* (Frankland and Frankland) Bergey et al. Laboratory tests and spray inoculation experiments on young Bartlett shoots revealed that the yellow organism had a definite inhibitory effect on the fire blight pathogen.

In 1964, Dye (245) proposed the name "*Erwinia herbicola* (Duggeli) nov. comb." for the yellow organism usually associated with *E. amylovora*. Two years later the bacteriology committee for "Bergey's

Manual" recognized *Pseudomonas herbicola* (Geilinger) as the first valid publication of this name and thus accepted the name as *E. herbicola* (Geilinger) Dye. Following a major taxonomic study of the genus *Erwinia*, Dye (248) recognized the herbicola group as one of four groups of *Erwinia* species, *E. herbicola* as the type species. He found that *E. amylovora* and *E. herbicola* shared many cultural and biochemical characters, with the principal exception of an acid reaction in purple milk, growth at 37° C (99° F), and a yellow water-insoluble pigment for the latter. In general, Lazar (567) agreed with the separation of Dye's *E. amylovora*, *E. carotovora*, and *E. herbicola* groups on the basis of cross-agglutination and gel-diffusion studies. Descriptions of other yellow-pigmented bacteria isolated from various plant materials reportedly fit the one for *E. herbicola* (541).

In Illinois, Smith and Powell (879, 880) and Smith (1134) compared disc electrophoretic protein patterns of *E. amylovora* with several yellow isolates collected from blighted apple or pear trees. They found the yellow isolates more comparable to *Xanthomonas pruni* (Smith) Dowson than to *E. amylovora*. In a study of 20 yellow bacterial isolates from Jonathan apple trees, all were Gram-negative, peritrichously flagellated, and with rods 1.1µm–2.9µm long and 0.6µm–0.9µm wide; their temperature requirements were almost similar to those of *E. amylovora* (1133).

Chatterjee and Gibbins (161–163) studied in detail the metabolic activities of *E. herbicola* and found that it produced phloretin when grown on a defined medium containing phlorizin as the sole source of carbon. They also observed that several strains of *E. herbicola* produced white variants at high frequency when grown in yeast broth at 37° C (99° F). These variants did not reverse to the parent strain, however, but varied in their extracellular diffusible antigens among themselves and with the parent strain (327). A variable but minor degree of cross-reaction with an isolate of *E. amylovora* was observed.

Chatterjee (1094) also presented evidence that all yellow isolates utilized arbutin, whereas only three isolates grew with phlorizin as sole source of carbon. These results suggested that the yellow organisms could tolerate higher concentrations of hydroquinone in the microenvironment than *E. amylovora*. The findings supported the hypothesis that the yellow isolates in vivo could act on arbutin with the

consequent release of hydroquinone, which might inhibit *E. amylovora*, whereas the yellow isolates could multiply to degrade more arbutin. This phenomenon has been suggested as having a role in the epidemiology of fire blight (164).

In Indiana, McIntyre et al. (612) observed an apparent relationship between several isolates of *E. herbicola* and virulent as well as avirulent isolates of *E. amylovora*. They obtained profiles from the hydrolysis of 27 naphthyl phosphoramides, sulfonamides, and acetamides and concluded that aminopeptidase profiles offer a rapid reproducible means of microbial identification to supplement morphological and cultural criteria.

During 1956–76, several investigators studied the nature and possible relationship between *E. herbicola* and *E. amylovora* in the overall fire blight syndrome. Farabee and Lockwood (296) frequently isolated a nonpathogenic yellow species of *Bacterium* from fire blight cankers on apple and pear trees in Ohio. Most of the isolates inhibited growth of *E. amylovora* by increasing the acidity of the culture media to a degree unfavorable for growth of the fire blight pathogen.

Baldwin and Goodman (62) isolated among other types a dominant yellowish-mucoid bacterium from dormant apple buds. They suggested that it was analogous with the “yellow” organism associated with fire blight for many years by Rosen (803). Goodman (339) later conducted studies with an avirulent yellow bacterium “closely related” to *E. amylovora*, which suppressed the growth of virulent isolates of *E. amylovora* in vitro. Rapidly growing apple shoots were protected against infection by a virulent strain of *E. amylovora* by prior inoculation with a yellow *Erwinia*-like isolate (341). In further studies, Goodman (340) mixed the yellow avirulent form (35 A-Y) with a white virulent form (35 A-W), both isolated from apparently healthy dormant apple buds. He then found that the longer they were incubated before introduction into the host, the less infectious the white virulent form became.

In Michigan, Riggle and Klos (790, 791) and Riggle (1128) conducted several studies on *E. herbicola*. They found large numbers of this organism on leaves of apple, cherry, and apricot but smaller numbers on pear. Pear blossoms inoculated with *E. herbicola* 24 hours before inoculation with virulent *E. amylovora* partially controlled fire blight (791). Laboratory studies indicated that *E. herbicola* reduced the pH of the substrate, which was inhibitory to *E. amylo-*

vora. Further studies supporting this hypothesis showed that filtration of a simulated nectar medium in which *E. herbicola* had been growing would not support growth of *E. amylovora* (790). However, growth of the latter resumed when amino acids were supplied and the pH was adjusted to neutrality.

In Canada, Erskine (279) showed by pathogenicity studies on pear slices that symptom development was delayed when mixtures of either *E. amylovora* plus *E. amylovora* bacteriophage or *E. amylovora* plus a yellow saprophytic bacterium was used as inoculum. Symptoms did not appear when *E. amylovora* and a lysogenic form of the yellow organism were inoculated together. The yellow organism may appear frequently in its lysogenic form in nature and serve as a reservoir of phage, which may affect the occurrence and severity of fire blight.

In other laboratory studies, Erskine and Lopatecki (281) showed by inoculated pear slices that variation of temperatures and sucrose concentration determined independently the equilibrium of a readily reversible alternation of predominance of the yellow bacterium and *E. amylovora*. These investigators suggested that *E. amylovora* may sometimes exist as an avirulent resident on the surface or within healthy host plants when environmental conditions favor growth of the yellow saprophyte rather than the pathogen. Furthermore, such conditions are more likely to occur in midsummer and the fall, with decreased humidity or diminution of sap flow and with increased sugar content in the host tissues.

These studies indicate that the yellow organism, reportedly associated with *E. amylovora* in the fire blight disease syndrome, may possibly be one and the same as *E. herbicola*. When fully understood it may be used in biological control of the blight pathogen.

Phytobacteriological Techniques

Apart from the materials and methods previously discussed here for culture media, inoculation techniques, and taxonomy and separation of pathogens, many other procedures and techniques have been used in fire blight research. For more information, see Goodman (344a).

Descriptions of these techniques by various researchers include among others those for lyophilization of bacterial pathogens, electron microscopy, histological studies of plant material, methods for flagella stain, bacteriophage studies, starch-gel zone electrophoresis, studies of glucoside metabolism in

diseased plant tissues, methods for the separation of closely related bacteria by gel diffusion test, single-cell isolation of bacterial cultures, and procedures for pathogen identification, including rapid detection through use of the hypersensitive reaction of plants. Additional phyto bacteriological literature is listed with most articles. Methods for bioassay of streptomycin in pear and apple tissue have been published by Coyier (188a) and Grove and Randall (374a).

For specific materials and techniques used in recent studies for advanced degrees at various universities relative to the fire blight organism and its host-parasite relationship, see the theses and dissertations grouped by the following subjects: (1)

Taxonomy and serology—Ark (1080), Chatterjee (1094), Dalzell (1095), El-Goorani (1098), Elrod (1099), Hendry (1106), Huang (1109), Schroder (1128a), and Shaffer (1129); (2) etiology and pathogenesis—Addy (1078), Burkowicz (1088), Gowda (1103), Huang (1110), Lewis (1114), McIntyre (1118), Pierstorff (1123), Plurad (1124), Reinhardt (1126), Sjulín (1132), and Wrathier (1139); (3) biochemistry—Ahn (1079) and Hildebrand (1107); (4) bacteriophagy—Baldwin (1082); and (5) *Erwinia herbicola*—Riggle (1128), Shaw (1130), and Smith (1133, 1134). For more specific and detailed fire blight studies, more sophisticated methods and techniques may have to be developed.

CHAPTER 8

DISEASE CYCLE

As far as we know, *Erwinia amylovora* passes its entire active life (primary and secondary cycles) in direct association with the living host. In 1898, Waite (993) made the first brief description of the organism's life cycle. Since then numerous life cycles have been proposed or sketched by various investigators. Modifications, additions, and improvements have been made by many.

For this handbook we prepared a new diagram of the life cycle of *E. amylovora* (fig. 16), based on all available information about the disease and its pathogen. The description starts with the primary infection in the spring (blossom period) and continues clockwise in the diagram through the summer ending with the formation of cankers in the fall (dormant period). Special emphasis is placed on resident bacteria present internally and externally in host tissues, as well as on all known means of dissemination and overwintering.

Primary Infection

The origin of primary infection in the spring has been the subject of much controversy through the years. Since some holdover cankers from the previous season were found to exude bacterial ooze in the spring, ooze was believed to be the principal source of primary inoculum, based on the assumption that insects visited the ooze and carried the organism to the blossoms and twigs where infection originated in the spring (416–418, 651). This theory was often discredited because (1) oozing frequently occurred after the first infections appeared; (2) insects only accidentally came in contact with ooze; (3) only flies were attracted by ooze but were not observed to visit flowers; and (4) ooze did not seem to be attractive to bees and other pollinating insects.

Overwintering Cankers

Sackett (826) was the first to distinguish between regular fire blight cankers and holdover cankers on pear, in which bacteria overwintered from one season to the next. Miller (651) in Wisconsin observed that cankers on apples showing no line of demarcation between diseased and healthy tissue were re-

sponsible for carrying the organism through the winter, whereas cankers on apples with a definite line of delineation (crack) at the margin of the cankered area were usually found to be inactive.

In New York, Specht and Beer (884a) used a novel method to detect smooth-margined cankers caused by *E. amylovora*. When infected pear and apple trees were photographed (through filters that removed radiation of less than 700 nm) with film sensitive to infrared radiation, cankers were readily detected. Conceivably such a technique might be modified for practical use in the field.

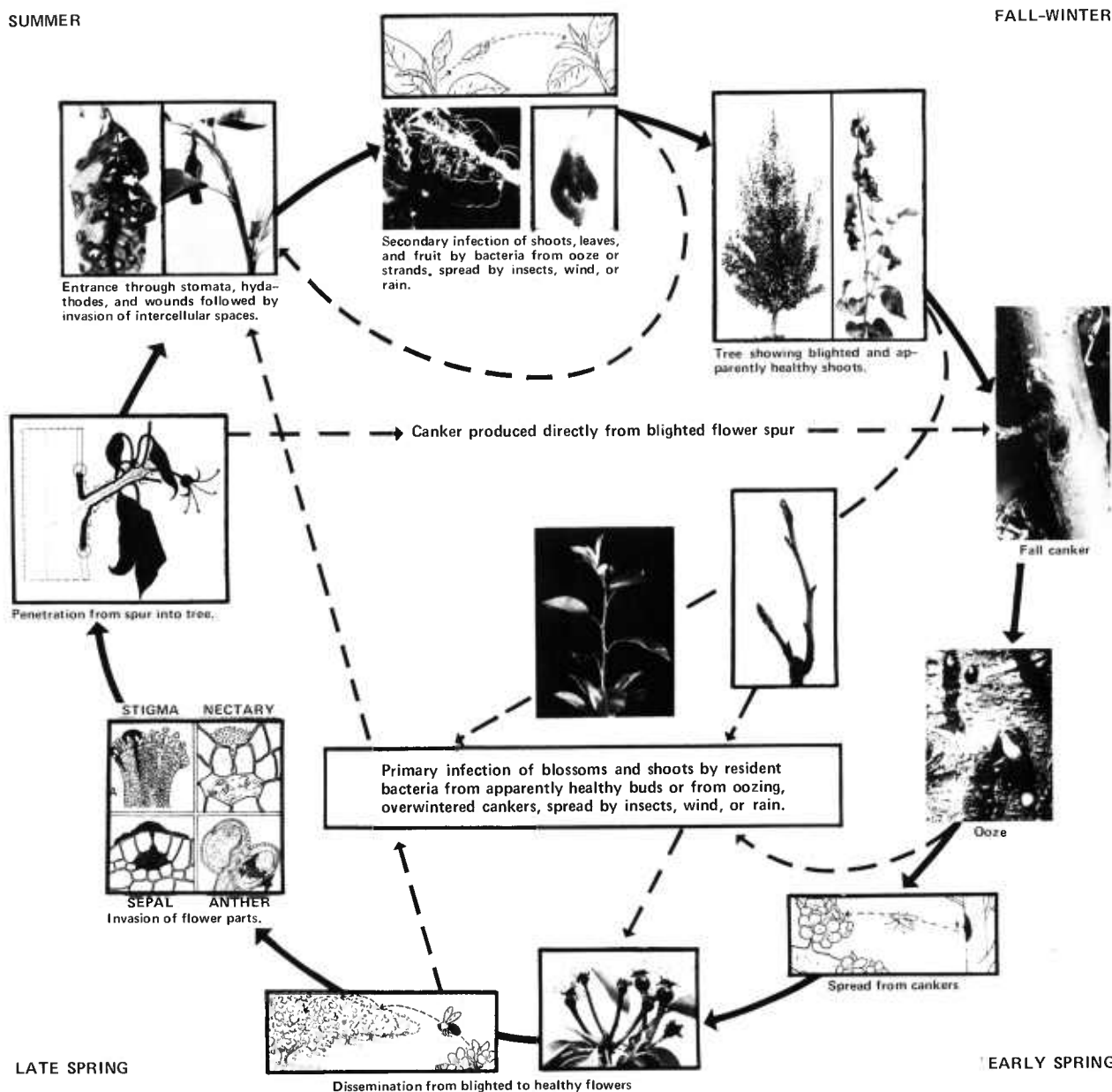
In other studies, Beer and Norelli (81c) recovered *E. amylovora* from intact canker margin surfaces of 15 percent of 130 cankers examined. The organism was recovered more frequently from cankers with indeterminate-type margins than those with determinate margins. Inoculation of nursery-grown apple trees early in the growing season produced cankers with determinate-type margins, whereas trees inoculated later produced cankers with indeterminate margins.

Viable infectious bacteria have been isolated from cankers on pear (742, 795a, 795c, 1050, 1051), apple (114, 416, 791, 795a, 804, 813), and hawthorn (256, 635, 638, 1097). Reinking (1127) reported all negative isolations from apple cankers in Wisconsin, whereas Rosen (804) reported the collection of "sterile" noninfectious ooze from apple cankers in Arkansas. Many of these investigators observed ooze production from no more than 12 percent of the cankers in any one orchard (114, 742, 804, 1051). In addition to cankers, the blight bacterium reportedly overwinters in diseased fruit (25, 335, 619), small twigs, and occasionally in twigs and branches left on the ground after pruning (44, 318).

Fire blight cankers vary from only 1 or 2 mm in the current season's shoots to 15–20 cm or larger in limbs and tree trunks. In a study of 100 cankers on 10-year-old seedling pear trees in Maryland, we found that 65 percent of the cankers were formed following invasion through the top of the tree downward and only 35 percent in the main trunk after invasion through a lateral branch (1050, 1051, 1075). In this

SUMMER

FALL-WINTER

FIGURE 16.—Life cycle of *Erwinia amylovora* (sketches after Hildebrand, 420).

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study nearly all the oozing cankers were in large scaffold limbs and tree trunks. The percentage of live tree tissue above the canker was correlated with the positive isolation of *E. amylovora* from these cankers. In Michigan, however, Ritchie and Klos (795a) isolated the pathogen from pear and apple cankers as small as 0.4 cm in diameter. They concluded that small cankers may be as important as large ones in overwintering *E. amylovora*.

In the spring some fire blight bacteria are carried by wind, rain, and insects from winter cankers to blossoms or young tender tissues of shoots where infection may start. The bacteria enter unwounded blossoms through natural openings (651, 804, 816). Hildebrand (417) reported that the bacteria enter the specialized nectar-secreting stomata of the flower's nectary, uncutinized stigmas, undehiscent anthers, and stomata on the sepals. The bacteria

multiply and advance into the intercellular spaces. After a few days the cells begin to collapse owing to plasmolysis, at which time discoloration manifested as necrosis sets in. After a few more days the flowers blight completely.

In pear flowers, invasion occurred more rapidly through nectaries and pistils, whereas in apple flowers the stigmas and the anthers were first invaded (417, 816). The morphological differences of open receptacles in pears versus closed ones in apples appear to account for this variation. Hildebrand (418) reported that he was able to initiate infection in apple blossoms with a single bacterial cell but failed to do so in pear blossoms.

Rosen (816) undoubtedly made the most detailed study of the penetration and invasion of *E. amylovora* into apple and pear blossoms. He concluded that (1) the nectarial surface is the most vulnerable to invasion; (2) nectar is an excellent medium for bacterial multiplication; (3) masses of bacteria can be traced through several layers of cells below the nectar chamber soon after blossom inoculation; (4) the stigmas of the apple pistils are receptive structures for invasion; and (5) bacteria travel through intercellular spaces, often actually penetrating into protoplasts. Ivanoff and Keitt (465) reported a correlation between the nectar concentration of apple and pear flowers and the growth of *E. amylovora*. Infection occurred freely when sugar concentrations were low but not at medium or high concentrations. These observations have been confirmed (196, 427, 465, 515, 935).

After killing the blossom, blight infection moves into the flower stem and then into the peduncle and spur, where it invades the leaves and finally the branch. At this time the infection, if walled off, produces a canker or it penetrates farther into the branch and then into the trunk, where it moves up and down and results sometimes in death of the tree. In some instances, a few to many limbs may be killed, with the infection penetrating into and girdling the trunk of the tree. As a result, those parts of the tree above the girdle usually die (1051).

At the time of or following flower infection, leaves and tender succulent shoots not associated with the flowers may also be invaded (197, 394, 433, 560). Insects, wind, and rain may carry the fire blight organism to these tissues, where by chance they are deposited, or the contaminated insects inadvertently introduce the bacteria into the host cells during feeding. In fact, twig or shoot infection may

occur in orchards where little or no blossom infection is found. At Beltsville, Md., where a heavy concentration of natural inoculum is usually found, records show that about 50 percent of natural infection occurs after the spring bloom (505).

Based on this information, combined with our experience and observations, we have concluded that some fire blight cankers are instrumental in the primary infection process but to a less extent than generally believed in the past.

Epiphytic *Erwinia amylovora*

It does not seem logical that the small number of oozing cankers supply sufficient inoculum to cause the great number of infections often observed in the spring, especially when little or no active blight was observed during the previous season. In addition to ooze from overwintered cankers, some other source of inoculum, occurring both in the spring and at other times during the growing season, has been suspected for a long time. This we refer to as resident bacteria in tree tissues and is shown schematically in the center of figure 16.

As early as 1929, Rosen (804) reported from careful histological studies that "the pathogen may actually pass upward or downward in some of the ducts without calling forth any disease symptom." He showed very conclusively that the xylem vessels were occupied by masses of bacteria, even though there was no definite proof of identity or pathogenesis. In 1933, Rosen (813) concluded that primary blossom blight may originate as (1) internal extensions of the previous year's blight; (2) bud infections in which the buds, though infected the year before by internal blight extensions, remain alive through the winter; (3) infections resulting from bacterial exudates produced the previous growing season; or (4) the well-known twig blight induced by inoculum from overwintered cankers. These masses of bacteria in the xylem appeared to be similar to cysts reported by Nixon (695) a few years earlier.

The fact that *E. amylovora* could spend part of its life cycle ostensibly as a resident organism in the tissues of its hosts apparently remained unnoticed for about 30 years. In 1962–63, Baldwin (1082) and Baldwin and Goodman (62) reported the isolation of *E. amylovora* from apple buds in Missouri. About 40 percent of the bacterial isolates from more than 750 apple buds were sensitive to 1 or more of 5 typing phages. Similar isolations from apparently healthy

apple and pear buds were confirmed by Dueck and Morand (238a) in Ontario, Canada.

We (508, 511) discovered that *E. amylovora* may live for long periods as residents in or on apparently healthy pear and apple tissues without producing blight symptoms. Bacteria were isolated from symptomless (1) side shoots developing from axillary buds below the base of cankers on apple and pear trees in the greenhouse, (2) suckers on blighted Bartlett trees in the field, and (3) dormant branches of three other *P. communis* cultivars without records of visible fire blight. All cultures of *E. amylovora* proved virulent upon reinoculation into young shoots of Bartlett trees in the greenhouse. *E. amylovora* also has been recovered after more than 70 days from symptomless stems of apple seedlings in Great Britain (575).

In California, Miller and Schroth (653, 654) and Miller et al. (655) developed a selective medium for *E. amylovora* in order to monitor the epiphytic populations on insects and pear tissues. They have shown conclusively that the blight organism can live as an epiphyte on flowers, fruits, and leaves of apparently healthy pear trees, as well as on the surface of inactive cankers and on *Pegomya* and *Minettia* insect species. The epiphytic population varied among orchards and trees and was detected from 2 to 4 weeks prior to the appearance of any blight symptoms.

Studies have revealed through use of the scanning electron microscope and photography the actual presence of *E. amylovora* on leaf and blossom surfaces of pear and apple. In Michigan, Sobiczewski and Klos (881a, 881b) showed that apple leaf wounds afforded both entry points and protective covers for the blight bacteria following artificial inoculation (fig. 17, A and B). Pear blossoms held at 25° C (77° F) had the greatest increase of *E. amylovora* population after 48 hours when epiphytic microflora became evident. At 10° (50°) and 15° (59°), population increase was slower and survival time longer (881b).

Natural epiphytic populations of *E. amylovora* on shoots, leaves, and buds were detected in the early 1970's in Michigan (915a) and Ontario (238a). However, the blight pathogen usually was seen only at the time of symptom initiation or following visible blight in the orchard. Monitoring during the 1973 growing season in Michigan showed that bacteria first appeared in late bloom (538). Under these conditions the prediction of blight epidemics would be impossible. However, an improved monitoring

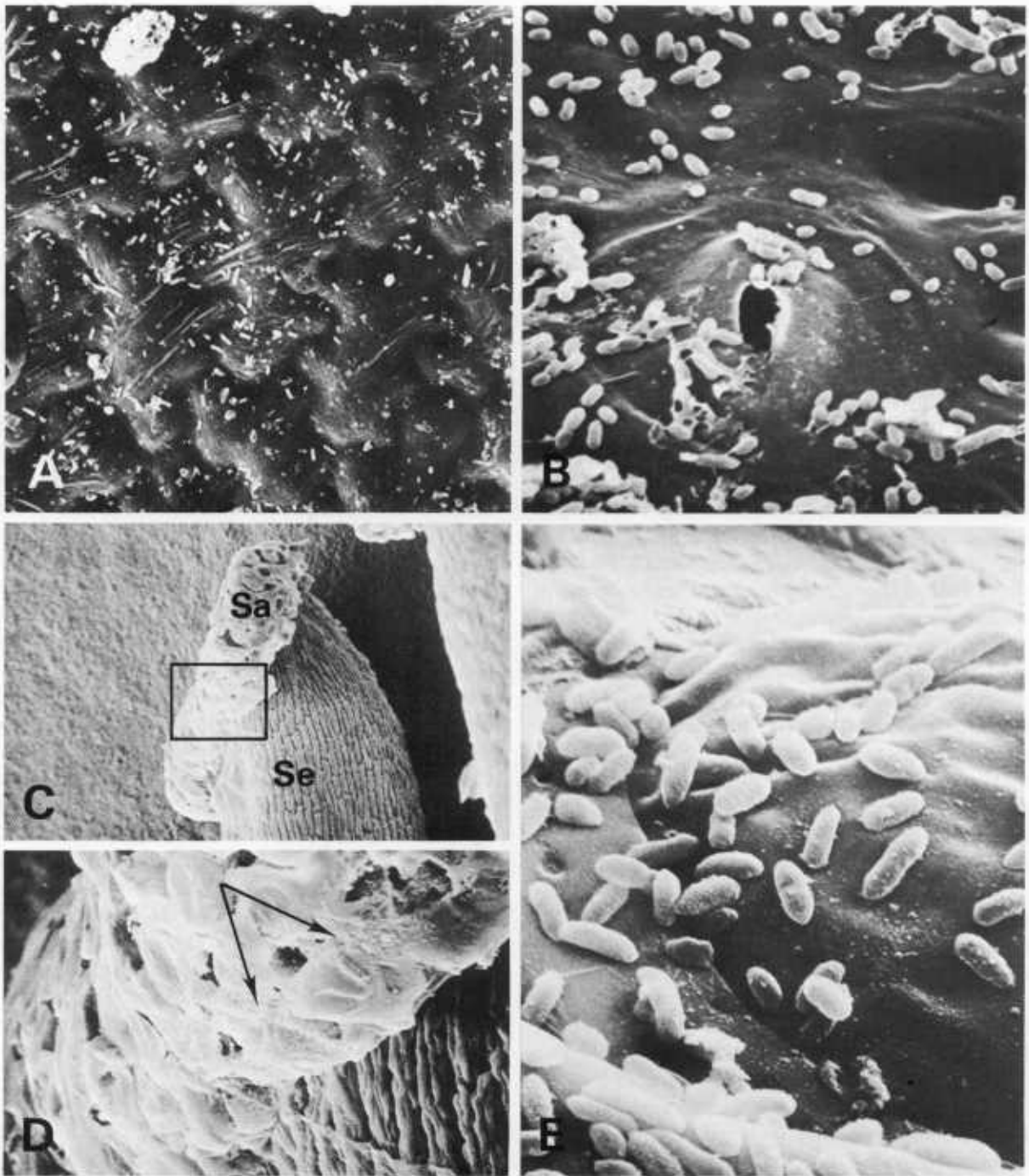
technique possibly could be used to advantage in a pest management program such as is employed in California.

In California, Thomson ¹¹ studied the epiphytic colonization of pear flowers collected from the field and found *E. amylovora* to be present almost exclusively on the stigmatic surface of the pistil (fig. 17, C and D). Under high magnification ($\times 15,000$), numerous bacterial cells, some dividing, were readily visible (fig. 17, E). He reported no sign of blight infection even though bacterial populations sometimes exceeded 10^6 cells per healthy pistil. In 1975 only 23 percent of Bartlett pear flowers that were open for 1 day were colonized with *E. amylovora*, whereas 70 and 100 percent of the flowers open for 3 and 5 days, respectively, were colonized. All of the flowers open for 7 days (petal fall) and 89 percent of the young fruits were colonized epiphytically. Thomson et al. (951a) suggested that this random occurrence was congruous with insect dissemination of the bacterium. Simulated rain in the field caused movement of *E. amylovora* from the stigmatic surface to other flower parts but without a resultant increase in infections (948a). Through the use of the immunofluorescent staining technique, Thomson and Schroth (948b) demonstrated epiphytic *E. amylovora* in pear blossoms in 3–4 hours, compared to 3–4 days with the Miller-Schroth selective medium. In pear orchards monitored during 1972–76, Zoller and Sisevich (1046d) determined that at least 110 degree hours above 18.3° C (65° F) were necessary before blossom populations developed to the point of epidemic blight.

In New York, Beer and Norelli (81a) studied inoculated blossoms on potted pears at various temperatures. They found that the time required for development of fire blight symptoms was negatively correlated with temperature and inoculum dose. The amount of infection was proportional to the inoculum dose but independent of incubation temperature and pear cultivar with an inoculum dose of about 10^4 cells per blossom. However, incubation temperature was positively correlated with a dose of 10^2 cells per blossom.

In the mid-1970's, Ritchie and Klos (795b) were the first to report the isolation of *E. amylovora* bacteriophage in aerial parts of apple and pear trees. In what numbers these phages are generally present and what role they have in nature and in the fire blight syndrome have yet to be determined.

¹¹ Pers. commun., Dept. Plant Path., Univ. Calif., Berkeley.



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FIGURE 17. —Scanning electron micrographs of apple and pear, showing presence of epiphytic *Erwinia amylovora*: A, Bacterial cells on upper surface of apple leaf 48 hours after inoculation ($\times 900$) (after Sobiczewski and Klos, 881a and 881b); B, bacterial cells on lower surface of apple leaf ($\times 5,000$); note size of bacteria in relation to stomatal pore (after Sobiczewski and Klos, 881a and 881b); C, pistil of Bartlett pear flower from field, showing terminal part of style (Se) and stigma (Sa) ($\times 150$); D, part of pistil shown in C with bacterial cells (arrows) evident only on stigma ($\times 250$); E, magnified part of stigma shown in D with individual bacterial cells ($\times 15,000$); note some cells undergoing binary fission. (C, D, and E, Courtesy S. V. Thomson, Dept. Plant Path., Univ. Calif., Berkeley.)

We consider that these facts and observations support the argument that the presence of resident epiphytic bacteria in and on the host tissues may be the most significant segment of the life cycle of *E. amylovora*. Even though epiphytic populations of *E. amylovora* may vary between trees and orchards, the resident bacteria afford a logical explanation for blight epidemics in new orchards without any oozing cankers or any previous record of fire blight (362, 1066).

Secondary Infection

Once primary infection occurs and the disease is advancing through the tissues, secondary infections may continue throughout the growing season. Sources of inoculum may be bacterial ooze or strands produced on shoots, leaves, fruit, or larger branches. They can be disseminated by rain, wind, insects, or birds. In addition, man may also spread the pathogen by means of contaminated pruning tools. The secondary infections are usually far more numerous than the primary ones and generally cause serious injury to the trees.

When leaves and succulent shoots become infected, the fire blight bacteria may enter host tissues directly or through wounds. Lewis and Goodman (582, 583) showed that the bacterium can enter through excretory glandular trichomes and hydathodes on the upper surface of Jonathan apple leaves and through lenticels on the stem. They stated that once the pathogen entered the leaf, it migrated rapidly in the stem via the phloem.

Numerous experiments and field observations also indicated that wounds offer definite avenues for the bacterium to enter the host. Types of injuries vary from small insect punctures and stem abrasions to large wounds caused by severe wind or hail. Young pear fruit especially is susceptible to blight infection during hailstorms (see chap. 11).

Secondary cycles may continue throughout the remainder of the growing season and each infection may terminate as a small or large canker.

Toward the end of the growing season the bacteria remain abundant in the edge of advancing infection, but as soon as the bark tissues die, most of the bacteria die also. Progress of the bacteria slows down and usually ceases with the formation of a crevice at the edge of the invaded tissue. Sometimes brown streaks may be found in the live bark tissue beyond the crevice. In these tissues the bacteria may be abundant throughout the following winter

and spring, and thus the life cycle of *E. amylovora* is concluded.

Dissemination

Dissemination of the fire blight organism is essential for distributing the pathogen and completing the disease cycle. *E. amylovora* is usually spread by rain, wind, insects, birds, or man.

Rain and Wind

Of the meteoric conditions, rain is probably the major factor in disseminating the pathogen from holdover or fresh inoculum (360, 516, 651). Gossard and Walton (360, 361) were the first to emphasize the importance of rain drip and windblown rain as a means of disseminating secondary inoculum, but they did not appreciate its possible significance in primary infection. They proved conclusively the effectiveness of rain in spreading the bacteria from blossom to blossom. Proof of the significance of water in primary infection was demonstrated by Brooks (114, 1086), Miller (651), Tullis (961, 1138), and Keitt et al. (516). They maintained that the greater part of primary infection resulted from inoculum that was rain splashed or blown from hold-over cankers to blossoms.

In a 3-year study on apples, Miller (651) showed that if a source of inoculum was present in the upper part of a tree, the area of secondary infection below it was cone shaped, caused by the downward spread of bacteria by spattering rain. Such a pattern would not result when blight inoculum was randomly spread by bees. On the other hand, Pierstorff (742, 1123) and Parker (722, 1122) concluded that meteoric water did not appear to spread the bacterium from flower to flower. They stated that the bacteria were spread by wind and rain throughout the orchard, no matter what their source, landing in many sites, some favorable and some unfavorable for infection. The favorable sites were usually those with young actively growing tissues.

Indirect effects of rainfall on the epidemiology of fire blight have also been reported. Thomas and Ark (935) and Ivanoff and Keitt (465, 515) pointed out that during dry weather the nectar in blossoms was too concentrated for bacterial growth, but rain diluted the nectar so that bacteria multiplied and caused more infection. In Arkansas, Shaw (860) demonstrated that apple and pear shoots were more susceptible during wet weather because of increased intercellular humidity, which favored infection and disease development.

Since the earliest observation by Stevens et al. (898) that wind was important in spreading the bacterium, many observers have noted that fire blight seems to spread in the direction of prevailing winds. In Iowa, Bauske (71, 73) studied in detail the wind dissemination of *E. amylovora*. He observed a relationship between the severity of blight epiphytotics in nursery rows and the exposure of pear trees to prevailing southerly winds, and he noted that spread of fire blight was sharply reduced through using wind barriers in the rows. He reported that water droplets containing the bacteria were easily transferred distances of up to 1 meter at a wind velocity near 14 miles per hour (22 km/h). Pear foliage injured by wind also facilitated infection (1083). Boyd (1085) determined that southerly winds were most frequent during May, June, and July in areas of southwest Iowa, when fire blight developed rapidly on pear and apple nursery trees.

Nearly identical observations were made in England by Glasscock (329, 330), where blight epidemics occurred on apples following a hailstorm with strong northwesterly winds from the direction of diseased hawthorn hedges. In one orchard with more than 700 infected trees, strong northwest winds accompanied by light hail occurred in July 1969, blowing from the direction of three hawthorn hedges suspected as sources of blight. Humid weather with temperatures of 22°–25° C (72°–77° F) followed the hail and continued until the blight symptoms were first noticed. In all cases, infection started in young succulent shoots. The highest number of shoot infections (90–140) was observed in trees nearest the infected hawthorn hedges. This number rapidly decreased to only a few infections a short distance away. We have made similar observations in our extensive pear cultivar and seedling plantings in Maryland after severe summer rainstorms without any hail.

With wind dissemination, the organism is usually carried in drops of dew or rainwater. However, *E. amylovora* may be produced as bacterial strands (72, 464, 509, 512), which can be blown for long distances by the wind. Strands have been reported in apple orchards in Illinois by Powell,¹² on pear in Washington (885), and on hawthorn in Great Britain and in the Netherlands (89, 254, 256, 637, 638) (fig. 7). They have been found on leaves, stems, fruit, and even in the spring on overwintered cankers. Strands vary from a fraction of a millimeter to several cen-

timeters in length and normally from 6 μ m to 35 μ m in width. Short, thick (100 μ m–300 μ m) strands have also been observed (fig. 7, D). Short fragments of strands, less than 1 mm long, are not too noticeable with the unaided eye but are readily seen with magnification. Bacterial strands are thought to be either wafted into wind currents and transported in the dry state over long distances or carried upward by wind currents into nearby clouds where they are dispersed in moisture and subsequently fall in raindrops at a distant location.

In Great Britain, Southy and Harper (883) demonstrated the survival of *E. amylovora* on small airborne particles in the laboratory at relative humidities between 40 and 90 percent. Significant numbers of organisms were viable after 2 hours' exposure to the open air. In preliminary wind-tunnel dissemination studies at East Malling, strands were produced over a range of constant environmental conditions when plants were incubated in a constant airflow of 0.78 meter per second, but their integrity was lost under constant humidity (254). When plants with strands were exposed to bursts of turbulent wind at 12.5 meters per second, 3 shoot infections were observed on a total of 30 target shoots.

Insects

In general, insects are probably the most important agents for spreading the blight pathogen. Since 1891, when Waite (986) first observed that bees and wasps spread the bacteria from flower to flower, these pollinating insects are frequently considered the main disseminators of the pathogen. After reviewing the extensive fire blight literature, however, we concluded that bees have a role in dissemination but not to the extent generally believed during the 1920's. Numerous observations and experiments since then revealed that (1) pollinating insects rarely were seen in contact with ooze produced by overwintering cankers; (2) flies, ants, and other crawling insects were frequently found in contact with or feeding on ooze; and (3) bees may be instrumental in disseminating the blight pathogen from flower to flower.

During this literature review we have listed the insects reportedly associated with the dissemination of fire blight (table 7). They represent 77 genera.

During the 1930's the role of bees in disseminating fire blight became extremely controversial. Many investigators were convinced that bees spread the organism from blighted to healthy flowers (358, 369,

¹² Pers. commun., Hort. Field Lab., Univ. Ill., Urbana.

TABLE 7.—*Insects associated with dissemination of fire blight*

Scientific name ¹	Common name	Host ²	Location	Reference
<i>Acalymma</i> spp. (as subgenus <i>Diabrotica</i>).	Cucumber beetles-----	Pear (b, s)---	Calif.-----	483
* <i>Adelphocoris rapidus</i> (Say)-----	Rapid plant bug-----	Apple (s)----	Mich., N.Y., Ohio -	358, 361, 905, 961
* <i>Alsophila pometaria</i> (Harris)-----	Fall cankerworm-----	Pear-----	Calif.-----	483
<i>Andrena varians</i> (Rossi)-----	-----	Pear (b)-----	Gt. Brit.-----	271
<i>Anthrenus</i> sp.-----	Dermestid beetle-----	Apple (b)----	Gt. Brit.-----	271
<i>Aphis mali</i> F.-----	-----	Pear (b)-----	Calif.-----	934
* <i>Aphis pomi</i> DeGeer-----	Apple aphid-----	Apple-----	Ontario-----	484
		Pear (s)-----	Calif., N.Y.-----	481, 483, 722, 901, 1018
		Apple (s)----	Kans., Mich., Ohio, Wis.	114, 128, 358, 361, 961
		ELR-----	Mo.-----	749, 750, 1121, 1124
<i>Aphis</i> sp.-----	Aphid-----	Pear (b)-----	Calif., Ohio, Gt. Brit.	271, 358, 934
	Green apple aphid-----	Apple (b, s)-	Kans., Mich., Mont., Ontario.	485, 641-643, 919, 920, 961
* <i>Apis mellifera</i> L.-----	Honey bee-----	Pear (b)-----	Calif., N.Y., Wis., Gt. Brit., Ontario.	40, 271, 357, 417, 426, 483, 515, 628, 644, 805-808, 939
		ELR-----	East Germany-----	82a
* <i>Attagenus megatoma</i> (F.) (as <i>A. piceus</i>).	Black carpet beetle-----	Pear (b)-----	Calif.-----	934
<i>Bibio albipennis</i> Say-----	March fly-----	----do-----	N.Y.-----	722
<i>Bombus hortorum</i> (L.)-----	Bumblebee-----	----do-----	Gt. Brit.-----	271
<i>Bombus terrestris</i> (L.)-----	-----do-----	----do-----	Gt. Brit.-----	271
Bombyliidae-----	Bee fly-----	----do-----	Calif.-----	483
* <i>Byrobia rubrioculus</i> (Scheut.) (as <i>B. arborea</i>).	Brown mite-----	ELR-----	Ohio-----	361
<i>Campylomma verbasci</i> (Meyer)----	Mirid-----	Apple (s)----	Mich., N.Y., Ohio -	358, 361, 579, 901, 902, 905, 961
* <i>Chlamydatus associatus</i> (Uhler).	Ragweed plant bug-----	----do-----	N.Y.-----	902
<i>Cosmopepla bimaculata</i> (Thomas) (as <i>C. carnifex</i>).	Pentatomid-----	----do-----	N.Y.-----	902
<i>Cynomyopsis cadaverina</i> (R.D.) (as <i>Cynomyia cadaverina</i>).	Fly-----	Pear (s)-----	N.Y.-----	722
<i>Dasyneura crataegi</i> Winn.-----	Gall midge-----	Haw-thorn (s).	Denmark-----	952
<i>Diabrotica soror</i> LeConte-----	Beetle-----	Pear (b)-----	Calif.-----	934
<i>Didea</i> sp.-----	Syrphid larva-----	ELR-----	Ohio-----	361
<i>Drosophila funebris</i> (F.)-----	Vinegar fly-----	Pear (s)-----	N.Y.-----	722
<i>Drosophila melanogaster</i> Mg.-----	-----do-----	ELR-----	Calif.-----	40
* <i>Dysaphis plantaginea</i> (Pass.) (as <i>Anuraphis roseus</i> and <i>Aphis sorbi</i>).	Rosy apple aphid-----	Apple (s)----	Mich., Ohio-----	361, 961
* <i>Edwardsiana rosae</i> (L.)-----	Rose leafhopper-----	Apple-----	N.Y.-----	901, 902
Elateridae-----	Click beetles-----	Pear (s)-----	Calif.-----	483
* <i>Empoasca fabae</i> (Harris) (as <i>E. mali</i>).	Potato leafhopper-----	Apple (s)----	Mich., N.Y., Ohio, Wis.	128, 358, 361, 901, 902, 906, 961
<i>Empoasca</i> sp.-----	Leafhopper-----	----do-----	Wis.-----	114
* <i>Eriosoma lanigerum</i> (Hausm.) (as <i>E. lanigera</i> and <i>Schizoneura lanigera</i>).	Woolly apple aphid-----	----do-----	Ohio, Pa., Ontario -	361, 485, 486, 714
* <i>Eristalis tenax</i> (L.)-----	Drone fly-----	Pear (b)-----	Gt. Brit.-----	271
		Apple (b)----	Gt. Brit.-----	271

See footnotes at end of table.

TABLE 7.—*Insects associated with dissemination of fire blight*—Continued

Scientific name ¹	Common name	Host ²	Location	Reference
* <i>Formica fusca</i> L.-----	Silky ant-----	Pear (s)-----	N.Y.-----	722
<i>Formica pallidefulva</i> <i>nitidiventris</i> Emery (as <i>F.</i> <i>pallidi-fulva</i> subsp. <i>schanfussi</i> var. <i>incerta</i>).	Ant-----	----do-----	N.Y.-----	722
<i>Formica</i> sp.-----	-----do-----	Pear (b)-----	Calif., Ohio-----	358, 483, 722, 934
		Apple (b)---	Calif.-----	483
<i>Glischrochilus fasciatus</i> (Oliv.)----	Sap beetle-----	Pear (s)-----	N.Y.-----	722
* <i>Hemerocampa leucostigma</i> (J. E. Sm.).	Whitemarked tussock moth.	Pear (b, s)---	Calif.-----	483
<i>Heterocordylus malinus</i> Reuter----	True bug-----	Apple (s)-----	N.Y.-----	905
* <i>Hippodamia convergens</i> Guer.----	Convergent lady beetle---	Pear (b)-----	Calif.-----	934
<i>Homoneura bispina</i> (Lw.) (as <i>Sapromyza bispina</i>).	Fly-----	Apple (s)-----	N.Y.-----	906
* <i>Hoplocampa testudinea</i> (Klug)----	European apple sawfly----	Pear (b)-----	Gt. Brit.-----	271
		Apple (b)---	Gt. Brit.-----	271
* <i>Hylemya antiqua</i> (Mg.) (as <i>Helemymia antiqua</i>).	Onion maggot-----	Pear (s)-----	N.Y.-----	722
<i>Ilnacora malina</i> (Uhler)-----	True bug-----	Apple (s)-----	Ohio-----	361
* <i>Lasius alienus</i> (Foerst.) (as <i>L. niger</i> var. <i>americanus</i>).	Cornfield ant-----	Pear (b)-----	N.Y.-----	722
* <i>Laspeyresia pomonella</i> (L.) (as <i>Carpocapsa pomonella</i>).	Codling moth-----	Pear (b, s)---	Calif.-----	483
		Apple (b, s)-	Calif.-----	934
<i>Lithophane</i> sp.-----	Fruitworm-----	Pear (b, s)---	Calif.-----	483
<i>Lucilia</i> sp.-----	Blow fly-----	Apple (b)---	Gt. Brit.-----	271
<i>Lygidia mendax</i> Reuter-----	True bug-----	Apple (s)-----	N.Y.-----	905
<i>Lygocoris invitus</i> (Say) (as <i>Lygus invitus</i>).	-----do-----	Pear (f)-----	N.Y.-----	905
<i>Lygocoris pabulinus</i> (L.)-----	Common green capsid----	Pear (s)-----	Gt. Brit.-----	271
* <i>Lygus elisus</i> Van Duzee-----	-----	Pear (f)-----	Colo.-----	1134a
* <i>Lygus lineolaris</i> (P. de B.) (as <i>L. pratensis</i> (L.)).	Tarnished plant bug-----	Pear (b, s)---	N.Y., Ohio-----	358, 481, 902
		Pear (s)-----	Calif., Mich., N.Y.	905, 906, 934
		Apple (s)-----	N.Y., Ohio-----	358, 361, 901, 902, 961
		----do-----	Ohio, Wis.-----	114, 128, 358
* <i>Macrosiphum avenae</i> (F.) (as <i>Aphis avenae</i>).	English grain aphid-----	-----do-----	Ohio, Wis.-----	114, 128, 358
* <i>Macrosiphum avenae</i> (F.) (as <i>Siphocoryne avenae</i>).	-----do-----	Apple-----	N.Y.-----	902
<i>Melanotrichus flavosparsus</i> (Sahlb.) (as <i>Orthotylus</i> <i>flavosparsus</i>).	Mirid-----	Apple (s)-----	Mich., N.Y., Ohio -	358, 361, 902, 905, 961
* <i>Melanotus oregonensis</i> (LeConte).	Oregon wireworm-----	Apple (b, s) --	Calif.-----	934
		Pear (b, s)---	Calif.-----	934
<i>Meligethes</i> sp.-----	Sap beetle-----	Pear (b)-----	Gt. Brit.-----	271
<i>Minettia</i> sp.-----	Fly-----	ELR-----	Calif.-----	654
* <i>Musca domestica</i> L.-----	House fly-----	Apple-----	Quebec-----	767
		Pear-----	Calif.-----	40
		ELR-----	Calif., Ohio, Ontario.	40, 358, 483, 484
<i>Musca</i> sp.-----	Fly-----	Pear (b, s, f)	Calif., N.Y., Ontario.	483, 486, 722, 934
		Apple-----	N.Y.-----	905
<i>Muscina assimilis</i> (Fall.)-----	Root maggot-----	Pear-----	N.Y.-----	722
* <i>Muscina stabulans</i> (Fall.)-----	False stable fly-----	----do-----	N.Y.-----	722
<i>Nabis ferus</i> (L.) (as <i>Reduviolus ferus</i>).	True bug-----	Apple-----	N.Y.-----	901, 902

See footnotes at end of table.

TABLE 7.—*Insects associated with dissemination of fire blight*—Continued

Scientific name ¹	Common name	Host ²	Location	Reference
<i>Neosciasia</i> sp.-----	Syrphid fly-----	Pear (b)-----	Calif., Gt. Brit.-----	271, 483
<i>Orsodacne atra</i> (Ahrens)-----	Chrysomelid beetle-----	-----do-----	Calif.-----	934
<i>Orthotylus marginalis</i> Reut.-----	Dark green apple capsid--	Pear (s)-----	Gt. Brit.-----	271
* <i>Paleacrita vernata</i> (Peck)-----	Spring cankerworm-----	Pear (b, s)---	Calif.-----	483
* <i>Panonychus ulmi</i> (Koch)-----	European red mite-----	-----do-----	Ohio-----	361
<i>Pegomya lipsia</i> (Walker) (as <i>Helemya lipsia</i>).	Fly-----	Pear (s)-----	N. Y.-----	722
<i>Pegomya</i> sp. (as <i>P. calyptrata</i>).	-----do-----	-----do-----	N. Y.-----	722
Pentatomidae-----	Stink bugs-----	ELR-----	Calif.-----	654
<i>Phaenicia sericata</i> (Mg.) (as <i>Lucilia sericata</i>).	Blow fly-----	Pear (b, s)---	Calif.-----	483
<i>Phaonia variegata</i> (Mg.)-----	Muscid fly-----	ELR-----	Calif.-----	40
* <i>Philaenus spumarius</i> (L.)-----	Meadow spittlebug-----	Pear-----	Gt. Brit.-----	270
<i>Plagiognathus politus</i> Uhler-----	Mirid-----	Pear (s)-----	Gt. Brit.-----	271
<i>Polistes</i> sp.-----	Paper wasp-----	Apple (s)---	Mich., N. Y.-----	901, 902, 906, 961
* <i>Pollenia rudis</i> (F.)-----	Cluster fly-----	Apple (b, s)---	Calif.-----	934
<i>Polymerus basalis</i> (Reuter) (as <i>Poeciloscytus basalis</i>).	-----do-----	Pear (b, s)---	Calif.-----	934
<i>Prenolepis imparis</i> (Say)-----	Ant-----	Apple, pear, quince.	N. Y., Quebec-----	767, 906
* <i>Psylla pyricola</i> Foerst. (as <i>P. simulans</i> Foerst.).	Pear psylla-----	Apple (s)---	Mich., N. Y., Ohio -	358, 905, 961
<i>Rhopalosiphum</i> sp. (as <i>R. prunifolium</i>).	Aphid-----	-----do-----	Calif.-----	934
<i>Rhynchaenus canus</i> Horn (as <i>Orchestes canus</i>).	Apple flea weevil-----	Pear (s)-----	N. Y., Gt. Brit.,	271, 481, 906
* <i>Rhynchaenus pallicornis</i> (Say) (as <i>Orchestes</i> <i>pallicornis</i>).	-----do-----	Apple (s)-----	Ontario.	
<i>Scaphytopius acutus</i> (Say) (as <i>Platymetopius acutus</i>).	Leafhopper-----	ELR-----	Ontario-----	1024
<i>Scatophaga stercoraria</i> (L.) (as <i>Scopeuma stercorarium</i> (L.)).	Anthomyiid fly-----	Apple (s)---	Ohio-----	361
* <i>Scolytus rugulosus</i> (Ratz.) (as <i>Ecoptogaster rugulosus</i>).	Shothole borer-----	-----do-----	Ohio-----	358
<i>Sephena cinerea</i> Kirkaldy-----	Slate gray plant hopper--	-----do-----	-----do-----	358, 361
* <i>Stictocephala bupalus</i> (F.)-----	Buffalo treehopper-----	Apple-----	N. Y.-----	901, 902
<i>Sylvicola fenestralis</i> (Scopoli) (as <i>Anisopus fenestralis</i>).	False crane fly-----	Pear (b)-----	Gt. Brit.-----	271
* <i>Tachypterellus quadrigibbus</i> (Say) (as <i>Anthonomus</i> <i>quadrigibbus</i>).	Apple curculio-----	Apple (s)---	Mich.-----	961
<i>Taedia colon</i> (Say) (as <i>Paracalocoris colon</i>).	True bug-----	Apple (s)---	Mich.-----	961
<i>Taeniocampa hibisci</i> Guenee (as <i>Orthosia hibisci</i>).	Fruitworm-----	ELR-----	Ohio-----	361
* <i>Taeniothrips inconsequens</i> (Unzel).	Pear thrips-----	Apple (s)---	Ohio-----	361
<i>Tetranychus</i> sp.-----	Spider mite-----	Pear (b, s, f)	Calif.-----	483

See footnotes at end of table.

TABLE 7.—*Insects associated with dissemination of fire blight*—Continued

Scientific name ¹	Common name	Host ²	Location	Reference
<i>Vespa</i> sp. -----	Wasp -----	Apple (b, s)-	Calif.-----	934
		Pear (b, s)---	Ontario-----	486

¹Scientific insect names were verified by the Systematic Entomology Laboratory, Agricultural Research Service. Names with an asterisk (*) are in the list of "Common Names of Insects Approved by the Entomological Society of America," December 1970. Names originally used in the literature are in parentheses.

²Recordings include experimental laboratory research (ELR) and host observations with special emphasis on blossom (b), shoot (s), or fruit (f).

427, 483, 515, 628, 743, 745, 806–808, 867, 939), whereas others disagreed with this view (212, 644, 734, 743, 801a). The latter were mainly those whose livelihood depended on bees. Since apparently healthy flowers may harbor fire blight bacteria, we believe that bees may also be instrumental in disseminating the pathogen from "infested" but apparently healthy flowers to healthy flowers. The extent of this spread depends largely on environmental factors that control bee activity and bacterial multiplication.

Rosen (808) reported successful isolation of *E. amylovora* from beehive material collected throughout the summer, winter, and early spring, as well as from bees taken from the hives in early spring before development of the disease. This observation was confirmed by Hildebrand and Phillips (427) by using contaminated food. This theory was opposed by Thomas and Vansell (939), Pierstorff (743), Pierstorff and Lamb (745), and Thomas and Ark (934). Gossard and Walton (361) stated that fertilized blossoms became resistant to infection sooner than did unfertilized ones. They concluded that blossoms pollinated for 72 hours were not likely to be infected and that susceptibility to infection did not exist in blossoms 144 hours after pollination. However, Miller (651) disagreed and suggested that flowers remained susceptible to infection much longer.

In contrast to Rosen's (808) findings, the longevity of *E. amylovora* in pure honey was found to range from 3 to 11 days (361, 745), but the organism could not be detected on the combs, frames, or in the honey taken from beehives 24 hours after inoculation (745). Bacteria remained viable in the viscera of honey bees for 48 hours but were not recovered from their heads 12 hours after inoculation (40). Gossard and Walton (361) reported survival of bacteria in aphid honeydew after 7 days and after 3 more days when moisture was added.

Apart from the fact that bees may carry the blight organism from flower to flower, the nectar concentration appears to be very important in that it may affect the multiplication of the bacteria deposited there. However, other factors may also limit blossom blight transmission by bees. The reports of Stewart (902) and Stewart and Leonard (906) on aphids and other sucking insects spreading fire blight have also been controversial. Many early investigators (chap. 1) considered piercing and sucking insects as important disseminating agents of fire blight. However, in thorough studies of these insects, Miller (651) and Tullis (961, 1138) concluded that aphids were rarely involved in either primary or secondary infections and therefore seemed to have a minor role in disseminating the blight organism.

In New York, Hildebrand (420), Parker (722, 1122), and Parker et al. (726) emphasized insect control as a means of effectively controlling fire blight. They claimed that aphids and leafhoppers had a relatively important role as inoculating agents of succulent terminals. In Missouri, Plurad et al. (749) proved through artificial feeding experiments that the blight pathogen could be found in the apple aphid within 5 minutes after feeding and remained there for at least 72 hours. Later they demonstrated that at least 70 bacterial cells had to be injected into the host plant for systemic infection of young apple shoots. The inability of the apple aphid to regularly introduce 70 or more cells into the host seemed to preclude its effectiveness as a vector. Similar results were reported by Thygesen et al. (952) from Denmark.

In Michigan, Jones (481) demonstrated the association of the pear psylla (*Psylla pyricola* Foerster) with fire blight infections in leaf axils and the base of flower clusters. He also noted feeding of the tarnished plant bug (*Lygus lineolaris*) on flower parts and opening buds. He confirmed observations by Stewart (901) that this insect may be important in

starting primary infections. Luepschen ¹³ mentioned that unusual occurrences of Bartlett fruit blight near harvesttime in western Colorado appeared to be associated with large populations of the tarnished plant bug on weeds under the trees. In further studies, Stahl (1134a) isolated from contaminated *Lygus* species equal numbers of *E. amylovora* from external and internal parts of the insect. He showed that these insects can successfully transmit the blight pathogen within a short time after acquiring the bacteria and suggested that they have a high potential for wounding pear fruit, which results in fruit blight if inoculum is present.

In 1965, Leonard (579) reported the first known record of *Atractotomus mali* (Meyer) in Connecticut. He considered it distinct from *A. crataegi* Knight known on hawthorn in Iowa and did not report either insect associated with fire blight. Whitcomb et al. (1019) isolated an *Erwinia*-like bacterium from internal parts of leafhoppers. Since leafhoppers have often been reported in the dissemination of fire blight, they conceivably could also harbor *E. amylovora*.

Hildebrand (420) was the only investigator to publish a series of unique cartoons depicting the life cycle of the causal organism and its dissemination by insects.

In Denmark, Bech-Andersen (77a) distinguished the following types of dissemination: (1) Short distance (0–100 m), such as rain splashing or certain insects that spread bacterial ooze from blighted hawthorns to fruit trees; (2) middle distance (100–5,000 m), accomplished by such vectors as pollinating insects between trees and nearby orchards; and (3) long distance (>5 km), most likely caused by migratory birds.

Birds

Without any experimental proof, birds have been mentioned as instrumental in disseminating fire blight (77, 369, 639, 690). Since the first outbreaks of fire blight along the coastal regions of northwestern Europe, migratory starlings were suspected as carriers of the pathogen. Reports from Kent indicated that branches were broken by large numbers of roosting birds (571). Bech-Andersen (77a) reported from Denmark in 1974 that (1) hawthorns serve as shelter and feeding places for such birds as starlings (*Sturnus vulgaris* L.) and warblers (*Phylloscopus*

trochilus (L.)); (2) viable *E. amylovora* bacteria were isolated from starling excrement and from their feet 8 days after these birds were artificially infested with the organism; and (3) starlings and warblers often complete their migration from England to Denmark in 2 to 3 days before continuing to Poland and the U.S.S.R. Considering that starlings are berry and fruit feeders and that large numbers have been observed in hawthorn shrubs and fruit orchards, these birds appear to have an important role in disseminating the blight organism.

Man

The blight pathogen may be spread by man himself on orchard equipment, fruit, and budwood. Pruning tools are the most important means of spreading bacteria from blighted to healthy branches. Pruning shears and saws used to remove blighted shoots and limbs can spread the organism if they are not properly decontaminated between cuts (507, 778, 989, 992). The organism may also be spread by hands, clothing, shoes, and wheels of orchard equipment if they have been in contact with the inoculum.

The expression “one rotten apple spoils the barrel” can certainly apply to pears in the spread of fire blight. Since internal inoculum has been reported in pear fruit, such infected fruit can be instrumental in short- or long-range dissemination of fire blight. Without definite proof, contaminated fruit boxes have been suggested as introducing the blight pathogen into Great Britain prior to the observed outbreak in 1957 (369, 571). Fire blight was first observed in a pear orchard near the farm gate where the assumed infested crates were stacked for future use.

Whether the blight organism can be transported on or in pome fruit has often been questioned. In Canada, McLarty (618) recovered viable *E. amylovora* bacteria from mature fruit of several artificially inoculated apple cultivars 5 months after ordinary storage. On the other hand, Dueck (237) found that the organism failed to survive for a 24-hour period on the surface of artificially inoculated apples. However, survival in the laboratory was excellent on the fruit surface when the bacterium was applied as natural ooze or in a water suspension.

Man may also spread the bacterium by shipping contaminated budwood, especially from trees with a history of fire blight. Many such observations have been reported, though few are documented in the

¹³ Pers. commun., Colo. Agr. Expt. Sta., Grand Junction.

literature. In Michigan, Klos¹⁴ reported a local nursery had a severe outbreak of fire blight in rootstocks budded the previous summer. In 1972, Burkowicz (124) stated that the localized occurrence of fire blight at the research station in Skierniewice,

Poland, was probably due to using imported infected propagating material.

Evidently the fire blight bacterium can be disseminated in many different ways and its movement is difficult to contain. Therefore grow resistant plant material, eliminate existing sources of infection, and apply eradivative and protective control measures as thoroughly as possible.

¹⁴ Pers. commun., Dept. Plant Path., Mich. State Univ., East Lansing.

CHAPTER 9

PATHOLOGICAL ANATOMY

In the earliest histological studies by Burrill (133) and Waite (991), slight mention was made of intercellular migration of the bacterium. Jones (484), Bachmann (55), Smith (878), Nixon (695), and Miller (651) showed that *E. amylovora*, following infection and early penetration, makes its way intercellularly by dissolving cell walls and middle lamellas. In 1927, Nixon (695) and Gibbons (1102) reported two phases in the life cycle of *E. amylovora*—the vegetative stage, including the intercellular migration in the form of zooglea, causing lysigenous cavities, and the pseudofructification stage, comprising intracellular migration with ultimately the formation of cysts in schizogenous cavities. Nixon's early drawings are in striking agreement with recent observations under the electron microscope. Similar observations were made by Haber (376) on apple leaf tissue and Wahl (985) on quince.

The most extensive histological studies on the mode of penetration and invasion of *E. amylovora* in apple and pear tissues were by Rosen (804, 816) at the University of Arkansas. He found that the nectarial tissues of apple blossoms consisted essentially of the same structures as those in pear blossoms. Also, the mode of bacterial invasion through nectarial tissue was similar in both types of flowers. However, he (816) observed the following differences in his studies:

(1) Pear blossoms, unlike apples, have a fully exposed nectarial region, forming a shallow, open, greenish, saucerlike dish. In apple blossoms the nectarial region is almost completely hidden by the enlarged, hairy base of the stamens and the funnel- or cup-shaped form.

(2) In pear blossoms the nectar forms an excellent medium for multiplication of the fire blight bacteria. Nectararhodes, free of any cuticular covering, serve as definite avenues of bacterial invasion.

(3) In apple blossoms the bacteria penetrate more frequently in stigmas, anthers, outer receptacle walls, and calyx lobes than in nectarial tissue. The outermost layer of stigma cells has no cuticle and the thin walls are easily infected by the pathogen. Open

anthers serve as excellent avenues of bacterial invasion.

(4) In both pear and apple, progressive penetration occurs in the subnectarhode chambers and stigmatic or stylar tissues mainly by means of intercellular spaces (fig. 18, *C*) and the localized dissolution of middle lamellae and delicate cell walls.

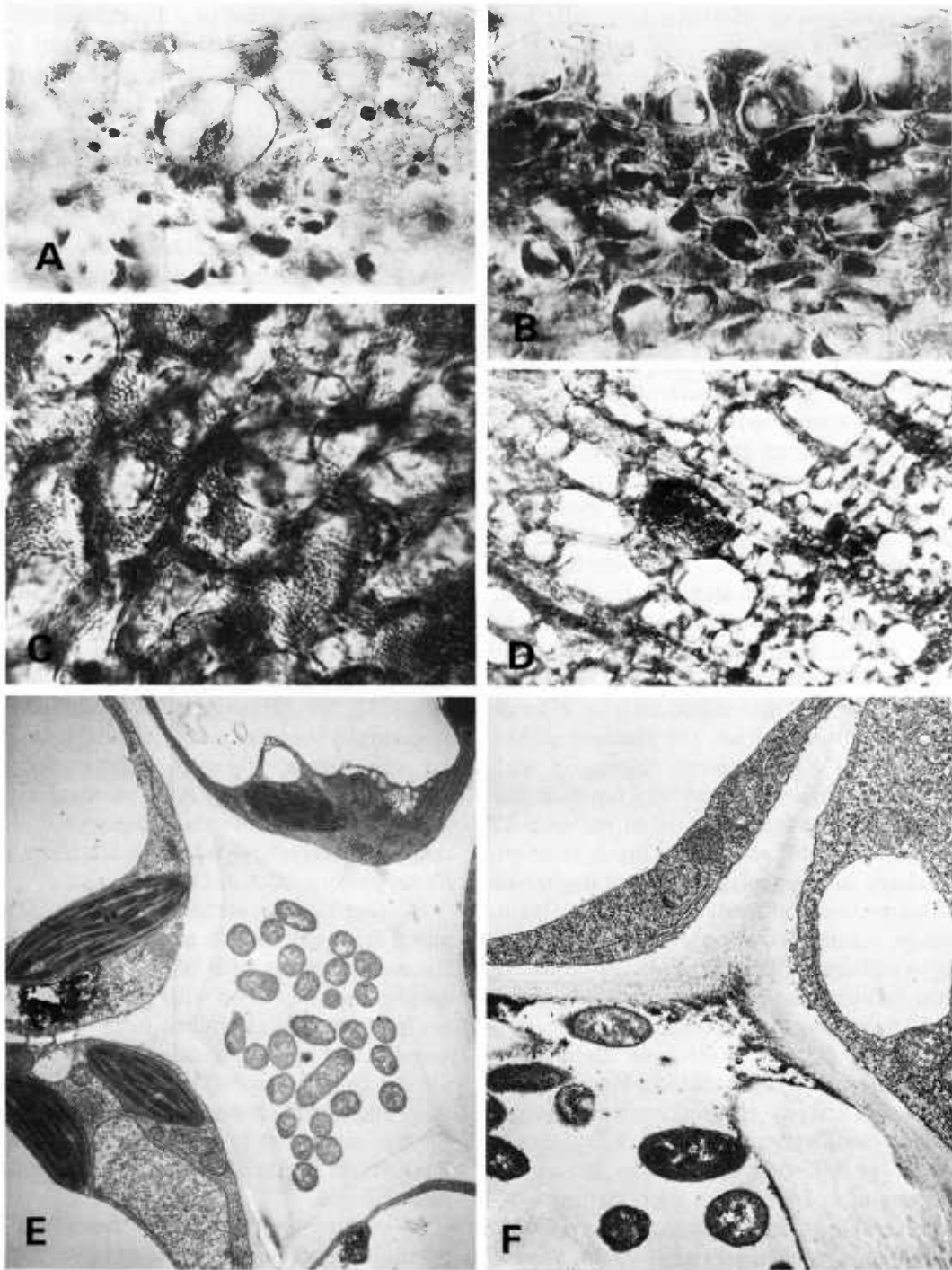
Rosen (816) illustrated these observations (fig. 18, *A* and *B*) and concluded that pear and apple flowers should be fully covered with a protective spray to control blossom blight.

Rosen (804) also made the most detailed cytological and histological study of infected pear petioles and pear and apple stems. In these tissues the cell walls of cortical tissues were noted to undergo a distinct swelling and lamellation, indicating the production of cell wall-destroying enzymes acting partly in advance of bacterial invasion.

He emphasized that cortical invasions are most common in infected stems of pear and apple but that the most serious invasions destroy the phloem and cambium. Rosen (804) published the earliest pictures of masses of *E. amylovora* bacteria in xylem vessels of apparently healthy Kieffer pear shoots (fig. 18, *D*). He also described masses of normal appearing, disintegrating, and finely granular gummy *E. amylovora* material.

Hildebrand (417) confirmed these observations on apple, pear, and quince flowers as to obtaining a more effective blossom blight control program. Greenhouse tests on dwarf pear trees showed that the blossoms were most susceptible to infection during the 2 days after opening. Hildebrand also showed details of the progressive invasion of the blight pathogen through stomata, substomatal chambers, and intercellular spaces during the first 3 days following inoculation.

In New York, Aldwinckle and Preczewski (16a) observed in many apple cultivars discolored streaks in the xylem extending in advance of externally visible lesions following artificial inoculation. They isolated pathogenic *E. amylovora* from the streaks and concluded that xylem streaking may indicate the



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FIGURE 18.— Mode of penetration and movement of *Erwinia amylovora* in pear and apple tissues: *A*, Longitudinal section of nectarial disk of Bartlett pear blossom, showing penetration of bacteria through nectarthode ($\times 950$) (after Rosen, 816); *B*, movement of bacteria from nectarthode into subnectarthodal chamber ($\times 950$) (after Rosen, 816); *C*, bacteria in intercellular spaces of Duchess pear petal ($\times 800$) (after Rosen, 804); *D*, bacteria in xylem vessel of apparently healthy Kieffer pear shoot ($\times 500$) (after Rosen, 804); *E*, presence of virulent cells in intercellular spaces of cortical tissue of apple shoot ($\times 9,000$) (after Huang, 1110); *F*, presence of virulent cells in xylem vessel of apple shoot ($\times 19,000$) (after Huang, 1110).

potential for rare severe infections in usually less susceptible apple cultivars.

Host Ultrastructure

Nearly all research on the ultrastructure of host tissues has been done at the University of Missouri. In 1968, Burkowicz and Goodman (125) reported a rapid increase in permeability of cellular membranes when immature pear fruit slices were inoculated with either virulent or avirulent strains of *E. amylovora*. However, avirulent bacteria did not spread beyond inoculated surface layers and their capacity to induce permeability changes was limited. The rate of pathological alterations in Jonathan apple leaves was correlated with the length of the bacterial generation time (126). Inoculum concentration and age of leaves were the primary factors that affected the rate and extent of the membrane permeability alterations. They concluded that the hypersensitive reaction was due to membrane damage, which permits rapid water loss from tissues, which in turn precludes the growth of bacteria in the intercellular spaces (345).

Addy and Goodman (7) and Addy (1078) found that polyphenol oxidase and peroxidase activity in apple leaves, infiltrated with either the virulent or the avirulent strain of *E. amylovora*, increased with time. Maximum difference in activity between the control and infected leaves was noted between 12 and 18 hours. Addy (6a) observed a linear relationship of leakage of electrolytes and total phenols when the leaves were infiltrated with either strain. This leakage occurred well in advance of visible browning symptoms, which were evident about 12 hours after infiltration. In California, Pitman and Cruess (748) found that *E. amylovora* had little or no pectinase activity in pectin hydrolysis studies.

Huang and Goodman (453, 454) and Huang (1110) made the most extensive electron microscopy studies on the modifications of the ultrastructure in Jonathan apples following infection by *E. amylovora*. One day after inoculation with virulent bacteria, no noticeable structural changes were found, but bacterial cells were observed in xylem vessels and in intercellular spaces (fig. 18, *E* and *F*). Two days after inoculation, ultrastructural modification included plasmolysis, aggregation of cytoplasm, disruption of chloroplast envelopes, and disorganization of lamellar structures. Virulent bacteria formed a protective layer in the host tissue, consisting of an electron-lucent zone and five filaments. They also

observed degradation of subcellular structures beyond recognition and the formation of lysigenous cavities as reported by Nixon (695) and Crosse et al. (197). In their 1976 report, Huang and Goodman (454a) concluded that ultrastructural changes induced by the fire blight toxin were much the same as those induced by the pathogen per se.

After inoculation with avirulent bacteria, Huang et al. (454b) and Huang (1110) observed the following types of host defense reactions in apple petioles: (1) Bacteria in intercellular spaces of cortical tissue were arrested and localized by the hypersensitive reaction; (2) long-distance translocation of bacteria in xylem vessels was stopped by an agglutination reaction accomplished by the aggregation of avirulent cells into clumps by host-formed granules; and (3) bacteria observed in living xylem parenchyma cells were digested within the vacuoles. These findings suggest that avirulent cells of *E. amylovora* are localized in petioles and do not translocate into stem tissue. The hypersensitive reaction of apple tissue to avirulent cells does not explain this phenomenon satisfactorily, as this reaction reportedly is a host defense mechanism that is operative only in living cells (534, 536). Huang (1110) concluded that ultrastructurally the effects of avirulent bacteria on cortical parenchyma cells were degeneration of subcellular organelles but without plasmolysis. This observation is similar to the ultrastructural modification of hypersensitive tobacco leaf tissues induced by *E. amylovora* (350, 351).

In other studies, structural protein (SP) was prepared from chloroplast membranes of tobacco leaf tissues infiltrated with 10^8 cells per milliliter of *E. amylovora* and mixed with chloroplast lipid. It did not reaggregate as well to form membrane structures similar to the original chloroplast membrane as did SP from water-infiltrated tissue. Huang et al. (449) suggested these changes may be responsible for the alteration in membrane permeability and integrity in bacterially induced hypersensitivity in plant tissues.

In studies on *Cotoneaster pannosus* Franch., Seemuller and Beer (849) concluded that cell wall degradation may not be an important factor in the development of fire blight. In Denmark, Hockenhull (428, 1107a) made a detailed anatomical study of healthy and diseased hawthorn following natural infection by *E. amylovora*. He found that the most common type of blight lesion involved the formation of a defense periderm, which isolated the diseased

tissues, causing them to shrink and dry up. Two types of cankers were distinguished, closed and open. In closed cankers, originating from shallow infections, the defense periderm formed a continuous barrier. In deeper infections in open cankers, cortical and phloem tissues are involved in the formation of the xylem or cambium, but the latter is destroyed and a typical wound healing reaction is initiated by healthy cambial cells.

Internal and Resident Bacteria

Following the initial studies by Miller (651), Nixon (695), and Rosen (804, 816) on resident fire blight bacteria in pear and apple tissues, additional research was undertaken during the 1960's on the prevalence of *E. amylovora* in these tissues and its recovery from symptomless stems and shoots on selective media. In 1963, Baldwin and Goodman (62) reported the isolation of *E. amylovora* from dormant Jonathan apple buds in Missouri. Forty percent of all isolates obtained were sensitive to one or more of the five typing phages. The 523 phage-sensitive isolates fell predominantly into 5 phage typing patterns, whereas 1 of the patterns, a combination of 2 phages isolated in England, typed 80 percent of all phage-sensitive isolates.

In morphological and anatomical studies of Jonathan apple tissues, Lewis and Goodman (582, 583) showed that hydathodes, glandular trichomes on leaves, and lenticels on the stems were natural openings for infection. They also found that the bacterium migrated very rapidly in the leaf and stem, and in the stem it moved via the phloem.

A few years later, Gowda and Goodman (363) detected the downward movement of *E. amylovora* exclusively in phloem 70 cm from inoculation in the stem apex, whereas visible disease symptoms were restricted to only 16 cm from this point. The maximum upward movement from inoculated roots into the stem was 40 cm. Such recoveries were confirmed in our studies at Beltsville with Bartlett pear and Jonathan apple, both in the greenhouse and the field (508, 511). Following surface sterilization of the shoots with 0.5 percent sodium hypochlorite, pure cultures of *E. amylovora* were obtained from sections 3 mm thick plated on nutrient-yeast-dextrose agar (fig. 12, A). The bacterium survived in both types of tissues for up to 6 months.

Figure 19 shows a comparison of the presence of *E. amylovora* in the tissues mentioned in the previous three studies. All platings were done on nutri-

ent-yeast-dextrose agar (NYDA). Lewis and Goodman (582) and Lewis (1114) spread a drop of inoculum over 6 mm of the serrated margin of uninjured upper surface of the sixth leaf from the shoot apex. Free hand sections were prepared from leaf and stem tissues, and microtome sections were made following routine histological procedures. The bacteria invaded the entire length of the shoot in approximately 7 hours, and 90 percent of the actively growing shoots developed fire blight symptoms (fig. 19, A).

Gowda and Goodman (363) and Gowda (1103) immersed about 6 cm of a decapitated root tip of a young Jonathan apple tree in a culture tube containing 5 ml of an aqueous suspension of *E. amylovora* (10^9 cells per milliliter). Two weeks after inoculation, the bacterium had spread a maximum of 40 cm into the symptomless aerial part of the shoot (fig. 19, C). Migration from the roots into aerial sections of the stem seemed to be limited to the second week following inoculation. In separate tests in which the inoculum was applied to the severed apex, typical blight symptoms were observed to a maximum length of 15–16 cm in 16 days, although bacteria had moved downward as much as 70 cm.

In our studies at Beltsville, virulent *E. amylovora* was readily isolated from the internal tissues of symptomless side shoots (75–90 cm) of Jonathan apple and Bartlett pear trees in the greenhouse (fig. 19, B). These shoots developed from axillary buds immediately below the base of the cankers when blight progress ceased (511). In addition, blight bacteria were recovered from many apparently healthy suckers on blighted Bartlett trees and from symptomless shoots of other pear cultivars in the orchard.

Covey and Fischer (184) obtained more bacteria from inoculated apple than pear shoots when sand was used to facilitate grinding of tissues. About 32 hours after injury the host-pathogen balance apparently shifted in favor of the pathogen, which then multiplied sufficiently to cause symptoms. It was of interest to note that the number of bacterial cells decreased within the first 24 hours. Similar results were reported in 1975 in recovery studies on pear blossoms in New York (81a).

Lewis and Goodman (582) reported that fire blight bacteria passed from the vein parenchyma into the petiole, where they seemed to multiply rapidly in the phloem and then moved into the xylem parenchyma, where bacteria were evident in conspicuous strands. This phenomenon was later confirmed by Crosse et

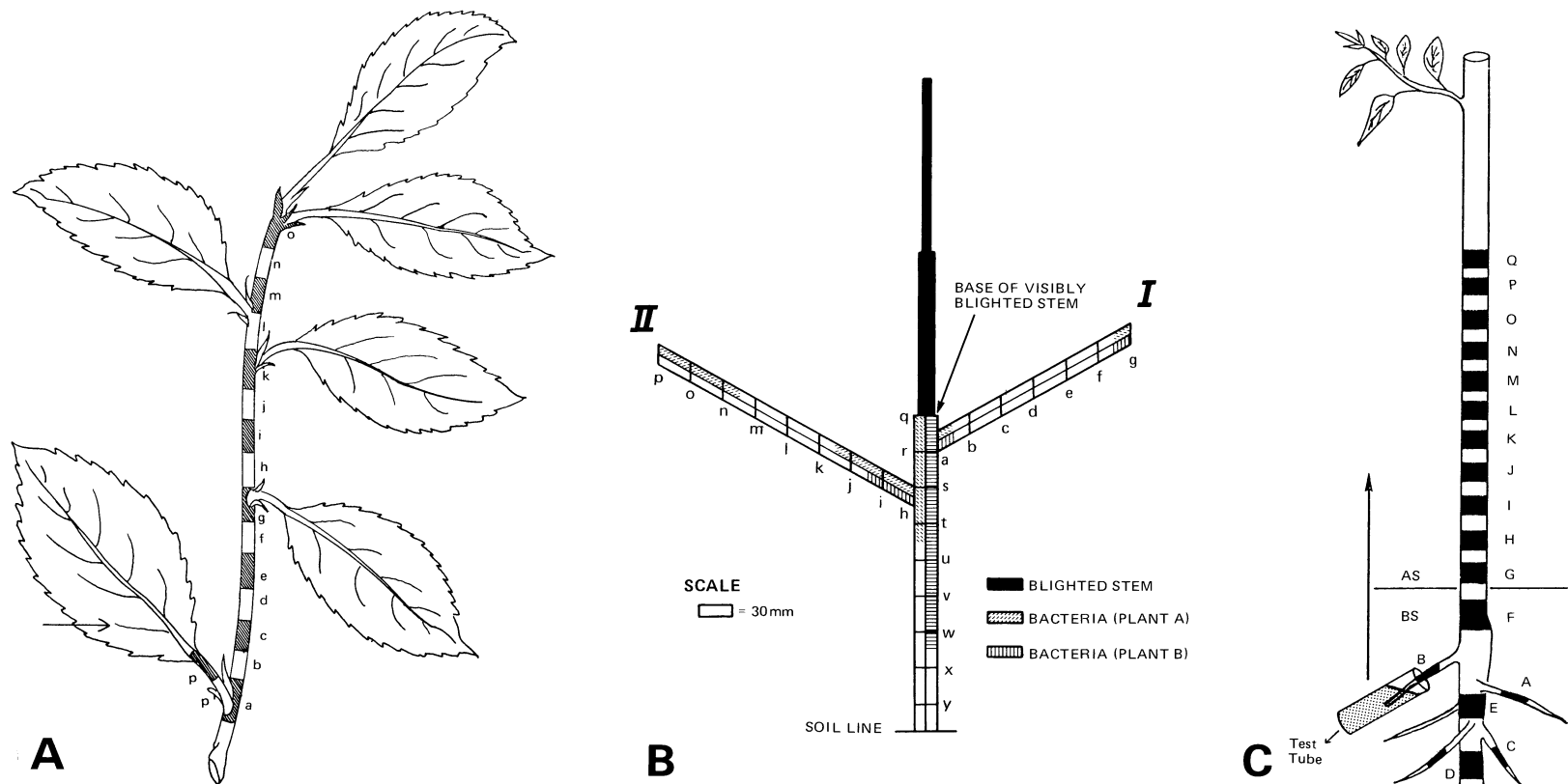


FIGURE 19.—Schematic diagrams showing movement of *Erwinia amylovora* in apparently healthy pear and apple tissues: *A*, From leaf surface through petiole and stem to shoot apex (after Lewis and Goodman, 582); *B*, from base of blighted shoot into side shoots developed from axillary buds after visible blight ceased to spread in main stem (after Keil and van der Zwet, 511); *C*, from root tip through stem into upper part of shoot (after Gowda and Goodman, 363).

al. (197). Gowda and Goodman (363) concluded that the pathogen moved downward from the stem apex via the phloem. Upward movement from the root was not determined but was believed to occur through the phloem.

In studies on overwintering of the blight pathogen inside living host tissue in Utah, Morrill (664, 1120) concluded that holdover bacteria were present in apparently healthy as well as diseased buds of apple and pear trees, pyracantha, chokecherry, and mountainash. Using a selective medium, Miller and Schroth (653, 654), Miller et al. (655), and Thomson et al. (950, 951) recovered *E. amylovora* from pear flowers in populations commonly ranging from 10^4 to 10^6 cells per flower. Up to 33 percent of the flowers were colonized by *E. amylovora* without any saprophytic bacteria, and the insects *Pegomya* sp. and *Minettia* sp. carried surface populations of blight bacteria ranging from 10^1 to 10^5 cells per insect. In Great Britain, Lelliott (575) readily recovered *E. amylovora* bacteria from symptomless stems as long as 70 days after inoculation. We emphasize again that fire blight bacteria have been isolated from dormant buds (62) and that infected buds have resulted in great losses of nursery trees (901, 999).

In 1943, Borden and Thomas (102) reported from California that Bartlett trees sprayed with a summer oil had 17 percent of the fruit infected with *E. amylovora*, whereas trees not sprayed with oil had

only 0.5 percent of the fruit infected. Moreover a shipment of apparently healthy pears, originating from orchards sprayed in the summer with oil-lead arsenate to control red spider mites, had 30–50 percent of the fruit infected when it arrived in Hawaii (972). It is possible that the oil sprays affected the epiphytic bacterial population and thus had a significant role in the spread of fire blight in these orchards. Internal fruit infections also have been observed in Great Britain (369). All reports appear to agree that the small external symptoms on the fruit surface are connected by a thin thread of infected tissue to large (up to 2 cm) pockets of infection in the center of the fruit.

We believe that there is sufficient evidence today that *E. amylovora* can enter its host through nectaries, hydathodes, lenticels, and other avenues and spread through the trees systemically as resident bacteria in or on shoots, roots, flowers, fruit, and other tissues (figs. 17–19). According to the laws of nature under which the healthy rather than the diseased state predominates, numbers of bacteria apparently remain low. Increased numbers of bacterial cells and the subsequent infection process depend on and are determined by many factors, such as degree of innate resistance, percent intercellular humidity, tree nutrition, environmental conditions, and injury caused by wind, hail, farm equipment, and so forth.

CHAPTER 10

BIOCHEMISTRY OF HOST TISSUES

Studies on the biochemical nature of pear and apple tissues in relation to fire blight resistance were started in the 1960's. Keil and Wilson (502) were the first to observe that leaf disks and stem cross sections from a blight-resistant cultivar of *Pyrus communis* L. were more inhibitory of *E. amylovora* than were comparable tissues from a susceptible cultivar. Significantly larger inhibition zones were produced by leaf disks and cross sections from Magness than from Bartlett leaves of the same age (fig. 20, A and B). Leaf ash was also demonstrated to be active, and the substances responsible for the bacterial inhibition were water soluble but insoluble in absolute methyl and ethyl alcohol.

Hildebrand and Schroth (412, 414, 415) and Hildebrand (1107) reported the first evidence of a disease-resistant compound, the glucoside 4-hydroxyphenyl beta-D-glucopyranoside (arbutin), in pear tissue, showing antibacterial activity against *E. amylovora*. This glucoside was hydrolyzed by glucosidase, splitting off the glucose and producing hydroquinone (quinol), which becomes antimicrobially active when oxidized to the semiquinone. Direct evidence for the antibacterial activity of hydroquinone was obtained by placing pear blossom sections and leaf disks on nutrient agar seeded with *E. amylovora* (fig. 20, C and D). Growth of the bacterium was not suppressed, however, near the cut end of major veins. The enzyme beta-glucosidase was also produced by *Pseudomonas syringae* in a medium containing large amounts of glucose (413).

In later tests Schroth and Hildebrand (846) found that all isolates of *P. syringae* synthesized large amounts of beta-glucosidase, whereas *E. amylovora* showed only slight activity. The maximum hydroquinone concentration in nutrient broth at which detectable growth of *E. amylovora* occurred ranged from 400 to 800 ppm, whereas *P. syringae* isolates grew at 1,200–1,800 ppm. They postulated that the low amount of beta-glucosidase in *E. amylovora* would probably not significantly affect pathogenesis in pear, but that the high amount in *P. syringae* would enable it to hydrolyze arbutin and thus possi-

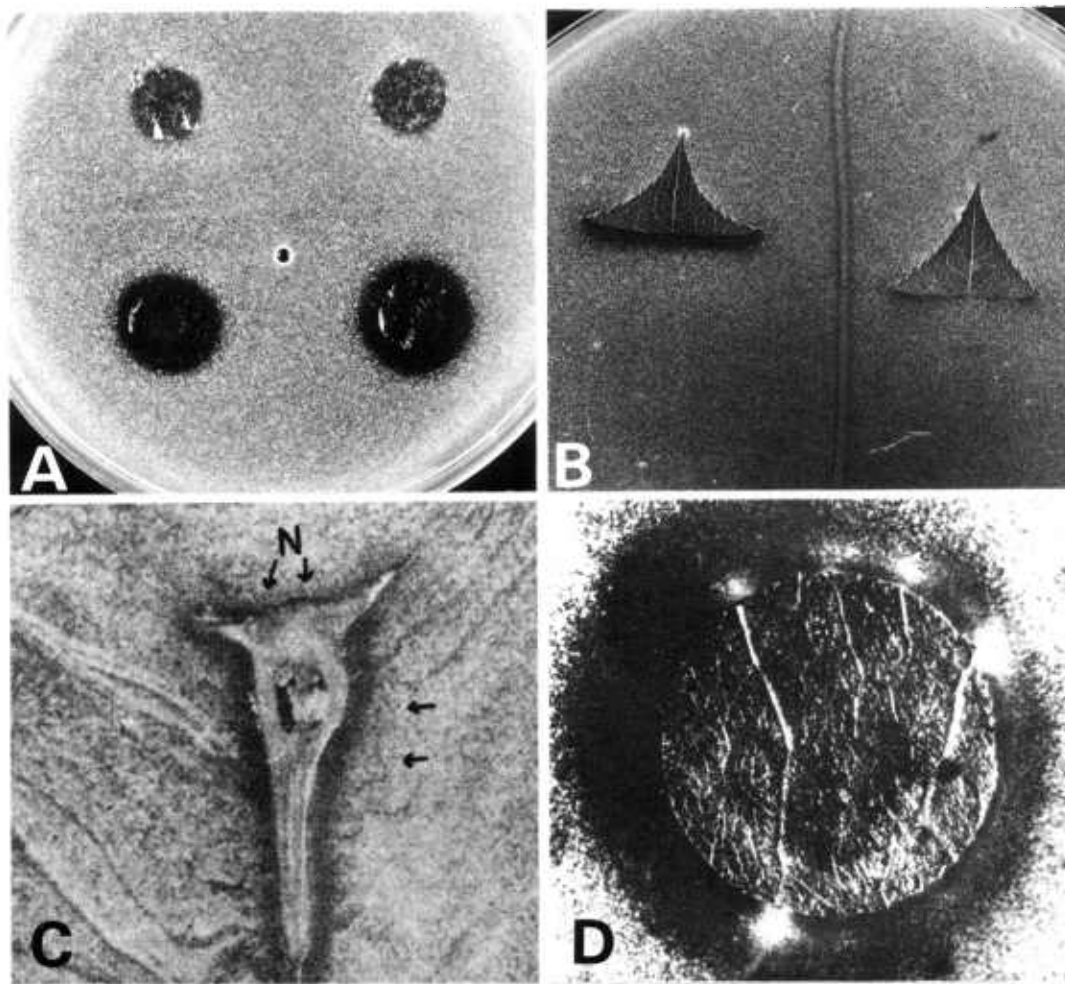
bly inhibit further advance in pear tissue (846).

A comparative study between fire blight-resistant and susceptible pear species revealed some striking differences in the arbutin-hydroquinone complex and associated enzymes in comparable tree tissues (410). A reagent composed of 0.2 percent *p*-phenylenediamine in 2 N ammonium hydroxide was used for the cytochemical demonstration of arbutin (dark blue to dark purple) in the tissues (845).

In 1967, Powell and Hildebrand (752) discovered a correlation between beta-glucosidase content of tissues and their antibiotic activity against *E. amylovora*. Nectarial tissue of the susceptible pear cultivar Forelle had a large amount of beta-glucosidase as compared with that of the resistant cultivar Old Home, but neither tissue exhibited antibiosis.

In addition, Hildebrand (480) found that aqueous extracts of pear leaf blade and woody tissues exhibited greater antibiotic activity than did extracts of petioles plus leaf midribs and bark. He noticed largest increases in antibiotic activity in extracts of tissues that showed the greatest amount of antibiosis in the tissue bioassay test. Also, arbutin was found in greater amounts in blight-resistant than in susceptible cultivars (410). The usual invasion routes of nectaries, lenticels, and cortex contained little arbutin regardless of the cultivar. From all these data it was concluded that other pathways may exist in pear leading to the formation of antibiotic substances from arbutin, including the formation of toxic substances and an interaction with the hydrolytic pathway (410, 753).

Smale and Keil (872) extensively studied the mechanism responsible for fire blight resistance in six cultivars of *P. communis*. They associated the following factors with mechanically injured leaves of highly resistant cultivars: (1) Presence of large amounts of arbutin and free hydroquinone in unaltered leaf homogenates, (2) accumulation and persistence of antibacterial concentrations of hydroquinone enzymatically released from arbutin during oxidation of leaf homogenates, and (3) disappearance of an unidentified antagonist of hydroquinone follow-



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FIGURE 20. — Bioassay of pear tissues on culture media seeded with *Erwinia amylovora*, showing varying zones of inhibition: A, Leaf disks cut from young pear leaves: Large zones from Magness and small zones from Bartlett; note disks were removed prior to photography (after Keil and Wilson, 502); B, leaf tips — left, Magness; right, Bartlett (after Keil and Wilson, 502); C, longitudinal section of pear blossom; note absence of inhibition zone around nectarial region (N) (after Hildebrand and Schroth, 412); D, leaf disk with well-defined inhibition zone except for bacterial growth near cut end of major veins ($\times 3.4$) (after Hildebrand and Schroth, 415).

ing cell disruption. They concluded that the balance between the rapid appearance and disappearance of antibacterial hydroquinone in mechanically damaged leaf tissue is a major determinant of relative blight resistance.

Preliminary studies ¹⁵ on leaves and stems of Bartlett, Magness, *Pyrus ussuriensis* 76, and *P. calleryana* cv. Bradford indicated no relationship between bioactivity and hydroquinone concentration within 36 minutes of oxidation.

Plurad (1124) sought to establish a relationship

between phloretin, the aglucon of phlorizin, and resistance of several apple cultivars to infection by *E. amylovora*. Although the level of phloretin in floral tissue was lower than that in stem tissue, comparable amounts were detected in blossoms of both resistant and susceptible cultivars. The antibacterial activity of phloretin and phlorizin was nearly comparable to that of arbutin.

Challice (151, 1092) and Challice and Westwood (154) studied in detail the genus *Pyrus* and reported no relationship between phenolic compounds in leaf and bark tissues resistant to fire blight, crown gall, and the woolly pear aphid. However, their results

¹⁵ Unpub. data, Fruit Lab., U.S. Dept. Agr., Beltsville, Md.

did indicate that under certain circumstances the phenolics may be used to differentiate between resistant and susceptible individuals.

Challice (152, 153, 1092) and Challice and Williams (156–158) reported many details on the nature of phenolic compounds in *Pyrus* species. They concluded that not all phenolics were distributed equally throughout buds, cork, green cortex, white phloem, and xylem. Some phenolics tended to be restricted to particular tissues at particular times.

In Minnesota, Ahn and Stushnoff (9) measured phenolic compounds in several apple cultivars from flowering to leaf fall and found greater amounts of catecholases and cresolases in resistant versus susceptible cultivars. They also found lower levels of enzyme and phenolic compounds in flowers than in stem tissue.

Hypersensitive Reaction

The hypersensitive reaction (HR) in plants is a resistance mechanism to pathogens that normally do not parasitize them. It is characterized by a rapid necrosis of tissue occurring usually within 24 hours after introduction of large numbers of micro-organisms into the intercellular spaces of the host (343, 411). In 1966, Klement and Goodman (534) showed that virulent strains of *E. amylovora* produced fire blight symptoms on inoculated apple shoots, whereas avirulent strains induced only small brown discolorations at the inoculation sites. Both types of bacteria started to multiply in the shoots, but the multiplication of the avirulent bacterium stopped 24 hours after infection.

Both types of *E. amylovora* and *Pseudomonas syringae* also induced the HR necrosis in tobacco leaves. Conductometric measurements of tissue leakage indicated that the two pathogens also induced significant changes in the selective permeability of the host cells (343, 535). Electron microscopy of the tobacco leaf tissue revealed a progressive degeneration of bounding membranes of chloroplasts, mitochondria, and cytosomes (351). Exposing healthy leaves to ammonia gas caused similar tissue necrosis as when inoculated with *E. amylovora* or three *Pseudomonas* species (352, 591). It was suggested that ammonia may be produced by these bacteria as a necrotoxin, which altered the tertiary structure of the membrane protein.

In studies of tobacco leaf tissue changes following the hypersensitive reaction, Huang and Goodman (445, 446) in 1970–72 reported the alteration and

reaggregation of structural protein from chloroplast membranes during development of the HR reaction. *E. amylovora* did not produce phosphatidase in vitro but did stimulate the synthesis of host phosphatidase D. Host phosphatidase activity was most stimulated by 10^6 cells per milliliter, a concentration that did not induce HR. Structural proteins (SP) were isolated from chloroplast membranes and all SP preparations migrated as a single boundary during ultracentrifugation (446, 450). In dialysis the SP from water-infiltrated tissues formed spherical aggregates, whereas the SP from bacteria-infiltrated tissues aggregated into irregular clumps. Since the lipids used in the experiments were identical, the inability to form membranelike structures was attributed to the alteration in SP properties by HR-inducing bacteria. The capacity of bacteria to induce HR on tobacco leaf tissue was detected within 2 minutes by measuring the oxygen consumption of mixtures of separated leaf cells and bacteria (447). This finding suggested the existence of a well-defined recognition system between the reactants.

In the mid-1970's, Goodman et al. (349) and Huang and Goodman (454) showed that in vivo agglutination of incompatible bacteria in plant tissue is a general defense mechanism but distinct from the hypersensitive defense reaction. They postulated that the agglutinating factor may migrate from the living xylem parenchyma cells into dead xylem vessels.

Induced Host Resistance

Following preliminary investigations during the 1930's on the antagonistic effect of various micro-organisms on *E. amylovora* (38, 722, 934), Goodman (339) reported in 1964 on the protection of Jonathan apple stem tissue against fire blight infection by introducing an avirulent yellow bacterium prior to inoculation with the blight pathogen. In vitro the virulent *E. amylovora* (35 A-W) and the yellow organism (35 A-Y) grew at the same rate, but the growth of 35 A-W was reduced significantly when the two cultures were inoculated together (340). The inhibitory effect of 35 A-Y on 35 A-W was also demonstrated in vivo and appeared to be due to acid production by the former. The initial inoculum (protecting strains) or inducer (IN), provided by either an avirulent isolate of *E. amylovora*, a yellowish *Erwinia*-like isolate, or *Pseudomonas tabaci* (Wolf and Foster) Stevens, protected the apple tissue from subsequent infection by a virulent strain of *E. amylovora* or challenge inoculum (CI) when inocu-

lated 30 minutes later (341). The duration of the protective effect reportedly was dependent on the number of “protecting” bacteria present in the apple tissue at the time the virulent inoculum was applied.

The association of a yellow saprophytic bacterium with *E. amylovora* has been known for many years (62, 86, 296, 401, 1051). *Xanthomonas pruni* (Smith) Dowson, *X. campestris* (Pammel) Dowson, *Bacillus subtilis* (Prazmowski) Cohn, and *B. cereus* Frankland and Frankland did not provide any protection against *E. amylovora* (339, 341, 613).

McIntyre (1118) studied the protection of Bartlett pear tissue by avirulent *E. amylovora*, *E. herbicola*, or *P. tabaci* at various intervals before inoculation with virulent *E. amylovora*. Fire blight symptoms were not delayed when CI was applied 0.5 hour after IN. Using young etiolated pear seedlings, McIntyre et al. (613, 614, 616) were able to determine that symptom expression could be delayed from 1 to 14 days, with maximum delay occurring when CI was inoculated 24 hours after IN. They also obtained a

delay in symptom expression when cell-free sonicates of both avirulent and virulent *E. amylovora* were used as inducers. Deoxyribonucleic acid (DNA) from *P. tabaci* and *E. herbicola*, bacteria that protected against fire blight, provided no protection, whereas DNA from virulent *E. amylovora* did protect (614, 615). The possibility of an interaction between host and bacterial DNA as a factor in protection is being explored. Wrather et al. (1041, 1139) found these same bacteria protected fruit of mature Anjou and immature Bartlett pear and Jonathan and Red Delicious apple cultivars against infection by *E. amylovora*. In these fruits, however, protection appeared permanent.

The host-parasite relationship in fire blight appears to be an intricate, complicated balance between *E. amylovora* and the various tissues of the host plants. The numerous biochemical interactions appear to have potentially great merit and in the future could lead to the production of plants possessing prolonged or permanent fire blight resistance.

CHAPTER 11

CONDITIONS AFFECTING DISEASE DEVELOPMENT

Fire blight development depends on the interaction between pathogen and host and is affected by the environment. Rather than a simple process, it is a complicated balance involving the bacterium with many host conditions and meteorological and edaphic factors. Each of them has to be optimum and synchronized for maximum blight development.

Host Conditions

Tree Growth and Vigor

Succulent shoot growth of pear, apple, pyracantha, hawthorn, or any other host plant usually is very susceptible to blight during an outbreak of the disease. Pear and apple trees alike should produce a slow, steady, uniform, and fairly vigorous growth. Such growth will usually develop stockier, harder twigs, which are much less susceptible to blight infection.

Succulent shoot growth is usually low in carbohydrates. Blake (94) reported such conditions in apple trees growing in clay loam during hot, dry summers in New Jersey. Trees with rather thick, medium dark-green leaves that cease their shoot growth by July 1 in New Jersey reportedly were high in carbohydrates and were the most resistant to fire blight. In preliminary work, Hewitt (404) found a positive relationship between high starch content in host tissues and susceptibility to fire blight. Miller (651) described a peripheral cork barrier delineating the superficial cankers on resistant apple cultivars. He concluded that "resistance is probably due, in part at least, to the laying down of a cork barrier by the host."

The various tissues of pear and apple trees differ markedly in their degree of blight susceptibility. Extensive inoculations in different tissues of 10 cultivars of *Pyrus communis* and a clonal selection No. 76 of *P. ussuriensis* at Beltsville showed that three cultivars were most susceptible to blossom blight, three to shoot blight, two others and the clonal selection to blight in 2-year-old branches, and one to trunk blight (1053, 1057). Green, immature fruit on all trees blighted within 2 weeks after inoculation.

Succulent shoots and woody trunk tissue in the resistant Magness pear differ considerably in their degree of blight resistance (1060, 1063). Reimer (780) was among the first to report this phenomenon in the pear cultivars Douglas, Orel, and Surprise following artificial inoculation.

Mature fruits of pear and apple are much more resistant to blight infection than young fruits of the same cultivar (936, 1062). A partial parallel between susceptibility and the anthocyanin pigment in the bark of pear seedlings has been reported (932). Thomas and Ark (936) did not observe any marked differences in the average extent of blight infections between two lots of pyracantha seedlings and bench-grafted pears, one showing the least and the other with the most red pigment.

Studies reported in 1972 on shoot infection revealed that low levels of inoculum can infect expanding leaves when placed on the exposed vascular system of a cut leaf (197). Also, young leaves on undamaged apple and hawthorn shoots were readily infected in early morning when thoroughly wetted before inoculation. Such wet treatment was effective in the evening with hawthorn but not with apple shoots (254). Billing (84a) concluded that both vascular damage and wetting in early morning favor blight infection.

Tree Nutrition

For many years nitrogen has been associated with vigorous growth and, in turn, has been correlated with fire blight infection (80b, 94, 303, 425, 584, 727, 899, 936). In addition, certain other elements usually applied as fertilizers may also affect blight susceptibility (303, 522, 580, 689, 727, 899, 1113). Nightingale (689) found that the relative concentration of carbohydrate and nitrogenous compounds within apple tissues and the balance of these one with the other were of much greater importance in determining the development of the fire blight organism within the tissue than the relative water content or the amount of resistance offered by the physical nature of the host cells. A relatively low carbohydrate, high organic nitrogen content correlated with

susceptibility and the reverse with resistance to fire blight. In addition, these studies showed that *E. amylovora* grew well on agar containing extracts from succulent twigs, low in carbohydrates and high in organic nitrogen, but grew poorly or failed to grow on that made from hard twigs, high in carbohydrates and low in organic nitrogen.

In a nitrogen-phosphorus-potassium factorial fertilizer test conducted over several years in the field on pears, Fisher et al. (303) and Parker et al. (727) found that adding potassium with nitrogen caused no increase in blight severity over nitrogen alone. However, adding phosphorus or phosphorus and potassium with nitrogen reportedly produced more succulent shoots and substantially increased susceptibility. Furthermore, inoculation of apple trees growing in sand culture with nutrient differentials supported the field results on pears.

In other nutrient solution studies on Bartlett pear, Kenworthy (522) and Lewis and Kenworthy (580) showed that the relationship between absorption of an element as measured by leaf analysis and concentration of nutrient solution can be significantly changed by interaction of the elements. Deficiencies of nitrogen, phosphorus, or calcium resulted in a significant increase in leaf potassium. On the other hand, excess nitrogen, phosphorus, or iron significantly decreased potassium in the leaf, whereas plants receiving no copper contained less potassium than check trees. High levels of potassium decreased the concentration of leaf calcium and magnesium by the same magnitude as withholding these two elements. In these studies the susceptibility of inoculated Bartlett pear trees appeared to be affected by the nutritional environment. Lowest susceptibility was found in trees with a high supply of calcium. A low supply of boron also appeared to reduce susceptibility. All other treatments, except minus phosphorus and minus iron, resulted in a slight or significant increase in susceptibility as compared with the check. Thus they concluded that withholding fertilizer applications would not necessarily increase resistance to fire blight.

In Virginia, Hickey (404a) confirmed that high rates of potassium increased the susceptibility of Jonathan apple trees on MM 106 rootstocks to fire blight when applying modified Hoagland solutions to trees in greenhouse sand culture. A 10×copper treatment appeared to increase susceptibility compared with the basic Hoagland solution, but the ef-

fect of high calcium (4 ×) was not significantly different.

In a 2-year study on Bartlett pear trees grown outdoors in washed quartz sand at Beltsville, less fire blight was observed in inoculated trees that received low nitrogen and high potassium plus an adequate supply of other macroelements and microelements, and greatest blight was seen in trees receiving high nitrogen and low potassium (499). Analysis of leaves from trees with intermediate potassium levels showed intermediate blight development (fig. 21). Fisher et al. (303) also indicated that Bartlett trees growing in New York State on poorly drained sites were low in potassium and showed more blight infection compared with trees growing in well-drained areas and containing higher potassium levels.

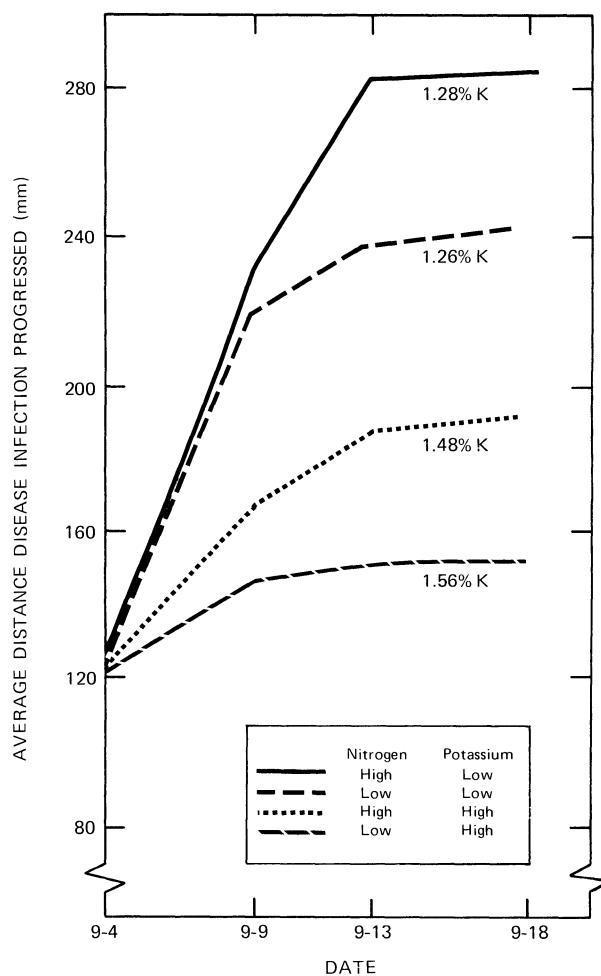


FIGURE 21.—Effect of nitrogen and potassium (K) amendments on fire blight infection in Bartlett pear trees in sand culture.

In other studies ¹⁶ at Beltsville, periodic leaf pH readings were made on several field-grown pear cultivars and Jonathan apple for two seasons to see whether any significant changes took place during the season and how pH could be assimilated into the fire blight syndrome. One gram of either old or young leaves was added to 50 ml of demineralized water and thoroughly mixed with a Waring blender. The pH readings were made on the resulting leaf-water suspension. Young leaves up to three-fourths grown of all seven pear cultivars—Bartlett, Stewart Bartlett, Dawn, DeVoe, Kieffer, Magness, and Moonglow—showed a striking increase in acidity from April 24 to June 13. On April 24 (full bloom to petal fall) all cultivars showed relatively high pH values (5.3–6.0). Such values are known to support optimum growth of *E. amylovora* in vitro (30, 87, 630, 901). On subsequent test dates (May 8 and June 13) the pH values of young leaves progressively decreased. Young leaves of Bartlett and Stewart Bartlett, both highly susceptible cultivars, never had pH values below 5.2 at any time during the study, whereas Magness, Kieffer, and Moonglow had pH values of 4.6, 4.9, and 4.9, respectively. No such increase in acidity was observed in Jonathan apple. As pear leaves became older, the pH appeared to stabilize and showed values less acid than those of young leaves sampled on the same date.

Based on these results, one may argue that the old leaves support growth of the fire blight organism more than young leaves. However, this is probably unlikely because other factors, such as morphology and phenolic potential, take over as leaves mature. It is therefore suspected that the pH of the sap of pear cultivars may in part affect the resistance of susceptible young leaves of a given cultivar. Further studies comparing young leaves and their petioles demonstrated that the latter always had higher pH values than the former. This appeared to correlate with our field observations and greenhouse inoculation studies (fig. 6, B and C). Studies also indicated lower pH values for leaves and petioles on resistant Magness and Moonglow cultivars compared with higher values for those on the susceptible Bartlett. Because some of the cultivars reacted similarly in the field, these data indicate that additional studies should be conducted to resolve the effect of sap pH on fire blight resistance.

Sands and McIntyre (835a) reported in 1975 on the

effect of potassium citrate and tartaric acid sprays in lowering leaf pH of the pear cultivar Clapp Favorite from 6.5 to about 4.0. Plants were treated with these acids and then spray-inoculated with *E. amylovora* 1 to 2 days later. Leaves were assayed with a selective medium 2 to 5 days after inoculation. Those from the water controls (pH 5.5–6.5) showed an average 3×10^3 cells per leaf, whereas the acid-treated leaves (pH 4.0–4.5) had approximately 50 cells per leaf.

Other greenhouse studies ¹⁶ at Beltsville indicated that leaf ash from young tender leaves, vulnerable to fire blight attack, can inhibit growth of *E. amylovora*. Spectrographic analysis of these leaves from plants growing in aluminum sulfate-amended soil showed no difference from leaves of plants growing in nonamended soils when analyzed for aluminum, boron, calcium, copper, iron, manganese, phosphorus, sodium, and zinc. However, an increase in potassium appeared to be positively correlated with *E. amylovora* inhibition. On a dry weight basis, if the potassium level of young tender leaves is below 1 percent, the inhibition zones appear to be materially reduced. We suspect that potassium is associated in some way with certain unidentified complex compounds responsible for resistance, because tests with potassium chloride and potassium sulfate at higher potassium ion concentrations than those found in leaves demonstrated no *E. amylovora* inhibition. One might also suspect that adding aluminum sulfate makes the soil more acid and allows roots to take up more potassium. However, sulfur lowers soil pH more than aluminum sulfate, but plants growing in soil amended with the latter contained more potassium.

At the University of Illinois, Reinhardt (1125) unsuccessfully attempted to increase sufficiently the copper content of young Jonathan apple trees so as to reduce the degree of blight severity following artificial inoculation. In later studies Bushong et al. (137) obtained a marked reduction in blight incidence in trees injected with various copper compounds in the trunk and foliar bordeaux spray treatments. Generally copper levels in succulent shoots were inversely proportional to the amount of fire blight. Marked differences in amino acid content occurred mainly in shoots of trunk-injected trees. However, neither protein nor nitrogen levels were affected by the copper treatments (1089).

In the mid-1970's, Aldwinckle and Beer (14a) studied the degree of artificial blossom blight in Golden Delicious apple trees on M 7 rootstocks under

¹⁶ Unpub. data, Fruit Lab., U.S. Dept. Agr., Beltsville, Md.

nitrogen-phosphorus-potassium nutrient regimes in greenhouse sand culture. They observed widest differences between nutrient treatments when about 10 bacterial cells were applied per blossom. Trees with high nitrogen and phosphorus contents had most infections, whereas in trees with low phosphorus content, those with higher potassium appeared more susceptible. One wonders whether nutrient measurements in leaves should be used to determine differences in degree of blossom blight.

Intercellular Humidity

Following his extensive studies of the effect of atmospheric and soil moisture on blight development in apples and pears, Shaw (860) conducted detailed studies on the amount of intercellular humidity (IH) in host plants, calculated by measuring the degree of turgor deficit of plant cells. He prepared tables showing the relationship between osmotic pressure and vapor pressure and between vapor pressure and relative humidity.

Figure 22 summarizes the data of this significant work on fire blight. Potted pear and apple plants at different atmospheric humidities and different soil moistures showed high IH and were very susceptible to fire blight when atmospheric humidity was high. When moisture content of the environment was low, both IH and degree of susceptibility were low. When the average was 97–98.5 percent, the plants were only slightly susceptible or were completely resistant to the pathogen; when IH was 99.5 percent, the plants were very susceptible. Plants with intermediate IH were intermediate in their degree of blight susceptibility.

We consider that the relationship between atmospheric humidity and IH is obvious and that it significantly affects the overall expression of the blight pathogen in its host tissues. IH probably is a major factor in causing differences in susceptibility in comparable groups of plants in environments varying in amount of moisture.

Meteorological Factors

The amount of fire blight on individual trees or in certain orchards in one season does not appear to be correlated with that of the preceding or succeeding season. The degree of disease is regulated by many factors, such as optimal temperatures, excessive rainfall, high relative humidity, and prevalence of insects. Weather is probably the most important factor in the epiphytology of fire blight, both in its

effect on the host and on disseminating the pathogen. In the host the bacteria develop best in rapidly growing meristematic tissues. Warm, rainy weather followed by periods of high humidity induces such growth not only in shoots but also in fruit and bark. Once the bacterium is introduced into such tissues, especially in a susceptible cultivar, the rapid and destructive development of the disease is assured (321).

Temperature

Development of blight infection is favored by moderately high temperatures, and often during bloom the temperature is low enough to retard infection considerably. The exact temperature limits have never been defined, but the following have been generally accepted: Minimum 18.5° C (65° F), optimum 21°–27° (70°–81°), and maximum 32°–35° (90°–95°).

Under controlled environmental conditions, Brooks (114) found that optimal temperatures for blight development in apple twigs were between 21° and 28° C (70°–82.5° F). This does not mean, however, that the disease does not develop below 21° (70°). Miller (651) stated that at 16° (61°) blight development was so slow that practically no differences could be detected between the degree of resistance in shoots of the apple cultivars Northwestern Greening and Wealthy. However, at 24° (75°) and 28° (82.5°) Northwestern Greening was distinctly more resistant than Wealthy.

In Wisconsin, Shaw (859, 1131) made detailed inoculation studies at various controlled temperatures. Apple cultivars Northwestern Greening and Yellow Transparent were grown at 16° C (61° F), 20° (68°), 24° (75°), and 28° (82.5°) and were placed at 24° following inoculation. Results showed that plants were most resistant at 16°, intermediate at 20° and 24°, and least resistant at 28°. Shaw concluded that fire blight resistance in apple was related to (1) the inherent characters of the cultivar, (2) the physiological and morphological maturity of the tissues, and (3) the environmental conditions to which the plants were subjected.

Several investigators reported the optimum temperature for the bacterium in culture to be 25°–28° C (77°–82.5° F) (30, 85, 87, 901). The bacteria in blighting shoots 2–6 mm in diameter reportedly withstood air temperatures for 4 hours at 48° (118.5°) or 30 minutes at 60° (140°) (934). In Colorado, Luepschen (596a) observed survival of *E. amylovora* at tem-

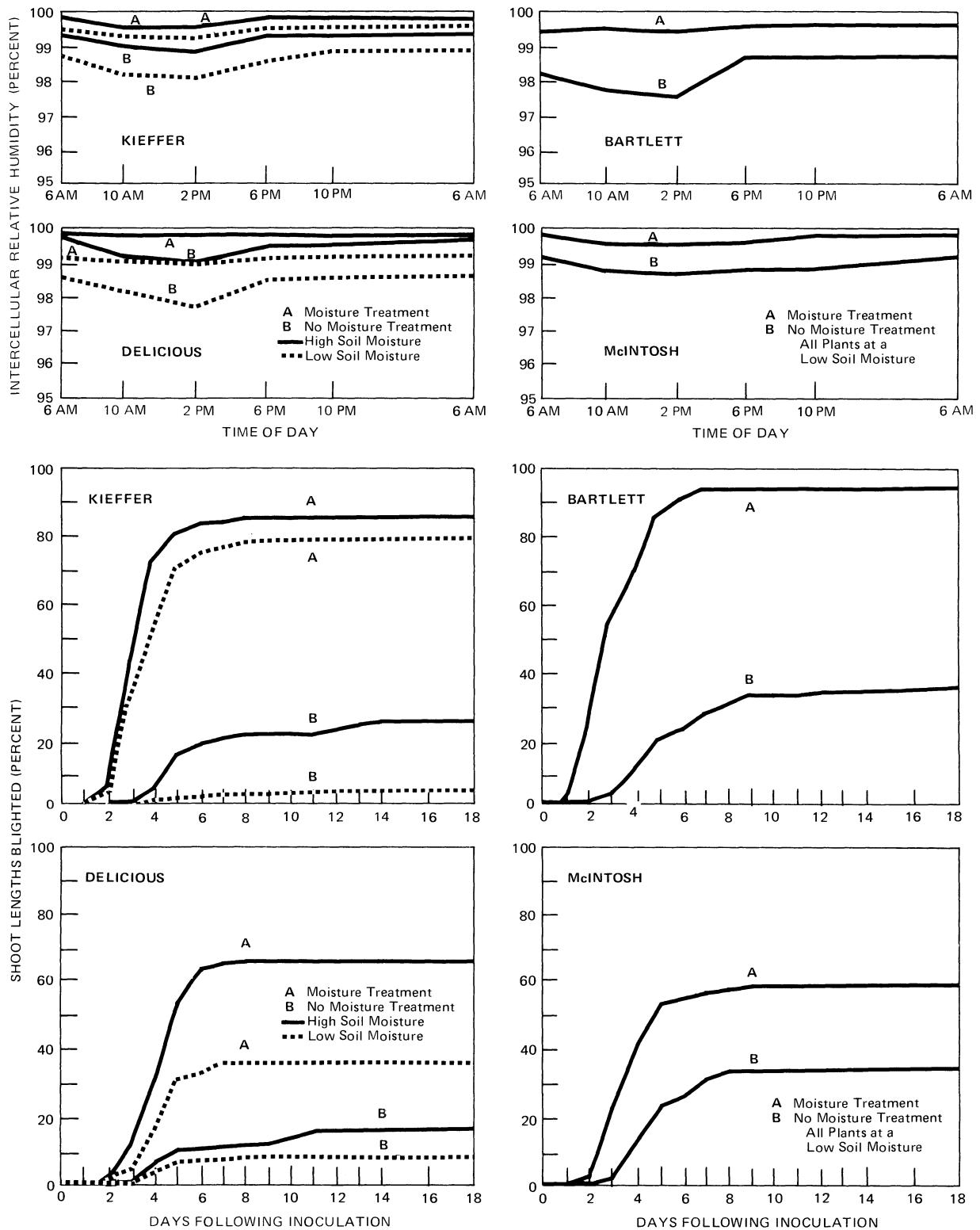


FIGURE 22. — Relationship between intercellular relative humidity and fire blight susceptibility in shoots of pear and apple at different atmospheric humidities and soil moistures (after Shaw, 860).

peratures up to 34° (93°) when Bartlett trees were spray-inoculated with 500 cc of 8-day-old broth cultures suspended in 500 gallons (1,890 liters) of water with 2 cc of Triton surfactant. There is probably no upper temperature limit for survival under natural conditions.

On the other hand, low temperatures retard or arrest the development of infections (756, 1126). In areas with mild winters, temperature is a limiting factor in the enlargement of cankers. Cankers entirely girdling the branches often increase several centimeters more during the fall and winter on the side exposed to the sun than on the opposite side. Thomas and Ark (936) demonstrated a relationship of low temperature to initiation of blight infection in California by inoculating alternate rows of pear seedlings on the north and south sides of the trunks in February. By early April, 15 percent of the trees

inoculated on the north side and 29 percent inoculated on the south side were infected.

In 1975, Thomson et al. (950) reported detailed studies of spring temperatures in several California counties during full and late season bloom in pear. Even though the correlation of temperature to the incidence of blossom blight has as yet been inconclusive, epiphytic populations of *E. amylovora* are monitored to improve the timing of bactericide applications for fire blight control.

In New York, Mills (656) claimed successful forecasting of blossom blight epiphytotics in apple using degree days above 18° C (65° F). He found positive correlations between degree days plus precipitation during bloom and severity of fire blight in the Lake Ontario fruit counties during 1918–54 (fig. 23). A few years later, Luepschen (1115) found in this area that, on days during bloom with maximum tempera-

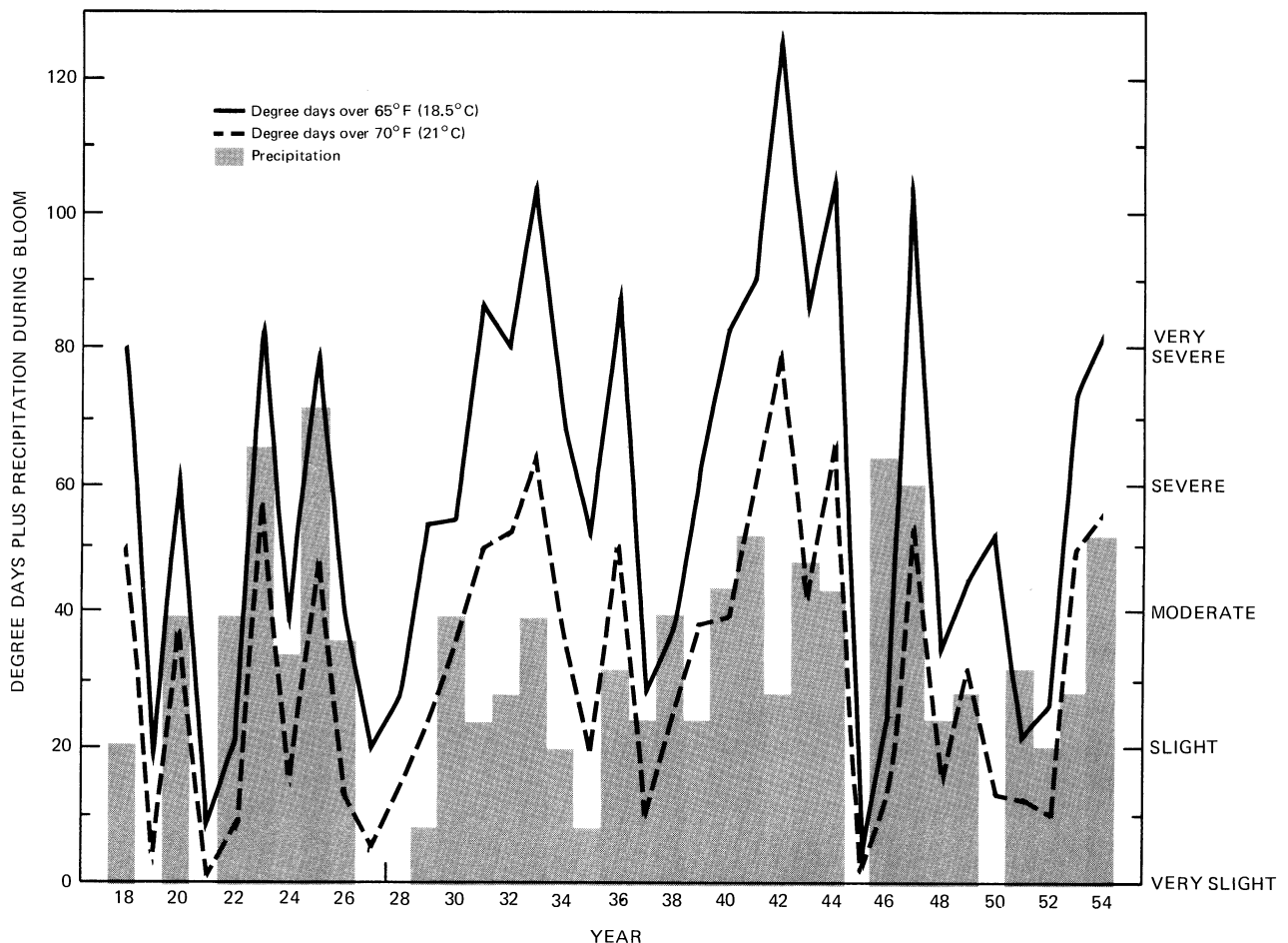


FIGURE 23. — Correlation among temperature degree days plus precipitation during bloom and fire blight severity in apple in New York during 1918–54 (after Mills, 656).

tures of 18.5° (65°) without rainfall but following rainy days, the mean relative humidity was as high or higher than on days when precipitation occurred. In controlled experiments, temperatures after blossom inoculation had a more significant role than those at the time blossom sprays were applied (598). Observations over a 5-year period indicated that serious blossom blight infections required a minimum of 2 favorable days for infection.

In Illinois, Powell (757, 758, 760, 761) worked out a rather unique method for predicting fire blight infections based on prebloom freezing temperatures and the number of "degree days" above 18° C (65° F) required for the organism to become active again. He concluded that 18 degree days Celsius (30 degree days Fahrenheit) between the last freeze and early bloom, combined with maximum temperatures of 21°–27° (70°–80.5°) and a light rain or high humidity, were adequate for fire blight infections. Principal factors reportedly interfering with blossom or twig infection are (1) inadequate number of degree days between latest prebloom freeze and early bloom, (2) maximum temperatures either lower than 18° (65°) or higher than 30° (86°) during early bloom, (3) drought preceding and during early bloom or during June 1–July 15, and (4) excessive rains during early bloom.

In Pennsylvania, Petersen (736) suggested using 60–100 ppm of streptomycin for blossom blight control based on Powell's temperature studies. In Arkansas, Rosen (817) showed an apparent correlation between blossom production regulated by frosts and prevalence of disease. Investigations in California by Thomson et al. (950) in 1975 showed no correlation between Mills' weather criteria and the presence of *E. amylovora* in blossoms.

In England, Billing (84, 84a) observed severe outbreaks of fire blight in apple and hawthorn in 1968 and 1969 when temperatures of 27° C (81° F) or higher followed heavy rainstorms in early July. In 1976, Billing (85a) proposed a method for assessing potential fire blight activity in the field in southeast England. It is based on potential doubling derived from in vitro growth rates of *E. amylovora* at different temperatures combined with a rain score derived from daily precipitation values. She found good agreement between accumulated potential doubling values and accumulated degree days, using both English and American temperature records. Highest potential fire blight activity occurred in warm, wet periods rather than in cool, dry ones.

In West Germany, Schroder (1128a) studied temperature-humidity limitations for blight development on 10 species of cotoneaster, crataegus, and pyracantha. Following artificial inoculation of the plants and incubation in a growth chamber, he was able to obtain blight symptoms at 15° C (59° F) and 55 percent relative humidity during the day and 10° (50°) and 70 percent relative humidity at night.

Rain, Humidity, and Hail

The relation of weather to dissemination of the blight pathogen is both direct and indirect (84). Observations and investigations by many workers, especially those by Miller (651), Brooks (114), and Tullis (961), demonstrated conclusively that rain is a very common and effective agent in disseminating the bacterium (chap. 8). Rainy weather followed by warm, cloudy weather, especially during blossoming and ultimate shoot growth, is very favorable to epiphytotic outbreaks of fire blight.

Periods of relatively high atmospheric humidity have been reported by many investigators to be frequently accompanied or immediately followed by rapid development of fire blight in apple and pear trees in the orchard. Brooks (114) observed the greatest amount of resistance in apple trees of the cultivar Fameuse when they were kept at 50 rather than 80 and 95 percent relative humidity after inoculation. Eighty percent appeared most favorable for infection, whereas 95 percent was slightly less favorable. Miller (651) reported no more blight resistance in young Northwestern Greening than in Wealthy apple shoots when they were placed in a saturated atmosphere at 26° C (79° F) following inoculation. Shaw (859) confirmed this observation when these two cultivars were subjected to high humidity for 72 or 96 hours after inoculation.

A high relative humidity reduces the sugar concentration in pear nectaries to permit growth of *E. amylovora*. Under natural conditions, sugar concentration in the nectaries is generally higher than lower (chap. 8).

For a long time, injury has been known to have an important role in the infection process (112, 114, 500, 575, 596a, 599, 651, 742). In 1966, Keil et al. (501) proved that considerably more infections occurred on artificially inoculated young Bartlett trees in the greenhouse when they were lightly sandblasted than when left uninjured. When trees were inoculated at various intervals from 0 to 64 days after injury, the disease was more severe when they were

inoculated within 6 hours after injury than at longer intervals (1052). More recently we showed that blight development was more severe within 24 hours after injury when trees were kept in a moist chamber than on the greenhouse bench (1062). Infection also developed on all injured pear fruit dipped in inoculum at the time of wounding (nail puncture) and on 70 percent of fruit bruised 2 days before or after inoculation. We found that infection took place mainly through leaf petioles whether the trees were injured or not (fig. 6, B). Crosse and Shaffer (198) reported that severe shoot blight resulted if the vascular system of Jonathan apple leaves was severed near the apex immediately before inoculation.

These facts indicate therefore that tissue injury providing access to the vascular system predisposes the development of fire blight. In the summer of 1967 our attention was directed to an epiphytotic of fire blight in an isolated pear orchard in northern Arkansas. A combination of heavy fertilization, abundant rainfall, and a severe hailstorm had caused blight in 80 percent of the trees in two orchards (1066). Without definite proof, the blight organism seemed to be present inside or on the surface of the pear branches.

Stewart (904) reported unusually severe outbreaks in two separate orchards in New York during the summer of 1914. The trees in these orchards were struck by a severe hailstorm and many blight infections were prevalent 2 weeks after the storm, originating in the wounds of the bark made by the hailstones. Similar observations were made in Colorado following a severe thunderstorm with hail (596a).

From California, Wilson (1029) reported that increased humidity due to sprinkler irrigation caused greater severity of fire blight in pear. In 1976, Spotts et al. (884b) reported measuring a ninefold increase in twig blight on water-misted trees of the cultivar Golden Delicious in Ohio over adjacent nonmisted trees.

The effect of wind on blight development primarily pertains to dissemination of the pathogen in the form of ooze droplets or bacterial strands (chap. 8).

Edaphic Factors

Soil Types

Usually blighted trees are more common in rich than in poor soil, in which tree growth is severely reduced. Rich soils, especially if manuring is prac-

ticed, result late in the season in extra succulence in branches, which in turn are susceptible to fire blight (899, 901). Trees in sod usually grow slower and the new shoots become hardy and woody earlier in the season (784, 955).

Blake (94) reported that trees were susceptible to blight when grown in dense soils where the water table was high at times or where they had limited root systems because of lack of aeration. He listed the following soil conditions in New Jersey that usually resulted in severe blight in apples and pears: (1) Very light, sandy soils that are subject to marked variations in water content; (2) shallow soils of any type as a result of being underlaid by ledges of rock or impervious clay; and (3) low areas where moisture is rather near the surface, aeration is somewhat unfavorable, or the trees continue to produce twig and shoot growth after the first of July, even during dry, hot days.

Before establishing a new orchard, select a fertile, well-drained site. Tree growth stops earlier in the season on dry soil than on poorly drained soil (784, 785). On well-drained soils, alfalfa or other deep-rooted legumes may be used as a permanent cover crop. Grass or alfalfa sod should be well mowed early in the season and then usually allowed to grow in midsummer to check tree growth. In New York, Hildebrand and Heinicke (425) observed in the same orchard that apple trees under alfalfa culture were less severely blighted than those in grass sod plus nitrogen or under cultivation. The number of infections did not differ measurably, but the extent of blight invasion from each infection was reduced under alfalfa culture. These results and observations were later confirmed by Toenjes (955) in Michigan.

Soil Moisture and Temperature

A relationship exists among soil moisture, tree growth, and percent intercellular humidity in the trees. Shaw (859) found the least blight in apple shoots where soil moisture was low. Soil temperatures of 12° and 32° C (54° and 90° F) were less favorable for blight development in Fameuse apple shoots than intermediate temperatures. He observed a positive relationship between blight resistance and lowered vigor in the shoots.

There is comparatively little information on the relationship of *E. amylovora* to the soil. Arthur (52) reported that the organism grew moderately well in soil extract. In 1895 after careful investigation, Waite (991) was unable to isolate the blight organism

from soils. From California, however, Ark (27) reported that *E. amylovora* could persist in the laboratory for 54 days in sterilized soil and for 38 days in unsterilized soil. He employed a special technique and used green, immature pear fruit dipped in soil suspensions to recover the blight organism (fig. 24). The bacterium was obtained from different orchards where it persisted for at least several weeks in dry or moderately moist soils.

Thomson (1137) in 1969 showed in detailed isolation studies that *E. amylovora* overwintered not only in soil but also on and within dead tissues, such as blighted stems, twigs, and fruit mummies. He recovered both virulent and avirulent *E. amylovora* isolates from apple or pear material and considered soil to be ideal for isolating the organism in March and April.

Cultural Practices

Cultivation and fertilization may markedly affect the amount and control of fire blight, particularly on pear trees. If cultivation and fertilization cause a rank, succulent growth, these trees are more likely to be affected by fire blight. Therefore never cultivate pear and apple orchards late in the season because it is likely to cause new growth, which may continue to spread fire blight. Severe pruning should also be avoided on susceptible cultivars, because it tends to produce rank, tender growth.

Growers should attempt to develop extensive, deep root systems by providing a favorable soil reaction and uniform soil fertility. Applications of nitrogen should be based on the need of the individual orchard and should be sufficient to provide only moderate growth. Foliar application of nitrogen may be used following the blossom period as a source of supplemental nitrogen. Usually sufficient nutrients will be obtained by the tree with applications of a 5-10-5 fertilizer at 1 pound per 100 square feet (0.5 kg per 25 m²). In general, a grower should study his trees and regulate growth in such a way that they will produce moderate shoot growth without unduly subjecting the trees to attack by fire blight.



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FIGURE 24. — Isolation of *Erwinia amylovora* from orchard soil beneath blighted pear tree after immersion of immature pear fruit in soil suspension (after Ark, 27).

There is considerable evidence that orchards planted on well-drained soils are much less subject to fire blight than those on wet soils. Fire blight problems have been reduced and tree productivity has been increased when poorly drained sites were improved by tiling. A new orchard site should be sufficiently limed to maintain a soil reaction of pH 5.5–6.5. The lime should be well worked into the soil, preferably by deep plowing or subsoiling.

During late winter or early spring remove all root sprouts and suckers from the main framework and trunk of the tree. Their removal may prevent summer infections that might destroy large branches or even entire trees. The removal of suckers from the main trunk and scaffold limbs should be repeated during the growing season. Wherever possible, also remove late season or “rattail” blooms. For further details on pruning, canker removal, and orchard sanitation, see chapter 12.

CHAPTER 12

CONTROL MEASURES

Fire blight cannot be controlled by any one measure alone. Every attempt must be made to keep fire blight out of the orchard. If this serious disease gets into the orchard, make every effort to eliminate or contain it so that trees are not lost and production is not impaired. Experience shows that the best control results when the grower follows an integrated program of chemical control combined with sanitation, pruning, eradication, tree nutrition, and insect control (8, 80*b*, 112, 188*a*, 234, 236, 298, 398, 627, 723, 724, 1048, 1064*a*).

Sanitation and Quarantine

Nurserymen or anyone propagating plants susceptible to fire blight should be responsible for using clean clonal or seedling stocks and budwood taken from plants free of the disease. Tracing fire blight infection back to the propagator is difficult. Sufficient evidence seems to indicate that fire blight can be spread from this source into an area where the disease has not previously been found (124). The grower, if possible, should be familiar with sanitary conditions of the nurseryman supplying his trees. Trees from a well-managed nursery may cost slightly more, but to obtain healthy plants is worth the price difference.

As a modified form of quarantine in some areas, a common practice is to avoid planting both apple and pear trees in the same orchard. In the early 1920's, laws were passed in America to prevent pear trees from being planted within 1.5–2.5 km of an apple orchard (78). Where this was done, less fire blight occurred in the apple orchards. Similarly the proximity of hawthorn to pear and apple has increased the incidence and severity of fire blight (87*a*, 179, 330, 638, 639, 681). Removal of hawthorn hedges in or near orchards has been suggested.

The most effective quarantine regulation is strict enforcement to prohibit importation of all fruit, seed, budwood, and other plant parts of all rosaceous plants from any country with fire blight. Soon after the introduction of fire blight into New Zealand about 1919, the Commonwealth of Australia passed a law prohibiting the importation of any plant parts

in the family Rosaceae from any country where fire blight was present (181). This enforcement has been continued ever since (1) and, together with the country's isolated location, undoubtedly has contributed to the absence of fire blight in Australia today. Since the introduction of fire blight into Western Europe, strict quarantine regulations have been adopted by Norway (288), Sweden (286, 289), and Switzerland (285).

Pruning

Sometimes if fire blight is not too severe, especially when only a few twigs are blighted in an orchard, the blighted parts can be pruned out without further spread of the disease. Often diseased branches and apparently healthy "rattail" blooms are regularly removed during the summer in orchards where a chemical control schedule is followed. Some of the largest pear orchards in the Pacific Coast States follow this practice (240). If pruning is done as soon as blight infection is observed, it will usually eliminate the diseased tissues as well as the inoculum that provides the bacteria for new infection (159, 498). It also destroys the dead tissue, which is vulnerable to invasion by rot organisms that affect fruit the following season (235).

Several years ago we experimentally demonstrated at Beltsville, Md., under severe disease conditions that fire blight could be contained by pruning alone (503). Ten-year-old fruiting Bartlett pear trees about 4 meters tall, in a virorous growing condition, were inspected once or twice each week between bloom and harvest. Each infection was pruned out as soon as it was observed. Cuts were made 15–45 cm below the visibly diseased part depending on the amount of apparently healthy tissue available for cutting. During the season, 135 pruning cuts, on an average, were made on each unsprayed tree, and although apparently free of blight, the trees were only one-third their original size at the end of the season. Similar trees not pruned died from blight infection. This simple experiment indicated that fire blight can be controlled by pruning even under severe disease conditions. Although following such a

procedure under similar conditions in large orchards is impractical, pruning can help control the disease.

On the other hand, Lake (1112) and Lake et al. (547) demonstrated in Minnesota that summer pruning of apples in early June markedly enhanced infection of fire blight. From Indiana, Gardner (320a) reported that ringing limbs of certain apple cultivars to induce early bearing resulted in considerable blight infection of the knife-cut girdle wounds.

In some fruit areas, pruning out blighted branches is particularly helpful when it supplements a chemical control schedule. Pruning tools should be dipped in a disinfectant between cuts to prevent spread of the bacteria. Several chemicals, including solutions of the corrosive sublimate, mercury cyanide, various denatured alcohols, and the common household sodium hypochloride, have been used successfully to decontaminate pruning tools (498, 507, 554, 726, 778, 992). Sodium hypochloride has been widely used in recent years because it is economical, easily accessible to the average household, and kills *E. amylovora* bacteria when the tool is dipped in a 10 percent solution for about 2 seconds (8, 507). Unfortunately it corrodes tool metal, but this can be prevented by rinsing in running water and oiling each day after use.

The fact that pruning tools can transmit the blight pathogen can best be demonstrated by an extreme example in 1906, when Waite and Smith (999) observed a nursery block of 10,000 pear trees completely destroyed by fire blight. Holdover blight cankers were present in the stock trees and pruning tools apparently became contaminated and transmitted the disease to nearly every tree.

Aldwinckle and Preczewski (16a) reported in 1976 a discolored streaking in xylem vessels in advance of externally visible blight symptoms in both field- and greenhouse-grown apple cultivars. Pathogenic *E. amylovora* was isolated from these vessels, and length of xylem streaking in advance of external lesions correlated with the standard error of lesion length. These facts again emphasize the importance of pruning far in advance of visible blight symptoms and the use of disinfectants between cuts.

Eradication

In addition to blighted twigs and branches, serious body blight, manifested as cankers in large limbs and the trunk, sometimes develops. Such blight infection often causes loss of the tree unless the bac-

teria in these cankers are eliminated or inactivated before the blossoms open. Several methods of eradicating the fire blight organism from cankers have been used. In the Pacific Northwest, cankers are scraped or scarified with a sharp-edged tool to allow them to dry out. Usually they are also painted with poisonous solutions, which kill the blight bacteria (199, 208, 437, 498).

Sometimes careful surgery is practiced, whereby the diseased bark is removed followed by proper disinfection. With this method the cut should be made several centimeters into the apparently unaffected wood of the canker margin. In some parts of the country, disinfectants are painted over the surface of the canker without any surgery. This method requires the least time and has proved effective in some orchards. Of the many chemicals tried in canker paint formulas, only a few have proved effective and relatively noninjurious to healthy wood. Combinations prepared by dissolving zinc chloride in denatured alcohol, water, and hydrochloric acid have been used extensively (150, 208-211, 228, 554, 602, 604, 608, 620, 941).

Both mercuric chloride and cyanide of mercury have been used alone but more successfully in combination, when they are referred to as Reimer's solution (66, 144, 199, 208, 209, 437, 469, 1045). This formula was improved by Day (208, 209) when he added glycerin, which allowed better penetration and prevented quick evaporation. Cardinell (144) of Michigan added fuchsin red to the Reimer-Day mercury and glycerin solution, which allowed one to tell at a glance which cankers had been treated. A third canker paint based on cadmium sulfate was developed by Parker et al. (726). The formula includes five parts cadmium sulfate solution plus two parts glycerin, two parts muriatic acid, and five parts denatured alcohol. This paint is applied to intact bark, and the dead spurs or small twigs are removed after treatment, not before (441, 498, 537). All these canker paints are poisonous and should not be used unless approved by your State government officials.

Experimental studies by Gardiner (319) using paints containing 550 ppm of streptomycin indicated that weekly applications on cankers in the spring and early summer may stop further development of the cankers and keep them inactive until they finally dry out. Coyier (188) also reported limited control of fire blight infection in cankers with 2,4-xylenol plus *m*-cresol (Bacticin) developed for treatment of crown gall in various fruit and ornamental trees.

Often it is difficult to detect all cankers on a tree. A technique based on infrared sensing has been devised by Specht and Beer (884*a*) in New York State and should alleviate this problem (chap. 8).

Eradication measures should also include eliminating all susceptible wild host plants adjacent to apple and pear orchards. Any susceptible escaped wild plants harboring the fire blight organism may serve as a source of inoculum for orchard trees. This has been shown conclusively in New Zealand (179, 681) and Great Britain (330), where blight spread from hawthorn into pear and apple orchards. The best and only control is to remove these plants.

Tree Nutrition

Any cultural practice that overstimulates growth usually makes the plant or tree vulnerable to serious fire blight infection. One such factor is the production of vigorous growth through applying too much nitrogen. Numerous investigators have associated fire blight infection with nitrogen (80*b*, 94, 188*b*, 303, 425, 584, 727, 899, 936). Blake (94) found that trees which became weak or rank in growth and high in nitrogen also became susceptible to fire blight. A relatively low carbohydrate and high nitrogen content appears to be correlated with fire blight susceptibility and the reverse with resistance (95, 689).

Shoot and body blight in four apple cultivars—Delicious, Northern Spy, McIntosh, and Rhode Island Greening—were markedly increased by application of nitrogen (425). Cultivation, which makes more nitrogen available to the plant, may also increase blight infection. Lewis and Kenworthy (580) found that trees supplied with high nitrogen contained the largest concentration of leaf nitrogen, and several other workers (303, 425, 859, 936) noted that high nitrogen levels enhanced fire blight infection. However, Lewis and Kenworthy also found that the level of nitrogen in other susceptible trees was no different from the level in the least susceptible trees.

The excessive or deficient supply of one element may have an important effect on the balance of elements in the composition of a plant and may affect its susceptibility to fire blight. Therefore the grower should supply his apple and pear trees with a balanced nutrition that will produce maximum yield of high-quality fruit without increasing blight. Such a nutrition program will have to be supplemented by other control measures, such as chemical sprays. For more detailed information on the effect of tree

nutrition and soil fertility on blight development, see chapter 11.

Chemical Control

Much has been published about fire blight control with chemicals. Data since 1920 have been summarized in table 8. Current chemical programs for fire blight control are based principally on protective schedules because available compounds possess poor eradivative properties (405, 503, 650). Periodic applications are required to keep the new growth protected, especially when environmental conditions are optimum for infection. To supplement this program, applications should also be made within 1 day following storms that cause tree injury (1062).

Two groups of chemicals, copper compounds and antibiotics, have had the most important role in controlling fire blight of apples and pears since the 1930's. Copper has been used since the 1900's and antibiotics since the mid-1950's.

Copper Compounds

As shown in table 8, copper compounds gave variable control ranging from poor to excellent (8, 176, 319, 423, 518, 597, 606, 607, 675, 746, 775, 781, 811, 812, 814, 862, 863, 975, 1117). Even in those orchards with satisfactory control, the growers usually complained about fruit russet caused by copper (519, 773, 815). Probably because of this injury, copper is not used more often. However, in some orchards where fruit is processed and russetting is not of great concern, copper is still widely used during the dormant and blossom periods, probably because it costs less than alternate treatments (756).

Copper sulfate plus lime (bordeaux mixture) has been used more often than any other form of copper. Fruit russet is directly proportionate to the copper content of the formula. A 2-6-100 ratio (2 pounds copper sulfate plus 6 pounds hydrated lime per 100 gallons of water) was used most frequently, usually applied one to three times only during the dormant and bloom periods because of injury to the fruit. Spray tests on pears in New Zealand by Dye (251) over a 5-year period failed to show any control of fire blight with bordeaux mixture, but adding streptomycin to this spray gave very effective control.

Other forms of copper have been tried with some success, especially in the Western States (240, 514, 525, 597, 762). More applications are usually applied with these copper compounds, but fruit russetting still limits their use. California investigators (59, 60,

TABLE 8.—*Summary of chemical compounds used to control fire blight on apple and pear*

Chemical compound	Tree	Concentration ¹	Number of applications	Disease severity ²	Disease control ³	Research location	Year	Reference
COPPER COMPOUNDS								
Bioquin ⁴ -----	Apple -----	1 lb/100	1-4	L-M	2	Ill. -----	1947	753a
	Pear -----	1 lb/100	1-4	L-M	2	Ill. -----	1947	753a
Bordeaux ⁵ -----	Apple -----	.5-1-100	14	M	2-3	Ill. -----	1959-60	755, 756
		1.5-6-100	3	S	0-1	N.Y. -----	1958-59	598
		2-6-80	2	M	2	N.Y. -----	1943	423
		2-6-100	5	M	3-4	Ark. -----	1932-33	811, 812, 814, 815
		2-6-100	1	M-S*	0-3	Ind. -----	1927-32	607, 608, 1117
		2-6-100	1	M	2	Iowa -----	1938	176
		2-6-100	2	L	1	Mo. -----	1954	334
		2-6-100	1-2	S	2	N.C. -----	1934	693
		2-6-100	2	L-M	2-3	N.Y. -----	1949	724
		2-6-100	2	M	1-2	N.Y. -----	1960	725
		2-6-100	1-3	M	1-3	S.C. -----	1933	675
		2-6-100	1-2	M-S	1-2	Tenn. -----	1931-34	862, 863
		2-6-100	6	M	3	Wis. -----	1936	514
		2-6-100; 6-12-100	1-5	M	1-3	Wis. -----	1926-37	518, 519, 746
	Pear -----	1-1.5-100	7	M	4	Canada -----	1951	319
		2-6-100	2	L-M	2-3	N.Y. -----	1949	724
		2-6-100	2	M	2	N.Y. -----	1954	378
		2-6-100	1-2	M	2-3	N.Y. -----	1960	725
		2-6-100	2	L-M	1	New Zeal. ---	1964-69	251
		6-12-100	3	S	1-2	Oreg. -----	1923-25	781
		10-10-100	2	M	2-3	Calif. -----	1943	975
Citcop ⁶ -----	-----do-----	1-2 gal/100	6-8	L-M	1	Calif. -----	1973	775
COCS ⁷ -----	-----do-----	1 lb/100	8	L-M	2-3	Calif. -----	1973	775
Coposil ⁸ -----	Apple -----	4 lb/100	6	L-M	3	Wis. -----	1936	514
Copper chelate -----	Pear -----	.5 lb/100	3	M	1	Oreg. -----	1957	525
Copper hydroxide (Kocide) -----	-----do-----	.25 lb/100	6	M-S	2	Calif. -----	1968-69	59
		.25-2 lb/100	6-8	L-M	2-3	Calif. -----	1973	775
		4-8 oz/100	3	L-M*	2-3	Colo. -----	1973	597
Copper-lime dust -----	-----do-----	-----	-----	L	2-3	Calif. -----	1956	35
		10-90%	-----	L	2	Calif. -----	1956	36
		-----	-----	L-M	2-3	Calif. -----	1956	39
		20-80%	7	M	4	Canada -----	1951	319
Copper oxalate -----	Apple -----	4 lb/100	6	L-M	3	Wis. -----	1936	514
Copper oxychloride -----	Pear -----	1 lb/100	3	M	3	Oreg. -----	1957	525

Copper phosphate + lime + bentonite -----	Apple -----	4+8+4/100	6	L-M	3	Wis. -----	1936	514
Copper sulfate -----	-----do-----	4 lb/100	1 (dormant)	L	2	Ill. -----	1954	762
Copper sulfate (tribasic) -----	Pear -----	8 oz/100	2	L-M*	1	Colo. -----	1973	597
		1 lb/100	5-7	M	2	Calif. -----	1954	240
Cuprioleat ⁹ -----	-----do-----	.5%	2	M	3	Denmark ----	1972	384
Cuprocide ¹⁰ -----	Apple -----	1.5 lb/100	6	L-M	3	Wis. -----	1936	514
ANTIBIOTICS								
Aureomycin -----	Pear -----	25 ppm	4	L-M	0	Calif. -----	1956	39
Neomycin -----	Apple -----	100 ppm	4	S	1	Ill. -----	1954	754
	Pear -----	10-50 ppm	3	L-M	2	Calif. -----	1956	39
Oxytetracycline (Terramycin) -----	Apple -----	30-120 ppm	5	L-M	0-1	Del. -----	1952	403
		60-120 ppm	3	L-M	2-3	Iowa -----	1953	863a
		60-120 ppm	3	M*	2-4	Ohio -----	1953	1032
		100 ppm	3	M*	1	Ohio -----	1954	1031
	Pear -----	10 oz/100	8	L-M	2-3	Calif. -----	1973	775
Penicillin -----	-----do-----	1,000 ppm	1	M*	0	Calif. -----	1946	824
Rimocidin -----	Apple -----	30-120 ppm	3	M	0-1	Del. -----	1952	403
Streptomycin nitrate -----	-----do-----	50-100 ppm	3	S	2-4	N.C. -----	1954	177
		100 ppm	2	M	1	N.Y. -----	1960	725
	Pear -----	100 ppm	1	M*	4	N.Y. -----	1963	1111
		100 ppm	5	M	4	Oreg. -----	1954	526
		200 ppm	5	M	3	Conn. -----	1956	650
Streptomycin sulfate -----	Apple -----	60-120 ppm	3	L-M	4	Ohio -----	1953-55	1031, 1032
		60-120 ppm	3	S	2-3	Iowa -----	1953	863a
		100 ppm	2	S	4	Pa. -----	1954	527
Streptomycin (15%) + oxytetracycline (1.5%) (Agrimycin 100).	-----do-----	30-120 ppm	5	L-M	2	Del. -----	1952	403
		50 ppm	9	M	3-4	Ill. -----	1967	759
		50-100 ppm	3-4	S	2-3	Mo. -----	1954	336
		50-100 ppm	2-10	M	3-4	Mo. -----	1969	856
		50-100 ppm	3	S	2-4	N.C. -----	1954	177
		50-200 ppm	8-9	L-S*	2-4	Md. -----	1964-65	505
		60-120 ppm	3	M*	4	Ohio -----	1953	1032
		100 ppm	6	L	3	Calif. -----	1956	39
		100 ppm	4	S	2-3	Ill. -----	1954	754
		100 ppm	4-10	M	2-3	Mo. -----	1970	857
		100 ppm	3	M-S	4	Ohio -----	1954	1033
		100 ppm	2	L	3-4	New Zeal. ---	1963	682
		100-250 ppm	4-7	L	4	Mo. -----	1953	333
		500 ppm	2	M	1-2	N.Y. -----	1964	480, 1111
	Pear -----	10-100 ppm	2	L	1-4	Calif. -----	1956	39
		25-100 ppm	-----	L	1-2	Calif. -----	1956	35
		50 ppm	17	L	?	Calif. -----	1968-69	59
		50 ppm	3	L-M	2	Colo. -----	1964	596
		50 ppm	2-4	S	4	Mich. -----	1962	537
		50-100 ppm	1	M*	1	N.Y. -----	1961	380
		50-100 ppm	1	M	3-4	N.Y. -----	1965	1044

See footnotes at end of table.

TABLE 8.—*Summary of chemical compounds used to control fire blight on apple and pear—Continued*

Chemical compound	Tree	Concentration ¹	Number of applications	Disease severity ²	Disease control ³	Research location	Year	Reference
ANTIBIOTICS—continued								
		50-100 ppm	1	M*	3-4	N. Y. -----	1968	1043
		50-100 ppm	6	M-S	3-4	Calif. -----	1970	59
		60 ppm	3	S	3	Oreg. -----	1955	524
		100 ppm	3	L-M*	2-3	Colo. -----	1973	597
		100 ppm	3	S	3-4	N. Y. -----	1958-59	598
		100 ppm	2	M	2-3	N. Y. -----	1960	1115
		100 ppm	3	M	2	N. Y. -----	1962	482
		100 ppm	4	S	4	Md. -----	1959-61	503
		100 ppm	1	S*	2-3	Md. -----	1971	1061
		100 ppm	5	M	4	Oreg. -----	1954	526
		100 ppm	2	L	3-4	New Zeal. ---	1963	682
		100 ppm	4	L-M	3-4	New Zeal. ---	1964-69	251
		100-200 ppm	2	M	4	N. Y. -----	1954	378
		200 ppm	5	M	3	Conn. -----	1956	650
		10 oz/100	8	L-M	2-3	Calif. -----	1971-73	775, 844
		.04%	2	M	3	Denmark ----	1972	384
Streptomycin + oxytetracycline -----	Apple -----	25 ppm + 50 ppm	4-6	S	1	Mo. -----	1955	337
		100 ppm	3	M-S	3-4	Ohio -----	1954	1033
		125-250 ppm + 250 ppm	4-7	L	3-4	Mo. -----	1954	334
		125-250 ppm + 250 ppm	4-7	M	3-4	Mo. -----	1953	333
	Pear -----	10 ppm + 100 ppm	-----	L	0-3	Calif. -----	1956	35
		30 ppm + 3 ppm	3-7	M	2-3	Calif. -----	1954	240, 241
		50 ppm + 100 ppm	1	M	1-3	N. Y. -----	1955	922
		60 ppm	10	M	4	Calif. -----	1958	34
		60 ppm + 6 ppm	3-7	M	2-4	Calif. -----	1954	240, 241
		100 ppm + 10 ppm	3-7	M	3-4	Calif. -----	1954	240, 241
		100 ppm + 10 ppm	2-4	S	2-3	Oreg. -----	1954	405
		100 ppm + 10 ppm	5	M	4	Oreg. -----	1954	524, 526
		200 ppm	5	M	3	Conn. -----	1956	650
	-----do -----	1,000 ppm; 10% copper	6	L	3	Calif. -----	1956	36
	-----do -----	1,000 ppm; 50 lb/A	10	M	2	Calif. -----	1958	34
	-----do -----	1,000 ppm; 50 lb/A	10	M	2	Calif. -----	1958	34
	-----do -----	2,000 ppm; 30-50 lb/A	10	M	2-3	Calif. -----	1958	34
	-----do -----	240-1,000 ppm	4-14	L	2-3	Calif. -----	1953-55	32, 33
		1,000 ppm	6	L	2	Calif. -----	1956	36
	-----do -----	1,000 ppm	6	L	2	Calif. -----	1956	36
Streptomycin-sulfur dust -----	-----do -----	1,000 ppm	6	L	2	Calif. -----	1956	36
Streptomycin + captan ¹³ -----	Apple -----	50 ppm + 2 lb	3	L-M	2-3	Canada -----	1955	174
Streptomycin + dichlone ¹⁴ -----	-----do -----	100 ppm + .5 lb	3	L-M	0	-----do -----	1956	174
Streptomycin + dimethyl sulfoxide (DMSO) -----	Pear -----	50 ppm + 1-2%	1	M	2	N. Y. -----	1965	1044
		50 ppm + 1%	1	L*	1	N. Y. -----	1968	1043, 1140
Streptomycin + glycerol -----	Apple -----	100 ppm + .5 gal/100	2	M	4	N. Y. -----	1960	725
	Pear -----	50 ppm + .5%	3	M*	2-3	N. Y. -----	1962	482

Streptomycin + glyodin ¹⁵ -----	Apple -----	100 ppm + .5 gal/100	2	M	3-4	N.Y. -----	1960	725
Streptomycin + maneb ¹⁶ -----	Pear -----	100 ppm + 1 pt	3	L-M	2-3	Canada -----	1956	174
Streptomycin + oil-----	-----do-----	50 ppm + 1 lb	1	M	2	N.Y. -----	1965	1044
Streptomycin-oxytetracycline + copper-----	-----do-----	50 ppm + 1%	3	M	1	N.Y. -----	1962	482
Streptomycin + oxytetracycline + zineb ¹⁷ -----	-----do-----	60 ppm + 10-42% copper	10	M	1-4	Calif. -----	1958	34
Streptomycin + Polyram ¹⁸ -----	-----do-----	30 ppm + 3 ppm + 2 lb	3-4	M	1	Calif. -----	1954	240, 241
Streptomycin STA (Merck)-----	-----do-----	50 ppm + 1 lb	1	M	2	N.Y. -----	1965	1044
Streptomycin STB (10%) (Merck) insoluble -----	Apple -----	100 ppm	4	S	2	Ill. -----	1954	754
	-----do-----	100 ppm	3	S	2	N.C. -----	1954	177
	Pear -----	100 ppm	2	M	3	N.Y. -----	1954	378
Streptomycin STC (Merck) insoluble-----	-----do-----	100 ppm	2	M	3	N.Y. -----	1954	378
Streptomycin STD (10%) (Merck) insoluble -----	-----do-----	100 ppm	3	S	4	N.C. -----	1954	177
Streptomycin STS (54%) (Merck) soluble -----	-----do-----	100 ppm	3	S	3	N.C. -----	1954	177
		100 ppm	2	M	4	N.Y. -----	1954	378
STS + oxytetracycline + calcium nitrate-----	-----do-----	75 ppm + 500 ppm calcium nitrate.	5	M	2	Conn. -----	1956	650
STS + oxytetracycline + glycerol -----	-----do-----	75 ppm + 500 ppm glycerol.	5	M	2	Conn. -----	1956	650
STS + oxytetracycline + kerosene-----	-----do-----	75 ppm + 500 ppm kerosene.	5	M	2	Conn. -----	1956	650
Thiolutin ¹⁹ -----	Apple -----	19 g/100	1	M	2	Mo. -----	1952	673, 674
		120-300 ppm	5	L-M	1-2	Del. -----	1952	403
CARBAMATES								
Ferbam ²⁰ (Fermate)-----	-----do-----	1 lb/100	1-4	L-M	0	Ill. -----	1947	753a
	Pear -----	1 lb/100	1-4	L-M	0	Ill. -----	1947	753a
Mancozeb ²¹ (Dithane M-45) -----	-----do-----	.2%	2	M	3	Denmark ---	1972	384
Maneb ¹⁶ (Manzate, Dithane M-22) -----	Apple -----	1-2 lb/100	2	M	1	N.Y. -----	1964	1111
		2 lb/100	2	M	2	Del. -----	1952	403
	Pear -----	1,000 ppm	1	M*	2	N.Y. -----	1963	1111
		1 lb/100	1	M*	2	N.Y. -----	1965	1044
		1 lb/100	1	M*	1	N.Y. -----	1968	1043
Nabam ²² (Dithane D-14) -----	-----do-----	1,000 ppm	1	M*	2	N.Y. -----	1963	1111
Polyram ¹⁸ -----	-----do-----	1 lb/100	1	M*	0	N.Y. -----	1965	1043, 1044
Zineb ¹⁷ (Parzate, Dithane Z-78) -----	Apple -----	2 lb/100	1-3	L	2-3	Colo. -----	1947-48	944
		2 lb/100	5-8	L-M	1-2	Del. -----	1952-53	402, 403
		2 lb/100	4	S	1	Ill. -----	1954	754
		2 lb/100	3	L-M*	2	Iowa -----	1953	863a
		2 lb/100	3	M	0-1	N.Y. -----	1954	598
		2 lb/100	1	L*	0-1	N.Y. -----	1962	482
		2 lb/100	3	L	2	Ohio -----	1953	1032
	Pear -----	.5-1.5 lb/100	3	L	2-4	Wash. -----	1952	884c
		2 lb/100	1-2	L	2-4	Colo. -----	1945-48	944
		2 lb/100	5	L	0	Oreg. -----	1954	524, 526
Ziram ²³ (Zerlate)-----	-----do-----	2 lb/100	1-3	M	2	Colo. -----	1948	944

See footnotes at end of table.

TABLE 8.—*Summary of chemical compounds used to control fire blight on apple and pear*—Continued

Chemical compound	Tree	Concentration ¹	Number of applications	Disease severity ²	Disease control ³	Research location	Year	Reference
MISCELLANEOUS								
ABG-1000 ²⁴ -----	Pear -----	20 ppm	4	L-M*	2	Colo. -----	1973	597
Bronopol SP. ²⁵ -----	-----do-----	.1-.4%	2	M	3	Denmark ----	1972	384
Captan ¹³ -----	-----do-----	2 lb/100	1	L-M	2-3	N. Y. -----	1961	380
		2 lb/100	1	M*	1	N. Y. -----	1962	482
Dichlone ¹⁴ -----	Apple -----	.5 lb/100	4	S	1	Ill. -----	1954	754
Dimethyl sulfoxide (DMSO)-----	Pear -----	2%	1	M	1	N. Y. -----	1965	1044
Emmi ²⁶ -----	-----do-----	600 ppm	1	S	3	Mich. -----	1962	316, 537
Expt. Fungicide 5379 -----	-----do-----	1 lb/100	3	L	2	Wash. -----	1952	884c
HPMTS ²⁷ -----	-----do-----	.3%	2	M	3	Denmark ----	1972	384
Lime -----	Apple -----	4 lb/100	6	L-M	0	Wis. -----	1936	514
MBR-10995 ²⁸ -----	Pear -----	150-300 ppm	4	L-M*	2-3	Colo. -----	1973	597
		150-600 ppm	6-8	L-M	2-3	Calif. -----	1973	775
OM-1562 ²⁹ -----	-----do-----	2 lb/100	1	L*	4	Mich. -----	1962	537
Phenacridane chloride ³⁰ -----	Apple -----	100-400 ppm	7	M	2-3	Ill. -----	1961	136
Phosphamidon ³¹ (Dimecron) -----	Pear -----	1 qt/100	1	L	0	Mich. -----	1962	316, 537
Puritized Agricultural Spray ³² -----	-----do-----	1 pt/100	1-2	L	0	Colo. -----	1948	944
TD-225 ³³ -----	-----do-----	800 ppm	1	L	1	Mich. -----	1962	537
UC-17525 ³⁴ -----	-----do-----	900 ppm	1	L	4	Mich. -----	1962	316, 537
UC-19297; ³⁵ UC-20712 ³⁶ -----	Apple -----	1,000 ppm	2	M	2-3	N. Y. -----	1964	480, 1111
Uni G 554 -----	Pear -----	.4%	2	M	3-4	Denmark ----	1972	384
Vanicide 51 ³⁷ -----	-----do-----	2 lb/100	3	L	0	Wash. -----	1952	884b
Vanicide Z-65 ³⁸ -----	-----do-----	2 lb/100	2	M	2	N. Y. -----	1954	378
Zinc sulfate -----	Apple -----	2 lb/100	1-2	L	1	Colo. -----	1948	944
	Pear -----	2 lb/100	1-2	L	0	Colo. -----	1948	944

¹Concentration: 1 oz=28 g, 1 lb=454 g, 1 pt=473 ml, 1 qt=946 ml, 1 gal=3.8 l; /A=per acre (2.5 acres=1 ha); /100=per 100 gal of water; bordeaux mixture (2-6-100) indicates 2 lb of copper sulfate plus 6 lb of hydrated lime per 100 gal of water; all other dash signs indicate a range.

²L=light, M=medium, S=severe; asterisk (*) indicates artificial inoculation.

³0=none, 1=poor (1-35 percent), 2=moderate (36-75 percent), 3=good (76-89 percent), 4=excellent (90-100 percent).

⁴Copper 8-quinolinolate.

⁵Pounds of copper sulfate plus pounds of hydrated lime in water.

⁶Copper salts of fatty and rosin acids.

⁷Copper oxychloride sulfate.

⁸Unidentified copper compound.

⁹Copper oleate "Cu-dol," 2.6 percent copper.

¹⁰Copper oxides.

¹¹Tetracopper calcium oxychloride, 55 percent (metallic copper, 45 percent).

¹²Hydrous aluminum silicate.

¹³N-[(Trichloromethyl)thio]-4-cyclohexene-1,2-dicarboximide.

- ¹⁴2,3-Dichloro-1,4-naphthoquinone.
- ¹⁵2-Heptadecyl-2-imidazoline acetate.
- ¹⁶Manganous ethylenebis(dithiocarbamate).
- ¹⁷Zinc ethylenebis(dithiocarbamate).
- ¹⁸Mixture of ethylenebis(dithiocarbamate)zinc and dithiobis(thiocarbonyl)iminoethylene)bis(dithiocarbamate)zinc.
- ¹⁹6-(Acetylmino)-4-methyl-1,2-dithiolo[4,3-b]pyrrol-5(4*H*)-one.
- ²⁰Ferric dimethyldithiocarbamate.
- ²¹Zinc ion and manganous ethylenebis(dithiocarbamate) complex.
- ²²Disodium ethylenebis(dithiocarbamate).
- ²³Zinc dimethyldithiocarbamate.
- ²⁴Unidentified experimental compound (Abbott).
- ²⁵2-Bromo-2-nitro-1,3-propanediol.
- ²⁶*endo*-1,4,5,6,7,7-Hexachloro-*N*-(ethylmercuri)bicyclo[2.2.1]hept-5-ene-2,3-dicarboximide.
- ²⁷2-Hydroxypropyl methanethiosulfonate.
- ²⁸New organic compound from 3M Co.
- ²⁹Copper salt of 2-pyridinethiol 1-oxide.
- ³⁰9-[4-(Hexyloxy)phenyl]-10-methylacridinium chloride.
- ³¹2-Chloro-2(diethylcarbamoyl)-1-methylvinyl dimethyl phosphate.
- ³²Phenylmercuric triethanolammonium lactate.
- ³³Pyrimidine compound.
- ³⁴*alpha*-(Bromoacetyl)valinamide.
- ³⁵*N*-Hydroxy-5-nitro-2-furancarboximidamide.
- ³⁶*alpha*-(2-Bromoacetoxy)acetanilide.
- ³⁷Sodium dimethyldithiocarbamate (27.6 percent) plus sodium salt of 2-benzothiazolethiol (2.4 percent).
- ³⁸Zinc salt of 2-mercaptobenzothiazole (65 percent).

657, 773–775) have been fairly successful in controlling blight in pear trees with copper hydroxide (Kocide) and other forms of copper, especially in orchards where the *E. amylovora* population has become resistant to streptomycin. In general, the copper compounds appear to give better blight control when disease severity is low to moderate, and they produce more phytotoxicity when applied during damp or wet periods.

Copper-lime dust has also been used on the west coast (35, 36, 39, 843). Under light disease conditions these dusts have given moderate to satisfactory control, but again fruit russetting limits their use. There is some evidence, however, that fruit russet may be associated with unfavorable weather conditions (370, 387).

Antibiotics

The most important development relative to fire blight control was the discovery and application of antibiotics in the early 1950's. It was natural for this development to take place, especially after the successful use of antibiotics in human diseases difficult to control.

The earliest studies on controlling fire blight with antibiotics were in 1951 by Murneek (673, 674) of Missouri. Thiolutin and streptomycin were applied once when 90 percent of the Jonathan apple blossoms were open. An average of 48 infections per tree developed with the thiolutin treatment and 94 with streptomycin compared with 224 in the untreated control. In the next 3 or 4 years, several other workers (32, 240, 333, 403, 1032) conducted additional field studies that proved the efficacy of streptomycin in controlling fire blight in both apple and pear orchards. In general, streptomycin gave better control of this disease than did copper and normally caused no fruit russet. The lack of injury probably appealed to many growers, even though the antibiotic program cost considerably more than the alternate copper schedule.

Streptomycin came into general commercial use during the late 1950's and early 1960's. Both streptomycin nitrate (177, 525, 650, 725) and streptomycin sulfate (35, 39, 52, 59, 82, 177, 333, 336, 344, 378, 380, 387, 403, 503, 524, 526, 527, 537, 596, 597, 650, 682, 754, 755, 844, 1031, 1032, 1043, 1044, 1061, 1115) were evaluated on apples and pears and both resulted in commercial control of fire blight. The sulfate form of streptomycin was generally used, whereas the nitrate form was only used occasionally.

In the early antibiotic research a widely used formulation contained a combination of 15 percent streptomycin sulfate and 1.5 percent oxytetracycline (Terramycin) (34, 35, 240, 241, 333, 334, 337, 405, 498, 524, 526, 650, 922). Laboratory studies showed *E. amylovora* developed resistance far more slowly with the combination than with streptomycin alone (273). This combination was used commercially for many years until the oxytetracycline was removed during the 1960's, apparently because the combination showed no advantage when used in the field.

One wonders whether streptomycin-resistant strains of *E. amylovora* would have occurred in California (657, 658, 949), Washington (182a), and Oregon (189) in 1971–72 if growers had been still using the combination of streptomycin and oxytetracycline. However, streptomycin-resistant *E. amylovora* has been found in areas where little or no streptomycin was used previously as well as in orchards where it was applied many times for several years. Conceivably one might substitute oxytetracycline for streptomycin in orchards where only resistant *E. amylovora* occurs.

On the other hand, data ¹⁷ from Beltsville tests indicate that such a substitution should not be made in orchards where only streptomycin-susceptible *E. amylovora* exists. These tests demonstrated that oxytetracycline was much inferior to streptomycin under these conditions. Surveys in 1972–74 revealed only two streptomycin-resistant isolates—one from a Golden Delicious apple tree regularly sprayed with streptomycin and one from an unsprayed tree. Beer and Norelli (81b) were unable to find any streptomycin-resistant isolates of *E. amylovora* in 19 orchards surveyed in western New York.

In one orchard in Washington, Covey (182a) made detailed isolations of resistant and susceptible *E. amylovora*. In 1972, all isolates were found to be streptomycin resistant, whereas in 1973, only half of the isolates were resistant. Based on streptomycin-resistance surveys, these mixed populations may make spray recommendations more complicated in the future.

During the early research, streptomycin was restricted to bloom application for fear that toxic residues might remain on the fruit if it was applied during the postbloom period. Because the bloom

¹⁷ Unpub. data, Fruit Lab., U.S. Dept. Agr., Beltsville, Md.

period on the west coast, especially for pears, extends over a long time, it was possible legally to make many applications. However, elsewhere in the country where the bloom period usually is short, only one to three applications were made. Obviously during long bloom periods young fruit might be present on trees still in bloom. However, in pome fruit-growing areas east of the Rocky Mountains much blight infection develops during the postbloom period. In fact, studies at Beltsville demonstrated that at least 50 percent of the blight infection on pears and apples occurs during this period (503). Streptomycin sprays extended into this period adequately controlled postbloom infection (503, 856, 857). The few blighted shoots found at this time in the streptomycin-sprayed trees could easily be removed by pruning. However, pruning of unsprayed trees took considerable time because of their many infections (498, 503).

At the same time, studies in California (657) and Beltsville¹⁷ demonstrated negligible streptomycin residue on pear fruit when sprays were discontinued 30 days before harvest. Similar studies on apples at Beltsville showed negligible residue if the sprays were stopped 50 days before harvest (504, 505). In New Zealand, little or no residue was detected on apples if the last spray was applied 5 weeks before harvest (252). Unfortunately this schedule was not followed in the Maryland studies, hence the 50-day limitation. Because of these residue studies a tolerance of 0.25 ppm of streptomycin residue was permitted by the U.S. Food and Drug Administration in July 1968 with a 30-day-to-harvest limitation on pears. Shortly thereafter a similar tolerance was set for apples with a 50-day-to-harvest limitation.

In general, the data in table 8 show that streptomycin applied to apples (39, 177, 333, 336, 403, 480, 505, 527, 682, 754, 759, 856, 857, 1031–1033) and pears (35, 39, 59, 378, 380, 482, 503, 524, 526, 537, 596, 598, 658, 682, 775, 1043) gave moderate to excellent control of fire blight. Sometimes satisfactory commercial control was demonstrated even under severe disease conditions. Streptomycin appeared to be superior to any other treatment in most tests reported and showed little or no phytotoxicity. It usually caused no fruit russeting, but occasionally slight chlorotic spotting of foliage was evident. This soon disappeared when spray applications were discontinued.

Most streptomycin applications are made during the daylight hours. However, Powell (759) of Illinois

first demonstrated that streptomycin is more effective if applied at night. Using spray intervals of 4–13 days (shorter following rainy periods), nighttime applications gave excellent control of fire blight on Jonathan apples compared with moderate control for the daytime schedule. Many growers have not yet accepted nighttime spraying, apparently because it deviates from their usual pattern of activity. However, if farmers once shifted to such a program, especially when better control can be obtained, they might be more willing to accept nighttime spraying.

Better control reported by Powell (759, 761) and Goodman (338) appears to be related to both temperature and relative humidity. Less streptomycin is required for a given degree of control at 18° C (65° F) or higher than at 10° (50°) or lower. Winter and Young (1034) and Petersen (736) also reported better control with streptomycin when applied during higher temperatures. There is also greater streptomycin absorption by leaf tissue at 95–100 than at 35–40 percent relative humidity. These interactions explain the increased control obtained with nighttime applications and the recommended 100 ppm of streptomycin during the bloom period when temperatures are cool.

Comparisons between concentrate and dilute sprays for fire blight control have been tested since 1972. In California, Beutel et al. (82) found that concentrate and dilute sprays of 50 and 200 gallons per acre (75 and 300 l/ha), respectively, of streptomycin on pears gave equally satisfactory control of blight. The more streptomycin they used, the better the control. In 1976, Beer (80a) showed similar results on apples in New York with streptomycin applied in 60 versus 360 gallons per acre (90 and 540 l/ha). However, significantly poorer control was obtained when streptomycin was applied in 25 gallons per acre (37 l/ha). In streptomycin tests on apples in Missouri comparing dilute and low volume sprays at 400 and 120 gallons per acre (600 and 180 l/ha), respectively, Shaffer and Goodman (858) demonstrated that about twice as much antibiotic was absorbed by fruit buds with the low volume sprays. These results suggested that one could reduce the antibiotic 50 percent and obtain the same degree of control as with dilute sprays. However, studies¹⁷ at Beltsville under severe fire blight conditions showed better control when streptomycin was kept near the level recommended on the label for dilute sprays.

Although streptomycin sprays were used more extensively than dusts, California investigators

(32-34, 36, 41, 42) formulated, developed, and made limited use of the latter. Dusts used at 50 pounds per acre (9 kg/ha) gave satisfactory fire blight protection, but when the dosage was reduced to 30 pounds (5.5 kg/ha), the amount of fire blight increased sharply (34). In the same tests, however, streptomycin sprays gave better control than the dust formulations. Copper A formulated with streptomycin in dusts gave satisfactory fire blight protection in some tests without evidence of fruit russet (36). Early studies showed that bentonite as a dilutant or extender for streptomycin was unsatisfactory because it failed to release the antibiotic (33). However, substituting pyrophyllite for the bentonite worked well (32, 33, 36). Some streptomycin dusts are still used under certain conditions in some fruit areas.

Streptomycin has also been used experimentally as an afterharvest fruit dip to eliminate surface-borne *E. amylovora*. These dip treatments were developed by Dueck (238) of Canada as a precaution against possible spread of the pathogen on fruit surfaces to fire blight-free areas. Of those compounds tested, streptomycin sulfate at 250 ppm and acetic acid at 1.0 M were most effective. Several combinations of these compounds killed all bacterial cells on the surface. When apples were immersed in a water suspension of bacterial ooze (8.2×10^6 cells per milliliter), a 10-minute dip in 1.0 M acetic acid was completely effective. In other dip tests with Bartlett pear fruit, Wilson (1028) demonstrated enhanced ripening but no control of *E. amylovora* with an isopropanol treatment. In Washington, Wright (1042) reported definite infection of healthy fruit through contact with diseased fruit but failed to do so when bacterial inoculum was added to a hot water dip (32° C, 90° F).

Most other antibiotics evaluated for control of fire blight in the field were less effective than streptomycin (37, 39, 43, 403, 754, 824). However, Billing et al. (87) in laboratory studies found various cultures of *E. amylovora* sensitive to chloramphenicol, streptomycin, and Terramycin but resistant to penicillin. In vitro tests conducted by Morgan and Goodman (663) and Morgan (1119) showed Aureomycin and neomycin equal to streptomycin, but polymixin, streptothricin, and viomycin were slightly better, whereas Chloromycetin was definitely less effective by the agar diffusion technique. Laboratory studies by Martinec and Kocur (630) showed also that 49 strains of *E. amylovora* were sensitive to tetracycline, erythromycin, and neomy-

cin but resistant to tyrothricin, nystatin, and bacitracin and variable with chlortetracycline. Colasito et al. (180) also noted that circulin in vitro was more effective than streptomycin. Both laboratory and field tests by Klos (537a) indicated that LMA-B-100 (spectinomycin) significantly controlled fire blight. However, in later studies by investigators in Michigan as well as several other States, it was found to be too phytotoxic for practical use.

Several attempts to improve the effectiveness of streptomycin by adding adjuvants to the antibiotic spray have had limited success (10, 334, 346, 365, 399, 482, 595, 598, 725). Fungicides and insecticides combined with streptomycin showed variable results (174, 854, 1044, 1111, 1140). Cing-Mars and Crete (174) reported some success when using glyodin and captan in combination with streptomycin on apples, but dichlone had no effect. Likewise, studies by Shaffer and Goodman (857) suggested that glyodin and sulfur aid control when added to streptomycin sprays on apples. They also found that sulfur, captan, Polybor, zineb, dodine, and endrin inhibited absorption of streptomycin. Carbaryl, DDT, lead arsenate, and parathion increased absorption of streptomycin, whereas dieldrin and phenyl mercuric acetate did not alter uptake of the antibiotic by apple leaves (854). In greenhouse trials, Hamilton and Szkolnik (380) found that captan reduced the effectiveness of streptomycin when exposed to simulated rain.

In laboratory experiments, Zehr (1043) found that maneb, Polyram, and glyodin supplemented the activity of streptomycin when they were combined in vitro, but dodine and captan had little or no effect. Combining fungicides in hope that they would enhance the bacterial action of streptomycin was not very successful with Polyram, maneb, and dimethyl sulfoxide in greenhouse and field tests (1044, 1140). Other investigators indicated variable results with certain miscellaneous compounds (80a, 379, 496, 568, 922). Additional laboratory and greenhouse studies indicated that adding glycerin to streptomycin sprays tended to increase the effectiveness of the antibiotic (365, 482, 725). However, field studies failed to demonstrate any significant increase with this combination compared with streptomycin alone. The addition of superior '70' oil to streptomycin lessened fire blight control in pear in New York State (482). In vitro studies by Keitt et al. (517) showed high toxicity of mercury compounds of *E. amylovora*, but sulfur was ineffective.

Carbamates

The carbamate compounds were used commercially for several years on vegetables and fruit to control various fungus diseases before anyone field tested them for fire blight on pome fruit. In Delaware, Heuberger and Poulos (403) and Heuberger et al. (402) conducted much of the early field testing of carbamates to control vegetable fungus diseases and were the first to evaluate these compounds on apples for control of fire blight. About the same time, Sprague ¹⁸ in Washington also tested them on pears. These investigators found that zineb gave moderate control of fire blight. However, blight severity in these studies was light to moderate, which probably accounted for the favorable results.

In other tests, usually under more severe fire blight conditions, carbamates failed to give satisfactory control of fire blight (480, 482, 524, 525, 598, 754, 1043, 1044). On some occasions, however, control on apples or pears with carbamates appeared to be acceptable (380, 384, 944, 1044). In general, under severe blight conditions the carbamates appear to be far less effective than the antibiotic streptomycin.

Miscellaneous Compounds

In the early 1930's, Thomas (940) determined in the laboratory by phenol coefficients the bactericidal efficiency of 14 disinfectants with respect to certain plant pathogens. Only mercuric chloride, ethyl mercury chloride, and all mercurial derivatives exhibited considerable activity against *E. amylovora*. In Denmark, Johansen (478) reported in 1969 that he had evaluated several commercial fungicides against *E. amylovora* in the laboratory. Maneb, mancozeb mercury, and copper were bactericidal, whereas thiram was bacteriostatic. In vitro studies by Jones (1111) also indicated that nabam, mane, and UC-19297 showed some promise for controlling fire blight.

Many miscellaneous compounds have been field tested for fire blight control, as shown in table 8. Most of them gave little or no control of the disease, and only a few appeared promising (136, 316, 378, 380, 403, 482, 514, 537, 597, 754, 775, 944, 1044, 1111). However, one new organic compound (MBR-10995) showed promise as a potential commercial bactericide for controlling fire blight (597, 775). In limited tests in several geographic areas, control with MBR-10995 appeared to be at least

equal to control with streptomycin. At Beltsville,¹⁹ 600 ppm of MBR-10995 were required to give control on apples or pears equal to control with 100 ppm of streptomycin. These results indicate that this compound should be considered in future evaluation trials.

An interesting approach for control of twig blight resulted from preliminary studies by Klos (537a) and Klos and Ritchie (538), who demonstrated that retarding tree growth with a chemical such as Alar significantly reduced the amount of blight in pear twigs during the summer.

In Belgium, Veldeman (976b) suggested indirect control of fire blight in hawthorn through chemical destruction of the flowers. He obtained good results in reducing blossoms and fruit set, with moderate to severe leaf damage, by spraying hawthorns with aqueous solutions of sodium hydroxide.

Most chemical and biological control treatments are usually applied as sprays or dusts. Recently a trunk injection technique has come into vogue. Holes are drilled into the tree trunk and concentrate or dilute materials are siphoned by either gravity feed or under pressure into the tree. Apple trees injected with thymol showed some resistance to the progress of *E. amylovora* (841). Tests ¹⁹ at Beltsville indicated that MBR-10995 injected into the trunks of fire blight-infected pear trees prolonged their life. Although these results were preliminary, they introduced a new approach to controlling diseases in trees.

Apparently additional screening of chemical compounds, including growth regulators, in laboratory, greenhouse, and field tests, as well as improved application techniques, should be conducted by industry, State, and Federal investigators to find a more effective, less expensive, but longer lasting control for fire blight.

Monitoring

Like fungicides, bactericides are frequently applied before any part of the plant becomes visibly infected. For fire blight, such a protective schedule sometimes includes from three to eight applications depending on the part of the country where the trees are grown. In California, many growers apply from 10 to as many as 18 applications (59, 657, 844). If the pathogen can be reliably monitored, the number of

¹⁸ Pers. commun., Tree Fruit Res. Cent., Wenatchee, Wash.

¹⁹ Unpub. data, Fruit Lab., U.S. Dept. Agr., Beltsville, Md.

applications can be reduced. In general, protective applications are restricted, because streptomycin is ineffective if applied after infection occurs (405, 503, 650). With such a program, there is always the possibility that serious fire blight would not have developed anyway, and thus much time, effort, and money would have been wasted.

Miller et al. (655) and Thomson et al. (950, 951) in California have conducted research on a system of monitoring pear flowers for the presence of *E. amylovora*. Their studies showed that, although over 50 percent of the healthy flowers in some orchards were infested with about 10^6 cells of *E. amylovora* per flower (fig. 17, C-E), subsequent disease incidence was only one to three infections per tree. Furthermore, these studies showed that the susceptibility of pear flowers to disease varied from year to year, during the season, and among flowers of a cluster. Because so many apparently healthy flowers and other plant parts harbor potentially dangerous *E. amylovora* (fig. 17), some way must be found to kill or inactivate them so that fire blight will not flair up when conditions are optimum for disease development.

Sutton and Jones (915a) in Michigan used a similar isolation method to detect *E. amylovora* in infected and apparently healthy apple tissues. *E. amylovora* was not detected in samples from 12 apple orchards before infections were prevalent in the orchards nor in the severely blighted orchards until numerous additional infections were apparent. More recently Beer and Oppenorth (81d) in New York isolated *E. amylovora* from the surface of some nonoozing fire blight cankers in one pear and four apple orchards, sometimes before blight symptoms appeared. However, the pathogen was not usually recovered from canker surfaces before bloom and not from blossoms in the early stages of bloom. These investigators pointed out that *E. amylovora* was not detected in blossoms in sufficient time to prevent infection by the immediate application of bactericides.

When a monitoring system is perfected for both pear- and apple-growing areas, we may expect more effective spacing of sprays, which will result in considerable savings for the grower. In California, Thomson ²⁰ estimated a savings of one-half to three-quarter million dollars during the 1975 growing season after growers used fewer spray applications based on the monitoring system.

Insect Control

Aphids, flies, ants, tarnish plant bugs, and leafhoppers have been implicated in the spread of fire blight (40, 145, 714, 726, 901, 902, 905, 906). Flies and ants are attracted to bacterial ooze, where their bodies may become contaminated. They then carry the fire blight bacteria to uninfected parts of the plant, where new infections may start if conditions are optimum. These insects should be kept under control with insecticide applications.

Bees rarely if ever feed on bacterial ooze and are not the principal agents involved in producing the first spring blight as once thought (chap. 8). However, bees after visiting blighted blossoms can spread fire blight to uninfected blossoms (357, 744, 750, 806-808, 933). Therefore keeping beehives out of an orchard during the pollination period is unnecessary, but blight should be controlled during bloom.

During the remainder of the growing season certain piercing and sucking insects often inhabit some legumes and other cover crops in or near the orchard. When such crops are harvested or plowed under, these insects may migrate to the fruit trees. Therefore insecticides are recommended in some areas as additives to regular fire blight spray control programs (183a).

Biological Control

Some investigators have attempted to control fire blight with biological means. Thomas and Ark (934) were among the first to test several isolates, mostly bacteria, in petri dish cultures for antagonism toward *E. amylovora*. Some of these isolates inhibited growth of this organism. Parker (722) also conducted studies during 1928-31, whereby he introduced into the blossoms the organisms that were antagonistic to the fire blight organism. The antagonists were mixed with *E. amylovora* and introduced into the blossoms together or sometimes separately. These studies indicated a tendency for some of the antagonists to reduce the percentage of fire blight infection. Ark and Hunt (38) continued to search during 1936-41 for other antagonists and found two isolates from soil, which in vitro tests were active against *E. amylovora*, as well as certain other phytopathogenic micro-organisms. In the early 1950's, Stessel et al. (897) screened about 70,000 colonies of soil micro-organisms in petri dish studies for activity against various plant pathogens. Three

²⁰ Pers. commun., Dept. Plant Path., Univ. Calif., Berkeley.

of these organisms exhibited considerable activity against *E. amylovora*.

In the mid-1960's, Goodman (340) reported in vitro and in vivo interactions between components of mixed bacterial cultures isolated from apple buds. Single-cell isolates were derived from a bud isolate 35A—a virulent white (35A-W) organism sensitive to five *E. amylovora* bacteriophages and an avirulent yellow (35A-Y) form sensitive to two phages. When mixed together, the yellow organism produced sufficient acid to inhibit growth of the virulent white organism and thus prevent it from causing infection. Also, about this time Klos (537a) showed that spraying Bartlett pear blossoms with an unidentified yellow organism 24 hours before inoculation significantly reduced blight infection.

Riggle and Klos (790, 791) and Klos and Ritchie (538), working with isolates of *E. herbicola* from fire blight cankers, also demonstrated buildup of acid inhibitory to *E. amylovora*. On the other hand, Chatterjee et al. (164) suggested that *E. herbicola*, a yellow organism often associated with *E. amylovora* in fire blight-diseased tissues, possesses a beta-glucosidase, which breaks down arbutin to hydroquinone and D-glucose. Hydroquinone accumulated in cultures of *E. herbicola* grown in arbutin broth to ca. 1,000 μ g per milliliter in 24 hours but to a much less extent in *E. amylovora* cultures. They

suggested that the accumulation of high levels of hydroquinone by *E. herbicola* might contribute to the fire blight resistance of the plant by inhibiting the metabolic activity of *E. amylovora* and reduce its effectiveness as a phytopathogen.

In tests in Great Britain with pear slices and hawthorn shoots, one isolate of *E. herbicola* often prevented infection when inoculated before *E. amylovora*, but there was little or no protection when they were applied together (254).

In Missouri, Goodman (341) later showed that *Pseudomonas tabaci*, as well as a yellow *Erwinia*-like isolate (35A) and avirulent isolates of *E. amylovora*, protected against infection from a virulent strain of *E. amylovora*. However, *Xanthomonas pruni* was unable to induce the protective effect. In California, Reil et al. (775) reported in 1974 that an application of bacteria antagonistic to *E. amylovora* gave some control of fire blight but not as effectively as a chemical treatment.

Although these biological control studies indicate some potentially useful control of the fire blight disease through antagonistic organisms, none of these control measures are sufficiently effective to replace chemical treatments. If some way can be found to enhance the activity of these organisms, they may be useful in the control program.

CHAPTER 13

NATURE OF RESISTANCE

Since the middle of the 19th century, differences in degree of fire blight resistance have been known to exist between cultivars of pear and apple. More recently such differentiation has been shown between species of *Pyrus* and *Malus* as well as among cultivars, species, and clonal selections of quince, hawthorn, pyracantha, and other genera of the family Rosaceae. However, blight resistance in plant material as discussed here is not necessarily innate.

Depth of blight penetration in plants is strongly affected by (1) the age, vigor, and nutrition of the host; (2) environmental factors, particularly temperature and humidity; (3) soil types, moisture content, and cultural practices; and (4) a combination of one or all of these factors with the time of bloom. Therefore the most realistic measure of the degree of blight resistance for any cultivar, seedling, or clonal selection can best be determined when the plant material is grown and tested under optimum conditions for blight development.

Plant material may be evaluated in many different ways and with various techniques for fire blight resistance. An attempt to grow uniform apple and pear seedlings for experimental use was reported at the Phytobacteriology Workshop in Missouri (344a). Because of the great diversity of techniques and results obtained by fire blight investigators, the procedures should be standardized in order to obtain uniform results.

To express the degree of fire blight resistance in pear and apple, many investigators have developed various blight rating systems. Following inoculation of succulent shoots of young pear material, Thompson et al. (948) established four blight-resistance classes based on the extent of infections. Lamb (550) measured the length of shoot killed and used values in excess of 100 percent to indicate infection in older wood. For large orchard trees, Mowry (667) developed a blight rating index using a factor obtained by multiplying the number of infected twigs times 5 and the age of infected wood times 20.

To score large numbers of clonal and seedling trees in the pear breeding program at Beltsville, a simple, efficient, and dependable rating system was

developed to estimate the severity of damage (1071). This system is based on (1) the number of branches infected, (2) the age of the wood into which the blight organism has penetrated, and (3) the overall percentage of tree blighted. The scale is a descending rating from 10 to 1 and is a visual estimate of tree damage. A score of 10 indicates a tree with complete absence of blight symptoms, whereas a score of 1 means a tree is entirely dead from fire blight. Figure 25 is a schematic diagram of a tree showing various degrees of blight and the location of blight for each percent score. This scoring system can also be used to determine the degree of blight resistance in apples.

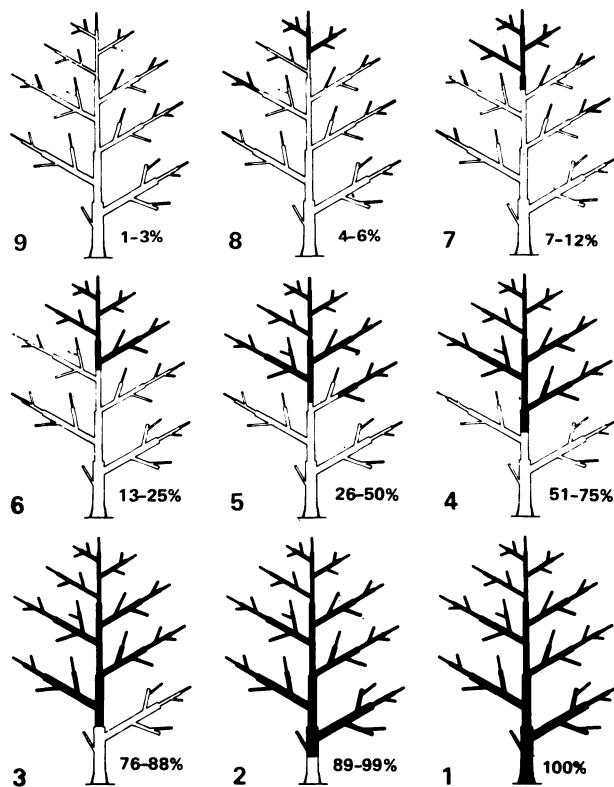


FIGURE 25.—Schematic diagram of USDA fire blight scoring system used to evaluate degree of blight resistance in apple and pear trees.

From these 10 blight scores, 4 classes of blight resistance are arranged as follows:

Resistance class	Score	Percent blighted
Highly resistant -----	10-8	0-6
Moderately resistant -----	7-6	7-25
Susceptible -----	5	26-50
Very susceptible -----	4-1	51-100

To simplify ratings of large numbers of cultivars, score 5 is combined with scores 4-1 into one susceptible class.

The tables in this chapter contain the names of most *Pyrus* species, as well as those of the best known pear and apple cultivars. The cultivars are divided into those named prior to 1920 and those since then (118, 119). The listing of degrees of blight resistance is based mainly on records of natural blight as given in the literature, although some ratings were assigned arbitrarily. Also, different sports of a cultivar may have lower or higher blight ratings than the original cultivar. For specific details on any one species, cultivar, or clonal selection, refer to the pertinent reference cited in the table.

Pear

The genus *Pyrus* has been classified under the subfamily Pomoideae and contains approximately 20 true species, all indigenous to Europe, Asia, and Africa (771, 1015). Challice (1092) and Challice and Westwood (155) made a detailed taxonomic study of the genus. Based on a total of 51 chemical and botanical characters, they classified the species into the following main groups: (1) East Asian pea pears, (2) larger fruited East Asian pears, (3) North African pears, and (4) European and West Asian pears.

In table 9 are listed the 21 true and 13 miscellaneous species, the latter classified as natural or arboretum hybrids. The following descriptions and records of blight resistance are for the five most economically important *Pyrus* species.

Pyrus communis

Practically all our cultivated varieties of pears have been derived from *P. communis* L., the native pear of Europe. It is also known as the common, domestic, or cultivated pear. The finest cultivars of this species are superior in quality to those of any other species. Although these cultivars vary considerably in their degree of blight resistance, none of the high-quality European pears are known to be sufficiently resistant to thrive in regions where fire blight is serious.

The losses by fire blight sustained by cultivars of *P. communis* have undoubtedly been greater than those by any other disease. In addition, fire blight has unquestionably been responsible for greater losses in American pears than all other pear diseases combined. Following 2 years of epiphytotic blight conditions at Beltsville, nearly 90 percent of the trees in a worldwide collection of more than 500 pear cultivars were destroyed (707). Most of the cultivars in the resistant blight classes were of oriental origin. Such cultivars as Kieffer, LeConte, and Garber, hybrids of *P. communis* cultivars with oriental pears, were long believed to be rather resistant (528, 716, 1011), but even these have often been blighted severely (707, 908, 909, 1037, 1070).

As with most other *Pyrus* species, many clonal selections and cultivars of *P. communis* are very susceptible to fire blight, whereas others are highly resistant. Cultivars such as Conference, DeVoe, Forelle, and Laxton's Superb are very susceptible, whereas Orient, Richard Peters, and Waite are highly resistant. In between these two extreme classes are two general groups of pears—cultivars that are rather consistently resistant to moderately resistant, such as Ayres, Mac, and Moonglow, and cultivars that show variable resistance, indicating that some trees are highly resistant and others moderately resistant to very susceptible (1070). Cultivars in this last group include Comice, Dawn, Duchess, Kieffer, and Maxine (Starking Delicious). Many other pear cultivars, such as Bartlett, Beurre Bosc, Beurre d'Anjou, and Clapp Favorite, are generally susceptible to fire blight. However, they are usually not as susceptible as those in the very susceptible group.

In table 10 are listed 400 cultivars of *P. communis*. Some of them, such as Kieffer, Old Home, and Carrick, may contain a fair degree of hybridization with other species. These cultivars bear the best known names used during the 1900's for which blight records are given in the literature. Of the 287 cultivars named prior to 1920, about 40 percent are classified as susceptible and 40 percent are only moderately resistant. They contain almost all the most familiar pear names. Eleven percent of the cultivars are resistant to highly resistant, including Beurre Fouqueray, Old Home, Orel, Professeur Molon, and Sudduth, and about 9 percent are variably resistant, such as Douglas, Duchess d'Angouleme, Garber, LeConte, Lincoln, and Winter Nelis.

TABLE 9.—Average degree of fire blight resistance in *Pyrus* species based on literature cited

Scientific name	Common name or type of hybrid	Native location	Degree of resistance ¹		Type of infection ²	Reference
Shoot Trunk						
TRUE, NATIVE PYRUS SPECIES						
<i>amygdaliformis</i> Vill. (syn. <i>parviflora</i> Desf.)	Almond pear -----	Asia (west), Europe (south)-----	M	S	A	140, 780
<i>betulaefolia</i> Bunge -----	Birchleaf pear-----	China (north, central)-----	S	---	N	381, 953, 960, 1072
			R	---	-----	599
			R-S	S	A	140, 780
<i>calleryana</i> Decne. -----	Callery pear-----	China (south, central)-----	---	M	A	780
			R	---	N	231, 479, 599, 667, 779, 953, 959
			S	---	N	22, 667
			S-R	---	A, N	140, 576, 1069, 1072
<i>caucasia</i> Fed. (syn. <i>pyraster</i>)-----	-----	U.S.S.R. (Caucasus), Europe, Asia (west)	---	---	-----	155
<i>communis</i> L. -----	Domestic pear ---	Europe, Asia (southwest)-----	S-R	S	A, N	140, 780, 948, 1037, 1072
			S-R	---	A	565
<i>cordata</i> Desv. -----	-----	France, Spain -----	---	S	A	155, 780
<i>dimorphophylla</i> Makino -----	-----	Japan -----	---	---	-----	155
<i>elaeagrifolia</i> Pall. -----	-----	Asia (west), Europe (southeast) -----	M-S	S	A	140, 780, 1072
<i>fauriei</i> Schneid. -----	-----	Korea -----	R-M	M	A	140, 780
<i>gharbiana</i> Trab. -----	-----	Morocco -----	---	---	-----	-----
<i>hondoensis</i> Nak and Kik. -----	Japanese pear---	Japan -----	R-M	S	A, N	780, 1069, 1072
<i>koehnei</i> Schneid. -----	Evergreen pear --	Taiwan (south)-----	S	R-S	A	140, 780
<i>longipes</i> Coss. and Dur. -----	-----	Africa (north)-----	S	S	A, N	780, 1072
<i>mamorensis</i> Trab. -----	-----	Morocco -----	---	S	A	780
<i>nivalis</i> Jacq. -----	Snow (perry) pear	Europe (south)-----	S	S	A, N	780, 1072
<i>pashia</i> Bush.-Ham. ex D. Don. -----	Pashi pear -----	India, Pakistan-----	S	M-S	A	140, 780
<i>pyrifolia</i> (Burm.) f. Nak. (syn. <i>serotina</i>)----	Sand pear -----	China, Korea, Japan -----	R-S	M-S	A, N	565, 780, 948, 1069, 1072
			R	---	N	479, 953, 959, 1037
			S	---	N	599
			---	S	A	780
<i>regelii</i> Rehd. (<i>heterophylla</i> Reg. and Schm.) -----	-----	Afghanistan, Turkestan -----	M-S	S	A, N	140, 780, 1072
<i>salicifolia</i> Pall. -----	Willowleaf pear---	Iran -----	S	---	A	140
<i>syriaca</i> Boiss. -----	-----	Asia (west)-----	R	R	A	780, 948
<i>ussuriensis</i> Maxim. (syn. <i>sinensis</i>) -----	Ussurian pear---	China (north), Manchuria, Korea, Siberia	R	---	N	22, 140, 381, 479, 550, 556, 667, 779, 1035, 1072
			M	---	N	953
			S	---	N	599
			S-R	---	A, N	565, 1069
MISCELLANEOUS PYRUS SPECIES AND HYBRIDS						
<i>balansae</i> Decne. -----	-----	Asia (west)-----	M	S	A	780

<i>breitschneideri</i> Rehd.-----	Natural hybrid ---	China (north)-----	R	R	A	780
			R-S	---	A	550
<i>canescens</i> Spach.-----	-----do-----	-----	S	S	A, N	780, 1072
<i>cotinifolia</i> Hort.-----	Arboretum	-----	---	S	A	780
	hybrid.					
<i>fascicularis</i> Hort.-----	-----do-----	-----	M	M	A, N	780, 1072
<i>glabra</i> Boiss.-----		Asia (west)-----	---	S	A	780
<i>malifolia</i> Spach.-----	Apple-leaved pear	-----	---	M-S	A	780
<i>michauxii</i> Bosc. ex Poir.-----	Natural hybrid ---	-----	S	S	A, N	780, 1072
<i>ovoidea</i> Rehd.-----		China (north)-----	R	R	A, N	381, 780
<i>persica</i> Pers.-----	Arboretum	-----	---	S	A	780
	hybrid.					
<i>phaeocarpa</i> Rehd.-----	Natural hybrid ---	China (north)-----	---	S	A	780
<i>serrulata</i> Rehd.-----	-----do-----	China (central)-----	M-S	M	A, N	780, 1072
<i>sinaica</i> Thouin.-----	-----do-----	-----	S	---	A, N	1072

¹R=resistant or 0-6 percent, M=moderately resistant or 7-25 percent, and S=susceptible or 26-100 percent of tree blighted.

²A=artificial inoculation, N=natural infection.

TABLE 10.—*Ratings of pear cultivars for fire blight resistance based on literature cited* ¹

Cultivar	Resistant (10–8)	Moderately resistant (7–6)	Susceptible (5–1)
CULTIVARS ORIGINATED BEFORE 1920			
Abbe Fétel-----	-----	-----	707
Alamo-----	-----	305	-----
Amelia Baltet -----	-----	389	-----
Ames-----	389	-----	-----
Amoot -----	-----	-----	1037
Andres Desportes-----	-----	-----	305, 707
Ansault-----	-----	-----	395
Baldwin -----	317, 439, 716	610, 706, 707, 909	550, 667
Bariker-----	-----	707	1067
Baronne Leroy-----	-----	-----	389, 707
Barrillet Deschamp-----	-----	389	-----
Barseek -----	-----	389	948
Bartlett (Williams; Williams' Bon Chretien).	-----	305	21, 104, 160, 274, 317, 389, 395, 400, 486, 528, 550, 587, 635, 667, 706, 707, 726, 769, 872, 909, 923, 948, 1011, 1012, 1037, 1066, 1070, 1136
Bayerische Winterbirne----	707, 1067	-----	-----
Belle de Beugny-----	-----	-----	389
Belle de Ferone-----	-----	-----	389
Belle Lucrative -----	-----	395	-----
Belle Poitevine-----	-----	-----	389
Belmont-----	-----	-----	1037
Bergamote d'Automne-----	-----	389	-----
Bergamote d'Ete-----	-----	389	-----
Bergamote Sargeret-----	-----	389	-----
Besi d'Hery-----	707	389	1067
Beurre Arenberg-----	-----	-----	706, 707
Beurre Auguste -----	-----	389	707
Beurre Baltet Pere-----	-----	389	439
Beurre Bosc -----	779	305	20, 104, 274, 317, 389, 395, 439, 528, 587, 660, 667, 706, 707, 726, 769, 1011, 1070, 1108
Beurre Chaudy -----	-----	389	-----
Beurre Clairgeau-----	-----	20	305, 389, 486, 550, 707
Beurre d'Alexander Lucas -	-----	389	104, 707
Beurre d'Amanlis -----	-----	389	-----
Beurre d'Angleterre-----	-----	389	707
Beurre d'Anjou -----	172, 305, 731	160, 274, 389, 395, 439, 528, 556, 706, 726, 769, 1011, 1108	298, 317, 550, 587, 667, 707, 908, 1037

See footnotes at end of table.

TABLE 10.—*Ratings of pear cultivars for fire blight resistance based on literature cited* ¹—Continued

Cultivar	Resistant (10–8)	Moderately resistant (7–6)	Susceptible (5–1)
CULTIVARS ORIGINATED BEFORE 1920—continued			
Beurre de Bollwiller -----	-----	389	707
Beurre de Jonghe -----	-----	-----	707
Beurre de Nantes -----	-----	389	-----
Beurre de Saint Nicolas ----	-----	389	-----
Beurre Diel -----	-----	305, 389	395, 707, 909, 1037
Beurre Dumont -----	-----	706	439, 667, 707
Beurre Flon -----	707	1067	-----
Beurre Fouqueray -----	707	389, 1067	-----
Beurre Giffard -----	-----	305, 389	68, 707
Beurre Gris -----	-----	-----	305, 389, 707
Beurre Gris d'Hiver -----	-----	-----	305
Beurre Hardy -----	-----	305, (2)	389, 395, 667, 706, 707, 1070
Beurre Millet -----	-----	389	-----
Beurre Phillipe Delfosse ---	-----	389	-----
Beurre Superfin -----	20, 305, 395	389	707
Bezi de la Motte -----	556	389	-----
Blanquet Precocoe -----	-----	389	-----
Blanquet Superfin -----	-----	389	-----
Bloodgood -----	395	305	-----
Bon Chretien Bonnamour --	-----	389	-----
Bon Chretien de Vermont --	-----	389	-----
Bonn d'Ezee -----	-----	389	-----
Bordeaux -----	-----	305	-----
Buffum -----	395	20, 389	550
Burkett -----	389, 776, 780	-----	-----
Butirra Capiaumont -----	-----	707, 1067	-----
Calebasse Madam Charles Furst.	-----	-----	439
Champion -----	1037	-----	-----
Charles Cogne -----	-----	-----	439
Charles Escaig -----	-----	706	707
Charnin -----	-----	-----	706, 707
Chasseurs -----	-----	389	-----
China -----	707, 1067	-----	-----
Citron de Carmes -----	-----	-----	389
Clapp Favorite -----	-----	-----	20, 21, 75, 160, 172, 274, 305, 317, 389, 395, 400, 439, 486, 528, 550, 587, 667, 706, 707, 726, 769, 923, 1011, 1067, 1070
Clarksville -----	-----	305	-----
Colonel Marchand -----	-----	389	-----
Colonel Wilder -----	-----	305, 389	-----
Columbia -----	-----	305, 389	-----
Comte de Lambertye -----	-----	389	-----

See footnotes at end of table.

TABLE 10.—*Ratings of pear cultivars for fire blight resistance based on literature cited* ¹—Continued

Cultivar	Resistant (10-8)	Moderately resistant (7-6)	Susceptible (5-1)
CULTIVARS ORIGINATED BEFORE 1920—continued			
Comte de Paris -----	-----	389	-----
Comte Lelieur-----	-----	389	-----
Conference-----	-----	192, 389, (2)	104, 667, 706, 707
Conkleton-----	-----	-----	389
Conner's Japan-----	-----	305	-----
Conseiller a la Cour -----	-----	389	-----
Dana Hovey -----	439	-----	68, 305, 389, 395, 667, 706, 707
Dearborn -----	395	-----	305
Delices d'Avril -----	-----	389	-----
Delices d'Hardenpont d'Anger.	-----	389	-----
Directeur Hardy -----	-----	389	-----
Dixie -----	389	-----	-----
Docteur Desportes-----	-----	389	-----
Docteur Jules Guyot -----	-----	192, 389	-----
Dorset -----	-----	305	389
Douglas -----	22, 389, 395, 550, 707, 904	317, 776, 1067	298, 528, 667
Doyenne Boussock-----	-----	395	20, 389, 707
Doyenne d'Alencon -----	-----	305	707
Doyenne d'Ete -----	-----	305	-----
Doyenne de la Grifferaye --	-----	389	-----
Doyenne de Saumur-----	-----	389	707
Doyenne du Comice -----	706, 1070	75, 389, 528, 769, 1011	305, 395, 587, 660, 667, 707, 1067
Doyenne Georges Boucher -	-----	-----	439, 707
Doyenne Goubalt-----	-----	-----	389, 707
Doyenne Gris-----	-----	389, 707, 1067	-----
Doyenne Madam Levavasseur.	-----	389	-----
Duchesse-----	-----	20, 21, 528, 769, 1011	160, 305, 486, 587
Duchesse d'Angouleme -----	172, 707, 1067, 1070	389, 706	667
Duchesse d'Angouleme Bronzee.	118, 707	389	-----
Duchesse de Berry d'Ete.	-----	389	439, 707
Duchesse de Bordeaux -----	-----	389, 706	707
Duchesse de Brissac-----	-----	389	707
Duchesse de Mouchy-----	-----	-----	389
Duchesse d'Orleans-----	-----	-----	707
Early Green Sugar -----	-----	389	707
Early Harvest-----	-----	389	-----
Early Sugar-----	305	-----	-----

See footnotes at end of table.

TABLE 10.—*Ratings of pear cultivars for fire blight resistance based on literature cited*¹—Continued

Cultivar	Resistant (10–8)	Moderately resistant (7–6)	Susceptible (5–1)
CULTIVARS ORIGINATED BEFORE 1920—continued			
Easter Beurre-----	-----	305	20, 389, 395
Elizabeth-----	-----	389	20, 395, 667, 707
Emile d'Heyst-----	-----	305	-----
Estella-----	389, 605	317, 780	298
Eureka-----	389	550	667
Eva Baltet-----	-----	389	-----
Fame-----	-----	305, 660	667
Farmingdale-----	214, 550, 626	389, 435, 780	667
Favorite-----	-----	-----	22
Figue d'Alencon-----	-----	389, 707, 1067	-----
Flemish Beauty-----	-----	159, 305, 556	20, 160, 298, 317, 395, 439, 486, 528, 550, 587, 610, 611, 667, 706, 707, 769, 908, 909, 923, 1011, 1108
Flemish Pear-----	-----	556	21, 621
Florida Sandpear-----	-----	776	-----
Fluke-----	-----	776	-----
Fondante de Moulins- Lille.	-----	389	-----
Fondante de Noel-----	-----	-----	707
Fondante des Bois-----	-----	389	-----
Fondante de Thiriott-----	-----	-----	194, 707
Forelle-----	-----	-----	305, 389, 707, 1067, 1070
Fox-----	-----	305, 389	-----
Fred Beandry-----	-----	305	-----
Frederick Clapp-----	-----	305	389
Garber-----	228, 528, 716, 1011	21, 305, 587, 769, 923	400, 667, 707, 804, 908, 909, 1037
General Galliene-----	-----	389	-----
German Sugar-----	-----	317, 780	298
Glou Morceau-----	-----	-----	305, 439, 707
Good Christian-----	-----	389	-----
Gregoire Bordillon-----	-----	389	-----
Greisa No. 1-----	-----	389	-----
Grosse Louise-----	-----	389	-----
Grune Jagdbirne-----	-----	-----	707
Hawaii-----	-----	-----	389, 707
Henri Desportes-----	-----	389	-----
Hessle-----	707	1067	-----
Hofrath's Birne-----	-----	389	-----
Hood-----	439	-----	-----
Hourdequin-----	-----	389	-----

See footnotes at end of table.

TABLE 10.—*Ratings of pear cultivars for fire blight resistance based on literature cited* ¹—Continued

Cultivar	Resistant (10-8)	Moderately resistant (7-6)	Susceptible (5-1)
CULTIVARS ORIGINATED BEFORE 1920—continued			
Howell-----	-----	20, 160, 556, 706	298, 305, 317, 389, 611, 707, 769, 908, 909, 1011
Idaho-----	-----	-----	20, 172, 395, 400, 528, 587
Japan Golden Russet-----	-----	305, 389	1037
Jargonelle-----	-----	-----	707, (2)
Jeanne d'Arc-----	-----	-----	707
Josephine de Malines-----	305	68, 75, 706	20, 707
Kieffer-----	305, 317, 395, 439, 528, 550, 611, 703, 706, 716, 1011, 1108	20, 21, 160, 317, 389, 587, 726, 769, 922, 932, 948, 1012, 1067, 1070, 1136	230, 274, 400, 707, 804, 908, 909, 1037
Koonce-----	-----	21	667, 908, 909, 1037
Krull-----	381, 707, 1067	776	-----
Krylov-----	381, 707, 1067	-----	383
Kuroi-----	-----	707, 1067	-----
Lady Clapp-----	-----	-----	389
Lawrence-----	1037	305, 389	20, 550, 667, 909
Lawson-----	20, 305, 395	389	667
Laxton's Wonderful-----	-----	-----	439, 707
LeBrun-----	-----	-----	389
LeConte-----	528, 703, 1011	389, 587, 769	20, 21, 305, 395, 400, 909, 1037
LeLectier-----	-----	-----	707
Lemon-----	214, 389, 780	-----	707
Leon Leclercq-----	-----	-----	707
Lieutenant Poidevin-----	-----	389	-----
Lincoln-----	67, 305, 395, 439, 582, 706, 804	21, 317, 389, 587, 923	550, 667, 707, 909, 1037
Longue Verte-----	-----	-----	389
Longworth-----	389, 435, 707, 780	667, 1067	-----
Louise Bonne de Jersey (Bonne Louise d'Avranche).	-----	75, 305, 395, (2)	20, 635, 707
Louis Pasteur-----	-----	389	550, 707
Louis Vilmorin-----	-----	389	707
Lucretia-----	-----	-----	305
Lucy Duke-----	776	395	389, 550, 707
Lyerlie-----	305	-----	-----
Madame Andre Leroy-----	-----	389	-----
Madame Caroline d'Airoles-----	-----	389	707
Madame Ernest Baltet-----	-----	706	439, 707
Madame Favre-----	-----	389	-----
Madame Hutin-----	-----	389	-----
Madame Lye Baltet-----	-----	-----	389
Madame Treyve-----	-----	389	707
Madeline-----	-----	-----	305, 395
Magnolia-----	-----	305	-----

See footnotes at end of table.

TABLE 10.—*Ratings of pear cultivars for fire blight resistance based on literature cited* ¹—Continued

Cultivar	Resistant (10–8)	Moderately resistant (7–6)	Susceptible (5–1)
CULTIVARS ORIGINATED BEFORE 1920—continued			
Margaret-----	-----	-----	395
Marie Louise-----	-----	389, 395	68, 707, (2)
Marguerite Marillat-----	-----	389	20, 707
Messire Jean-----	-----	389	-----
Miller-----	550	-----	-----
Monchallard-----	-----	-----	389, 707
New Zealand Winter Bartlett.	-----	-----	706, 707
No Blight-----	93	-----	-----
Notaire Lepin-----	-----	-----	389, 707
Old Home-----	67, 96, 213, 214, 371, 389, 439, 626, 779, 780, 948, 1136	317, 435, 550, 706, 707, 1067	667
Olivier de Serres-----	-----	-----	707
Omer Pache-----	-----	-----	389
Onondaga-----	-----	305	395
Orel-----	389, 776	-----	-----
Osband-----	-----	-----	20
Ozark-----	-----	305	-----
Para de Rosetta-----	1037	-----	-----
Passe Colman-----	-----	395	707
Passe Crassane-----	-----	-----	389, 707
Petit Blanquet-----	-----	389	707
Phillipe Chaveau-----	-----	-----	439
Pierre Corneille-----	-----	-----	707
Pineapple-----	389, 792–794, 908, 909, 1037	-----	230
Pitmaston-----	-----	389	-----
Poete Beranger-----	-----	389	-----
Pound-----	-----	305	707
Precoce de Trevoux-----	-----	389	75, 635, 707
Prenices de Maria Lesueur.	-----	389	-----
President Drouard-----	-----	-----	395, 707
Prince Marianne-----	-----	-----	104
Professeur Grosdemage-----	-----	389	707
Professeur Molon-----	707, 1067	-----	-----
Ramsey-----	-----	-----	909
Reeder-----	305, 395	389	-----
Reliance-----	-----	389, 707	-----
Riehls Best-----	395	-----	305
Robert de Neufville-----	-----	-----	439
Roi Charles de Wurtemberg (RCW).	660	305, 389	707
Rosee de Juillet-----	-----	389	707
Rosseney-----	-----	305	-----
Rousselet de Reims-----	-----	389	-----
Royale Vendee-----	-----	-----	389
Rutter-----	395	20, 305	-----

See footnotes at end of table.

TABLE 10.—*Ratings of pear cultivars for fire blight resistance based on literature cited* ¹—Continued

Cultivar	Resistant (10-8)	Moderately resistant (7-6)	Susceptible (5-1)
CULTIVARS ORIGINATED BEFORE 1920—continued			
Saint Andre-----	-----	389	-----
Saint Ghislain-----	-----	-----	389, 707
Saint Giles-----	-----	-----	439, 707
Seckel-----	172, 305, 395, 611, 706, 1108	21, 68, 160, 274, 317, 389, 528, 550, 556, 587, 726, 769, 923, 948, 1011	298, 400, 667, 707, 908, 909, 1037
Selenga-----	-----	-----	383
Senateur Bell-----	-----	389	-----
Serrurier-----	-----	389	-----
Shaparh-----	1037	-----	-----
Sheldon-----	706	305, 550	20, 389, 439, 528, 587, 667, 707, 909
Sir Harry Veitch-----	-----	-----	439, 707
Sladky-----	707, 1067	-----	383
Smyth-----	-----	389	-----
Snyder-----	-----	305, 389	-----
Sodak-----	609	-----	-----
Southern Queen-----	909	-----	-----
Souvenir d'Emile Coue-----	-----	-----	439, 707
Souvenir du Congress-----	-----	-----	305, 307
Spalding-----	-----	-----	909
Stark Tyson-----	96	-----	-----
Stout-----	-----	389	-----
Stuttgarter Geisshirtel-----	-----	-----	707
Succes de la Meilleraye-----	-----	389	707
Sucre Vert-----	-----	389	707
Sudduth-----	67, 96, 395, 707, 1067	-----	-----
Sugar Top-----	707	1067	-----
Summer Doyenne-----	-----	395	20
Superb-----	-----	389	-----
Surprise-----	214, 389, 776, 780	-----	707
Suzette de Bavey-----	-----	-----	389, 707
Taronta-----	-----	-----	1037
Tedrow Beauty-----	-----	389	707
Thompson-----	706	-----	707
Thornley-----	-----	389	707
Tolstoy-----	63	-----	-----
Triomphe de Vienne-----	-----	-----	389, 707
Triumph-----	-----	305	-----
Tyson-----	395, 706	20, 305, 389, 528, 587, 707, 1037	667, 908, 909
Urbaniste-----	-----	-----	395
Uvedale St. Germain-----	-----	-----	389
Variolosa-----	214, 626, 780	-----	-----
Vermont Beauty-----	305	21, 948, 1037	389, 660
Verte Longue d'Automne-----	-----	389	-----

See footnotes at end of table.

TABLE 10.—*Ratings of pear cultivars for fire blight resistance based on literature cited* ¹—Continued

Cultivar	Resistant (10–8)	Moderately resistant (7–6)	Susceptible (5–1)
CULTIVARS ORIGINATED BEFORE 1920—continued			
Vicar of Winkfield -----	-----	305	20, 389, 395
Vice President Aubert-----	-----	707	1067
Walker -----	317	-----	-----
Wallis Kieffer -----	-----	-----	550
Warner-----	556	389	-----
White Doyenne -----	-----	305, 389	20, 395
White Star -----	-----	389	-----
Wilder-----	395, 716	-----	909, 1037
Wilder Early -----	395	389, 707	20, 1067
Winter Bartlett-----	-----	389	660
Winter Cole-----	706	707, 1067, (2)	-----
Winter Nelis-----	305, 395, 599	68, 389, 528, 587, 703, 706, 769, 1011	172, 298, 660, 667, 707, (2)
Worden Seckel-----	706	305, 389, 395	667, 707
Yermak -----	-----	-----	383
Zoete Brederode -----	-----	-----	707
Zuckerbirne-----	-----	-----	389
CULTIVARS INTRODUCED SINCE 1920			
Aurora-----	-----	706	118, 1009, 1070
Ayres-----	118, 233, 667, 706	389, 610, 707, 1067	-----
Bantam-----	12, 118, 439	-----	667
Beierschmitt-----	-----	68, 389, 439, 706	667, 707, 948, 1070
Bristol Cross -----	-----	192	706, 707
California-----	-----	-----	119, 372
Campas-----	118, 439, 706	-----	667, 707
Carrick-----	232, 317, 439, 948	118, 861	-----
Cayuga-----	439, 706	118	667, 707, 909
Caywood-----	-----	-----	707
Chapin-----	-----	-----	707
Christmas Holiday-----	-----	-----	707
Clyde -----	-----	-----	707
Colette -----	-----	706	707
Covert-----	-----	-----	104, 667, 707
Dabney-----	706, 707, 716, 1067	118, 233, 667	-----
Dawn-----	706, 707	117, 118, 1067, 1070	872, 948, 969
DeVoe-----	-----	118	439, 667, 706, 707, 955, 1067, 1070
Dropmore -----	-----	(3)	-----
Dymond-----	-----	118	-----
Early Faulkner -----	118	-----	-----
Early Seckel-----	706	-----	707
Eldorado-----	328, 1070	-----	-----
Eller -----	-----	118	-----
Enie-----	93	-----	-----
Ewart-----	-----	118, 389, 439, 442, 550, 660, 706	667, 707
Finland-----	118, 381	-----	-----

See footnotes at end of table.

TABLE 10.—*Ratings of pear cultivars for fire blight resistance based on literature cited* ¹—Continued

Cultivar	Resistant (10–8)	Moderately resistant (7–6)	Susceptible (5–1)
CULTIVARS INTRODUCED SINCE 1920—continued			
Finsib-----	-----	-----	383
Funks Colorado-----	118	-----	-----
Gilmore Pride-----	-----	118	-----
Golden Spice-----	-----	(4)	-----
Gorham-----	-----	389, 706	68, 274, 383, 667, 707, 726, 909, 1070
Grand Champion-----	-----	389	667
Hansen Seedless-----	382	-----	-----
Harbin-----	381	118	-----
Harper-----	317	-----	-----
Henderson Special-----	118	-----	-----
Highland-----	-----	-----	118, 119, 553
Honeysweet-----	474a	-----	-----
Hoskins-----	118, 233, 716	-----	-----
Illinois Bartlett-----	667	118	-----
John-----	(5)	-----	-----
Johnson-----	118	-----	-----
Late Faulkner-----	118	-----	-----
Laxton's Early Market-----	-----	706	439, 707
Laxton's Foremost-----	-----	-----	118, 439
Laxton's Progress-----	-----	-----	118, 439, 442, 706, 707
Laxton's Record-----	-----	-----	707
Laxton's Satisfaction-----	-----	-----	118, 439
Laxton's Superb-----	-----	-----	75, 118, 192, 194, 439, 571, 707, 796
Laxton's Victor-----	-----	-----	118, 439, 707
Lee-----	436	118	707, 1070
LeRoi (Red d'Anjou)-----	-----	(6)	-----
Luscious-----	-----	119	-----
Mac-----	436	118, 1070	-----
McIlhenny-----	-----	118	-----
Magness-----	67, 68, 117, 118, 317, 474, 706, 707, 861, 872, 1065, 1067, 1070	274, 948, 1066	667, 1060, 1063, 1067
Manning Miller-----	-----	118	-----
Marks-----	-----	119	-----
Max-Red Bartlett-----	-----	706	439, 667, 707
Mendel-----	93	528, 909	587
Menie-----	93	-----	-----
Mericourt-----	118	-----	-----
Miner-----	93, 118, 442	-----	667
Ming-----	118, 381	707, 1067	667
Moe-----	93, 118, 550, 707	1067	-----
Mooers-----	117, 118, 233, 707, 1067	-----	667

See footnotes at end of table.

TABLE 10.—*Ratings of pear cultivars for fire blight resistance based on literature cited* ¹—Continued

Cultivar	Resistant (10–8)	Moderately resistant (7–6)	Susceptible (5–1)
CULTIVARS INTRODUCED SINCE 1920—continued			
Moonglow -----	118, 317, 471, 667, 872, 969, 1066, 1070	274, 706, 707	-----
Morgan-----	118, 317, 707, 1067	-----	-----
Nikto -----	-----	118	-----
Nixon -----	-----	118	-----
Nye Russet Bartlett -----	-----	-----	118, 389
Okolo-----	-----	707, 1067	-----
Olia-----	-----	-----	707
Orcross-----	118	-----	-----
Oregon 18 -----	118	-----	-----
Orient-----	118, 227, 230, 439, 610, 706, 707, 716, 827, 871	317	298, 667
Ovid-----	-----	-----	667, 707
Packham's Triumph -----	-----	706	68, 118, 389, 707, 1037, (2)
Parker-----	-----	93	118, 400, 528, 587, 667, 707
Patten -----	93	118	400, 528, 587, 667
Peter-----	(5)	-----	-----
Phelps -----	-----	389	1108
Philesson-----	-----	118	667
Philip -----	-----	(5)	-----
Pontotoc -----	119, 716	707, 1067	-----
Pulteney -----	-----	389	439, 707, 1108
Reed -----	550	118	-----
Regal Red Comice -----	-----	(6)	-----
Richard Peters-----	96, 118, 389, 696, 706, 707, 1067	820	667
Rogue Red-----	-----	118, 589	-----
Russet Bartlett-----	-----	706	707
Saponsky -----	97, 381	118	-----
Shea-----	-----	118, 439, 706	707
Simon-----	-----	(5)	-----
Sirrine-----	-----	118	551
Southworth -----	-----	118	-----
Spartlett-----	-----	119, 146	-----
Stanley-----	-----	706	707
Star -----	436	-----	118, 707
Starking Delicious (Maxine). -----	118, 317, 389, 436, 439, 473, 706, 709, 861, 948	550, 667, 707, 1070	-----
Starkrimson -----	-----	-----	667, 707
Stewart Bartlett-----	-----	118, 886	97, 115, 185, 707, 953, 1070
Sungari-----	609	-----	-----
Sure Crop -----	118, 706	707	667
Tait Dropmore -----	-----	118	667, 707
Tait 1 -----	439	-----	550

See footnotes at end of table.

TABLE 10.—*Ratings of pear cultivars for fire blight resistance based on literature cited* ¹—Continued

Cultivar	Resistant (10–8)	Moderately resistant (7–6)	Susceptible (5–1)
CULTIVARS INTRODUCED SINCE 1920—continued			
Tanya-----	118	-----	383
Texking-----	118	-----	-----
Thomas-----	-----	-----	707
Tioma-----	-----	-----	707
Vistica Nectar-----	118	-----	-----
Waite (Canner)-----	118, 317, 439, 550, 610, 660, 706, 707, 709, 716, 1067	-----	667
Willard-----	-----	706, 707	-----

¹Blight susceptibility classifications are primarily as originally published; some ratings were assigned arbitrarily. Resistant is 0–6 percent, moderately resistant is 7–25 percent, and susceptible is 26–100 percent of tree blighted.

²Pers. commun., Dye, D. W., Dept. Sci. and Indus. Res., Auckland, New Zealand.

³Pers. commun., Cumming, W. A., Canada Dept. Agr., Morden, Manitoba.

⁴Pers. commun., Stushnoff, C., Univ. Minn., St. Paul.

⁵Pers. commun., Nelson, S. H., Univ. Saskatchewan, Saskatoon.

⁶Pers. commun., Lombard, P. B., South Oreg. Agr. Expt. Sta., Medford.

In the last part of the table are listed 113 cultivars named and released since 1920 (118, 119). Of these, about one-third are reportedly predominantly resistant, one-third susceptible, and of the remaining one-third, one-half are moderately resistant and the other half variably resistant and susceptible. For 22 percent of the pears introduced since 1920, there was no mention of a blight rating.

Early published records of blight resistance in certain pear cultivars were later followed by contradictory reports. Dawn was at first reported as fairly susceptible to fire blight (948, 969), but in later tests it proved to be more resistant (474, 1067). On the other hand, Stewart Bartlett was recommended as a replacement for Bartlett based on considerable blight tolerance (886), but later it was shown to be as susceptible as Bartlett (115, 185, 1070).

Besides the four classes of cultivars—highly resistant, moderately resistant, variably resistant, and susceptible—there appears to be a fifth class, namely cultivars that are resistant to blossom and shoot blight but are very susceptible to trunk blight (pl. 4, C and D). The most recent example of this type of blight was observed in 8- to 10-year old Magness trees at Beltsville (1060, 1067, 1070) and in

young trees in isolated orchards in north-central Arkansas (1006). In all cases, the fire blight pathogen appeared to have entered the trees either through natural wounds in the trunk (1060, 1063) or through severe hail damage in older branches of the tree (1066). At Beltsville, trunk blight has also been observed in several Giant Seckel trees (female parent of Magness) as well as in 12 clonal accessions of different *Pyrus* species.

In general, trunk blight has been fairly uncommon, since previously it had only been recorded by Reimer (780). Following extensive artificial inoculations, he reported this phenomenon only in the cultivars Douglas, Orel, and Surprise and in several *Pyrus* species (table 9) and oriental cultivars (table 11).

Pyrus calleryana

The callery pear (*P. calleryana* Decne.) is native to South and Central China, especially in the Yangtze Kiang River Valley (780). The trees are medium to large, very vigorous, and usually bloom early. This species can be readily distinguished from all other species, especially *P. communis*, by its

TABLE 11.—*Ratings of oriental pear cultivars for fire blight resistance based on literature cited*¹

Cultivar	Resistant (10–8)	Moderately resistant (7–6)	Susceptible (5–1)
Ba Li Hsiang-----	389, 550, 707, 780, 859, 1067	-----	-----
Champa Li-----	-----	-----	707
Chieh Li-----	605, 707, 780, 1067	-----	-----
Chien Pa Li-----	389, 780	-----	-----
Chin Li-----	-----	-----	707
Chiu Tze-----	-----	-----	780
Chojuro-----	-----	-----	707
E Li-----	-----	780	-----
Fo Chin Hsi-----	-----	-----	780
Guar Li-----	-----	-----	707
Hau Kai-----	-----	-----	707, 780
Hsiang Sui Li-----	389, 605, 707, 780, 1067	-----	-----
Huang Hsiang Sui-----	389, 780	-----	-----
Hung Guar Li-----	389, 780	-----	-----
Hung Li-----	389, 707, 1067	780	-----
Ishi Wase-----	-----	-----	707
Kikusi-----	-----	-----	707
Kuan Hung-----	-----	-----	780
Lo Suan Li-----	780	-----	707
Ma Li-----	-----	780	-----
Man Yuan Hsuang-----	780	-----	707
Ma Ti Huang-----	780	-----	-----
Meigetsu-----	-----	-----	667, 707
Mein Suan Li-----	780	-----	-----
Mhikie-----	-----	-----	707
Mieajo-----	-----	-----	707
Mikado-----	-----	389	-----
Mi Li-----	389, 780	-----	707
Nai Tze Hsiang-----	-----	780	-----
Nan Li-----	-----	-----	780
Nyisiki-----	-----	389	707
Okusankichi-----	-----	-----	707
Pai Li-----	389, 435, 667	780	707
Pan Chien Sui-----	389, 780	-----	-----
Ping Ding-----	-----	780	707
Ping Li-----	389	780	707
Seigyoku-----	-----	-----	707
Suan Li-----	707, 780	1067	-----
Ta Mo Pan-----	-----	707, 780	-----
Tang Li-----	707, 780, 1067	-----	-----
Ta Suan Li-----	707	780	1067
Ta Tau Huang-----	707, 780	1067	-----
Tzu Ma Li-----	389	780	-----
Tzu Su Li-----	1037	-----	-----
Ya Kuang Li-----	389	780	707
Yakumo-----	-----	-----	707
Yarr Li-----	-----	-----	780
Yui Li-----	-----	-----	1037

¹Blight susceptibility classifications are primarily as originally published; some ratings were assigned arbitrarily. Resistant is 0–6 percent, moderately resistant is 7–25 percent, and susceptible is 26–100 percent of tree blighted.

medium to large, ovate, green leaves with a glossy surface and marginal teeth along the edge.

Nearly all selections, including the Bradford cultivar, are highly resistant to fire blight, *Fabraea* (*F. maculata* Atk.) leaf spot, and insect pests. However, other *P. calleryana* accessions are reportedly susceptible to fire blight (140, 780, 1072). When more than 400 open-pollinated Bradford seedlings were rated at Beltsville, the distribution was as follows: Highly resistant (10–8), 42 percent; moderately resistant (7–6), 19 percent; and susceptible (5–1), 39 percent. Bradford appeared to be rather variable in transmitting its high degree of resistance to its progenies (1072). Reimer (780) reported that only 11 percent of the trees inoculated in the trunk showed severe infection.

Pyrus ussuriensis

The ussurian pear (*P. ussuriensis* Maxim.) is native to extreme northern China, Manchuria, and eastern Siberia and is the hardiest of all pears. The trees are moderately vigorous, and the wild forms and some cultivated varieties bloom earlier than any other species. The flowers are larger than those of any other pear and vary from pink to white (780).

In *P. ussuriensis* two general groups are recognized: Group I, representing the true native species, and group II, which includes the domestic hybrids between this and other species.²¹ In the species planted at Beltsville, clones of the wild type (group I) were the most resistant of all the species tested and were assigned a mean blight score of 9.4 (highly resistant) (1072). However, 11 clones of the hybrid type (group II) showed considerable susceptibility (mean score of 4.3). Of the 36 accessions with *P. ussuriensis* parentage, such as Illinois 76 and Pai Li, 64 percent of the clones were rated moderate to highly resistant.

In the collections of oriental cultivars and clonal selections at Beltsville (table 11), those representing group I (Ba Li Hsiang, Hsiang Sui Li, and Suan Li) all showed high resistance, whereas those in group II (Pai Li and Ya Kuang Li) succumbed to blight (707). This reemphasizes the belief that cultivars closest to the wild type are more resistant to fire blight than hybrids with one susceptible parent. Of the 48 cultivars listed in table 11, approximately one-third were assigned to each of the 3 blight classes.

Reimer (780) reported that some cultivars of *P. ussuriensis* (Guar Li, Chin San, Hu Pi Hsiang, and Ta Tze Hsiang) produced a high percentage of blight-resistant seedlings, whereas seedlings of other cultivars (An Li, Chieh Li, Chien Pa Li, and Hau Kai) proved too susceptible to be of any value. He emphasized, however, that this may have been due in part to the effect of the unknown pollen parent, particularly so with Chieh Li and Chien Pa Li, which are highly resistant cultivars. From his trunk inoculation studies, Reimer (780) found that seedlings of the cultivated types of *P. ussuriensis* ranked second in resistance after those of *P. calleryana*. The proportion of infected trees varied from 20 percent in Ba Li Hsiang to 77 percent in Chieh Li. The extremely high degree of resistance in the former was confirmed at Beltsville (707, 1067).

Pyrus pyrifolia

The sand pear (*P. pyrifolia* (Burm.) f. Nak.) is synonymous with *P. serotina*. It is native to Central and East China and Japan. Cultivars of this species are also grown in China and Japan. The tree is very vigorous and productive but does not bloom as early as *P. ussuriensis*. Leaves are very large, with a long, tapering point and coarsely serrated margins. The fruit is usually round or slightly flattened. Table 11 includes several cultivars with *P. pyrifolia* parentage.

Inoculation tests by Reimer (780) and observations on natural blight in Beltsville (1072) have shown that this is another extremely variable species, ranging from highly resistant to very susceptible. Many cultivars with *P. pyrifolia* parentage, such as Campas, Hawaii, and Twentieth Century, have died from blight at Beltsville (707). Of the 49 clones with this species parentage (Okusankichi and Meigetsu), only 28 percent were in the resistant classes (10–8, 7–6) (1072). Reimer (780) reported that *P. pyrifolia* cultivars ranked third in resistance regarding trunk blight.

Pyrus betulaefolia

The birchleaf pear (*P. betulaefolia* Bunge) is indigenous to Central and North China. The tree is moderately vigorous with horizontal or drooping branches. The young shoots and leaves are very distinct from those of all other species; usually they are covered with a light grayish pubescence. Blossoms are very small and are produced in great abundance. The fruit is borne in clusters of from 5 to 10 and is smaller than that of any other species.

²¹KIKUCHI, A. SPECIATION AND TAXONOMY OF CHINESE PEARS. [English transl. from Japanese.] [Unpublished. Copy on file Dept. Hort., Oreg. State Univ., Corvallis.]

Severe fire blight in *P. betulaefolia* has been reported (140, 605, 780, 960, 1072). However, Reimer (780) found, among seedlings of this usually susceptible species, 18 seedlings that were highly resistant to fire blight. As reported for hybrids of the previous four species, those of *P. betulaefolia* varied from highly resistant to extremely blight susceptible.

In general, our observations at Beltsville agree with those of Reimer (780) that the five most important *Pyrus* species, ranked in descending order as to their degree of blight resistance, are *ussuriensis*, *calleryana*, *betulaefolia*, *pyrifolia*, and *communis*. In each species, however, the range of resistance makes impossible the assignment of a certain degree of resistance to a given species.

Apple

Rehder (771) listed 24 species of apples or crab apples indigenous to China, Japan, Siberia, and the United States. The cultivated forms have variously been designated *Malus pumila* Mill., *M. sylvestris* Mill., and *M. domestica* Borkh. (958). Cummins and Aldwinckle (203) reported that several clonal selections of *M. × atrosanguinea*, *M. fusca*, *M. prunifolia* (Willd.) Borkh. *xanthocarpa*, and *M. surgenti* Rehd. are highly resistant to artificial shoot tip inoculation. There are numerous other species, which include the many crab apple cultivars.

The flowering crab apples are excellent ornamental trees, valued for their flowers, foliage, and fruit. However, many of the crab apple cultivars are very susceptible to four common diseases, including fire blight. The indigenous crab apples in the United States were presumably one of the native hosts from which the blight pathogen spread to the cultivated apples and pears introduced from Europe. Therefore this host has been exposed to blight infection more than any other genus in the family Rosaceae. In Colorado, Crandall (190) observed in alternating rows of Martha and Whitney crab apple cultivars that the Whitney trees were severely attacked, but not a single Martha tree was blighted.

Studies on the nature of resistance in crab apple have been conducted in many parts of the country (63, 381, 870). The most extensive were by den Boer and Collins (98) in Iowa, Nichols (685–688) in Pennsylvania, Kozel and Dugan (543) in Ohio, and Jefferson (476) at the U.S. National Arboretum. One of the largest collections with about 1,100 trees in

300 cultivars of flowering crab apples in America is presently maintained by the Des Moines Water Works in Iowa (98).

The following crab apple cultivars and selections have consistently been found resistant to fire blight and four other serious crab apple diseases (476, 687):

Adams ¹
Ames White
Baskatong
Beverly ¹
Burton
Centennial ¹
Gibbs Golden Gage
Golden Gem
Golden Gem (BD 1155-58)
Golden Gem (PLT 788-58)
Henry Kohankie
Honeywood 14
Malus hybrid (scab immune clone - GR700-58)
Minnesota 1492
Morden 19-27
Mount Arbor Special
Professor Sprenger
Robinson ¹

¹Commercially available.

These four diseases are apple scab (*Venturia inaequalis* (Cke.) Wint.), powdery mildew (*Podosphaera leucotricha* (Ell. and Ev.) (Salm.)), cedar apple rust (*Gymnosporangium juniperi-virginianae* Schw.), and frog eye leaf spot (*Pysalospora obtusa* (Schw.) Cke.). In addition to these multiresistant trees, several other crab apple cultivars are resistant to fire blight alone (476, 687). Descriptions of crab apple origin, as well as flower and fruit characteristics, have been published (476, 687, 688).

As with pears, there are marked differences among species and cultivars of apples in their response to attack by fire blight. In table 12 are listed 390 cultivars of apples, including the best known names used during the 1900's for which blight records are given in the literature. Of the 193 cultivars introduced before 1920, about 28 percent are classified as resistant, 27 percent moderately resistant, 28 percent susceptible, and 17 percent variably resistant and susceptible.

In the last part of the table are listed 197 cultivars named and released since 1920 (118, 119, 1007, 1009). They comprise only 32 percent of the 620 cultivars listed (118, 119). Of the 197 cultivars for which blight ratings were reported, 41 percent are listed as resistant, 26 percent moderately resistant, 17 percent susceptible, and 16 percent variably resistant and susceptible.

TABLE 12.—*Ratings of apple cultivars for fire blight resistance based on literature cited* ¹

Cultivar	Resistant (10-8)	Moderately resistant (7-6)	Susceptible (5-1)
CULTIVARS ORIGINATED BEFORE 1920			
Adenburg-----	301	-----	-----
Akin-----	17	-----	22, 622
Alexander-----	17, 769	698	22, 160, 298, 317, 396, 611, 622, 666, 667, 725, 919, 920, 1011
Amur-----	-----	698	-----
Ananas Berzenicki-----	-----	-----	104
Anaros-----	-----	-----	698
Anis-----	-----	-----	698
Antonovka-----	-----	698, 946	665
Arkansas (Black Twig)-----	17, 22, 539, 610, 622, 827	850	301, 666, 667
Arobka-----	-----	-----	396
Athabaska-----	698	-----	-----
Autumn Strawberry-----	22, 622, 859	-----	-----
Babbit-----	396, 850	-----	-----
Bailey Sweet-----	-----	-----	396
Baldwin-----	17, 22, 396, 622, 769, 1011	274, 317, 400, 528, 667, 714, 850, 919, 920	160, 298, 587
Ballarat-----	17	6	-----
Baltimore-----	-----	-----	850
Baxter-----	22, 622	-----	-----
Beauty of Boskoop-----	75	-----	-----
Bellflower-----	-----	-----	850
Ben Davis-----	17, 22, 63, 114, 611, 622, 769, 1011	21, 317, 400, 404, 528, 714, 850, 919, 920, 923	298, 301, 587, 713
Benoni-----	17	-----	21, 22, 622, 923
Bentley Sweet-----	-----	850	-----
Bietigheimer-----	-----	22, 622	-----
Bismarck-----	22, 539, 622	-----	396
Black Ben Davis-----	22, 539, 946	622, 666, 667	114
Black Gilliflower-----	-----	17, 22, 622	396
Blushed Calville-----	-----	-----	698
Bonum-----	-----	693	-----
Canada Red-----	-----	850	-----
Champion-----	22, 622	-----	-----
Charlancoff-----	114	-----	698
Charles-----	-----	-----	698
Charles Ross-----	573	-----	-----
Chenango-----	-----	-----	17, 21, 22, 622
Collins-----	923	-----	-----
Columbia-----	539, 665, 698	-----	-----
Constantine-----	-----	-----	396
Cox Orange Pippin-----	17, 396, 573	946	666, 667
Cranberry Pippin-----	17, 75, 396	-----	-----
Crawley Beauty-----	573	-----	17
Crusoe-----	-----	-----	698

See footnotes at end of table.

TABLE 12.—*Ratings of apple cultivars for fire blight resistance based on literature cited* ¹—Continued

Cultivar	Resistant (10–8)	Moderately resistant (7–6)	Susceptible (5–1)
CULTIVARS ORIGINATED BEFORE 1920—continued			
Delaware Red-----	-----	920	-----
Delicious (Red Delicious) ---	6, 17, 22, 105, 114, 396, 425, 513, 622, 693, 769, 827, 850, 919, 1011	63, 274, 301, 317, 528, 666, 667, 919, (2)	298, 587, 920
Dr. Mathews-----	22, 160, 622, 666, 667	-----	-----
Domine-----	-----	-----	22, 622
Duchess of Oldenburg (Oldenburg).	17, 21, 22, 63, 301, 396, 539, 587, 611, 622, 698, 827, 919, 920, 923	114, 317, 528, 665, 769, 1011	160, 587, 666, 667, 850
Dudley-----	17, 22, 114, 622, 651	-----	611
Early Cooper-----	-----	-----	301
Early Harvest-----	22, 611, 622	17, 404, 693, 946	301, 666, 667, 850, 923
Early Ripe-----	22, 622	-----	667
Egremont Russet-----	17, 573	-----	-----
Elsa-----	-----	698	-----
English Codling-----	-----	-----	94
Esopus Spitzenburg (Spitzenburg).	-----	919	17, 22, 396, 434, 528, 622, 769, 804, 850, 920, 1011
Fallawater-----	17	622	-----
Fall Pippin-----	17	1011	22, 396, 528, 769, 827
Fameuse (Snow)-----	17, 946	22, 63, 622, 919, 1011	114, 160, 274, 611, 651, 666, 667, 920
Fanny-----	622	-----	-----
Five Crown-----	827	179	-----
Florence-----	665	698	827
Gano-----	22, 63, 611, 622	400, 850, 920, 923	301
Giant Geniton-----	22	-----	-----
Gideon-----	17, 396	-----	-----
Gilbert Winesap-----	827	-----	-----
Golden Delicious-----	17, 22, 75, 223, 668, 693, 945, 946	301, 317, 400, 528, 666, 667, 859, (2)	587
Golden Pippin-----	-----	-----	396
Golden Russet-----	-----	400	17
Golden Summer-----	-----	404	-----
Golden Sweet-----	-----	22, 404, 622, 946	667
Golden Winesap-----	17, 22, 622	-----	-----
Granny Smith-----	-----	(2)	-----
Gravenstein-----	17, 22, 396, 622, 821	528, 919, 946, (2)	587, 611

See footnotes at end of table.

TABLE 12.—*Ratings of apple cultivars for fire blight resistance based on literature cited* ¹—Continued

Cultivar	Resistant (10–8)	Moderately resistant (7–6)	Susceptible (5–1)
CULTIVARS ORIGINATED BEFORE 1920—continued			
Grimes (Grimes Golden, Grindstone).	17, 22, 301, 396, 622, 769, 946, 1011	21, 63, 114, 404, 528, 769, 850, 919, 920, 923	274, 587, 610, 667, 713, 806
Hawley-----	17	-----	396
Hibernal-----	731	63, 317, 665, 919	298, 698
Hibkee-----	-----	-----	698
Hoover-----	-----	17, 693	-----
Horse-----	-----	404	946
Hubbardston-----	17, 396	22, 622, 859	-----
Huntsman-----	17, 22, 622	859	396
Hyslop-----	17	22, 622	611, 698
Ingram-----	22, 622	770, 859	611, 923
James Grieve-----	-----	17	104
Janet-----	-----	-----	859
Jefferis-----	946	17, 22, 622	-----
Jonathan-----	22, 622	17, 63, 528, 769, 770, 919, 920, 1011, 1047	21, 75, 114, 274, 301, 317, 396, 400, 404, 587, 611, 666, 667, 804, 827, 923, 946
Keetosh-----	-----	698	-----
Kildare-----	827	-----	-----
King-----	-----	946	528, 611, 769
King David-----	17, 22, 622, 827, 946	400, 850	-----
Kinnard-----	-----	622	-----
Lady-----	17, 850, 946	-----	396
Lady Sweet-----	22, 622	-----	396
Lawver-----	-----	22, 622, 919	396
Limbertwig-----	-----	693	-----
Liveland Raspberry-----	17, 22, 622	-----	-----
Lowell-----	-----	-----	22, 622
Lowry-----	17	662, 946	-----
McIntosh-----	17, 22, 105, 223, 622, 651, 769, 946, 1011	63, 114, 274, 317, 400, 528, 859, 919, 920	160, 396, 425, 587, 610, 611, 850
MacMahon-----	22, 946	63, 919	114, 404, 611, 651, 920
Maiden Blush-----	946	17, 404, 1047	22, 396, 622, 667, 713, 804, 850, 923
Malinda-----	17	859	-----
Mann-----	17	850	-----
Markham-----	-----	-----	827
Melon-----	22	-----	622
Minkler-----	-----	22, 622, (3)	-----
Missouri Pippin-----	-----	859, 923	-----
Morden Russet-----	698	-----	-----
Moscow pear-----	665, 698	-----	-----

See footnotes at end of table.

TABLE 12.—*Ratings of apple cultivars for fire blight resistance based on literature cited*¹—Continued

Cultivar	Resistant (10–8)	Moderately resistant (7–6)	Susceptible (5–1)
CULTIVARS ORIGINATED BEFORE 1920—continued			
Mother -----	17, 22, 622	-----	396
Nero -----	-----	622	22
Northern Spy -----	17, 22, 611, 622, 769, 1011	94, 274, 317, 400, 528, 919, (3)	298, 396, 587, 699, 850, 946
North Western-----	22	-----	-----
Northwestern Greening-----	114, 400, 622, 651, 850, 984	17, 63, 274, 528, 587, 919, 920	666, 667
Ontario-----	17, 611	-----	-----
Opalescent-----	-----	17, 527	666, 667
Ortley-----	17, 22, 622	-----	396
Osman-----	-----	-----	698
Paragon-----	22, 622, 827, 946	17	66, 667
Patten-----	22, 622, 665	-----	-----
Patten Greening-----	-----	698	-----
Pedro-----	698	-----	-----
Pennock-----	765, 1011	528, 587	-----
Petrel-----	665, 698	-----	-----
Pewaukee-----	-----	665, 769	396
Pioneer-----	665	698	-----
Piotosh-----	17	-----	698
Polgo-----	827	-----	-----
Prince-----	-----	-----	698
Ralls-----	-----	22, 622, 946	22, 396
Ramsdale-----	22	-----	-----
Ramsdell Sweet-----	622	-----	-----
Redant-----	698	665	-----
Red Astrachan-----	17, 22, 396, 622	667	-----
Red Canada-----	17, 22, 539, 622	-----	396
Red June (Wilson Red June).-----	22, 622	404, 693	22, 274, 622, 946
Red Melba-----	827, 946	-----	946
Rhode Island Greening-----	-----	528, 665, 726, 1011	17, 22, 94, 160, 274, 396, 425, 587, 622, 667, 769, 827, 850
Romanite Little Red-----	22, 622	-----	-----
Roman Stem-----	-----	17, 22, 622	-----
Rome (Rome Beauty)-----	693, 946	528, 769, 919, 920, 1011	17, 22, 274, 301, 317, 396, 587, 622, 662, 666, 667, 850, 923
Rostherns-----	-----	-----	698
Roxbury Russet-----	17, 396	22, 622, 946	-----
St. Clair-----	945	-----	667
St. Lawrence-----	17	-----	396
Salome-----	17, 22, 622	850	114
Scarlet Pimpernel-----	573	-----	-----
Schoharie-----	17	622	-----
Scugog-----	-----	698	-----
Senator-----	22, 622	-----	-----

See footnotes at end of table.

TABLE 12.—*Ratings of apple cultivars for fire blight resistance based on literature cited* ¹—Continued

Cultivar	Resistant (10-8)	Moderately resistant (7-6)	Susceptible (5-1)
CULTIVARS ORIGINATED BEFORE 1920—continued			
Shannon Pippin-----		404	
Shiawassee-----	17		22, 622
Smith's Cider-----			713, 850
Smokehouse-----	946	17, 528, 666, 667, 769, 1011	396, 587, 713, 827
Sonora-----	827		
Spilaw-----			827
Stark-----		17, 22, 622, 769, 1011	587, 850
Starr-----	827	528	94, 587, 666, 667, 1011
Stayman (S. Winesap)-----	17, 22, 301, 622, 769, 827, 923, 946, 1011	274, 317, 528, 539, 610, 920	75, 587, 666, 667
Sturmer-----		6	
Sulton-----	396, 693		
Summer Rambo (Rambo)---	17, 622, 945	528, 946	587, 769, 850, 1011
Sutton (Sutton Beauty) ----		17	22, 396, 622, 850
Swaar-----	396		
Sweet Bough-----	396		22, 622
Sweet Russet-----			698
Tolman Sweet-----	396	22, 622	17, 21, 114, 160, 274, 611, 666, 667
Tompkins King-----	396	17, 919, 920, 946	22, 622, 726, 850
Twenty Ounce-----		17, 726, 769, 1011	22, 94, 396, 622, 666, 667, 946
Vandevere-----	22, 622		17
Wagener-----	17, 22, 396, 573, 622	666, 667, 919, 920, 946	400, 528, 587, 726, 769, 827
Walkers Beauty-----	622		
Wapella-----		17, 698	
Washington Strawberry----	396		
Watkens Beauty-----	22	622	
Waukon-----			698
Wealthy-----	17, 22, 396, 622	21, 63, 143, 528, 665-667, 698, 920, 1011	114, 223, 274, 298, 301, 317, 400, 587, 611, 651, 769, 827, 923
Weissemer Dessert-----		22	
White Ohio Pippin-----	827		
White Pippin-----	17, 850		22, 622
Williams Red (Williams) ---	17, 22, 528, 622, 769, 945, 946, 1011	587	666, 667
Willow (Willow Twig)-----			21, 22, 274, 298, 317, 396, 666, 667, 923
Windsor-----			22, 622

See footnotes at end of table.

TABLE 12.—*Ratings of apple cultivars for fire blight resistance based on literature cited*¹—Continued

Cultivar	Resistant (10–8)	Moderately resistant (7–6)	Susceptible (5–1)
CULTIVARS ORIGINATED BEFORE 1920—continued			
Winesap-----	17, 21, 22, 301, 622, 693, 827, 946	317, 666, 850	667
Winter Banana (Banana)---	827	17, 22, 622, 666, 667, 919	298, 317, 920
Winter Pearmain-----	-----	22, 622, 667	396
Wolf River-----	17, 22, 622	63, 400, 656, 919	920, 946
Yellow Bellflower-----	17, 22, 622, 946	667	-----
Yellow June-----	-----	404	-----
Yellow Newtown (Newtown Pippin, Albermarle Pippin Green Newtown).	-----	17, 946	22, 396, 622, 667, 850
Yellow Transparent (Transparent).	17, 396	22, 622, 666, 667, 770, 919, 920, 1011	21, 63, 94, 114, 160, 274, 301, 317, 400, 404, 513, 528, 587, 610, 611, 651, 665, 769, 804, 850, 859, 946
York Imperial-----	-----	21, 528, 769, 770, 850, 1011, 1047	17, 22, 301, 513, 587, 610, 622, 662, 666, 667, 713, 859, 923
CULTIVARS INTRODUCED SINCE 1920			
Abbott-----	-----	-----	(4)
Acheson-----	-----	-----	143, 665
Adanac-----	(4)	-----	-----
Advance-----	-----	-----	118
Almey-----	17, (3), (5)	-----	-----
Alton-----	17	-----	-----
Anderson-----	-----	(4)	-----
Anoka-----	827, 946	-----	666, 667
Atlas-----	17	143, 665, (6)	-----
Bancroft-----	17, (6)	-----	-----
Barrie-----	-----	-----	(4)
Barry-----	-----	-----	17, 667, 946
Battleford-----	-----	-----	698
Beacon (Fenton, Miller Red).	118, 121	17, 143, 665, 946	317, 666, 667, 827, 984
Bismar-----	609	-----	-----
Blair-----	17, (6)	-----	-----
Blaxtayman-----	827	-----	-----
Blaze-----	17, 945, 946	118, 223, 666, 667	-----
Breakey-----	-----	698	-----
Brightness-----	-----	(4)	-----
Burgundy-----	-----	17	1010
Caravel-----	17, 946, (3), (6)	-----	-----
Carlton-----	17	-----	-----

See footnotes at end of table.

TABLE 12.—*Ratings of apple cultivars for fire blight resistance based on literature cited* ¹—Continued

Cultivar	Resistant (10-8)	Moderately resistant (7-6)	Susceptible (5-1)
CULTIVARS INTRODUCED SINCE 1920—continued			
Carroll-----	17, (5)	-----	-----
Chieftain-----	17	118, 216, 274	-----
Chipman-----	-----	-----	(4)
Christmas Red-----	(4)	-----	-----
Close-----	17, 946, 954	75, 666, 667	-----
Collet-----	(5)	-----	-----
Conard-----	17, (7)	-----	667, 946
Cortland-----	22, 769, 1011	17, 75, 143, 274, 425, 528, 665-667	400, 587, 945
Crandall-----	945	17, 223	667
Crimson Spy-----	(6)	-----	-----
Dawn-----	-----	-----	(4)
Delcon-----	17, 223, (7)	274	667, 946
Dr. Bill-----	665	-----	-----
Dowingland-----	-----	-----	118
Dunning-----	-----	-----	17
Early McIntosh-----	17, 22	667, 946	-----
Early Vance Spur-----	-----	119	-----
Edgar-----	17, (6)	-----	-----
Edith Smith-----	-----	-----	(4)
Empire-----	17, 699, 946	1008, (3)	-----
Empire Red-----	-----	143, 665	-----
Exeter-----	-----	-----	(4)
Faurot-----	17	118, (7)	666, 667, 827
Fireside-----	17, 665	118, 274	666, 667, 946, 984
Folwell-----	-----	-----	400
Fyan-----	17	(7)	-----
Gala-----	-----	-----	(3)
Garland-----	17, (5)	-----	-----
Geneva McIntosh-----	17	(3)	-----
Geneva Ontario-----	17	-----	-----
George-----	-----	-----	143, 665
Gertie-----	(5)	-----	-----
Glennal-----	665	-----	-----
Glenton-----	(5)	-----	17, 667
Goalie-----	-----	118	-----
Godfrey-----	(5)	665	-----
Goldo-----	17	-----	118
Goodland-----	(5)	-----	-----
Greendale-----	945	17	667, 946
Greene Spy-----	17	-----	-----
Grove-----	118, 946	17, (7)	223
Haralson-----	17, 143, 223, 539, 665, 698, 946	274, 317	-----
Harvester-----	(4)	-----	-----
Hawkeye Greening-----	-----	143, 665	667
Heaver #5-----	(4)	-----	-----
Holiday-----	17, 946	-----	(8)
Honeygold-----	-----	17, 440	118, (9)

See footnotes at end of table.

TABLE 12.—*Ratings of apple cultivars for fire blight resistance based on literature cited* ¹—Continued

Cultivar	Resistant (10–8)	Moderately resistant (7–6)	Susceptible (5–1)
CULTIVARS INTRODUCED SINCE 1920—continued			
Hume -----	17, (6)	-----	-----
Idajon -----	-----	667	118
Idared -----	-----	118, 223	17, 274, 298, 667, 946, (3)
Jerseymac -----	-----	17	-----
Jerseyred -----	118, 539, 946	-----	666, 667
Joan -----	-----	17, 118, 143, 665, 946	274
Jonadel -----	17, 223, 539, 559, 946	274, 666, 667	118
Jonagold -----	-----	17, (3)	-----
Jonagram -----	(7)	946	17, 223
Jonamac -----	-----	-----	17
Jono -----	-----	17, 119	-----
Joyce -----	17, 539, 698	-----	-----
July Delicious -----	945	-----	-----
Julyred -----	667, 945	17, 946	-----
Kendall -----	-----	17, 666, 667	118, 946, 1007
Kidd's Orange -----	-----	(3)	-----
Kingscourt -----	(4)	-----	-----
Lakeland -----	-----	17, 118	223, 666, 667, 946
Laking -----	(6)	-----	-----
Lambton -----	-----	-----	(4)
Lawfam -----	(6)	-----	-----
Lina -----	609	-----	-----
Linda -----	827	17	-----
Lobo -----	17, 22, 946	143, 665	-----
Lodi -----	22, 945	143, 665	17, 75, 227, 274, 298, 317, 610, 666, 667, 946
McLean -----	(4)	-----	-----
Macoun -----	17, 22	666, 667, 946	(3)
Maga -----	-----	609	-----
Manan -----	-----	-----	(5)
Manbee -----	143, 665, (5)	-----	-----
Mandan -----	17, 118	-----	-----
Manitoba -----	143, 665, 698	-----	-----
Manitoba Spy -----	-----	698	-----
Manred -----	(5)	-----	-----
Mantet -----	17	-----	666, 667, 698, 946
Manton -----	-----	698	-----
Martin -----	118	-----	-----
Medina -----	22, 946	17, 666, 667	-----
Melba -----	17, 22, 223, 984	143, 665, 667	274, 298
Melrose -----	17, 946	-----	(8)
Merton Russet -----	-----	-----	(3)
Metzgar -----	-----	-----	118
Milton -----	-----	665, 667, 946	17
Minjon -----	17, 946	143, 665	223, 274, 667
Mollie's Delicious -----	945, 946	17	610, 925

See footnotes at end of table.

TABLE 12.—*Ratings of apple cultivars for fire blight resistance based on literature cited* ¹—Continued

Cultivar	Resistant (10-8)	Moderately resistant (7-6)	Susceptible (5-1)
CULTIVARS INTRODUCED SINCE 1920—continued			
Monroe-----	17	667, 946, (3)	-----
Morden Russet-----	(5)	-----	-----
Moris-----	(5)	-----	-----
Mortof-----	(5)	-----	-----
Mount-----	-----	-----	143, 665, 698
Mutsu (Crispin)-----	75, 945	105, 946, (3)	17, 223, 274, 667
Newfane-----	-----	223, 667, 946	17
Niagara-----	-----	-----	17, (3)
Norspy-----	-----	667	946
Ogden-----	17	-----	-----
Oriole-----	17	143, 665, 946	274, 667
Orleans-----	17, 22, 223, 946	-----	-----
Ostem-----	698	-----	-----
Oxbo-----	946	609	-----
Park-----	(4)	-----	-----
Patricia-----	17, (6)	223, 665	-----
Patterson-----	-----	(4)	-----
Paulared-----	17	(3)	298
Piotet-----	-----	-----	(6)
Prima-----	17, 215	-----	298
Priscilla-----	119, 1025	17	-----
Prolific-----	-----	(4)	-----
Puritan-----	17, 946	667	-----
Quebec Belle-----	(10)	17	-----
Quinte-----	17, 946, (6)	-----	-----
Ranger-----	17, (6)	-----	-----
Raritan-----	-----	17	945
Red Atlas-----	(6)	-----	143, 665
Red Baron-----	17	(9)	-----
Redford-----	17	-----	-----
Redhook-----	946	17	667
Red Prince-----	17, 668	-----	-----
Red Sauce-----	-----	-----	17, 827
Redsnow-----	(6)	-----	-----
Red Standard-----	17	-----	-----
Redwell-----	17	118	274
Redwin Spy-----	(6)	-----	-----
Regent-----	17	-----	118
Reid-----	-----	17, (4)	-----
Rescue-----	-----	665	698
Reward-----	-----	(4)	143, 665
Richared Delicious-----	17	105	-----
Roanoke-----	946	-----	-----
Roseman-----	(5)	-----	-----
Ruby-----	946	667	(8)
Rutherford-----	-----	(4)	-----
Sadow-----	17	-----	118
Secor-----	17	-----	528, 558, 667, 827
Seeando Red Rome 262-----	-----	-----	827
Semlar-----	609	-----	-----

See footnotes at end of table.

TABLE 12.—*Ratings of apple cultivars for fire blight resistance based on literature cited*¹—Continued

Cultivar	Resistant (10–8)	Moderately resistant (7–6)	Susceptible (5–1)
CULTIVARS INTRODUCED SINCE 1920—continued			
Sharon-----	17, 667	223, 558, 665	274
Shenandoah-----	17, 946	-----	-----
Sir Prize-----	1025a	-----	-----
South Dakota Golden-----	609	-----	-----
Spangelo-----	-----	665, (5)	-----
Spartan-----	17, 75, 223, 946	274	666, 667
Spencer-----	17	667	-----
Spigold-----	946	17	-----
Spijon-----	17	-----	-----
Starking Delicious-----	827	-----	-----
Stevenson-----	-----	665, (5)	-----
Summerred-----	-----	17	946
Superior-----	-----	118	-----
Sweet Delicious-----	17, 946	-----	-----
Sweet McIntosh-----	17	-----	-----
Tolmo-----	609	-----	-----
Toshkee-----	17, (6)	-----	-----
Trenton-----	(6)	-----	-----
Turley-----	22, 223, 622, 827, 946	17, 274	-----
Tydemans' Early Red-----	-----	-----	17, 118
Ultra Red Delicious-----	-----	119	-----
Unity-----	-----	(4)	-----
Victory-----	-----	-----	17, 118, 665–667
Volga-----	609	-----	-----
Wakaga-----	-----	609	-----
Watts-----	-----	-----	698
Wayne-----	-----	17	699, 946, (3)
Webster-----	17	-----	-----
Wedge-----	17, 400	-----	-----
Wellington-----	17	610	-----
Winter Queen-----	(4)	-----	-----
Wright-----	17, (7)	118	-----
Yellow Sweet-----	-----	-----	118

¹Blight susceptibility classifications are primarily as originally published; some ratings were assigned arbitrarily. Resistant is 0–6 percent, moderately resistant is 7–25 percent, and susceptible is 26–100 percent of tree blighted.

²Pers. commun., Dye, D. W., Dept. Sci. and Indus. Res., Auckland, New Zealand.

³Pers. commun., Cummins, J. N., N.Y. State Agr. Expt. Sta., Geneva.

⁴Pers. commun., Nelson, S. H., Univ. Saskatchewan, Saskatoon.

⁵Pers. commun., Cumming, W. A., Canada Dept. Agr., Morden, Manitoba.

⁶Pers. commun., Hutchinson, A., Hort. Res. Inst., Vineland Sta., Ontario.

⁷Pers. commun., Hansen, K. W., Mo. State Fruit Expt. Sta., Mountain Grove.

⁸Pers. commun., Ferree, D. C., Ohio Agr. Res. and Devlpmnt. Cent., Wooster.

⁹Pers. commun., Stushnoff, C., Univ. Minn., St. Paul.

¹⁰Pers. commun., Coulombe, L. J., Res. Sta., St. Jean, Quebec.

Aldwinckle and Preczewski (16a) in 1976 reported results of artificial shoot inoculations on 92 apple cultivars in the field and 79 in the greenhouse. They observed a strong correlation in the amount of blight between the two locations. In general, their blight ratings confirm the data in table 12.

Since 1946 the U.S. Plant Introduction Station at Glenn Dale, Md., has introduced and evaluated hundreds of apple cultivars. In addition to those in table 12, Ackerman (4, 5) published ratings of natural fire blight for a 3-year period of 63 early-ripening and 58 late-blossoming apple cultivars, most of which were introduced from Europe. The majority of the cultivars showed less than 5 percent of the tree blighted, indicating a high degree of resistance.

Studies by Ahn (1079) indicated that the mechanism responsible for fire blight resistance in apple shoots is closely related to catechol oxidase activity in the host tissues. Extracts from resistant cultivars Starking Delicious and Haralson showed higher total catechol oxidase activity than susceptible cultivars Beacon and Wealthy. However, total phenol and flavonol content did not correlate with resistance to *E. amylovora*, but leucoanthocyanin content appeared to be higher in resistant than in susceptible cultivars.

Rootstocks

Pear and apple cultivars in the United States are usually propagated on seedling or clonal rootstocks. For many years both cultivars were propagated on the so-called French seedlings imported from France prior to the 1930's (953). Since that time seeds of commercial cultivars from domestic sources have replaced imported seed. Also, many cultivars, especially apples, are grown on clonal rootstocks.

Pear

For several centuries, quince has been used as a pear stock, mainly because of its dwarfing effect. A series of clonal stocks, designated as Quince A, B, C, and Provence, have been developed from it. Unfortunately these stocks are winter tender, incompatible with most pear cultivars, and usually susceptible to fire blight and Fabraea leaf spot (953). In addition, Adams quince was reported in 1972 to have been developed in Belgium (656a). It appears to enhance precocity and increase yields in the cultivar Doyenne du Comice, but we know of no available information regarding its susceptibility to fire blight.

About 1915, Reimer (780, 782) began the search for pear rootstocks and interstocks resistant to fire

blight. Following extensive trips to China he imported and tested seed from several native oriental *Pyrus* species. He found *P. ussuriensis* and *P. calleryana* fairly resistant to blight, whereas *P. pyrifolia* and *P. betulaefolia* were susceptible (table 9). In addition, rootstocks of *P. pyrifolia* and *P. ussuriensis* were susceptible to pear decline and produced serious black end on fruit of the scion cultivar (590, 953). In New York, Kieffer performed more successfully on several oriental pear species, whereas Bartlett, Seckel, and Anjou were most successful on French roots (959).

Blight-resistant seedling stocks were also developed by Reimer (780, 782) by crossing Old Home and other resistant cultivars with Farmingdale. When he compared Bartlett, Bosc, and Howell on French seedling roots and Old Home-Farmingdale roots, 60 percent of those on French seedling were blighted following artificial inoculation of the susceptible scion cultivars, whereas only a few of the latter stocks were blighted. These resistant stocks are being used considerably as body stocks, interstocks, or rootstocks (371, 1014). In a 1975 report, Lombard and Westwood (590) identified pear rootstocks that are resistant to the woolly pear aphid (*Eriosoma pyricola* Baker and Davidson) and various diseases, including fire blight and decline. These rootstocks are adapted to a wide variety of soil conditions and sites and produce trees larger or smaller than standard.

In extensive rootstock trials in California, Day (213, 214) found that Old Home interstock on quince roots planted with the graft union 25–30 cm below ground produced Old Home roots above the quince and thus furnished blight resistance below ground as well as in the trunk and scaffold branches. However, Higdon (406) reported unidentified graft union failure in 15-year-old trees with Oregon-18 trunks on Oregon-18 × Farmingdale seedling roots and on 6-year-old Forelle trees topworked onto P-87 trunk stocks.

In addition to these pear stocks, stocks of several other genera of Pomoideae are graft compatible with *Pyrus*. English hawthorn (*Crataegus oxyacantha* L.) has been reported to have dwarfing effects and to be particularly tolerant of cold, wet soils (958). Olden (708a) reported that *Amelanchier canadensis* (L.) Medic. promoted earlier fruiting than quince, although anchorage was inferior, and that *Sorbus aucuparia* L. was also compatible enough with pear. However, these species are susceptible to fire blight

and have never been extensively used in pear production. Degrees of dwarfing have been recognized for several years in seedling selections of the USDA pear breeding program at Beltsville. US 309 and US 342, both seedlings from Michigan 437 × RCW, propagated on Bartlett seedling rootstock, show definite dwarfing and a high degree of fire blight resistance. Additional research is needed to determine the effect of the dwarfing character of these selections on commercial scion cultivars.

Apple

The history of apple rootstocks dates back much farther than that of pear. The Greeks and Romans were familiar with dwarf, self-rooting forms of apples (958). Following selection of several types of rootstocks in western Europe, the well-known Malling rootstocks were classified in Great Britain during 1912–25. The Malling-Merton rootstocks with Northern Spy as one parent were developed in 1925–50.

We have summarized the fire blight susceptibility data for the most common Malling and Malling-Merton rootstocks evaluated by other investigators (15, 16, 105, 200, 204, 223, 224, 668, 728, 799, 945). The mean blight ratings for natural infection plus artificial inoculation of ungrafted rootstocks were placed in four general categories (table 13). Thus, of the 28 clonal rootstocks, 9 were in the light susceptibility class, 12 in the moderate, 5 in the severe, and 2 in the very severe class (513).

In assessing the degree of blight resistance of the various rootstocks, we should distinguish between the direct damage of fire blight to the rootstock itself and the effect of the rootstock on increasing susceptibility in the grafted scion cultivar. Cultivars such as Jonathan, Mutsu, Golden Delicious, Raritan, and Lodi varied in their degree of blight susceptibility depending on the rootstock (105, 668, 945). In addition,

after several severe blight years at Beltsville, we observed very severe fire blight in York Imperial on M 26 rootstock in contrast to light infection when on M 111 or seedling rootstock (513). This high incidence of fire blight on M 26 has been reported by many others (105, 200, 224, 254, 798, 799). However, M 26 to date has had no effect on the susceptibility of Golden Delicious in large orchard plantings in Pennsylvania. Similar results were reported by Ahn (1079) using McIntosh on M 9, M 26, and M 111.

The increased sensitivity of the scion cultivar to blight infection on different clonal rootstocks is well established. This has been attributed to an earlier flower production induced by the rootstock, which provides more infection sites for the blight pathogen. Thus the rootstock also may have altered certain physiological processes in the tree, producing more flowers and also rendering the scion cultivar more blight susceptible. Therefore the two factors appear to be concomitant rather than causal.

In an extensive rootstock breeding project in New York, Cummins and Aldwinckle (15, 16, 200, 201) screened large numbers of seedlings from controlled crosses during their first year of growth for susceptibility to collar rot, the woolly apple aphid (*Eriosoma lanigerum* (Hausmann)), and fire blight. They found *Malus prunifolia* (Willd.) Borkh. *xanthocarpa*, *M. × sublobata* (Zab.) Rehd., *M. × robusta* (Carr.) Rehd., and a high proportion of seedlings in progenies from crosses with them to be blight resistant. In 1974 they (202) reported an interesting correlation between different degrees of suckering of apple rootstocks and incidence of fire blight. In 2- to 7-year-old orchards, tree mortality was highest on M 9, M 26, and Alnarp 2 rootstocks. In Arkansas, Rom (798) observed a relationship between burrknots on 4-year-old Jonathan trees on different rootstocks and fire blight lesions on the stocks.

TABLE 13.—*Classification of most common Malling and Malling-Merton apple dwarfing rootstocks for fire blight susceptibility*¹

Susceptibility class	Clonal rootstock No.	
	Malling	Malling-Merton
Light-----	2, 7, 15	102, 103, 104, 105, 110, 111
Moderate -----	1, 4, 8, 10, 12, 13, 25, 27	106, 107, 109, 112
Severe-----	6, 9, 16	113, 114
Very severe-----	3, 26	-----

¹Data compiled from Anthony and Clarke (26), Cummins and Aldwinckle (200), Doll (223), Parker et al. (728), and Rom and Slack (799).

Artificial Inoculation

Techniques

Many techniques have been tested and employed for artificial inoculation of plant material to determine the degree of fire blight resistance in pears, apples, pyracantha, cotoneaster, and other rosaceous hosts. The oldest method, which is still used, includes variations of needle inoculation of the succulent shoot tip. In 1925, Reimer (780) placed a drop of bacterial ooze or pure culture of *E. amylovora* on the shoot tip or other part of the tree to be inoculated and passed a needle several times through this drop into the tissue. In 1934, Shaw (859) extensively studied the variations in fire blight resistance among 31 rosaceous species of several genera, including *Pyrus*. In addition to Reimer's needle-puncture method, he used a hypodermic needle to inject about 0.1 ml of concentrated bacterial suspension into the shoot tip. Bruner (1087) reported in 1953 of dipping a dissecting needle into a bacterial suspension and then puncturing the leaf axils or stem internode of the plants. These three methods of inoculation have since been used by many scientists studying fire blight (81, 97, 139, 444, 550, 564, 565, 948, 1090, 1091, 1101, 1108, 1136).

At Beltsville we have experimented with several techniques of tissue injury in combination with spray inoculation (501, 1054, 1062). Sandblasted and spray-inoculated pear trees in the greenhouse on raised beds (fig. 26, A) showed that petioles were most commonly infected (fig. 6, B and C). Occasionally stems became infected through wounds caused by large sand particles. Vascular tissues in the leaves supported the blight pathogen better than interveinal tissue. Sandblast injury of petioles and midribs often resulted in systemic infection. Crosse et. al. (197) and Crosse and Shaffer (198) reported similar findings with Jonathan apple.

In Canada, Layne (563, 564) reported that the needle inoculation method was more effective than spray inoculation on 7- to 10-month-old pear seedlings. Following inoculation he placed the plants in a humidity chamber maintained at 90–100 percent relative humidity for 3 days. This method, though slow and laborious, resulted in 90–100 percent infection compared with only 60 percent infection without a humidity chamber.

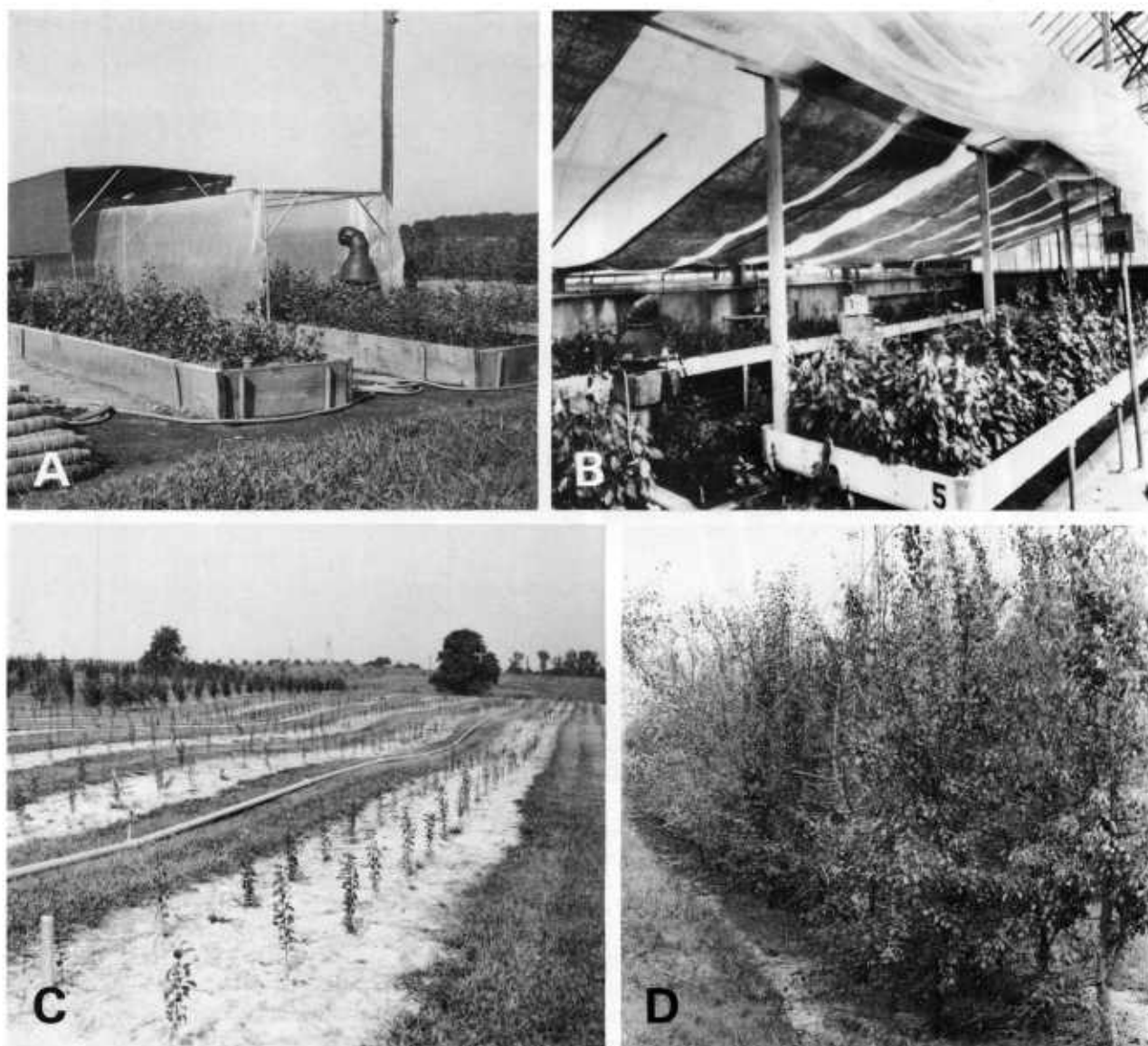
Several investigators have successfully inoculated pear blossoms by spraying them with a bacterial suspension (417, 651, 742, 1057). In Maryland, Dune-

gan et al. (242, 243) reported on field inoculation of 9-year-old pear seedlings during bloom. They sprayed the trees with an aqueous suspension of *E. amylovora* and an abrasive applied with an orchard sprayer. Blight developed in 52 percent of the trees the first year, and with additional sprays it developed in 57 percent of the trees the following year. In New York, Beer (80) obtained as much as 40 percent infected blossom clusters when 6-year-old Idared apple trees were sprayed in full bloom with a backpack-type gasoline-powered mist blower. He has also reported techniques for field evaluation of spray materials to control fire blight of apple and pear blossoms (80c).

Carpenter and Shay (147) and Carpenter (1090, 1091) were the first to attempt the development of a mass inoculation technique to screen seedlings in their pear breeding program. When leaves and succulent shoots were sprayed with a bacterial suspension at 15 pounds per square inch (1 kg/cm²), only 10 percent of the plants became infected. When 2-year-old nursery trees without succulent shoots were sprayed at 50 pounds per square inch (3.5 kg/cm²) with Carborundum added to the inoculum, 39 percent of the trees were blighted. They concluded that there was no visible resistance in the seedlings prior to the 8-leaf stage but that intermediate types of resistance existed at the 18- to 24-leaf stage.

Maximum movement of the blight organism in plant tissue is usually obtained when inoculated plants are kept under optimum environmental conditions for blight development. Small lots of plants are usually placed for 3 to 14 days in growth chambers or small humidity chambers maintained at 26° C (79° F) and 80–100 percent relative humidity (565, 1054, 1058, 1068). During 1966–69, several types of humidity chambers were tested at Beltsville, mainly as enclosures over raised beds of seedlings in the field (fig. 26, A). Maintaining optimum temperatures was difficult, but fair success was obtained in May and June when a layer of burlap shading was used above the plastic chamber.

As a result of these techniques, we decided to handle large populations of seedlings at Beltsville with a specially prepared rapid inoculation device (fig. 27) under a large plastic canopy over the greenhouse bench (fig. 26, B). The inoculation apparatus consisted of a set of large aluminum forceps containing a florist pin holder on one side and a sponge on the opposite side (1059, 1068, 1075, 1077).



PN-6390

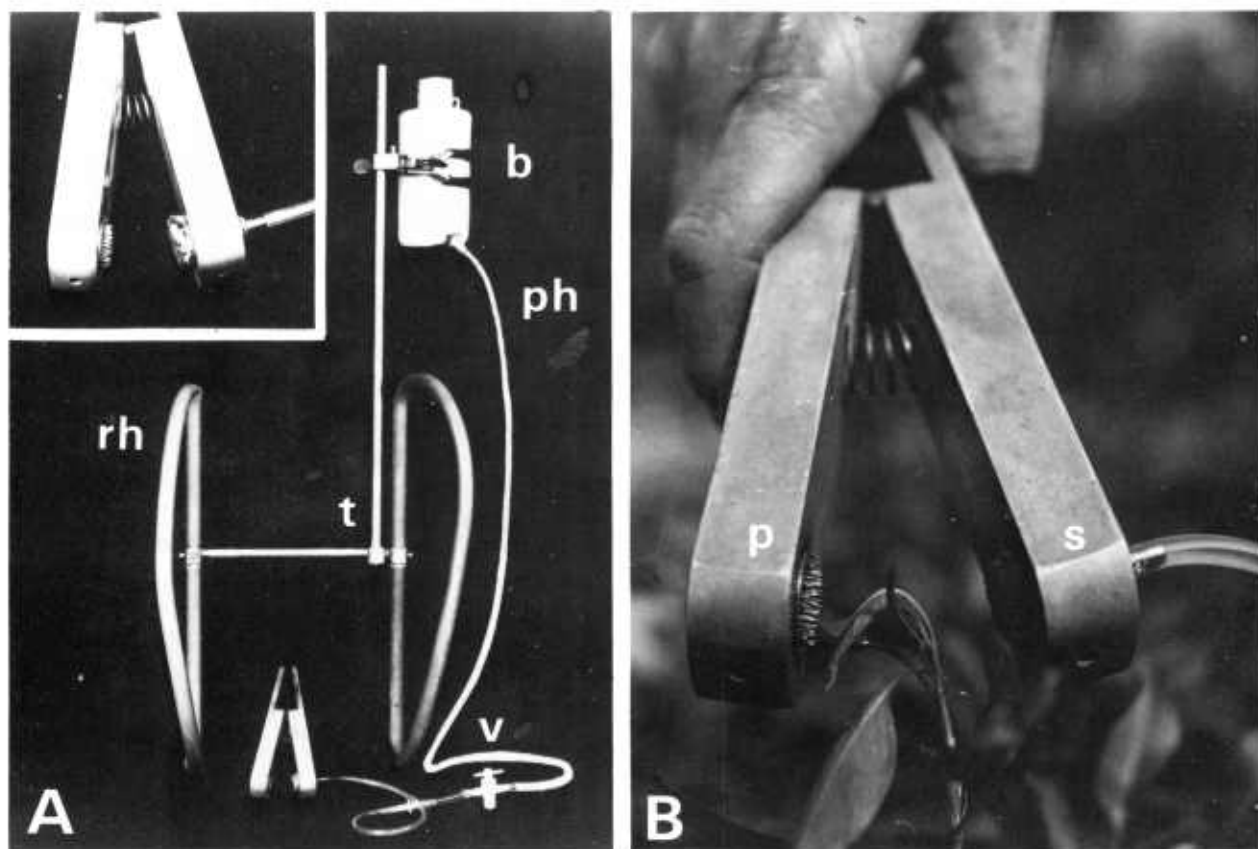
FIGURE 26. — Methods used in inoculating and planting pear seedlings at Beltsville, Md.: A, Small plastic enclosure with supplemental burlap shading for experimental control of temperature and humidity over raised beds of inoculated seedlings; B, environmental control under plastic structure in greenhouse for optimum blight development in inoculated pear seedlings; C, 1-year-old seedlings in double rows in field; D, blight in double rows of 6- to 8-year-old seedlings.

The sponge was attached by a hose to a bottle of inoculum and clamped to a backpack made of aluminum tubing. With this inoculator, two technicians could inoculate rapidly and uniformly about 4,500 pear seedlings per day with approximately 4 gallons (15 l) of inoculum.

Following inoculation, the tentlike structure was closed and two humidifiers were activated to provide a relative humidity of 85–100 percent within the enclosure. With the regular greenhouse heating sys-

tem and the aid of two large window fans and a wet pack on the opposite side of the greenhouse, the temperature during April and May was maintained between 21° and 27° C (70°–80.5° F). The use of this inoculation device resulted in a high percentage of blighted seedlings (1074, 1077). Although such screening has provided desirable selection pressure in determining blight resistance, it may eliminate a higher percentage of trees than necessary.

Wrather (1139) reported in 1973 of successfully



PN-6391

FIGURE 27.—Apparatus for rapid inoculation of seedlings with *Erwinia amylovora* at Beltsville, Md.: A, Backpack equipment, consisting of aluminum tubing (*t*) and rubber hose (*rh*), showing plastic inoculum bottle (*b*) attached to inoculator (insert) by plastic hose (*ph*); flow of inoculum may be regulated by valve (*v*); B, closeup of inoculator, consisting of aluminum forceps with hinge and spring attachments; florist pin holder (*p*) and sponge (*s*) are in opposite wells.

inoculating etiolated pear and apple seedlings by puncturing the stem and placing a drop of inoculum with a known number of cells per milliliter in the opening. He found the seedlings as resistant to fire blight as mature plants following exposure to light for 14 days. In Michigan, Ritchie and Klos (795) needle-inoculated similar young seedlings to study *E. amylovora* isolates for pathogenicity. Ahn (1079) studied the wilting response of several apple cultivars, mountainash (*Sorbus*), and hawthorn (*Crataegus*) species to phenolic compounds. Differences in wilting time between susceptible and resistant apple cultivars were significant when shoot tips were inserted in 4-methylcatechol 0-0 diacetic acid.

From East Germany, Schaefer et al. (840a) reported more successful blight development in young apple and pear trees in the greenhouse with a "needle prick" (Nadelstich) than a "squeeze-bruise" (Quetsch) inoculation method.

Inoculum

In all these inoculation techniques not much is known about the actual concentration of inoculum or number of bacterial cells necessary to produce infection and symptom expression. In 1937, Hildebrand (418) conducted one of the early inoculation studies with small numbers of *E. amylovora* cells. When single cells were introduced into nectaries of excised apple flowers, 60 percent became infected; with 10 or more cells per nectary, all flowers became infected. However, similar tests with intact flowers on pear trees in the greenhouse failed to produce infection. In 1976, Aldwinckle and Beer (14a) reported that they obtained blossom infection in Golden Delicious apples using as few as 10 cells per blossom.

Initiation of shoot blight appears to require more cells per inoculation for infection to develop. Powell (758) demonstrated a direct relationship between inoculum concentration per milliliter and incubation

period in Jonathan apple. With 200 cells, no infection resulted; with 2×10^4 cells, 40 percent of the shoots were blighted after incubation for 7–10 days, whereas with 2×10^7 cells, 100 percent of the shoots were infected after 4–5 days. Lelliott (575), on the other hand, in field studies showed a mean ED_{50} (dose at which 50 percent of plants respond) of 2×10^6 cells per milliliter for leaf infection and 6.6×10^6 cells for stem infection. Wounded seedling leaves required 20 times fewer cells for infection than did unwounded leaves.

Preliminary studies²² at Beltsville indicated that fewer cells were required to produce disease symptoms in apples than in pears. Furthermore, fewer cells of a streptomycin-sensitive strain of *E. amylovora* appeared to be required to produce symptoms than of a streptomycin-resistant strain. If repeated studies show this to be true, one might expect the streptomycin-sensitive strain to eventually overcome the resistant strain.

Sources of bacterial inoculum have varied among investigators from a bacterial suspension produced by extraction from freshly blighted tissue in vacuo (475, 948) to a cell suspension prepared from a virulent *E. amylovora* culture grown on solid or liquid media in vitro (565, 1054, 1068), as well as a mixture of several cultures (147, 765). In our research²² at Beltsville we have usually applied concentrations of 5×10^7 cells per milliliter from a single isolate and results have generally been comparable with the previously mentioned types of inocula.

Disease Evaluation

The degree of blight resistance in young seedlings has usually been expressed by measuring the total length of the seedling at time of inoculation and the visually blighted part when blight ceased to move any farther. From this, the percent blighted tissue could thus be calculated. Seedlings with a trace to 25 percent of the shoot blighted are usually classified as highly resistant (scores 10–8), from 26 to 50 percent as moderately resistant (scores 7–6), and more than 50 percent as susceptible to very susceptible (scores 5–1). In a slight variation of this system, Thompson et al. (475, 948) and Thompson (1136) established four resistance groups based on the average length of blighted tissue per tree as follows: 0–1.9, 2–9.9, 10–19.9, and 20 or more inches (0–4.9, 5–24.9, 25–49.9, and 50 or more cm).

In our studies at Beltsville a general correlation was observed in degree of shoot blight resistance between young budded pear trees artificially inoculated in the greenhouse and mature trees of the same cultivars naturally blighted in the field (1057). Similar results were reported from New York on degree of blight between young apple cultivar trees in the greenhouse and nursery (16a).

Breeding Programs

Breeding programs to improve pear and apple trees for blight resistance were started in the United States about the mid-19th century. At this time, blight was reported in various cultivars and the first plant exploration trips were made to Europe, Asia, and the Orient to collect resistant germ plasm. Table 14 summarizes the most significant pear and apple breeding programs and selection-evaluation sites in North America since about 1870–80. Detailed summaries of pear and apple breeding programs in North America prior to World War II have been published (11, 623, 624).

Pear

Nearly all pear cultivars introduced from Europe proved susceptible to fire blight. In the dry, irrigated valleys of the Pacific Coast States, where nights are relatively cool, the disease is less serious than in the Eastern and Central United States. By 1840 the sand pear (*P. pyrifolia*) was growing in America and became widely distributed in the eastern part of the country. Soon after, hybrids between the sand pear and cultivars of the common pear (*P. communis*) began to appear. Garber, Kieffer, LeConte, Pineapple, and more recently Ayres, Mooers, and Orient are the best known of these gritty, coarse-fleshed fruit hybrids. Because of their culinary quality, however, they were widely grown in home orchards and small commercial plantings.

All pear breeding programs in North America had one main objective, i.e., to obtain high-quality dessert pears with a high degree of fire blight resistance. Of the inactive pear breeding programs not in existence today, the one by Patten in Iowa in 1867 is probably the oldest. His work was mainly to develop pears sufficiently hardy to thrive in the upper Mississippi Valley. He grew mainly open-pollinated seedlings of *P. ussuriensis*, which have proved more hardy than pears from any other source (730, 731). In 1922 the cultivar Patten (Orel 15 \times Beurre d'Anjou) was introduced by the Iowa Agricultural Exper-

²² Unpub. data, Fruit Lab., U.S. Dept. Agr., Beltsville, Md.

TABLE 14.—Active and inactive pear and apple breeding programs and selection-evaluation sites in North America

Location	Period (approximate)	Plant	Research activity ¹	Breeder or evaluator	Reference
UNITED STATES					
California:					
Palo Alto -----	1920-35	Pear -----	BP	Wight, W. F. ² -----	624
Davis -----	1928-	Pear, apple -----	BP, ES	Chandler, W. H., Tufts, W. P., Griggs, W. H. -----	372
Georgia:					
Experiment -----	1912-36	Apple, pear -----	ES	Parish, J. J., Stuckey, H. P. -----	908, 909, 1037
Blairsville, Byron -----	1959-	-----do -----	BP, ES	Hardigree, J. B., ² Thompson, J. M. ² -----	386, 945, 946
Idaho: Moscow -----	1909-40	Apple -----	BP	Vincent, C. C., Longley, L. E. -----	981
Illinois:					
Urbana -----	1908-22	-----do -----	BP	Crandall, C. S. -----	191
	1922-	Apple, pear -----	BP, ES	Anderson, H. W., Dayton, D. F., McMunn, R. L. -----	21, 22, 215, 622
	1942-68	Pear -----	BP, ES	Hough, L. F., Barrett, H. C. -----	67, 68, 435
Carbondale -----	1951-	Apple, pear -----	ES	Mowry, J. B. -----	666-668
Indiana: Lafayette -----	1945-	Apple -----	BP, ES	Shay, J. R., Williams, E. B. -----	121, 215, 861, 1025, 1136
	1947-	Pear -----	BP, ES	Carpenter, T. R., Janick, J. -----	147, 473, 474-475, 948, 1090, 1091
Iowa:					
Charles City -----	1868-1932	Apple, pear -----	BP, ES	Patten, C. G. -----	730, 731
Ames -----	1880-1960	Apple -----	BP	Budd, J. L., Beach, S. A., Lantz, H. L. -----	556-559, 624
Kentucky: Lexington -----	1950-55	Pear -----	ES	Olney, A. J. -----	709
Maryland:					
College Park -----	1906-35	Apple, pear -----	BP	Auchter, E. C., ² Close, E. C. -----	54
Beltsville -----	1890-1932	Pear -----	BP	Waite, M. B., ² Shear, E. ² -----	624
	1932-60	-----do -----	BP, ES	Magness, J. R., ² Moon, H. H. ² -----	624, 660
	1960-	-----do -----	BP, ES	Brooks, H. J., ² van der Zwet, T. ² -----	116, 117, 707, 1054, 1065, 1068, 1070-1073
Michigan:					
South Haven -----	1916-35	-----do -----	BP, ES	Wight, W. F., ² Johnston, S. -----	479, 624
East Lansing -----	1945-	Apple, pear -----	ES	Tukey, H. B., Carlson, R. F. -----	146, 958, 960
Minnesota: St. Paul -----	1890-	-----do -----	BP, ES	Wilcox, A. N., Alderman, W. H., Stushnoff, C. -----	9, 12, 13, 912
Mississippi: State College -----	1925-	Pear -----	ES	Overcash, J. P. -----	716, 871
Missouri:					
Columbia -----	1905-60	Apple, pear -----	ES	Whitten, J. C., Chandler, W. H., Murneek, A. E. -----	624
Mountain Grove -----	1901-	-----do -----	BP, ES	Faurot, F. W., Shepard, P. H., Hansen, K. W. -----	624
New Jersey: New Brunswick -----	1948-	-----do -----	BP, ES	Hough, L. F., Bailey, C. H. -----	57, 58, 436
New York:					
Ithaca -----	1888-92	-----do -----	BP, ES	Bailey, L. H., Cox, H. R., Hsiong, S. L. -----	186, 443, 444, 1108
Geneva -----	1892-	Pear, apple -----	BP, ES	Howell, G., Beach, S. A., Oberle, G., Lamb, R. C. -----	200, 386a, 549-552, 1009, 1087

		Apple-----	BP, ES	Klein, L., Cummins, J. N., Way, R. D., Aldwinckle, H., Hamilton, J.	14, 17, 200-204, 1006-1010
North Carolina: Raleigh -----	1955-	Pear -----	ES	Clayton, C. N. -----	624
North Dakota: Mandan-----	1915-66	Apple, pear-----	BP, ES	Pfaender, M., ² Baird, W. P., ² Oitto, W. A. ² -----	118
Ohio: Wooster-----	1915-66	-----do-----	ES, BP	Keil, J. B., Howlett, F. S. -----	439-442
	1966-	Pear -----	BP, ES	Oitto, W. A., ² Blake, R. C. ² -----	705, 706, 1070
Oregon:		-----do-----	ES, BP	Reimer, F. C. -----	776, 777, 779, 780, 782
Talent -----	1911-50	-----do-----	ES	Lombard, P. B. -----	140, 589, 590
Medford -----	1950-	-----do-----	ES	Westwood, M. N. -----	140, 1014, 1015
Corvallis -----	1961-	-----do-----	ES	Nixon, E. L. -----	696
Pennsylvania: State College -----	1929-39	-----do-----	ES	Hansen, N. E., McCrory, S. A. -----	381, 609
South Dakota: Brookings -----	1895-1945	Apple, pear-----	BP, ES	McClintock, J. A. -----	599-601
Tennessee:		Pear, apple -----	ES	Drain, B. D. -----	227, 229-233
Knoxville -----	1921-30	Pear -----	BP, ES	Drinkard, A. W., Horman, F. W., Moore, R. C., Oberle, G. D.	662, 700, 701
Merricourt-----	1931-60	Apple-----	ES, BP		
Virginia: Blacksburg -----	1910-				
CANADA					
British Columbia: Summerland ---	1930-	-----do-----	BP, ES	Lapins, K. O. -----	623, 624
Manitoba: Morden-----	1916-70	-----do-----	BP	Kerr, L., Ure, R., Quamme, H. A. -----	623, 624
Nova Scotia: Kentville-----	1950-	Apple, pear-----	BP, ES	Bishop, C. J., Crowe, A. D. -----	198a-198c
Ontario:					
Ottawa -----	1899-1968	Apple-----	BP	Hunter, A. W. S., White, F. H., Macoun, W. T., Spangelo, L. P. S.	93, 207, 459, 623, 624
Vineland -----	1913-	Apple, pear-----	BP, ES	Dickson, G. H., Anderson, E., Tehrani, G., Hutchinson, A.	219
Harrow-----	1962-	Pear -----	BP, ES	Layne, R. E. C., Quamme, H. A. -----	563-566, 764a, 765
Quebec: Saint Jean -----	1968-	Apple-----	BP	Rousselle, G., Lereau, M. -----	
Saskatchewan: Saskatoon-----	1925-	-----do-----	BP	Patterson, H., Nelson, S. H. -----	623, 624

¹BP=breeding program; ES=evaluation site.

²Employed by USDA.

iment Station. Between 1918 and 1928, crosses and backcrosses between Patten's seedlings and *P. communis* cultivars were made, but much of this work was lost when the station was closed in 1932.

A similar program of breeding hardy, blight-resistant pears was conducted by Hansen (381) at the South Dakota Agricultural Experiment Station in Brookings. Several cultivars were named, such as Finland (Finland Early Yellow × OP), Ming (*P. ovoideae* × Louise Bonne de Jersey), Hansen Seedless (*P. sinensis* × Marguerite Marillat), Tanya (Ideal × *P. ussuriensis*), and Valya (Lincoln × Russian sand pear).

During 1925–60, a major pear breeding and selection-evaluation program was carried out in Tennessee. Started under McClintock (599, 600), it was continued and expanded by Drain (227). About 1933, McClintock discovered a resistant pear seedling and later named it Late Faulkner. Since 1925 the work consisted mainly of crossing resistant species, such as *P. pyrifolia*, *P. calleryana*, and *P. ussuriensis*, with the more resistant cultivars of *P. communis*. By 1943, of 1,586 seedlings containing one-fourth *P. pyrifolia*, more than 50 percent developed no fire blight; in 710 seedlings with one-eighth *P. pyrifolia*, 70 percent did not develop blight (229). Several pear cultivars have been introduced from this program (118, 230, 231), such as Ayres (Garber × Beurre d'Anjou), Dabney (Seckel × Garber), Carrick, Hoskins, Mericourt (all three from Seckel × Late Faulkner), Mooers (Duchess d'Angouleme × Late Faulkner), Morgan (Bartlett × Late Faulkner), and Orient (*P. communis* × *P. sp.* China).

Between 1942 and 1968, another large pear breeding program was conducted at the University of Illinois at Urbana. Pear species and cultivars had been tested since 1919 (21, 22). In addition, some very resistant pear trees (Old Home, Farmingdale, and Longworth) were discovered in and near Illinois. Hough (435) used primarily cultivars and selections of Chinese species, such as Pai Li and *P. ussuriensis* 76, and crossed them with several *P. communis* cultivars. Later Barrett (67, 68) continued this program and broadened the base of blight-resistant material, using Lincoln, Old Home, Sudduth, and several resistant Illinois selections. In 1968, this work was discontinued. Many selections from Hough's program were moved to Rutgers University in New Jersey and have been used extensively there by him as well as in the USDA program at Beltsville. Many selections from Barrett's pro-

gram are currently under observation at the N.Y. Agricultural Experiment Station at Geneva.

Other past pear breeding programs, smaller but of importance in their time, were active in California (Palo Alto), Georgia (Experiment), Kentucky (Lexington), Maryland (College Park), Minnesota (St. Paul), New York (Ithaca), North Dakota (Mandan), and Pennsylvania (State College). From the Pennsylvania program originated the highly resistant Richard Peters cultivar (Kieffer × OP) (696).

Of the active pear breeding programs, the most productive was at the N.Y. Agricultural Experiment Station at Geneva. This program has consisted mainly in hybridizing *P. communis* cultivars to produce high-quality fruit (549, 550). Between 1920 and 1945, the following 11 cultivars were introduced: Cayuga, Caywood, Chapin, Clyde, and Early Seckel (all open-pollinated seedlings of Seckel); Covert, Ovid, and Willard (all Bartlett × Dorset seedlings); Gorham (Bartlett × Josephine de Malines); and Phelps and Pulteney (Winter Nelis × Russet Bartlett seedlings). Most recent introductions were Aurora (Marguerite Marillat × Bartlett) in 1964, Sirrine (seedling) in 1970, and Highland (Bartlett × Comice) in 1974 (551, 553). It should be emphasized, however, that all these introductions from New York are blight susceptible and must be protected in areas where fire blight is a problem.

The pear breeding program in New Jersey was undertaken by Bailey and Hough (57, 58) in 1948. It provided some very interesting and important blight-resistant selections, many with *P. pyrifolia* and *P. ussuriensis* parentage. An apparently blight-resistant pear seedling (NJ 1) was used extensively in this breeding program. The tree and foliage are intermediate between *P. pyrifolia* and *P. communis* cultivars. This selection has medium-sized, very short pyriform, green-skinned fruit, which is not buttery but contains a few stone cells. In 1968, Hough and Bailey (436) introduced three blight-resistant pear cultivars for the fresh market—Star and Lee (both from a cross of Beierschmitt × NJ 1) and Mac (Gorham × NJ 1). At Beltsville the cultivars Star and Lee were found to be susceptible, whereas Mac was moderately resistant (707, 1070).

The oldest continuous pear breeding program is that of the U.S. Department of Agriculture at Beltsville. In 1908, Waite (fig. 3) started hybridizing pears at Arlington Farms in Virginia (990). He intercrossed the moderately resistant Kieffer, Seck-

el, and Anjou cultivars with the susceptible Bartlett. Many thousands of seedlings were inoculated with the blight organism, but few resistant seedlings were recovered. One selection of unknown parentage was introduced in 1938 as the Waite cultivar (fig. 28, A), but it was never widely planted.

In 1938 the breeding program was moved from Arlington to Beltsville, where it was under the direction of Magness (624, 660). Several European cultivars with the most blight resistance, such as Roi Charles de Wurtemberg (RCW), were intercrossed with promising selections from preceding programs. In 1960 three new pear cultivars were introduced (fig. 28, B–D). Magness (Seckel seedling SPI 49490 × Comice) is a male sterile, high-quality dessert pear, resistant to twig blight but susceptible to trunk blight (1060, 1063). It was later found susceptible to blossom blast caused by a *Pseudomonas* species (506). Moonglow (US-Mich. 437 × RCW) is a medium-quality dessert and processing pear, with moderate resistance to fire blight. Dawn (US-Mich. 437 × Comice) is a high-quality dessert pear, which at first was thought to be susceptible to fire blight but later proved fairly resistant (1070). Figure 29, A and B, shows that numerous Magness, Moonglow, and Dawn trees were alive following severe blight epiphytotics. The missing Magness trees died from trunk blight. The many empty spaces due to loss of trees from fire blight indicate the relative resistance of these three cultivars to this disease.

In 1960, Brooks et al. (117) continued the pear breeding program when five objectives were initiated: (1) Extensive collection of species and cultivars from around the world for evaluation of blight resistance; (2) evaluation and use of several oriental *Pyrus* species, hybrids, and cultivars as parents; (3) planting of large numbers of seedlings annually for evaluation on a 10-year rotation schedule; (4) mass inoculation of seedlings in the greenhouse for evaluation of blight resistance; and (5) establishment of genetic studies on blight inheritance, tree juvenility, and fruit characteristics. Since 1966 a cooperative program has been maintained with the Ohio Agricultural Research and Development Center at Wooster (117, 706).

The extensive planting of many pear cultivars collected worldwide to evaluate their blight resistance resulted in the loss of about 90 percent of the trees (fig. 29, C) and about 50 percent of the trees in a planting of commercial cultivars (707, 1070). The best known resistant and susceptible cultivars are

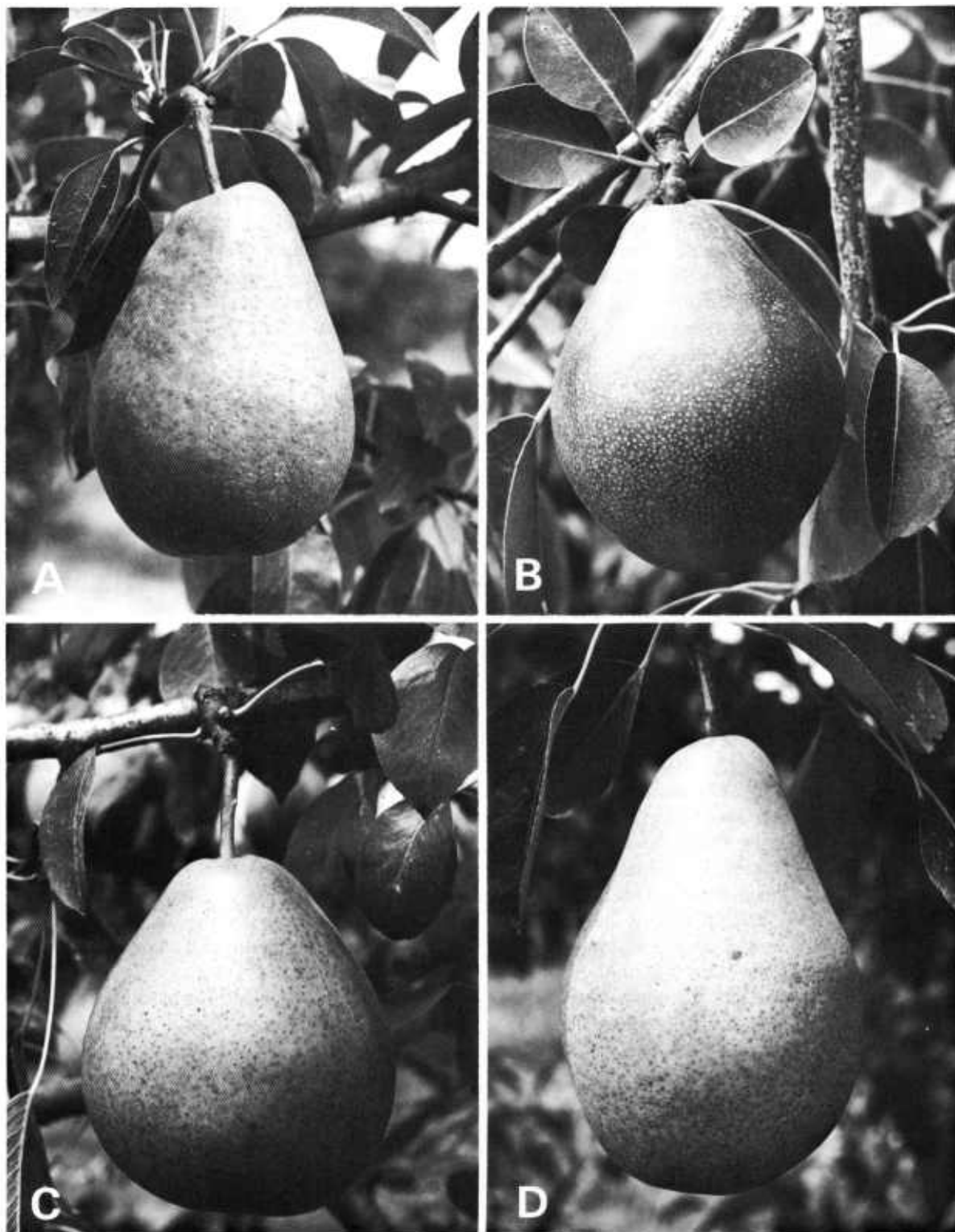
listed in table 10. Degree of resistance also was examined in 107 selections in 17 *Pyrus* species (table 9), 85 selections from controlled interspecific crosses, and a large number of species hybrids (1069, 1072). Degree of blight resistance varied among species, clones, and selections within species and species hybrids. In interspecific crosses, resistance was not consistently transmitted either by crossing a highly resistant with a very susceptible species or by crossing two highly resistant ones. The highest overall resistance appeared to result from crossing two moderately resistant parents (1072).

Combinations of low and intermediate levels of fire blight resistance within *P. communis* have resulted in numerous resistant selections with fair to good fruit quality (1057a). Subsequent combinations of these and other additive sources of resistance have resulted in such resistant cultivars as Magness and Moonglow.

Nearly 32,000 pear seedlings at Beltsville and 10,000 at Wooster, Ohio, from more than 600 progenies derived from controlled pollinations have been planted as of 1975 and are being evaluated for blight resistance, fruit quality, tree vigor, and time and amount of flowering (1073). At Beltsville the seedlings have been spaced 4 feet in the row and in 3-foot-wide double rows, which are 16 feet apart (1.2 × 1.0 × 5.0 m) (fig. 26, C and D; fig. 29, D). Thus, we were able to plant 1,400 trees per acre (3,500/ha), and the trees will have attained sufficient growth so that all required data can be collected within 8–10 years from the planting date. In addition, 3,000 seedlings screened for blight resistance in the greenhouse are being evaluated for natural blight in the field to determine the relationship between natural and artificially induced blight. All data are computerized so that genetic studies can be made for these characteristics.

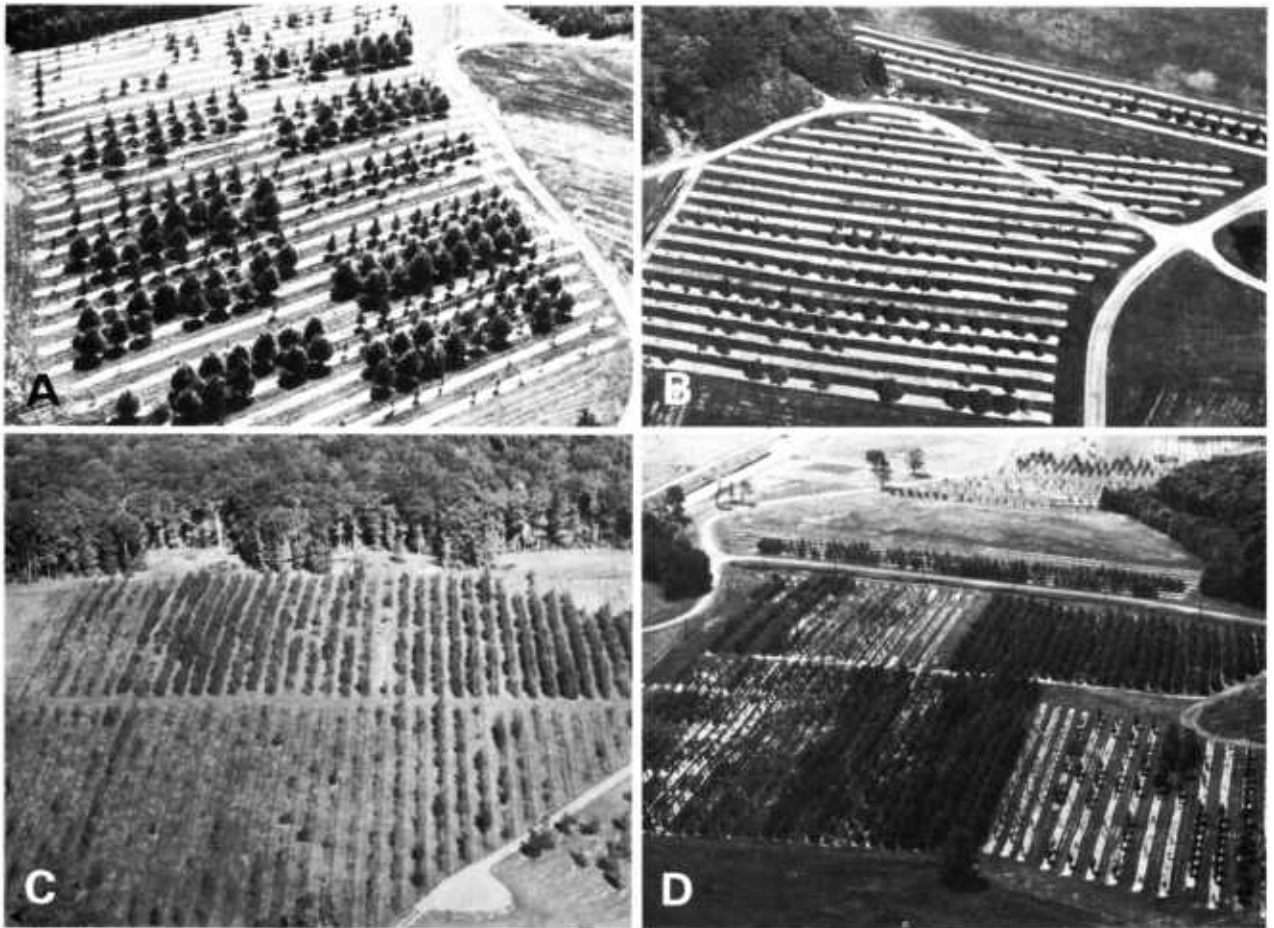
One of the first significant contributions from this computerized breeding program is the determination of a dominant gene, *Se*, causing sensitivity in *P. communis* to fire blight (947, 1076). A total of 13 cultivars and 4 selections are *Sese* and 3 selections are *sese*. At this time we question previous reports of the apparent existence of dominant genes *EW*₁ and *EW*₂, carrying resistance in *P. pyrifolia* and *P. ussuriensis*, respectively (19, 229, 948, 1136).

In the mid-1970's, Bell (1084) and Bell et al. (81e) reported on a possible correlation between pear fruit quality and fire blight resistance, based on data collected in the USDA pear breeding program. They



PN-6392

FIGURE 28.—Pear cultivars released by the U.S. Department of Agriculture: A, Waite; B, Magness; C, Moonglow; D, Dawn.



PN-6393

FIGURE 29. — Aerial view of USDA pear plantings at Beltsville, Md.: A, Randomized and replicated block of three pear cultivars: Large trees, Magness; medium-sized trees, Moonglow; smallest trees, Bartlett; B, single-row planting of major pear cultivars: Magness, row 1 (bottom); Bartlett, rows 2 and 3; Moonglow, row 4; and Dawn, row 5; C, planting of 2 trees each of 500 pear cultivars collected worldwide; seedling progenies in upper half of photograph; D, several blocks of pear seedlings planted in double rows, as shown in figure 26, C and D. Note: With few exceptions all missing trees in these plantings were destroyed by fire blight.

concluded that blight resistance and fruit quality of the progenies studied were not genetically linked or physiologically associated and that simultaneous selection for resistance and high fruit quality appeared feasible. Possibly the breeder should concentrate on germplasm of high fruit quality available within *P. communis* and discard susceptible seedlings (474b). Bell et al. (81f) also studied regressing progeny means on midparental phenotypes and obtained heritability estimates for fire blight resistance in pear. They determined that approximately half of the variability in resistance in pear is additive, but also they found evidence for nonadditive genetic effects compatible with the qualitative gene for sensitivity reported by Thompson et al. (947).

Between 1916 and 1919, the USDA pear program also maintained a cooperative breeding project with the Michigan Agricultural Experiment Station at South Haven. Parent trees in this program had either moderate blight resistance or desirable fruit quality. Of all progenies, seedlings from Barseck (Bartlett \times Seckel) \times Bartlett had the best fruit quality in combination with moderate resistance to fire blight. One selection from this parentage, US-Mich. 437, has since been used extensively as a parent at Beltsville. Also, Johnston (*in* Brooks and Olmo, 118) in 1935 introduced the cultivar Campas (parentage unknown) for canning purposes.

Another of the large pear breeding programs in North America is that of the Canada Department of

Agriculture (CDA) at Harrow, Ontario. This program was started in 1962 by Layne (561, 564) in order to produce high-quality, blight-resistant pears for southwestern Ontario. The program consists of crossbreeding most of the known sources of blight resistance with the best commercial cultivars of high fruit quality (566). All seedlings from controlled pollinations are artificially inoculated and the resulting seedlings grouped into four blight-resistance classes according to the amount of blight.

Studies at Harrow on about 7,500 seedlings in 48 progenies have shown that both quantitative and qualitative inheritance of fire blight may be involved (565). The breeding value of the most efficient *P. communis* sources (Magness, Maxine, and US-Mich. 437) appeared to be superior to the *P. ussuriensis* and *P. pyrifolia* sources, principally because of the larger, higher quality fruit associated with *P. communis*.

The first phase of a cooperative study between CDA and USDA has been completed. Its purpose was to determine the possible correlation of fire blight resistance of young pear seedlings inoculated in the greenhouse with mature seedling trees naturally infected in the field (765, 1057, 1074). Preliminary results indicated a general correlation, and early screening appears useful in breeding fire blight-resistant pears by eliminating the most susceptible seedlings.

In 1947-48, the CDA Research Station at Ottawa introduced a series of four blight-resistant pear cultivars—Enie, Menie, Miney, and Moe—to be grown in home gardens in eastern Ontario and Quebec (93, 459). Menie was selected from a cross of Kurskaya × Flemish Beauty, whereas the other three cultivars originated from the cross Zuckerbirne × Clapp Favorite. This station was closed in 1968.

Lombard and Westwood (590) and Westwood et al. (1015) have maintained a large collection of *Pyrus* species, hybrids, and cultivars at Corvallis and Medford, Oreg. This material has been evaluated for resistance to fire blight and for use as rootstocks against *Phytophthora* root rot, blast, pear decline, and root aphids (140).

Other active pear breeding programs and selection-evaluating sites are located in California (Davis), Georgia (Byron), Illinois (Carbondale), Indiana (West Lafayette), Michigan (East Lansing), Mississippi (State College), Missouri (Mountain Grove), and North Carolina (Raleigh), the provincial

station at Vineland, Ontario, and the station of the CDA at Kentville, Nova Scotia.

Recent pear cultivar introductions are Rogue Red (Seckel × Farmingdale seedling) from Oregon in 1969, Spartlett (Bartlett seedling) from Michigan in 1973, California (Max-Red Bartlett × Comice) from California in 1974, and Honeysweet (Seckel × US 220) from Indiana in 1976. The first three cultivars are only moderately resistant to fire blight (146, 372, 589), whereas Honeysweet appears to be rather resistant (474a).

Soon after the appearance of fire blight in Europe in 1957, a pear breeding program was undertaken in England. By 1966, several inoculation techniques were evaluated at the John Innes Institute to determine seedling resistance to *E. amylovora* (631). This program is being continued at East Malling. Alston (19) reported in 1972 that among such other breeding criteria as late maturing, long storage, and dwarf tree habit, the main goal against fire blight is to avoid parent trees that produce secondary blooms.

Apple

Objectives in apple breeding have varied in different sections of North America. Because fire blight has usually been less severe on apples than on pears, the main objective has not been to combine blight resistance with superior fruit quality, although some breeders have been advocating this since 1930. Throughout most of the central United States increased winter hardiness is highly desirable as in the northern Great Plains, New England, and Canada. An extensive review of apple breeding prior to 1938 was published by Magness (624).

In breeding for disease resistance, scab probably has been considered more important than fire blight. However, fire blight is a serious disease on Jonathan, Wealthy, York Imperial, and several other cultivars. On the other hand, Delicious, Ben Davis, and the Winesap family of cultivars are fairly resistant.

One of the first apple breeding programs was begun in 1868 by Patten in Charles City, Iowa. He introduced several cultivars, and some selections from his work were later used extensively by the Iowa Agricultural Experiment Station at Ames by Budd et al. (558, 559) until about 1960. In 1909 another extensive apple breeding program was begun by Vincent and Longley (981) in Idaho. Results from nearly 12,000 seedlings indicated that the

cultivars Jonathan, Wagener, and Esopus Spitzenburg provided the highest dessert quality when used as parents, whereas seedlings derived from Ben Davis had the best keeping quality. About the same time, Crandall (191) started a breeding program at Urbana, Ill., which was later continued by Dayton et al. (215) and Mowry (666, 667).

At the Ohio Agricultural Research and Development Center in Wooster, apple breeding was begun by Keil in 1915 and continued in 1929 by Howlett. Other apple breeding programs, nearly all of which were terminated by World War II, were in Georgia (Experiment), Maryland (College Park), Missouri (Columbia), New York (Ithaca), North Dakota (Mandan), and South Dakota (Brookings). The program at Mandan was directed by the U.S. Department of Agriculture. Between 1952 and 1965, the following apple cultivars were introduced at Mandan: Custer, Dakota, Garrison, Heart River, Killand, Mandan, Peace Garden, Prairie Gold, Stephens, and Thorberg (118). For additional apple cultivars introduced from these programs, see the extensive review by Magness (624) and the fruit variety register by Brooks and Olmo (118). Those reported cultivars with ratings for fire blight resistance are listed in table 12.

Of the active apple breeding programs, the oldest is that of the N.Y. State Agricultural Experiment Station at Geneva started by Beach. The main objectives initially were to produce high-quality, productive, late-keeping cultivars that would be fully hardy under New York State conditions. Many well-known cultivars were used to obtain thousands of seedlings for evaluation of these characters. During 1914–68, 52 apple cultivars were introduced (1007). The best known of these were Cortland (Ben Davis × McIntosh), Early McIntosh (Yellow Transparent × McIntosh), Empire, originating from an open-pollinated seedling in an orchard containing only McIntosh and Delicious trees (1008), Lodi (Montgomery × Yellow Transparent), Macoun (McIntosh × Jersey Black), Milton (Yellow Transparent × McIntosh), Monroe (Jonathan × Rome Beauty), Niagara (Carlton × McIntosh), and Wayne (Northwestern Greening × Red Spy). Recent apple introductions from Geneva include Jonamac (McIntosh × Jonathan) in 1972 and Burgundy from a cross of Monroe × (Macoun × Antonovka) in 1974 (1008, 1010). Of these cultivars, Lodi and Wayne appear to be susceptible, whereas the remainder are moderately resistant to fire blight (table 12).

In 1975, Gardner (1101) reported that he had identified near immunity to fire blight in several clonal selections of *Malus* species, following numerous shoot tip inoculations in the greenhouse and field nursery. From crosses between these resistant clones and the susceptible M 9, M 16, and M 27 rootstock clones, about one-eighth of the seedlings in each progeny exhibited the resistance level of the resistant parent. In progenies from crosses between the susceptible Malling parents, 90–100 percent of the seedlings were killed by fire blight, and of the survivors more than 50 percent of the shoot lengths were blighted. Gardner concluded that resistance appeared to be oligogenic, with control by dominant additive genes carried in the heterozygous condition.

A comprehensive apple breeding program is being carried out in Indiana. It was undertaken in 1945 by Shay et al. (861) and continued by Dayton et al. (215) and Williams et al. (1025). It is a highly cooperative endeavor among the agricultural experiment stations in Indiana, Illinois, and New Jersey. Names of new cultivars carry the prefix PRI, an acronym formed by the three cooperating institutions—Purdue, Rutgers, and Illinois. Four new cultivars have been introduced from this program: Prima (14-510 × N.J. 12324a) in 1970, Priscilla (Starking Delicious × 610-2) in 1972, and Sir Prize (Golden Delicious (4 ×) × 14-152) in 1975. These three cultivars are not only highly resistant to scab but also to fire blight in the field in Indiana (215, 1025, 1025a). In addition, Priam (Golden Delicious × 26829-2-2) × Jonathan) was introduced in France in 1974. This cultivar is only slightly susceptible to mildew; its resistance to fire blight was not mentioned (215a).

In 1959 the USDA undertook a minor apple breeding program at Blairsville, Ga., to serve the Southeastern United States (386). The principal objectives were fire blight resistance and superior horticultural characteristics, including late blooming, early maturity, and fruit color. Following blight epidemics in 1963, 1967, 1970, and 1971, Thompson (946) reported fire blight ratings on approximately 300 fruiting apple cultivars and selections on various rootstocks and 100 nonbearing cultivars. In addition, he published data on tree precocity. Also, about 12,000 seedlings from controlled pollinations are being evaluated. The headquarters for this breeding program has been moved to Byron, Ga.

Other locations for current apple breeding programs and selection-evaluation sites are Illinois

(Carbondale), Michigan (East Lansing), Minnesota (St. Paul), Missouri (Mountain Grove), Virginia (Blacksburg), and Vineland, Ontario.

Pyracantha

At the U.S. National Arboretum in Washington, D.C., Egolf (260a) has maintained a large pyracantha breeding program since 1959. Cold hardiness and disease resistance have been emphasized. Since 1960, 80,000 seedlings have been produced, from which 72 selections have been test planted for evaluation. Mass inoculations of the plants have been performed with the rapid inoculator (fig. 27) to screen them for fire blight resistance (262). The cultivar Shawnee, considered a spontaneous hybrid of *Pyracantha koidzumii* (Hyata) Rehd. and *P. crenato-serrata* (Hance) Rehd., was introduced in 1966 and the cultivar Mojave (*P. koidzumii* × *P. coccinea* Roem. cv. Wyatt) in 1970 (259, 260). Both are resistant to fire blight and scab (*Fusicladium pyrinum* (Lib.) Fekl. var. *pyracanthae* Thuem.).

Hawthorn and Cotoneaster

A breeding and selection-evaluation program has been undertaken in Denmark since 1970 to find blight resistance in hawthorn (*Crataegus*) (882). Large numbers of plants and clonal selections of several species from various countries in Western Europe are being evaluated for fire blight resistance in the field (489). Blight-resistant cultivars of hawthorn are of utmost importance because they are extensively used as windbreaks for fruit orchards and generally as ornamental shrubs.

At the U.S. National Arboretum, Egolf (261) has inoculated large numbers of cotoneasters to select possible resistant germplasm. In West Germany, Zeller and Meyer (1046b, 1046c) are evaluating numerous hawthorns and cotoneasters against natural blight infection. A cooperative endeavor is underway among fire blight investigators from Denmark, West Germany, and the Netherlands to hybridize, select, and evaluate these host plants for resistance to fire blight and for important horticultural characters.

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SURVEY OF FIRE BLIGHT RESEARCH IN THE UNITED STATES AND CANADA

In 1974, an ad hoc committee²⁵ of the Apple and Pear Disease Workers surveyed the fire blight research in the United States and Canada. The purpose of this survey was to determine the following facts about this research: (1) Studies in progress, (2) nature of the research, (3) personnel involved, (4) supporting agencies, and (5) location. The questionnaire was returned by 71 professional workers from 26 States of the United States and 2 Provinces of Canada.

Table 15 summarizes the pertinent data. The committee found that 47 professional investigators devoted part or full time to fire blight research in the United States and Canada. About 9.6 scientific man-years (SMY) were spent on fire blight research in the United States and 2 SMY in Canada during 1974. Included with scientists in the United States were seven professional investigators (1.3 SMY) employed by commercial companies, who evaluated new chemicals for fire blight control. For each SMY in the United States, there were 2.7 support person-

nel compared with about 2.2 in Canada. Among the 42 U.S. investigators, 27 were considered to be working in pathology, 10 in horticulture, 4 in bacteriology-physiology, and 1 in biochemistry.

Breeding of pears, apples, or both for fire blight resistance and evaluating progenies from these programs predominated the research activity of many professionals. Although one cannot determine from the questionnaires exactly how much time an investigator devoted to breeding, we know from personal contact that about 3.5 SMY were spent on research associated with breeding. Georgia (USDA), Indiana, Maryland (USDA), New Jersey, Ohio (cooperative with USDA), and Canada (Harrow, Ontario) had active breeding programs. Minor programs were conducted in California, Michigan, Minnesota, New York, and North Carolina, where 1–10 percent of a professional investigator's time was spent principally on variety evaluation.

The largest breeding program (2.0 SMY), which was supported by the U.S. Department of Agriculture, was devoted to breeding pears resistant to fire blight. This research was conducted at Beltsville, Md., and Wooster, Ohio. In addition, 0.25 SMY was spent on fire blight resistance in apples (USDA–

²⁵This committee included H. L. Keil (chairman), H. S. Aldwinckle, S. V. Beer, R. P. Covey, A. L. Jones, E. J. Klos, W. R. Landis, W. J. Moller, J. D. Moore, and T. van der Zwet.

TABLE 15.—*Data on fire blight research in the United States and Canada, 1974*¹

Location	Investigator	Discipline	Full-time effort Number	Support personnel Percent	Source of support	Objectives
UNITED STATES						
California:						
Berkeley -----	Schroth, M. N. ---	Pathology -----	30	5.1	} State, Fed. Ext., Hatch, Indus.	Study ecology, biology, and variation of <i>Erwinia amylovora</i> ; chemical and biological control; monitor bacterial population on pear trees.
	Moller, W. J. -----	-----do -----	30	---		
	Zoller, B. G. -----	-----do -----	40	---		
Davis -----	Ryugo, H. -----	Physiology -----	10	.05	State -----	Evaluating hybrid resistance in pears.
	Starr, M. P. -----	Bacteriology -----	25	.5	-----do -----	Study ecological genetics of <i>Erwinia</i> , particularly virulence in <i>E. amylovora</i> .
Richmond -----	Landis, W. R. ² ---	Pathology -----	1	1.0	Food and Mach. Corp. -----	Field evaluation of chemicals for blight control.
Colorado: Grand Junction ----	Luepschen, N. S. -----	-----do -----	20	1.0	State, Hatch, Indus. -----	Evaluating new chemicals for blight control and field inoculation techniques.
Delaware: Wilmington -----	Davidson, S. -----	-----do -----	25	.5	Dupont -----	Evaluating new chemicals for blight control.
Georgia: Byron -----	Thompson, J. M. -	Horticulture -----	25	---	Fed. (USDA) -----	Breeding and evaluating apple selections for blight resistance.
Illinois: Urbana -----	Ries, S. M. -----	Bacteriology -----	10	.1	Hatch -----	Evaluating new chemicals for blight control and effect of mulching on blight control.
Indiana: Lafayette -----	Kuc, J. ² -----	Biochemistry -----	10	3.0	} USDA coop. agreement -----	Study biochemical factors in resistance; factors contributing to symptom development; in vivo and in vitro studies of substances synthesized by infected host; inducement of resistance factors by avirulent strains of <i>E. amylovora</i> .
	Williams, E. B. ---	Pathology -----	10	---		
	Janick, J. -----	Horticulture -----	15	.3	State, Hatch -----	Breeding pears for blight resistance.
Maryland: Beltsville -----	van der Zwet, T. --	Pathology -----	100	1.5	Fed. (USDA) -----	Breeding pears for blight resistance; genetic studies of blight inheritance; improvement of inoculation techniques; study relation of artificially inoculated seedlings with naturally infected trees; determining degree of resistance

	Keil, H. L.-----	-----do-----	50	.5	Fed. (USDA)-----	in various pear tissues; study pathogenicity of single and mixtures of <i>E. amylovora</i> isolates; developing dwarf-resistant pear varieties.
						Evaluating new chemicals for blight control; determining <i>Erwinia</i> cell numbers to produce blight symptoms; determining if tissue developed after infection acquires any resistance; determining role of bacterial strands in dissemination; effect of tree injections on eradication and control; determining susceptibility of apple dwarfing rootstocks.
Michigan: East Lansing-----	Klos, E. J.-----	-----do-----	20	.7	State, Indus.-----	Evaluating new chemicals for blight control; study ways to increase effectiveness of compounds; determining role of yellow <i>Erwinia</i> ; altering tree physiology by fertilizer and biological compounds to reduce susceptibility; monitoring <i>E. amylovora</i> populations; surveying for resistant individuals; study role of insect vectors.
	Carlson, R. F.----	Horticulture-----	1	--	State-----	Breeding and selecting pear varieties resistant to blight.
	Jones, A. L.-----	Pathology-----	5	}	Fed. Ext.-----	Developing better timing of fire blight treatments; monitoring <i>E. amylovora</i> populations.
	Sutton, T. B. ² ----	-----do-----	15			
Minnesota: St. Paul-----	O'Malley, J.-----	-----do-----	100	1.5	3M Co.-----	Evaluating new chemicals for blight control.
	Stushnoff, C.-----	Horticulture-----	10	.5	State-----	Breeding and evaluating apple selections for blight resistance.
Missouri: Columbia-----	Goodman, R. N. -	Pathology-----	25	}	1.2 State, Natl. Sci. Found., Hatch, Indus.	Study host specificity, biochemical properties, and mode of action of <i>E. amylovora</i> toxin; developing bioassay with toxin for evaluating blight resistance of pear and apple seedlings.
	Huang, H. S. ² ----	Bacteriology-----	100			
New Jersey: New Brunswick	Hough, L. F.-----	Horticulture-----	10	.05	State, Hatch-----	} Breeding pears for blight resistance.
	Bailey, C. H.-----	-----do-----	10	--	-----do-----	
New York:						
Geneva-----	Aldwinckle, H. S.	Pathology-----	20	2.5	-----do-----	} Evaluating new chemicals for blight control; developing inoculation techniques to evaluate resistance of apple cultivars and seedlings in breeding program.
	Szkolnik, M.-----	-----do-----	10	--	-----do-----	
	Gilpatrick, J.-----	-----do-----	10	--	-----do-----	
	Cummins, J. N. --	Horticulture-----	4	--	-----do-----	
	Lamb, R. C.-----	-----do-----	1	--	-----do-----	Breeding and evaluating apple rootstocks for blight resistance.
	Way, R. D.-----	-----do-----	5	--	-----do-----	Breeding and evaluating pear seedlings for blight resistance.
See footnotes at end of table.						Breeding and evaluating apple selections for blight resistance.

TABLE 15.—*Data on fire blight research in the United States and Canada, 1974*¹—Continued

Location	Investigator	Discipline	Full-time effort Number	Support personnel Percent	Source of support	Objectives
UNITED STATES—continued						
Ithaca-----	Beer, S. V.-----	Pathology-----	50	1.9	State, Hatch-----	Evaluating control practices; study epidemiological, physiological, and biological factors affecting blight infection and resistance.
Middleport-----	Harnish, W.-----	-----do-----	1	2.0	Food and Mach. Corp.-----	Evaluating new chemicals for blight control.
	Perry, R. S.-----	-----do-----	1	2.0		
North Carolina: Goldsboro-----	Brooks, D. H.---	-----do-----	5	.1	Imper. Chem.-----	Field testing of chemicals for blight control.
Raleigh-----	Clayton, C. N.---	-----do-----	1	.01	State-----	Evaluating pear seedlings in greenhouse and field for blight resistance.
Ohio: Wooster-----	Blake, R. C.-----	Horticulture-----	100	---	Fed. (USDA)-----	Breeding pears for blight resistance.
Oregon: Medford-----	Cameron, H. R.--	Pathology-----	5	---	State, Hatch-----	Evaluating susceptibility of potential rootstocks.
Virginia: Blacksburg-----	Drake, C. R.-----	-----do-----	8	---	State, Indus.-----	Determining whether pear industry can be established in Virginia.
Winchester-----	Hickey, K. D. ² ---	-----do-----	5	.1	State, Indus.-----	Evaluating new chemicals for blight control.
Washington: Wenatchee-----	Covey, R. P.-----	-----do-----	40	.4	State-----	Evaluating new chemicals for blight control; study effect of environmental factors and bacterial population on blight development; surveying extent of streptomycin resistance.
Yakima-----	Biehn, W. ² -----	-----do-----	2	.7	Ciba-Geigy Corp.-----	Evaluating new chemicals for blight control.
CANADA						
British Columbia: Summerland.	Lopatecki, L. C. ² -	-----do-----	10	---	Canad. Dept. Agr.-----	Study characteristics of <i>E. amylovora</i> bacteriophage and its role in blight etiology; in vitro and in vivo studies of <i>E. amylovora</i> and related nonpathogenic bacteria.

	McIntosh, D. L.--	-----do-----	10	.75	Canad. and Brit. Columbia Dept. Agr.	Monitoring populations of <i>E. amylovora</i> in irrigated and nonirrigated pear and apple trees; study elimination of <i>E. amylovora</i> from fruit being exported.
Ontario:						
Guelph-----	Gibbins, L. N.----	Bacteriology- physiology.	30	2.0	Natl. Res. Council of Canada.	Study oxidative metabolism of <i>E. amylovora</i> through aerobiosis and anaerobiosis transition; bacteriocinogeny, lysogeny, and nature of temperature-induced variation in <i>E. herbicola</i> .
Harrow-----	Quamme, H. A.--	Horticulture-----	100	1.0 .5 }	Canad. Dept. Agr. -----	Breeding and evaluating blight-resistant varieties of pear and dwarfing rootstocks; study inheritance of resistance; developing satisfactory control measures by studying epidemiology and environmental factors; monitoring <i>E. amylovora</i> in orchards.
	Bonn, W. G.-----	Pathology-----	50			
<hr/>						
Part- and full-time professional fire blight investigators in—						
U.S. -----			42.0	(SMY 9.6)		
Canada -----			5.0	(SMY 2.0)		
Support personnel for fire blight research in—						
U.S. -----			25.9	(MY)		
Canada -----			4.3	(MY)		

¹A November 1977 survey indicated only minor changes in personnel and percentage of full-time effort.

²No longer at this location.

Georgia). New Jersey devoted 0.2 SMY and Indiana 0.15 SMY to their pear breeding programs. The Canadian Department of Agriculture supported 1 SMY to breeding pears resistant to fire blight. Also, a small amount of time was used in evaluating rootstocks for fire blight resistance.

New chemicals for fire blight control were tested in California, Colorado, Illinois, Maryland (USDA), Michigan, New York, Virginia, and Washington. An estimated 2–3 SMY were devoted to this work by the academic institutions. In addition, at least seven commercial companies were developing new chemicals for fire blight control. This commercial effort amounted to about 1.4 SMY, which seemed hardly enough when *E. amylovora* strains resistant to streptomycin have been found in several areas of the United States. Resistance of *E. amylovora* to streptomycin was studied in California, Maryland (USDA), and Washington.

Studies on the etiology, biology, and ecology of *E. amylovora* were conducted in California, Colorado, Illinois, Maryland (USDA), Michigan, Missouri, New York, and in British Columbia, Canada. In addition, epidemiology was investigated in Indiana, Maryland (USDA), Michigan, New York, Washington, and Ontario.

Techniques for monitoring bacterial populations were being developed in California, Michigan, Washington, and Canada. As soon as they are perfected, we anticipate much more activity in this

phase of fire blight research. In California, researchers were spending a small amount of time studying the ecological genetics of the genus *Erwinia*, particularly the virulence of *E. amylovora* to its host. In Canada, some time was devoted to bacteriology-physiology studies.

In the United States, fire blight research was supported by funds of Federal and State governments and by industry. Without industry, this left about 8.3 SMY dependent on government for support. Federal money for fire blight research was appropriated through the Agricultural Research Service, Extension Service, Hatch funds, and the National Science Foundation. About 4–5 of the 8.3 SMY devoted to fire blight research were supported by Federal sources and the remainder by State funds. The Canadian Government completely supported the 2 SMY.

If we consider that fire blight usually causes more damage to pears and apples in the United States than in Canada and that the United States produces 16 and 7 times more pears and apples, respectively, then the U.S. Government appears to support proportionately far less fire blight research than the Government of Canada. Since much of the fire blight research in the United States is fragmented, better coordination of this research is needed so that a concerted effort can be made to solve the many problems associated with the disease.