# Fire Blight Epidemiology: Factors Affecting Release of Erwinia amylovora by Cankers

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## ABSTRACT

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Cankers with different characteristics in one pear and two apple orchards were studied to determine which were effective producers of primary inoculum and when inoculum was produced. *Erwinia amylovora* was recovered at least once from intact canker margin surfaces of 19 of 122 cankers that were swabbed weekly from April through July. Fifteen of the 19 active cankers initially yielded *E. amylovora* during a 2-wk period after bloom. Cankers from which *E. amylovora* was recovered generally had indeterminate-type (smooth) margins and were located on wood at least 4 yr old. The pathogen was recovered from a significantly greater proportion of cankers, the margins of which had been covered with moist pads, than from similar cankers that were exposed to ambient moisture. *Erwinia amylovora* was recovered from blossom buds or blossoms collected from clusters in the immediate vicinity of two cankers that had extended before bloom, but the pathogen was isolated from these two canker surfaces only after bloom. Only clusters that were included in the pathogen-positive blossom samples became infected. Inoculation of nursery-grown apple trees early during the growing season produced cankers with determinate-type margins; later inoculation yielded cankers with indeterminate-type margins. When these cankered trees were potted, chilled, and then placed under controlled-environment conditions, *E. amylovora* was recovered from a significantly greater proportion of trees with indeterminate-type canker margins than from those with determinate-type canker margins. More of the cankered trees grown at 21 C yielded *E. amylovora* than those grown at 17 C or 28 C.

*Additional key words*: bacteria, plant disease, infrared detection.

Fire blight, which is caused by *Erwinia amylovora* (Burr.) Winslow et al., continues to limit pear production and is becoming increasingly important to apple culture in the northeastern United States (2). The disease varies in severity from year to year and from location to location (6, 20) probably because of variation in environmental conditions (11, 15) and differences in amounts of initial inoculum.

The principal sources of primary inoculum are the margins of cankers formed the previous season (9, 20). Cells of *E. amylovora*, which are produced in ooze on the surface of "hold-over" cankers [sensu Sackett (19)] may be transmitted to new infection courts (blossoms, leaves, and stems) by rain, wind, or insects (6). Although the pathogen has been detected in pome-fruit blossoms prior to the appearance of symptoms (4, 20, 26), little attention has been given to detection of primary inoculum at its source. Numerous workers have reported that the majority of cankers formed one season do *not* become active hold-overs and produce visible ooze the following year (5, 7, 10, 12, 14, 17, 18, 25, 26). However, inoculum may be produced by a greater proportion of cankers without obvious ooze (4, 26).



The factor(s) that influence whether cankers become active and those that influence initiation of activity are not well known. Most early workers generally considered cankers situated on larger tree limbs to be more important sources of inoculum than those on small twigs. However, there are several reports of successful pathogen overwintering in twigs 3-13 mm in diameter (12, 14, 25). In a more recent study by van der Zwet (27), six of the seven cankers that were observed to produce ooze were located on tree structures more than 6 yr old. The early workers considered cankers with "smooth" (vs. "rough") margins ["indeterminate" vs. "determinate", sensu Tullis (25), "open" vs. "closed", sensu Hockenhull (8)] more important as sources of primary inoculum. Only cankers with smooth margins were reported to have produced ooze in van der Zwet's (27) study. The results of studies of fire blight histopathology in infected *Crataegus monogyna* by Hockenhull (8) suggested that in closed cankers the pathogen is isolated from host sources of nutrients and moisture by complete "defense periderms". The further development of the pathogen thus is inhibited and such cankers would be unlikely to become active hold-overs in the following season.

The time of inoculum production relative to the phenological development of host trees varies considerably from year to year. If inoculum is present in

abundance during bloom and environmental conditions are suitable for dissemination and development of infection, severe blossom blight may be expected.

The purpose of the present study was to determine which cankers are more likely to release inoculum and to relate inoculum release to tree phenology and environmental conditions. Factors leading to the development of cankers with a high probability of releasing the pathogen were considered also. A preliminary report has been published (3).

## MATERIALS AND METHODS

**Orchard studies.**—The presence of *Erwinia amylovora* on canker surfaces and in selected blossoms was determined during the 1975 growing season in two apple (*Malus pumila* Miller) orchards and one pear (*Pyrus communis* L.) orchard in Wayne County, New York. Most trees in the three orchards had two to 20 fire blight cankers that had been initiated during the 1974 growing season (Table 1). Before tree growth resumed, each tree was examined and cankers were selected for subsequent monitoring. We selected representive cankers of all types located on tree structures of all ages in Orchards A (apple) and B (pear). In Orchard C (apple), many cankers with indeterminate-type margins were present and only these were selected for monitoring. An electronic infrared sensor [Find-R-Scope (FJW Industries, Mt. Prospect, IL 60056)] was used as an aid in detecting cankers with indeterminate margins (24). To provide a point of reference for subsequent canker extension, margins were outlined with yellow paint applied with a brush.

Each selected canker was characterized by location on the tree, margin type, and age of infected tissues. The location of the margin with respect to tree structure (trunk, scaffold, limb, terminal shoot, or fruiting spur) and the age of the oldest tissue that the lesion had affected also were noted. Each canker margin was rated for degree of determinate character (Fig. 1). "Determinate" cankers had margins with considerable amounts of cracked bark at the juncture between live and dead tissue. The bark on "indeterminate" canker margins was not cracked visibly;

TABLE 1. Orchards in which fire blight cankers were monitored by swabbing intact canker margins during May, June, and July, 1975[a]

| Orchard | Cultivar | Age (yr) | Cankers monitored[b] (no.) | Active cankers[c] (no.) |
|---|---|---|---|---|
| A | Idared | 9 | 55 | 10 |
| B | Bartlett | 10 | 53 | 4 |
| C | Rhode Island Greening | 4 | 14 | 5 |

[a]All orchards were located in Wayne County, New York, and had sustained severe fire blight damage the previous growing season, 1974.

[b]The margins of 7, 10, and 2 cankers in Orchards A, B, and C, respectively, had been covered with moist cotton pads (feminine sanitary napkins) and overwrapped with black polyethylene film to retain moisture.

[c]Number of cankers from which *Erwinia amylovora* was recovered at least once by swabbing during the 1975 monitoring period. Cankers for monitoring had been selected before growth started in the spring.

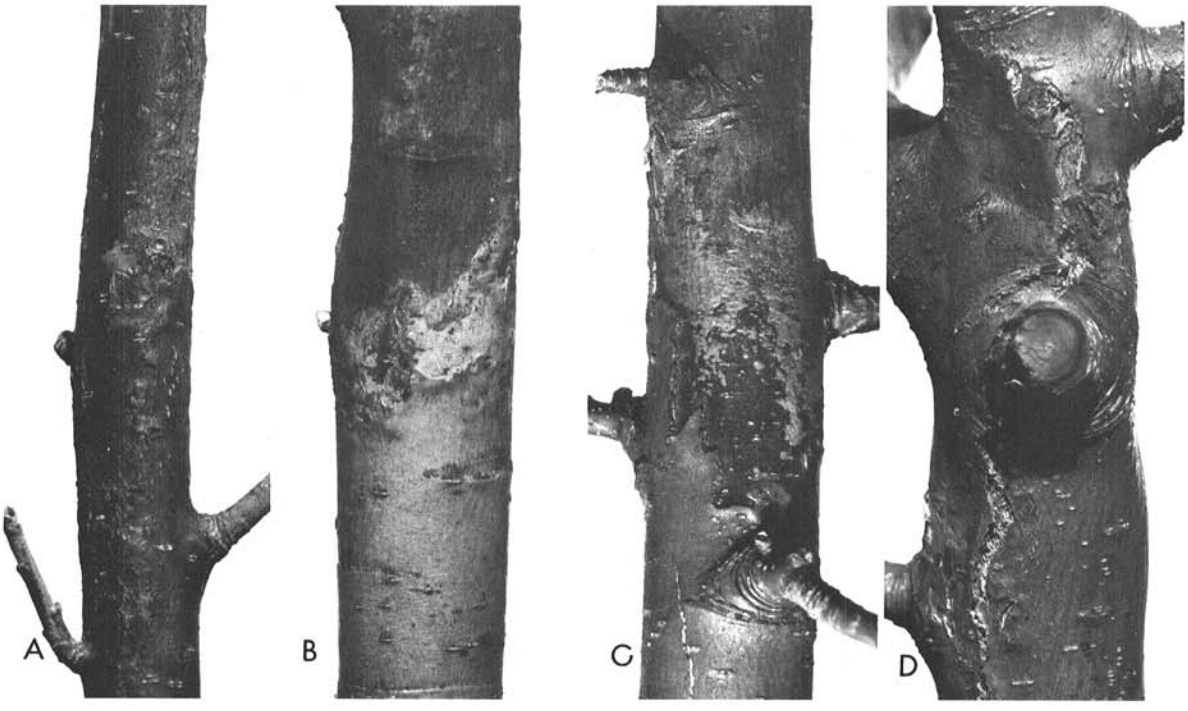


**Fig. 1-(A to D).** Representative fire blight canker margin types on *Malus pumila* 'Idared': **A)** indeterminate, **B)** almost-indeterminate, **C)** almost-determinate, and **D)** determinate.

two intermediate categories ("almost-determinate" and "almost-indeterminate") also were used.

To determine if moisture, external to the canker margin, affected the activity of *E. amylovora*, matched pairs of cankers in each orchard were selected based on all rated characters. The margin of one member of each pair (chosen at random) was covered with one or more feminine sanitary napkins previously saturated with sterile tap water. The wet napkins were secured with paper-covered wire and then covered with black polyethylene sheeting to prevent drying. The pads usually were replaced weekly. All orchards were treated with 8-8-100 Bordeaux mixture plus 1% oil (9.6 gm copper sulfate, 9.6 gm spray lime, 10 ml "60-second" spray oil per liter water) at the green-tip to half-inch (12.7 mm) green growth stage (13) before napkins were placed.

Orchards were visited weekly beginning on 22 April to observe cankers and to collect samples. During each visit, weather data were gathered from recording hygrothermographs and simple rain gauges. Daily rainfall data were obtained from a recording rain gauge located between Orchard A and Orchard B. Each canker was examined to determine if ooze was present on the surface and if the lesion had extended beyond the previously painted margin.

To determine if *E. amylovora* was present on intact canker margin surfaces, methods similar to those used previously by Beer and Opgenorth (4) were employed. Sterile cotton-tipped hospital applicators (Van Waters and Rogers, Inc., Rochester, NY 14603) were moistened with cold 50 m*M* potassium phosphate buffer, pH 6.5, and the margin and adjacent 4 cm of healthy bark were swabbed. After swabbing, the applicators were held in 5 ml of the same cold buffer in capped test tubes until they were processed further within 18 hr. Plating procedures, media, and *E. amylovora* identification procedures were as described previously (4). The relationships between canker activity and canker characteristics or environmental variables were analyzed by the chi-square method (23).

Flower buds, blossoms, or young fruits were sampled for *E. amylovora* as described previously (4). Each week, composite samples of five reproductive structures were collected from within 50 cm of all cankers that showed visible extension and from the vicinity of several cankers that did not. Composite samples of 50 or 100 reproductive structures were collected at random from the entire orchards.

**Production of cankers by artificial inoculation.**—Apple trees (cultivar Idared) were propagated by bench grafting scion wood to M. 7 rootstocks for the purpose of studying canker formation and activity under controlled conditions. The trees were grown for 2 yr in a nursery. To produce fire blight cankers, trees were inoculated on 14 July and 5 September 1974 by two techniques. Succulent lateral shoot tips were injected with a suspension of *E. amylovora* [strain 27-3 (21)] containing approximately $10^{10}$ cells/ml with a hypodermic needle. Other trees were inoculated on the main leader by making "X"-shaped cuts approximately 15 cm and 70 cm above the soil surface with a scalpel previously dipped in suspensions of the pathogen. Some noninoculated trees became infected by natural means shortly before the second set of inoculations was made. These were considered as "late-inoculated" trees in subsequent studies. After normal leaf fall in November, all infected trees were dug, bundled, and packed in moist sawdust.

Cankers were rated following the criteria used for cankers on orchard trees. In addition, the distance from the graft union to the canker margin, the tree circumference, and lesion dimensions were determined. Shoot tissue (alive or dead) distal from the canker margins was removed to leave at least 60 cm of scion wood. The pruned trees were potted in crocks (18 cm diam × 18 cm height) in a mixture of peat, perlite, and vermiculite (1:1:1, v/v) containing a complete fertilizer. Potted trees were placed at 2 ± 2 C for 3-6 mo to break dormancy.

To determine if growth temperature affected *E. amylovora* activity in cankers, ten sets of three trees each were selected based on similarity in size, inoculation type,

TABLE 2. Relation of canker margin character to activity of 55 fire blight cankers on Idared apple trees (Orchard A, Wayne County, New York)[a]

| Margin character[b] | Cankers monitored (no.) | Cankers active (no.)[c] | Cankers active (%) |
|---|---|---|---|
| Indeterminate | 3 | 1 | 33 |
| Almost-indeterminate | 8 | 3 | 38 |
| Almost-determinate | 32 | 4 | 13 |
| Determinate | 12 | 2 | 17 |

[a]Cankers were selected for monitoring before growth started in the spring. The intact margin area of each canker was swabbed weekly, to determine if *Erwinia amylovora* was present on the surface.

[b]Cankers were rated based on the extent of bark cracking at the margin and depression of the dead tissue relative to contiguous healthy tissue.

[c]Number of cankers from which *E. amylovora* was recovered at least once during the 15-wk monitoring season.

TABLE 3. Recovery of *Erwinia amylovora* from matched pairs of fire blight cankers as affected by moisture external to the canker margin in two apple orchards (A and C) and one pear orchard (B)[a]

| | Canker pairs (no.) | Active cankers[b] (no.) Wet[c] | Active cankers[b] (no.) Dry |
|---|---|---|---|
| Orchard A | 7 | 4 | 1 |
| Orchard B | 10 | 3 | 0 |
| Orchard C | 2 | 2 | 1 |
| Total | 19 | 9 | 2 |

[a]Pairs of cankers were selected in each orchard before growth started on the basis of location in trees, age of tissues infected, margin character and margin area.

[b]Number of cankers in each orchard from which *E. amylovora* was recovered at least once from the intact margin area during the season following formation. The probability that the observed distribution of activity among wet and dry cankers occurred by chance alone was 0.1, 0.1, and 0.01 in Orchards A, B, and A, B, and C together (total), respectively.

[c]The canker margin area of "wet" cankers was covered with water-saturated feminine sanitary napkins overwrapped with black polyethylene film; "dry" cankers were not covered.

inoculation date, canker characteristics, and storage time. One member of each set was placed in one of three controlled environment chambers at 17 C, 21 C, or 28 C ± 1 C, 70-80% relative humidity, and 14.0 klux for 14 hr per day. Isolation of *E. amylovora* from canker surfaces was attempted weekly in a manner similar to that used with cankers of orchard trees. Sampling was continued for 5 wk after *E. amylovora* first was isolated.

## RESULTS

*Erwinia amylovora* was recovered at least once from the surfaces of 19 of 122 (16%) fire blight cankers that were swabbed in three pome-fruit orchards during the season following their formation (Table 1). Because the proportion of cankers in Orchard A that yielded the pathogen was greater than in the other two orchards, the results from Orchard A will be discussed in detail.

**Association of canker characteristics with subsequent pathogen activity.**—Cankers with indeterminate-type margins (Fig. 1) became active in higher proportion than cankers with determinate-type margins (Table 2). The relationship between margin type and recovery of the pathogen was significant ($P = 0.20$). Only cankers (10 of 32 monitored) that were located on trunks and limbs at least 4 yr old yielded *E. amylovora*. None of 23 cankers on branches, terminal shoots, or fruiting spurs 1 to 3 yr of age yielded the pathogen.

The data from Orchards B and C were similar to those from Orchard A. *Erwinia amylovora* was recovered from only four cankers in Orchard B throughout the season (Table 1). These four were located on trunks and limbs ≥ 5 yr old; none of 11 monitored cankers on younger branches yielded the pathogen. Three of the four had indeterminate-type margins; the fourth had an almost-determinate margin. In Orchard C, *E. amylovora* was recovered from five of 14 cankers with indeterminate-type margins. The margins of three of the five were in tissues 4 yr old or older.

Considering the data from Orchards A and B together, in which cankers of all margin types had been monitored, there was a significant correlation ($P = 0.02$) between margin type and recovery of *E. amylovora*. There was no significant correlation between the extent of limb girdling by cankers or canker margin length and recovery of *E. amylovora*.

**Effect of external moisture on canker activity.**—Nine of the 19 cankers that had been covered with wet sanitary napkins yielded *E. amylovora*, whereas only two of the 19 uncovered pair members yielded the pathogen (Table 3). Statistical analysis of the combined matched canker data from the three orchards by the Fisher sign test (23) indicated that covering the canker margins significantly ($P = 0.01$) affected recovery of *E. amylovora*.

**Initiation of pathogen activity in cankers.**—During the 1975 growing season, *E. amylovora* was isolated from the surfaces of 10 out of 55 monitored cankers in Orchard A (four of the ten had been covered with moist cotton pads). *Erwinia amylovora* was not recovered from any canker surface until after petal fall on 27 May (Fig. 2). However, extension of two cankers first was noted on 13 May, and the pathogen was recovered from blossom buds taken from the immediate vicinity of these two cankers, but not from others, on that date. The pathogen was isolated from the surfaces of one of these two cankers on 27 May and from the other on 3 June. On 11 June, the pathogen was isolated for the first time from the surfaces of five other cankers and on 18 June, the pathogen was isolated for the first time from two others. *Erwinia amylovora* was recovered from more cankers (seven) on 11 June than on any other date. Most cankers that were active yielded the pathogen twice, usually on successive sampling dates, indicating a relatively short period of activity during the growing season.

In Orchard B, *E. amylovora* was first recovered from one canker surface on 11 June; two others yielded the pathogen on 18 June. Of the 50 remaining cankers, one yielded *E. amylovora* late in the season. In Orchard C, five cankers initially yielded the pathogen also on 11 or 18 June. Thus, considering the cankers in the three orchards together, *E. amylovora* was recovered initially from the

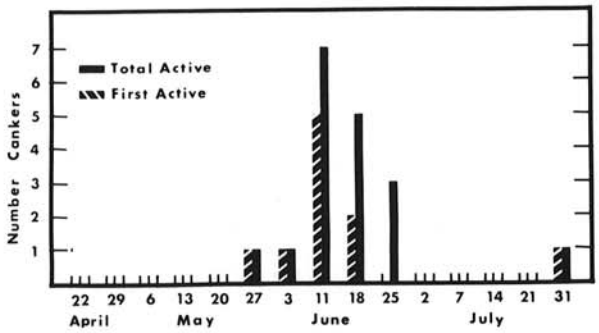


**Fig. 2.** Recovery of *Erwinia amylovora* from 55 fire blight cankers in Orchard A. Intact canker margins and contiguous healthy bark were swabbed with sterile moist cotton-tipped applicators at weekly intervals. Washings of the applicators were plated on two media selective for *Erwinia amylovora*. Representative colonies were tested for pathogenicity on immature apple or pear fruit. Cankers were considered active if *E. amylovora* was recovered from the intact surface. Full-bloom occurred on 20 May.

TABLE 4. Effect of relative time of inoculation on the character of the resulting fire blight canker margins[a]

| Canker margin character[b] | Number of trees[c] | |
|---|---|---|
| | Early inoculation | Late inoculation |
| Indeterminate | 2 | 15 |
| Almost-indeterminate | 11 | 66 |
| Almost-determinate | 90 | 30 |
| Determinate | 17 | 0 |
| Total | 120 | 111 |

[a]Lateral shoots or trunks of *Malus pumila* 'Idared' trees, growing in a nursery, were inoculated "early" (14 July) or "late" (5 September) in the growing season. All infected trees were dug after leaf-fall and the character of the canker margins was rated.

[b]Cankers were rated based on the extent of bark cracking at the margin and depression of dead tissue relative to contiguous healthy tissue

[c]There was a significant relationship ($P = 0.005$) between time of inoculation and resulting margin-type.

surfaces of almost 80% of those that ever yielded the pathogen during a seven-day period (11-18 June). As the three orchards were subject to similar environmental influences, these results suggest that canker activity is subject to seasonal environmental or host influences.

**Presence of Erwinia amylovora in blossoms and development of blossom infection.**—*Erwinia amylovora* was isolated from blossom or blossom bud samples taken from the vicinity of two cankers in Orchard A that had extended 1 - 4 cm, 1 wk before bloom on 13 May, and during bloom on 20 May. The pathogen was not isolated from 10 other blossom samples taken from the vicinity of other cankers, some of which also had visible evidence of extension, or from any canker surfaces swabbed at the same times. Composite samples of blossom buds, blossoms, or young fruits collected at random did not yield *E. amylovora*. The absence of *E. amylovora* from these samples may be explained by the small number of reproductive structures sampled, relative to the total number present. In addition, the cankers from which *E. amylovora* was recovered generally were located inside the tree canopy, but the random reproductive structure samples were taken from the periphery of the canopy because most of these structures were located there. Blossom blight developed only on clusters that had been included in the blossom or blossom bud samples from which *E. amylovora* had been isolated earlier as mentioned above.

**Effect of time of inoculation on type of canker margin produced.**—Inoculation of young apple trees in the nursery resulted in 231 fire blight cankers. Eighty-nine percent of the cankers that resulted from early inoculation had determinate-type margins (Table 4). The remaining cankers had indeterminate-type margins. In contrast, 72% of the cankers produced by late inoculation had indeterminate-type margins. There was a highly significant relationship ($P = 0.005$) between time of inoculation and margin type produced. Lateral shoot inoculation resulted in a higher proportion (65%) of determinate-type cankers than did X-cut inoculation (50%), but time of inoculation affected resulting margin character more strongly than inoculation type.

**Effect of margin character on production of Erwinia amylovora in cankers on potted trees.**—*Erwinia amylovora* was recovered from 7 of 15 trees with indeterminate-type cankers that had been produced as a result of artificial inoculation (Table 5). The pathogen was recovered from only one of the determinate margin cankers of similarly incubated trees. Canker margin character was significantly correlated ($P = 0.04$) with recovery of the pathogen; these data are consistent with the orchard study data.

**Effect of temperature on the production of Erwinia amylovora by fire blight cankers.**—When artificially inoculated potted trees were grown at 21 C, *Erwinia amylovora* was recovered from four of five indeterminate-type fire blight cankers (Table 5). The pathogen was recovered from only one and two cankers on matched trees grown at 17 C and 28 C, respectively. There was a significant relationship ($P = 0.15$) between incubation temperature and canker activity. Incubation temperature similarly affected recovery of *E. amylovora* from determinate cankers. The pathogen was recovered from only one determinate-margin canker from a tree that had been grown at 21 C. Considering cankers of both margin types together, 50% of those on trees grown at 21 C released *E. amylovora*, whereas only 10% and 5% of those grown at 28 C and 17 C, respectively, released the pathogen.

TABLE 5. Relation of canker margin type, incubation temperature, and production of *Erwinia amylovora* from canker surfaces of potted *Malus pumila* 'Idared' trees[a]

| Margin type | Temperature (C) | Cankers sampled (no.) | Cankers active[b] (no.) |
|---|---|---|---|
| Indeterminate | 28 | 5 | 2 |
| | 21 | 5 | 4 |
| | 17 | 5 | 1 |
| | Combined | 15 | 7 |
| Determinate | 28 | 5 | 0 |
| | 21 | 5 | 1 |
| | 17 | 5 | 0 |
| | Combined | 15 | 1 |

[a]Fire blight cankers were produced on 2-yr-old trees growing in the nursery. After they were dug the trees were graded for canker and tree characters. Trees were potted, given a cold treatment to break dormancy, and then placed in controlled-environment chambers. The surface of canker margins and contiguous healthy tissue was swabbed weekly to determine the presence of *E. amylovora*.

[b]Number of cankers from which *E. amylovora* was recovered at least once.

## DISCUSSION

Under orchard conditions, only a small proportion of fire blight cankers that develop during the year become hold-over cankers the following season (5, 10, 14, 17, 18, 25, 27). Thus, in vivo canker studies necessarily must involve large numbers of cankers and even then, precise replication is difficult because of differences in host trees, orchard management, types of infection, and environmental conditions. The dynamics of canker activity are particularly difficult to study. Many earlier workers attempted isolations of *E. amylovora* from dormant cankers with considerable success (20). Brooks (5) and Ritchie and Klos (16) used excised cankers for studies of *E. amylovora* survival. Successful isolation of the pathogen from dissected dormant or excised cankers, however, does not mean that those cankers would have become sources of inoculum in the spring. Whether the results of such studies can be extended with validity to orchard situations is questionable.

Our studies indicate that certain dormant canker characteristics, namely, margin type and age of tissues infected, can be used as criteria to select cankers that have a higher probability of releasing *E. amylovora* in the future than those selected at random. In both orchard studies and studies under controlled environmental conditions, margin character significantly affected the probability of recovering *E. amylovora* from cankers. Our results thus confirm and extend the observations made by Brooks (5), Miller (10), and van der Zwet (27), that cankers with indeterminate ("smooth") margins are more likely to become active hold-overs than those with

determinate ("rough") margins. Our results also confirm the observations of several earlier workers (9, 20) that cankers on older and larger tree parts are more important as potential sources of inoculum.

The removal of cankers with indeterminate margins from old and large tree structures should be emphasized in winter pruning programs because such cankers have a significantly greater probability of releasing the pathogen than others. However, we found that all cankers with determinate margins are not benign; therefore, they should be removed too. Cankers with indeterminate margins are particularly difficult to see and therefore are less likely to be removed during dormant pruning. Infrared reflectance techniques (24) were useful in visualizing cankers in the present studies, and they may prove useful to commercial fruit growers. The information provided by the present studies has already facilitated further in vivo studies (S. V. Beer, *unpublished*). Using margin type and size and age of affected tree structures, a group of cankers on pear was selected which yielded 55% hold-overs during the 1976 season. Rosen's (17) and Hockenhull's (9) observations that some cankers with margins that appeared to be indeterminate, actually had cork layers beneath the outer bark, may explain our failure to recover *E. amylovora* from all the indeterminate-type cankers included in our studies.

Whether an effective defense periderm (8) is formed at the lesion edge very likely is a function of the relative time when lesion extension and host cortex activity cease during the growing season (9). Infections that were initiated on nursery-grown trees early during the growing season resulted in determinate-type margins; those initiated later generally developed indeterminate-type margins. Our findings in commercial orchards agree with the results of artificial inoculations. A high proportion of the cankers found in Orchard C were the indeterminate type. The orchard owner had reported that most of the blight in Orchard C developed after a late-season hail storm the preceding season. Substantially smaller proportions of indeterminate-type cankers were found in Orchard A and Orchard B. In these two orchards, most cankers resulted from infection of primary blossoms. Thus, our results suggest that the time when infections are initiated in the field influences the type of canker margin formed. Although all cultivars included in our studies are considered highly susceptible to fire blight (1, 2), the possibility that the differences in the proportion of indeterminate cankers in Orchard C vs. Orchards A and B were due to cultivar differences cannot be dismissed. Several earlier workers (5, 10, 14) noted that a higher percent of cankers were hold-overs on susceptible than on resistant cultivars.

In controlled environment studies, an incubation temperature of 21 C was more favorable for the initiation of pathogen activity than higher or lower temperatures. We can only speculate on possible effects of environment on the initiation of pathogen activity in the field because conditions were similar in all three monitored orchards. Of the 19 monitored cankers from which *E. amylovora* was recovered during the season, 15 yielded the pathogen on 11 June, or 18 June. The 11 June, collection date was preceded by generally rainy weather; some rain fell during six of the previous 9 days. The mean temperature for the period (average of daily maximum and minimum) was 16.5 C. Earlier in the season, higher temperatures had occurred, but with less rainfall. In the 2-wk period before bloom (20 May), rain fell on only 2 days with a total accumulation of 1.2 cm.

Orchard cankers that were maintained in a moist environment yielded *E. amylovora* in significantly greater proportion than those that were subject to ambient moisture, but the time of initial isolation and duration of pathogen release apparently were not affected. The additional moisture provided by the moist pads may have favored survival of *E. amylovora* or retarded the development of defense periderm (9, 22) until other conditions, including host factors, had become more favorable for pathogen activity.

The relationship between the time of primary inoculum production and host phenology is critical. Since hold-over cankers are thought to be the major source of fire blight primary inoculum (6, 9, 20), if cankers do not release *E. amylovora* until after bloom, development of substantial new blossom infection is unlikely. Additional studies of *E. amylovora* canker relationships, in several geographical areas are needed. Knowledge of the relationships between host physiology, pathogen activity and environmental influences may provide a basis for predicting the timing of primary inoculum production and thus the severity and seasonal development of fire blight.

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