Reaction of Terminal Shoots of Apple Cultivars to Invasion by Erwinia amylovora

Herb S. Aldwinckle and J. L. Preczewski

Department of Plant Pathology, New York State Agricultural Experiment Station, Geneva 14456.
The authors thank J. Barnard for statistical advice and computer services; H. L. Gustafson and R. E. Gibbs for technical assistance; and Betty Bixler for clerical services.

Accepted for publication 2 June 1976.

ABSTRACT

ALDWINCKLE, H. S., and J. L. PRECZEWSKI. 1976. Reaction of terminal shoots of apple cultivars to invasion by Erwinia amylovora. Phytopathology 66:1439-1444.

Young trees of 92 apple (*Malus pumila*) cultivars were trained to single shoots in a field nursery. After 8 weeks' growth the shoot tips were inoculated with a virulent isolate of *Erwinia amylovora* by injection. Resultant fire blight lesions were measured 6 weeks after inoculation when infection had ceased to extend visibly. Statistically significant differences in cultivar reaction were observed, especially in resistant cultivars. In 79 apple cultivars tested similarly in the greenhouse, statistically significant differences in cultivar reaction also occurred, but with greater separation of the susceptible cultivars. There was a strong correlation between the results of the field and greenhouse tests. Some of the resistant cultivars also possessed other desirable characters and should be considered for use in apple breeding. Discolored streaks were observed in the xylem extending in advance of the visible cortical lesions, particularly in many of the resistant cultivars. Gram-negative, rod-shaped bacteria were observed in the xylem streaks, and pathogenic *E. amylovora* was isolated from them. Length of xylem streaks from the point of inoculation was not correlated with cortical lesion length; but, the length of xylem streaking in advance of the cortical lesion was correlated with the standard error of the lesion length. Xylem streaking may indicate a potential for occasional severe infections in normally resistant cultivars.

Additional key words: disease resistance, apple cultivars, *Malus sylvestris*.

Fire blight, which is incited by *Erwinia amylovora* (Burrill) Winslow et al., is a serious bacterial disease of apple (*Malus pumila* Miller), pear (*Pyrus communis*), and rosaceous ornamentals in the United States and England, and it is spreading into continental Europe (10, 24). After a century of research, control measures still are inadequate although useful control can be achieved by combining good cultural practices, sanitation, and chemical sprays (24, 29). Resistant cultivars would greatly supplement these practices.

No commercial cultivars of apple or pear are completely resistant to fire blight (10, 29) but great differences in susceptibility exist. There have been several reports on the incidence and severity of fire blight in different apple cultivars (1, 4, 16, 19, 26), apple rootstocks (9, 14), and pear cultivars (19, 20).

There are several objections to assessments of cultivar susceptibility based on the severity of natural infections. Variation in rootstock (14), tree age (25), nutrition (2, 21), orchard topography, and soil type (11) may obscure cultivar differences even when cultivars are grown in the same area or under the same climatic conditions. Inoculum pressure probably depends on the proximity of overwintering cankers (5) and on epiphytic populations of *E. amylovora* (27), and is unlikely to be uniform on all trees.

Vegetative susceptibility ultimately determines the fate of a cultivar as far as fir blight is concerned. If infections can readily progress into older tissue, trees may be severely damaged and rapidly killed. A cultivar that resists extension of infections into older tissue may sustain many blossom or shoot infections that result in only a light pruning effect and perhaps some loss of yield in that year. Therefore, it is equally as important to predict the severity of infections as to know the probability of new infections. To eliminate the effects of inoculum pressure and to attain 100% infection it is necessary to use a massive dose of inoculum.

Artificial inoculation of pear seedlings (15, 32), pear cultivars (20), apple seedlings (18), and apple clonal rootstocks (22) has been reported. Shaw (25) reported the reaction of 25 apple cultivars in the greenhouse to artificial inoculation with *E. amylovora*. Many of those 25 cultivars are now rare, and only three of the 13 cultivars that make up over 90% of current United States apple production (28) were tested. Shaw's (25) results were not statistically analyzed.

Fire blight infection of vegetative tissue usually has been equated with visible cortical lesions. Infection of xylem extending further than the visible lesions was reported by Rosen (23) and Shaw (25) but with little information on cultivar differences.

We report the results of artificially inoculating 92 apple cultivars in the field and 79 cultivars in the greenhouse with *E. amylovora* under uniform conditions. Included were the 13 most important U.S. cultivars (28) and many promising introductions.

MATERIALS AND METHODS

Apple cultivars were bench-grafted on domestic seedlings (seed parent: cultivar Delicious). Fifteen replicates of each cultivar were planted as three five-tree blocks in a field nursery on 2 May 1974. Each was trained to a single shoot for maximum uniformity and maintained in vigorous growth by regular fertilization and pest control. On 25 July 1974, plants were inoculated by a modification of a method used by others (22, 30). *Erwinia amylovora* strain 27-3, a virulent isolate from apple in New York (obtained from S. V. Beer) was grown in nutrient broth at 22 C for 24 hours. The broth culture (determined by dilution plating to contain approximately 10^{10} cells/ml) was used directly as inoculum. Because of inherent cultivar differences in stem diameter, a standard volume of inoculum was not used. A 0.46-mm diameter (26-gauge) hypodermic needle was inserted through the stem just above the youngest unfolded leaf. Sufficient inoculum was introduced to fill the wound and leave visible drops at both ends of the wound. Lesion length and total shoot length were recorded on 5 September 1974, when all lesions had ceased extending. The mean daily temperature after inoculation was 19.9 C (9.4-30.6 C) with a mean daily relative humidity (RH) of 77%.

Another group of similar grafted plants was planted in a peat-perlite-vermiculite (1:1:1, v/v) mixture in 13-cm diameter plastic pots and grown in a greenhouse. Following a first flush of growth, when the plants were well established, each was cut back to one bud and trained as a single shoot. After 8 weeks' growth, the shoot tips were inoculated as above. Lesion and shoot lengths were determined 6 weeks after inoculation. The mean daily temperature during the experiment was 19.7 C (14.4-24.4 C) with a mean daily RH of 51%. Shoots were dissected and the extent of visible discoloration in the xylem was recorded. Transverse sections of shoots with discolored xylem were examined microscopically, both after staining with acid fuchsin and unstained, with oil-immersion optics at ×1,000.

Isolation of *E. amylovora* from the discolored tissue was attempted by plating out segments of flamed pieces on nutrient dextrose agar. Resulting bacterial colonies were suspended and diluted in sterile distilled water and plated on modified Miller-Schroth medium (MSS) (17, 27). Colonies morphologically typical of *E. amylovora* on MSS were transferred to nutrient broth and incubated for 24 hours at 22 C. To test pathogenicity, shoot tips of potted Rome Beauty and Jonathan apple trees were inoculated with the broth culture as described above and observed for typical fire blight symptoms. Additionally, drops of the same cultures were placed on the surface of immature Jonathan apple fruits. The epidermis was then pierced several times through the drop. Pathogenicity was indicated by subsequent ooze production.

For both field and greenhouse tests the mean percentage of the total new shoot length affected (percent lesion length) was calculated. Lesions that extended into previous season's growth were recorded as 100%. The cultivar means for percent lesion length were separated by Duncan's multiple range test after arc-sin transformation for normality. Relationships between field and greenhouse percent lesion lengths; between length of xylem streaking and cortical lesion lengths; and between length of xylem streaking and the standard error of the mean of the cortical lesion length were determined by calculating correlation coefficients.

RESULTS

The mean lengths of fire blight lesions and the percent lesion lengths on 92 apple cultivars and selections were determined in the field test (Table 1). Many cultivars were very severely blighted and the most susceptible 42 cultivars did not differ significantly in percent lesion length. The resistant cultivars such as Britemac, Quinte, Primegold, NY 55140-19, and Priscilla showed greater differences in percent lesion length.

Symptoms developed in the greenhouse test involving 79 cultivars were less severe (Table 1), perhaps because of generally lower RH and less favorable edaphic conditions than in the field. Greater differences among the susceptible cultivars such as Burgundy, Twenty Ounce, Rome Beauty, York Imperial, and McIntosh were noted.

The positive correlation between percent lesion lengths of cultivars in the field test and those of the same cultivars in the greenhouse test was highly significant ($r = 0.56$; $P = 0.01$). Thus, the two tests complemented each other. However, in Table 1 the cultivars are ranked separately for each test according to their mean percent lesion length for ease in interpreting the statistical differences.

During evaluation of lesions in the greenhouse test it was observed that many individual shoots had longitudinal dark brown streaks in the stele extending further than the visible cortical lesion. Histological studies indicated that the streaks were confined to the primary xylem. The length of xylem streaking in advance of each cortical lesion was determined for each cultivar (Table 1).

There was no significant correlation between length of xylem streaking and length of cortical lesion in either the greenhouse test or the field test. There was, however, a highly significant positive correlation ($r = 0.32$; $P = 0.01$) between length of xylem streaking and the standard error of the mean of the cortical lesion length in the field test.

Short, Gram-negative rods were observed in the lumen of xylem vessel elements and tracheids of sections of streaked tissue. Pathogenic *E. amylovora* was isolated from such tissues.

DISCUSSION

All apple cultivars tested were susceptible to *E. amylovora* in the sense that infection took place following inoculation with a massive dose (approximately 10^6-10^7 cells). The data reported gave a measure of the susceptibility of vegetative tissue to lesion extension. These data cannot be compared directly with observations of incidence and severity of natural infections, the only other information available on cultivar susceptibility, since natural infections depend on many uncontrolled factors. The data at best can be regarded as the potential of a cultivar to be damaged by fire blight under field conditions most favorable for the disease.

Nevertheless, it is evident that the relative susceptibility ranking of well-known cultivars in our controlled tests was generally in the same order that would be expected

TABLE 1. Relative reaction of terminal shoots of field- and greenhouse-grown apple cultivars to artificial inoculation[w] with *Erwinia amylovora*

Field-grown

Cultivar	Cortical lesion length[x] (cm)	Cortical lesion length[x] (%)
York Imperial	42.3	100.0 a
Yellow Transparent	43.3	100.0 ab
Idared	51.8	100.0 abc
McIntosh	46.2	100.0 abc
Milton	46.6	100.0 abc
Niagara	43.8	100.0 abc
Opalescent	43.6	100.0 abc
Rhode Island Greening	44.8	100.0 abc
Rome Beauty	39.7	100.0 abc
Summerred	51.4	100.0 abc
Tolman Sweet	46.7	100.0 abc
Tydeman's Early Worcester	39.9	100.0 abc
Virginiagold	53.8	100.0 abc
Wagener	48.3	100.0 abc
Wayne	53.6	100.0 abc
Wealthy	42.3	100.0 abc
Yorking	43.0	100.0 abcd
Honeygold	47.2	100.0 abcd
Mollie's Delicious	47.2	99.9 abcd
Puritan	53.2	99.9 abcd
Yellow Newtown	41.5	99.8 abcd
Lodi	54.9	99.7 abcd
Twenty Ounce	46.1	99.6 abcd
Macoun	33.6	99.5 abcd
Burgundy	58.2	99.4 abcd
Macspur	48.4	99.3 abcd
Jonathan	47.1	99.1 abcd
Webster	43.4	98.9 abcd
Julyred	40.4	98.7 abcd
Scotia	39.3	98.6 abcd
Paulared	42.5	98.1 abcd
Mutsu	48.8	97.4 abcde
Grimes Golden	44.9	97.4 abcde
Duchess of Oldenburg	33.9	97.0 abcdef
Jerseymac	49.2	97.0 abcdef
Ben Davis	42.8	96.5 abcdef
Sungold	33.1	96.4 abcdef
Monroe	48.5	95.9 abcdef
Jonagold	31.5	95.5 abcdef
Spigold	39.6	95.5 abcdef
Nured McIntosh	34.5	95.3 abcdef
Magnolia Gold	45.8	94.9 abcdef
Gravenstein	38.0	94.6 bcdef
NY 58553-1	41.5	93.7 cdefg
Ring's Wealthy	39.5	93.5 cdefg
Jenkins	37.9	92.1 cdefgh
Horton Twenty Ounce	36.6	92.0 cdefghi
Empire	39.3	91.2 cdefghi
Jonnee	36.9	91.1 cdefghi
Jonamac	33.9	91.0 cdefghij
Golden Delicious	39.8	90.7 cdefghij
Spijon	37.0	90.6 cdefghij
Early McIntosh	39.0	90.1 cdefghij
Holly	32.8	89.3 cdefghijk
VPI 6	42.6	86.4 defghijk
Ozark Gold	45.0	84.2 efghijk
Spartan	30.4	84.0 efghijk
Arkansas Black	28.1	83.9 efghijk

Greenhouse-grown

Cultivar	Cortical lesion length[y] (cm)	Cortical lesion length[y] (%)	Xylem streaking[z] (cm)	Xylem streaking[z] (%)
Burgundy	40.2	95.2 A	0	0
Opalescent	28.8	83.7 AB	4.0	13.5
Twenty Ounce	37.9	82.7 B	0	0
Yellow Newtown	38.7	81.7 B	0	0
Grimes Golden	24.7	77.7 BC	4.1	11.6
Rome Beauty	30.3	70.9 BCD	3.0	6.6
Niagara	32.0	70.1 BCDE	6.8	20.1
Idared	29.0	69.6 BCDE	2.1	6.1
Tolman Sweet	18.0	68.3 BCDEF	3.0	17.0
York Imperial	32.0	67.6 BCDEF	5.6	20.6
Jenkins	19.3	64.4 CDEFG	1.0	2.7
Julyred	24.6	62.1 DEFG	5.0	16.4
Monroe	28.4	59.5 DEFGH	3.8	10.8
Yorking	25.6	58.8 DEFGH	3.7	11.1
Jonagold	25.5	57.1 DEFGHI	6.0	13.4
Jonnee	26.0	56.5 DEFGHI	8.2	22.0
Barry	24.6	54.8 EFGHI	0	0
Baldwin	19.0	51.4 FGHIJ	7.2	22.7
Yellow Transparent	24.7	51.2 FGHIJ	3.0	6.2
VPI 6	27.1	51.1 FGHIJ	0	0
Lodi	23.0	50.5 FGHIJ	0	0
Wagener	20.0	50.1 FGHIJ	3.6	15.6
Tydeman's Early Worcester	20.4	49.1 FGHIJK	8.8	39.1
Milton	24.3	48.8 FGHIJK	4.1	9.9
Honeygold	17.3	48.4 FGHIJK	5.1	19.3
Jonamac	24.1	47.3 FGHIJK	9.1	21.2
Webster	21.0	46.8 FGHIJKL	5.0	10.5
Nured McIntosh	24.8	46.7 FGHIJKL	4.6	9.4
Jonalicious	17.0	46.6 FGHIJKL	3.3	8.9
NY 18491	15.0	46.4 FGHIJKL	15.5	52.5
Macoun	14.3	45.8 GHIJKL	11.2	39.3
Magnolia Gold	23.3	44.9 GHIJKL	8.0	17.5
Spigold	15.9	43.6 HIJKL	10.7	31.1
Spartan	16.0	42.3 HIJKL	7.3	23.0
Mutsu	17.3	40.1 IJKL	8.7	25.4
Ben Davis	16.3	39.7 IJKLM	8.8	27.6
Sungold	14.1	37.5 IJKLMN	10.1	32.7
Holly	19.8	37.2 IJKLMNO	16.5	39.5
Summerred	13.4	36.1 JKLMNO	9.2	28.9
Jonadel	16.6	36.1 JKLMNO	7.8	25.0
McIntosh	16.7	35.7 JKLMNO	14.1	36.2
Scotia	12.6	35.7 JKLMNO	8.2	22.1
Turley	14.1	35.3 JKLMNO	20.0	60.5
Paragon	13.7	32.4 JKLMNOP	9.0	26.7
NY 58553-1	15.9	32.3 JKLMNOP	11.8	26.6
Jerseymac	10.5	32.2 JKLMNOP	17.2	62.0
Ozark Gold	14.1	32.0 KLMNOP	1.7	3.9
Wealthy	13.4	31.9 KLMNOP	13.8	39.0
Northern Spy	12.7	31.0 KLMNOP	6.3	23.0
Wayne	12.7	29.4 LMNOP	17.1	47.8
Cortland	11.8	28.3 LMNOP	18.5	57.3
Purdue 187-6	14.3	27.5 LMNOP	27.4	62.0
Spijon	11.6	26.4 LMNOPQ	3.0	6.9
Mollie's Delicious	10.0	25.9 LMNOPQ	14.6	39.5
Golden Delicious	11.0	24.0 MNOPQ	5.7	14.0
Winesap	10.4	23.4 MNOPQR	17.8	51.6
Melrose	12.2	23.1 MNOPQRS	7.4	13.4
Starkspur Golden Delicious	11.1	22.9 NOPQRS	4.2	13.2
Primegold	9.6	21.5 NOPQRS	29.6	72.5

TABLE 1. continued

Field-grown		
	Cortical lesion length[x]	
Cultivar	(cm)	(%)
NY 18491	39.9	83.5 fghijk
Nured Rome	34.9	83.4 fghijk
Turley	34.9	82.7 fghijk
Northern Spy	30.3	82.3 fghijkl
Paragon	41.1	78.6 ghijklm
Delicious	36.0	77.7 hijklm
Young America	29.1	77.1 hijklmn
Prima	30.8	76.1 hijklmn
NY 55140-9	34.6	76.0 hijklmn
Baldwin	34.1	75.3 ijklmn
Wellington	30.9	73.5 ijklmn
Melrose	34.7	72.2 jklmn
Vermont Spur Delicious	23.8	70.9 jklmn
Starkspur Golden Delicious	32.1	68.9 klmno
Carroll	27.4	60.9 lmnop
Priscilla	25.0	60.4 lmnop
Winesap	22.3	57.1 mnopq
Stayman	25.0	56.5 nopq
Viking	18.1	47.3 opqr
NY 55140-19	22.2	44.2 pqr
Starkrimson Delicious	12.1	42.7 pqrs
Dolgo	21.6	38.7 pqrs
Jonadel	17.8	32.5 qrs
Primegold	14.4	32.4 qrst
Northwestern Greening	15.6	31.7 rst
Hawaii	16.9	29.2 rst
Jonalicious	11.7	28.8 rst
Quinte	12.9	22.8 stu
Purdue 1279-2	12.1	19.7 stu
Crimson Beauty	6.5	11.3 tuv
Britemac	10.9	9.7 uv
NY 55158-2	6.7	8.8 uv
Ottawa 523	7.3	5.5 v
Purdue 187-6	3.9	4.4 v

Greenhouse-grown				
	Cortical lesion length[y]		Xylem streaking[z]	
Cultivar	(cm)	(%)	(cm)	(%)
Puritan	9.0	21.4 NOPQRS	11.6	32.2
Prima	9.7	20.6 OPQRS	8.3	25.7
Early McIntosh	8.9	16.5 PQRS	19.1	50.1
Delicious	8.8	16.3 PQRS	8.8	25.5
Purdue 1279-2	7.2	14.6 PQRS	35.1	82.3
Empire	6.3	13.8 PQRS	12.8	36.2
Carroll	6.3	13.8 PQRS	13.8	37.1
Wellington	4.3	12.9 PQRS	3.0	12.5
NY 55140-19	4.0	12.6 QRS	17.8	71.5
Ring's Wealthy	5.3	12.4 QRS	20.3	67.8
Hawaii	5.5	11.8 QRS	5.3	11.2
NY 55158-2	5.1	10.9 RS	25.2	61.8
Northwestern Greening	3.9	9.4 RST	21.0	60.4
Quinte	3.5	9.2 RST	24.7	67.2
Starkrimson Delicious	3.3	8.4 RST	20.6	70.5
Crimson Beauty	2.3	8.2 RST	13.6	57.1
Priscilla	3.7	8.0 ST	26.0	63.8
Viking	3.0	7.3 ST	21.7	63.0
Britemac	1.0	1.8 T	21.6	79.6
Ottawa 523	1.6	1.8 T	38.0	85.4

[w]Inoculation was by direct injection of a nutrient broth culture (22 C for 24 hours containing ~ 10^{10} cells/ml) applied by inserting a 0.46-mm diameter (26-gauge) hypodermic needle through the stem just above the youngest unfolded leaf and filling the wound with the inoculum suspension as the needle was withdrawn.

[x]Means of 15 replicates of each cultivar. Percent (%) = [lesion length (cm)]/[total shoot length (cm)] × 100. Percent lesion lengths followed by same letter did not differ significantly ($P = 0.05$) according to Duncan's multiple range test on arc-sin transformed data (within field test only).

[y]Means of seven replicates of each cultivar. Percent (%) = [lesion length (cm)]/[total shoot length (cm)] × 100. Percent lesion lengths followed by same letter did not differ significantly ($P = 0.05$) according to Duncan's multiple range test on arc-sin transformed data (within greenhouse test only).

[z]Means of seven replicates of each cultivar. Length (cm) of discolored streaking in xylem that extended further than cortical lesion. Percent (%) = [length of xylem streaking (cm)]/[total shoot length (cm)] × 100.

from field observations based on natural infection (1, 26). For example, Jonathan, Rhode Island Greening, Rome Beauty, and York Imperial were highly susceptible in both tests, while Delicious, Stayman, and Winesap were resistant.

Of more immediate interest to horticulturalists is the performance of cultivars recently introduced (6). Britemac, Hawaii, Priscilla, Quinte, and Viking were very resistant; Carroll, Melrose, Prima, and Primegold were resistant. They may be useful in breeding (7) although there is no information on the heritability of their resistance. Resistance to fire blight in other apple cultivars and *Malus* species is variable in its mode of inheritance (12). Burgundy, Honeygold, Julyred, Lodi, Milton, Monroe, Niagara, Summerred, Tydeman's Early Worcester, Virginiagold, and Webster were conspicuously susceptible.

Some of these cultivars are resistant to other diseases.

Prima and Priscilla are resistant to *Venturia inaequalis,* the incitant of apple scab (7). Priscilla is also resistant to *Gymnosporangium juniperi-virginianae,* the incitant of cedar apple rust, as are Britemac, Carroll, Hawaii, Melrose, and Viking (3).

Spur type sports generally were less susceptible than their parent cultivars. In the field test, Starkrimson Delicious was significantly less susceptible than Delicious, and Starkspur Golden Delicious significantly less susceptible than Golden Delicious. Since these differences were based on percent lesion length, they were independent of any reduction in actual shoot length in the spur types.

In this research, streaking in the xylem was observed to extend beyond visible cortical lesions in many cultivars (25). Bacterial cells were observed microscopically (8, 23) and pathogenic cells of *E. amylovora* were isolated (13, 25). The bacteria presumably gained access to the xylem vessels of the stem via the needle puncture at the time of inoculation (8). The positive correlation of the xylem streaking with the standard error of the cortical lesion supports the concept that xylem-transmitted *E. amylovora* might initiate invasion of the cortex (25). This may explain why cultivars that usually produce short cortical lesions but long xylem streaks will occasionally develop much longer cortical lesions. Interestingly, in many of the least susceptible cultivars extensive xylem streaking did occur, although there was no negative correlation between streak length and cortical lesion length. Similar xylem streaking has also been observed in naturally infected shoots in the field (13, Preczewski, *unpublished*).

Although *E. amylovora* appears to invade the cortex from the xylem only rarely (25) and activation of internal bacteria has not been achieved, internal *E. amylovora* was suggested (13) as the source of inoculum for fire blight following hail-damage to healthy trees and in an outbreak in an extremely isolated planting of Magness pears (31).

The possibility that xylem streaking may initiate severe branch, trunk, or rootstock lesions on normally resistant cultivars calls for further investigation. Account must be taken of this phenomenon in breeding and selecting apple cultivars for resistance to fire blight.

LITERATURE CITED

1. ALDWINCKLE, H. S. 1974. Field susceptibility of 46 apple cultivars to fire blight. Plant Dis. Rep. 58:819-821.
2. ALDWINCKLE, H. S., and S. V. BEER. 1976. Nutrient status of apple blossoms and their susceptibility to fire blight. Ann. Appl. Biol. 82:159-163.
3. ALDWINCKLE, H. S., R. C. LAMB, and H. L. GUSTAFSON. 1976. Nature and inheritance of resistance to Gymnosporangium juniperi-virginianae in apple cultivars. Phytopathology 66: (In press).
4. ALDWINCKLE, H. S., R. D. WAY, K. G. LIVERMORE, J. L. PRECZEWSKI, and S. V. BEER. 1976. Fire blight in the Geneva apple collection. Fruit Var. J. 30:42-55.
5. BEER, S. V., and D. C. OPGENORTH. 1976. Erwinia amylovora on fire blight canker surfaces and blossoms in relation to disease occurrence. Phytopathology 66:317-322.
6. BROOKS, R. M., and H. P. OLMO. 1972. Register of new fruit and nut varieties. 2nd ed. University of California Press, Berkeley. 708 p.
7. BROWN, A. G. 1975. Apples. Pages 3-37 *in* J. Janick and J. N. Moore, eds. Advances in fruit breeding. Purdue University Press, West Lafayette, Indiana. 623 p.
8. CROSSE, J. E., R. N. GOODMAN, and W. H. SHAFFER, JR. 1972. Leaf damage as a predisposing factor in the infection of apple shoots by Erwinia amylovora. Phytopathology 62:176-182.
9. CUMMINS, J. N., and H. S. ALDWINCKLE. 1973. Fire blight susceptibility of fruiting trees of some apple rootstock clones. HortScience 8:176-178.
10. EDEN-GREEN, S. J., and E. BILLING. 1974. Fireblight. Rev. Plant Path. 53:353-365.
11. FISHER, E. G., K. G. PARKER, N. S. LUEPSCHEN, and S. S. KWONG. 1959. The influence of phosphorus, potassium, mulch, and soil drainage on fruit size, yield, and firmness of the Bartlett pear and on development of the fire blight disease. Proc. Am. Soc. Hortic. Sci. 73:78-90.
12. GARDNER, R. G. 1976. Studies on inheritance of fire blight resistance in Malus. Ph.D. Thesis, Department of Pomology, Cornell University, Ithaca, New York. 71 p.
13. KEIL, H. L., and T. VAN DER ZWET. 1972. Recovery of Erwinia amylovora from symptomless stems and shoots of Jonathan apple and Bartlett pear trees. Phytopathology 62:39-42.
14. KEIL, H. L., and T. VAN DER ZWET. 1975. Fire blight susceptibility of dwarfing apple rootstocks. Fruit Var. J. 29:30-33.
15. LAYNE, R. E. C., C. H. BAILEY, and L. F. HOUGH. 1968. Efficacy of transmission of fire blight resistance in Pyrus. Can. J. Plant Sci. 48:231-243.
16. MC MUNN, R. L. 1939. An evaluation of ninety-six apple varieties at the 21-year period under Illinois conditions. Proc. Am. Soc. Hortic. Sci. 36:379-383.
17. MILLER, T. D., and M. N. SCHROTH. 1972. Monitoring the epiphytic population of Erwinia amylovora on pear using a selective medium. Phytopathology 62:1175-1182.
18. MOORE, R. C. 1946. Inheritance of fire blight resistance in progenies of crosses between several apple varieties. Proc. Am. Soc. Hortic. Sci. 47:49-57.
19. MOWRY, J. B. 1964. Maximum orchard susceptibility of pear and apple varieties to fireblight. Plant Dis. Rep. 48:272-276.
20. OITTO, W. A., T. VAN DER ZWET, and H. J. BROOKS. 1970. Rating of pear cultivars for resistance to fire blight. HortScience 5:474-476.
21. PARKER, K. G., N. S. LUEPSCHEN, and E. G. FISHER. 1961. Tree nutrition and fire blight development. Phytopathology 51:557-560.
22. PARKER, K. G., N. S. LUEPSCHEN, and A. L. JONES. 1974. Inoculation trials with Erwinia amylovora to apple rootstocks. Plant Dis. Rep. 58:243-247.
23. ROSEN, H. R. 1929. The life history of the fire blight pathogen, Bacillus amylovorus, as related to the means of overwintering and dissemination. Ark. Agric. Exp. Stn. Bull. 244. 96 p.
24. SCHROTH, M. N., S. V. THOMSON, D. C. HILDEBRAND, and W. J. MOLLER. 1974. Epidemiology and control of fire blight. Annu. Rev. Phytopathol. 12:389-412.
25. SHAW, L. 1934. Studies on resistance of apple and other rosaceous plants to fire blight. J. Agric. Res. 49:283-313.
26. THOMPSON, J. M. 1972. Fire blight ratings, bloom dates, and precocity of apple varieties tested in the southeast. Fruit Var. Hortic. Dig. 26:84-97.
27. THOMSON, S. V., M. N. SCHROTH, W. J. MOLLER, and W. D. REIL. 1975. Occurrence of fire blight of pears in relation to weather and epiphytic populations of Erwinia amylovora. Phytopathology 65:353-358.
28. U. S. DEPARTMENT OF AGRICULTURE ECONOMIC RESEARCH SERVICE. 1975. Page 38 *in* The Fruit

Situation, March 1975. Washington, D.C. 54 p.
29. VAN DER ZWET, T. 1967. Review of fire blight control measures in the United States. Trans. Ill. State Hortic. Soc. 101:63-71.
30. VAN DER ZWET, T. 1970. Evaluation of inoculation techniques for determination of fire blight resistance in pear seedlings. Plant Dis. Rep. 54:96-100.
31. VAN DER ZWET, T., H. L. KEIL, and B. C. SMALE. 1969. Fire blight in the Magness pear cultivar in north central Arkansas. Plant Dis. Rep. 53:686-689.
32. VAN DER ZWET, T., W. A. OITTO, and M. N. WESTWOOD. 1974. Variability in degree of fire blight resistance within and between Pyrus species, interspecific hybrids, and seedling progenies. Euphytica 23:295-304.