Amylovorin-Induced Shoot Wilting: Lack of Correlation with Susceptibility to *Erwinia amylovora*

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ABSTRACT

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Amylovorin, a polysaccharide isolated from ooze produced on the surface of *Erwinia amylovora*-infected apple and pear fruit, has no host-specificity and cannot be used to screen plant material for resistance to fire blight. The cut ends of excised shoots of *Cotoneaster pannosa*, *Spiraea vanhouttei*, and 19 *Malus pumila* (apple) cultivars were placed in aqueous solutions of amylovorin under controlled environmental conditions and observed for wilting for up to 12 hr. There was no significant difference in the mean time required for wilting of *C. pannosa* and *S. vanhouttei* shoots, although only *C. pannosa* was susceptible to *E. amylovora*. When shoot tips (6 cm long) of apple cultivars were placed in amylovorin solution and evaluated hourly for degree of wilting, there were significant differences in mean wilt indices of the cultivars. However, the differences were not correlated with the susceptibility of the cultivars to infection by *E. amylovora*. Shoot flexibility of both *C. pannosa* and *M. pumila* shoots was significantly correlated with sensitivity to wilting after placement in amylovorin solutions.

Additional key words: host-specific toxin, water relations.

Fire blight of rosaceous plants, which is caused by *Erwinia amylovora* (Burrill) Winslow et al, is characterized by rapid necrosis of infected host tissues (2). Prior to the development of obvious necrosis, succulent infected tissues often appear wilted and water-soaked, and ooze containing bacteria is forced to the exterior surfaces (6).

Pierstorff (13) first reported that preparations from bacteria-free ooze induced wilting of excised rosaceous shoots. The isolation of wilt-inducing polysaccharides from bacteria-free ooze was reported independently from two laboratories in 1974 (9,10). Goodman et al (10), who isolated the polysaccharide and named it amylovorin, reported that solutions of it induced wilting of the cut shoots of three apple and seven pear cultivars and that time required to cause wilting was negatively correlated with the reported susceptibility of the cultivars to *E. amylovora*. Cut shoots of several nonrosaceous plants that are immune to fire blight did not wilt when placed in amylovorin solutions. Based on these observations, amylovorin was characterized as a host-specific phytotoxin.

The results of previous work in our laboratory (16) indicated that amylovorin induced wilting of excised *Cotoneaster pannosa* shoots by causing water deficits. By contrast, wilting of *C. pannosa* tissues infected by *E. amylovora* resulted from loss of membrane

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semipermeability.

The present studies were undertaken to test the reported host specificity of amylovorin to determine if amylovorin might be used, as had been suggested by Goodman et al (10), as a screening agent for determining the fire blight susceptibility of apple cultivars. Preliminary experiments had indicated that certain factors unrelated to genotype (shoot flexibility and transpiration rate) influenced the sensitivity of cut shoots of apple, pear, and cotoneaster to wilting when placed in amylovorin solutions (15). In experiments with nine apple cultivars, we found no significant relationship between susceptibility to *E. amylovora* and sensitivity to amylovorin (7). We now report further attempts to confirm the host-specificity of amylovorin, and to identify other sources of variation that affect the sensitivity of rosaceous shoots to amylovorin-induced wilting.

MATERIALS AND METHODS

Amylovorin isolation and purification. Amylovorin was isolated and purified from ooze produced on immature Bartlett pear fruits infected with *E. amylovora* by procedures described previously (16). In certain experiments, amylovorin supplied by R. N. Goodman and purified from ooze produced on infected Jonathan apple fruits was used. The two amylovorin preparations could not be distinguished by compositional analysis and serological methods (8).

Plant material and growing conditions. *Cotoneaster pannosa* Franch. and *Spiraea vanhouttei* (Briot) Zab. plants were obtained from Aldridge Nursery, Inc. (Von Ormy, TX 78073), and Interstate Nurseries, Inc. (Hamburg, IA 51640), respectively. Additional plants were grown from rooted cuttings in a peat-vermiculite mix (1:1, v/v) in 15-cm-diameter clay pots. Apple cultivars were propagated clonally and grown in a mixture of equal volumes of peat, perlite, and vermiculite as described previously (3). All plants were grown in a greenhouse at 24 ± 3C with a photoperiod of at least 14 hr and sufficient fertilizer and water to maintain vigorous extension of vegetative shoots.

Susceptibility of cotoneaster and spiraea to *Erwinia amylovora*. The susceptibility of vegetative shoots of *C. pannosa* and *S. vanhouttei* to infection by *E. amylovora* was determined by artificial inoculation. A turbid aqueous suspension of a 22-hr nutrient agar culture of *E. amylovora* was injected by hypodermic syringe and needle into the stem within 0.5 cm of the shoot apex of plants growing in the greenhouse. Three strains of *E. amylovora* were used: Ea 273, a New York strain from a naturally infected Rhode Island Greening apple tree, and Mac 715 and H 430, two Michigan strains (from E. J. Klos) from a naturally infected McIntosh apple tree and from a naturally infected Bartlett pear tree, respectively. These strains are maintained in the Cornell University Collection of Phytopathogenic Bacteria as strains 273, 138, and 131, respectively. Three cotoneaster shoots and three spiraea shoots were inoculated individually with each strain; for controls, three shoots of each species were injected with sterile distilled water. After inoculation, shoots were examined for fire blight symptoms at 3–5 day intervals for the next 60 days.

Wilting of shoots in amylovorin solution. All assays for wilting were conducted in walk-in controlled environment chambers because preliminary trials had indicated that environmental conditions during assay strongly affected the results. Tests with cotoneaster and spiraea shoots were conducted at 26 ± 0.5 C, 80% RH, and 19 klux. Assays with apple shoots were conducted at 24 ± 0.5 C, 80% RH, and 19 klux. Shoots selected for assays were excised with a razor blade and immediately plunged into water. An additional portion (at least 3 cm long) of the shoot base was excised under water. Shoot bases were submerged until each shoot was transferred to an individual vial containing amylovorin solution or water. Shoots transferred to vials containing water served as controls in each experiment. The flexibility of apple shoots was determined, by methods described below, before excising shoots for assay.

Cotoneaster and spiraea shoots were observed for wilting continually during the assays. A shoot was considered wilted when the upper portion of the shoot had bent 90 degrees with respect to the lower portion; the time elapsed was then noted. All experiments with cotoneaster and spiraea shoots were conducted with amylovorin from pears.

Apple shoots were rated at hourly intervals by the following scale (Fig. 1): 0 = shoot fully turgid; 1 = leaf lamina flaccid, stem turgid; 2 = stem bent 0–30 degrees from vertical; 3 = stem bent 30–60 degrees from vertical; 4 = stem bent 60–90 degrees from vertical; and 5 = stem bent 90 degrees or more from vertical. Leaf turgidity was estimated by stroking with the forefinger. Stem angles were determined with the aid of a protractor card held behind each shoot.

Apple cultivars were assayed for sensitivity to amylovorin in two experiments. In the first experiment, nine cultivars were assayed using two amylovorin preparations, one isolated from apple and the other from pear. Four shoots of each cultivar were placed in solutions (100 μg/ml) of each amylovorin preparation; the test was repeated the following day. In the second experiment, which was conducted 4 mo later, 13 cultivars (including three that had been tested in the first experiment) were assayed using only amylovorin (100 μg/ml) isolated from infected pear fruits.

Measurement of shoot flexibility. The correlation of shoot flexibility with sensitivity to wilting in amylovorin was examined in a sample of 42 cotoneaster shoots. The flexibility was estimated by attaching a 3.5-g weight within 0.5 cm of shoot apices. The distance in centimeters (to the nearest 0.5 cm) from the shoot apex to the horizontal tangent to the arc induced by the weight was used as an index of shoot flexibility (Fig. 2). Then shoots were removed from plants and recut under water to a length of 10 cm. The time required for these shoots to wilt in solutions of amylovorin (1.0 mg/ml) from pear was determined as described above.

The correlation of apple shoot flexibility with sensitivity to

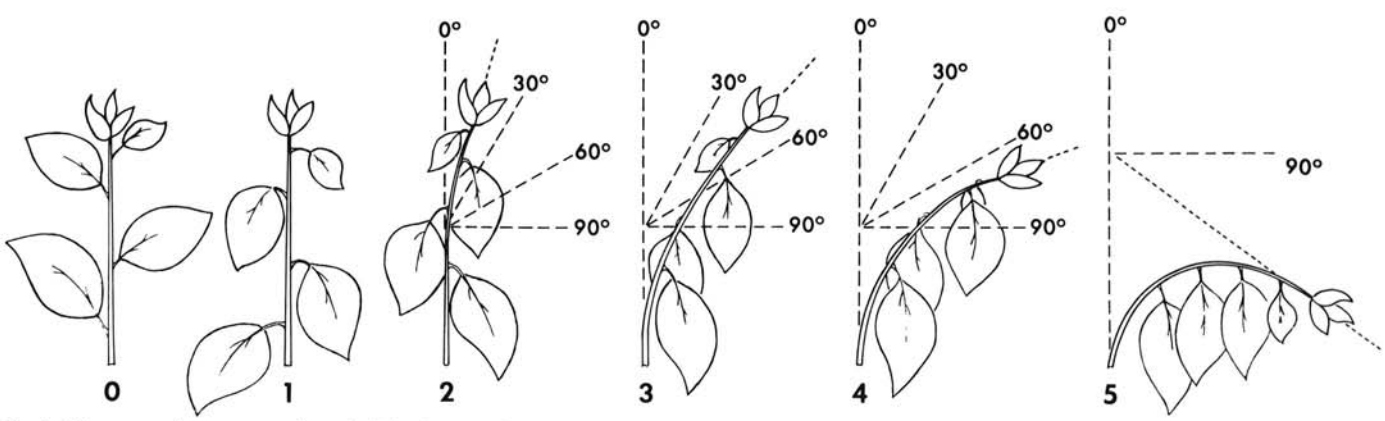

Fig. 1. Diagrammatic representation of wilt indices used for apple shoots. Rating is determined by leaf turgor and angle formed between the upper and lower portions of the shoot. 0 = Shoot and leaves fully turgid; 1 = Leaf lamina flaccid, stem turgid; 2 = Stem bent 0–30 degrees from vertical; 3 = Stem bent 30–60 degrees from vertical; 4 = stem bent 60–90 degrees from vertical; and 5 = stem bent >90 degrees.

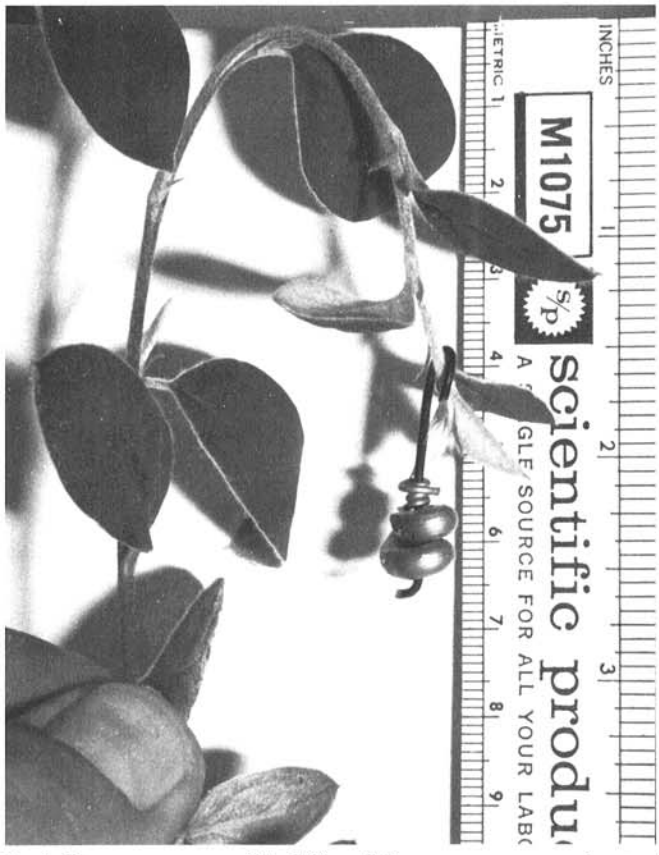

Fig. 2. The measurement of flexibility of *Cotoneaster pannosa* shoots. A 3.5-gm weight was attached to the stem within 0.5 cm of the apex. The distance in cm from the shoot apex to the horizontal tangent to the arc induced by the weight was determined (5.0 cm for shoot illustrated).

wilting in amylovorin was specifically tested with shoots of the Rome Beauty cultivar. The flexibility of shoots on trees that had been cut back to single buds and then grown for 2–9 wk was estimated by measuring the relative force required to displace each shoot apex 1 cm. A system of weights, hooks, nylon monofilament line, and a pulley was used in combination with a 10-g capacity dial balance to apply force to each shoot apex (Fig. 3). The wilt index of 15 shoots ranging in flexibility from 2.1 to 5.9 g was determined 12 hr after placing them in solutions of amylovorin (100 μg/ml) from pear.

Determination of transpiration rates. The relationship between shoot transpiration rate in water and sensitivity to wilting in amylovorin was examined in a sample of 24 cotoneaster shoots. Flexibility measurements were made as described above, and then transpiration rates of the detached shoots in vials of water were determined. The loss in weight with time of each shoot plus its vial was assumed to be due to transpiration because evaporative losses from vials without shoots were negligible. Transpiration rates were converted to a leaf area basis after tracing leaf outlines onto graph paper, weighing the leaf tracings, and calculating leaf areas from a standard curve. After a steady transpiration rate was achieved, shoots were transferred to solutions of amylovorin from pear (1.0 mg/ml), and the time required for wilting was determined as described above.

RESULTS

Susceptibility of cotoneaster and spiraea shoots to *Erwinia amylovora*. Vegetative shoots of *C. pannosa* were susceptible to all three strains of *E. amylovora* tested. Typical fire blight symptoms were observed on eight of the nine inoculated shoots within 6 days after inoculation; the ninth shoot (which had been inoculated with strain H 430) exhibited symptoms within 14 days. No evidence of infection was observed when shoots of *S. vanhouttei* were inoculated with the same strains of *E. amylovora*. Inoculation of shoots of *S. vanhouttei* was repeated 60 days after the initial

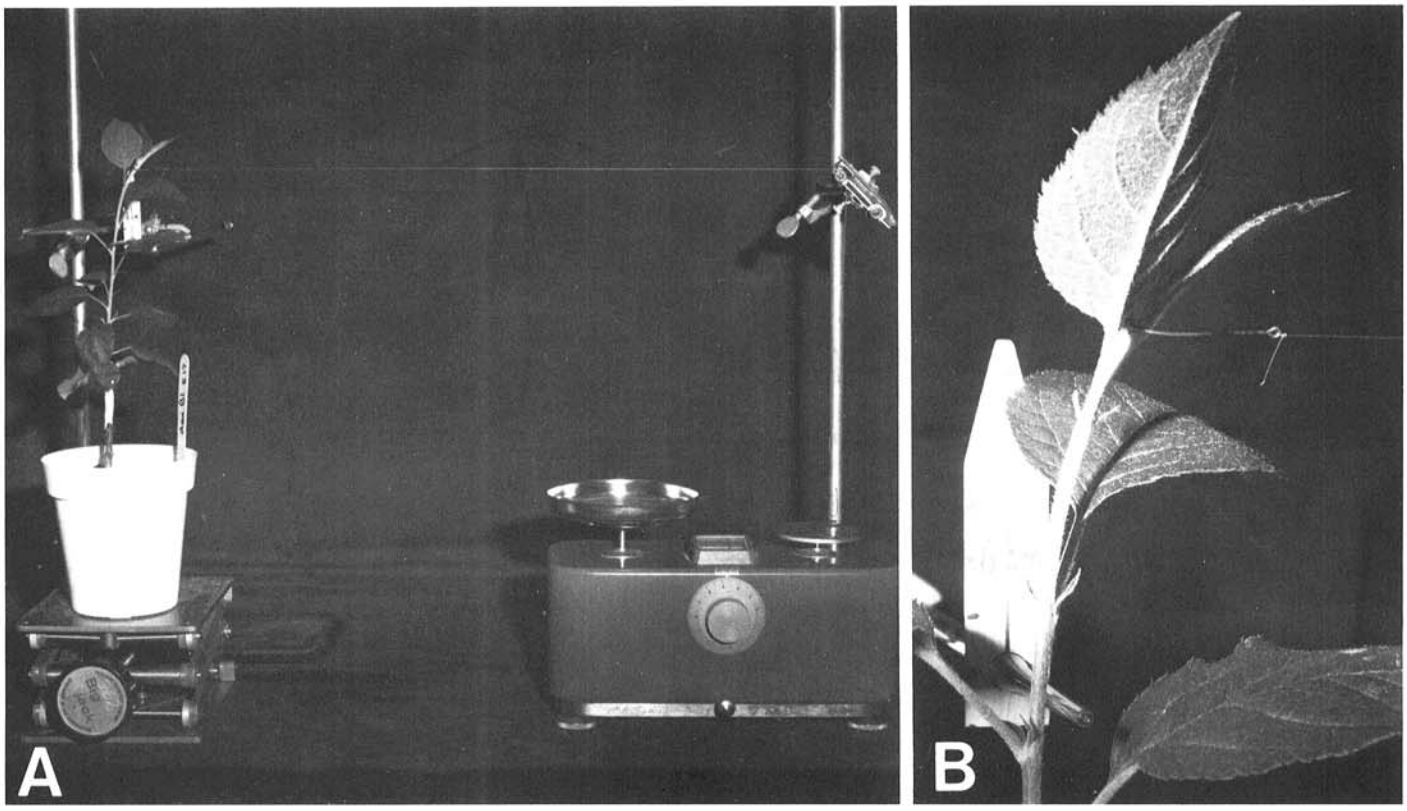

Fig. 3. Measurement of flexibility of apple (*Malus pumila*) shoots. **A,** Apparatus for measuring shoot flexibility. A dial balance is used to apply a variable force to the shoot tip. Force is transmitted to the shoot tip through a length of nylon monofilament fishing line and a modified fish hook. A model car is used to provide a low friction pulley. **B,** Shoot tip that has been displaced laterally 1 cm by force applied by the apparatus. Note that the distance from the fulcrum (a glass pipet) to the shoot apex is 6 cm. Following flexibility measurements, shoots were excised and placed in amylovorin solutions.

inoculation. Drops of a 20-hr nutrient broth culture of *E. amylovora* (strain Ea 273) were applied to the cut surfaces of stems immediately following removal of the apical 2-mm portions. No evidence of fire blight infection was observed with this procedure.

None of the shoots of either species that had been injected with water showed symptoms of fire blight.

Sensitivity of cotoneaster and spiraea shoots to wilting in amylovorin solution. The mean time required for twenty 10-cm shoots of *S. vanhouttei* (resistant to *E. amylovora*) to wilt in amylovorin solution (500 μg/ml) was 52.6 ± 40.8 min (mean ± S.D.), which was not significantly different from the mean time required for twenty 10-cm shoots of *C. pannosa* (susceptible to *E. amylovora*) to wilt (77.6 ± 40.5 min). Shoots of both species that remained in water did not wilt.

Sensitivity of apple cultivars to wilting in amylovorin solutions. In the first experiment there were highly significant differences among apple cultivars in sensitivity to amylovorin solutions (Table 1). There was no significant difference between the response of the first group of four shoots in any cultivar-amylovorin source combination and the response of the second group of four shoots in the same combination tested the following day (Table 1). During the first 3 hr, none of the shoots wilted, but after 6 hr differences in relative sensitivity of the cultivars to wilting induced by each amylovorin preparation became apparent. Subsequently, the mean wilt indices of all cultivars increased and only minor changes occurred in the relative sensitivity of the cultivars. After 10 hr, the mean wilt index of shoots treated with amylovorin from apple was significantly greater than the mean wilt index of shoots treated with amylovorin from pear. However, cultivar-amylovorin source interaction was not statistically significant.

Despite large differences in sensitivity to amylovorin-induced wilting among the cultivars used in the first experiment, there was no relationship between this sensitivity and the reported susceptibility of these cultivars to *E. amylovora* (Table 2). When the percent cortical lesion length following artificial inoculation was used as a measure of susceptibility to the pathogen (3), there was no significant linear correlation between susceptibility and sensitivity to amylovorin from either apple ($r = -0.717$) or pear ($r = -0.728$). No significant relationship between susceptibility to the pathogen and mean sensitivity to amylovorin was detected by Spearman's rank correlation test (17) ($r_s = -0.633$) either.

The second experiment also demonstrated that apple cultivars differed significantly in their sensitivity to amylovorin (Table 3). The mean wilt index of shoots from 13 apple cultivars after 12 hr in amylovorin solution ranged from 1.0 for Northern Spy to 5.0 for Hawaii. As in the first experiment, no relationship between the sensitivity of these cultivars to amylovorin-induced wilting and their reported susceptibility to *E. amylovora* could be detected by

TABLE 1. Sensitivity of shoot tips of nine apple cultivars to wilting in amylovorin solutions from two sources and the susceptibility of vegetative shoots to inoculation with *Erwinia amylovora*

Cultivar	Wilt indices[w] of apple shoots exposed to amylovorin from: Apple	Pear	Mean[y]	Percent cortical lesion length[x]
Turley	4.5 a[z]	3.8 a	4.1 a	38.2 c
Rome Beauty	4.4 ab	3.5 a	3.9 ab	63.6 abc
Arkansas Black	4.1 abc	3.6 a	3.9 abc	50.6 bc
Prima	3.9 abc	3.3 ab	3.6 abc	37.5 c
Golden Delicious	2.8 abcd	1.9 bc	2.3 bcd	58.7 abc
Ben Davis	2.4 cd	2.1 abc	2.3 cd	77.4 a
McIntosh	2.5 bcd	1.1 c	1.8 d	61.7 abc
Tolman Sweet	2.6 abcd	1.1 c	1.8 d	80.5 a
York Imperial	1.4 d	0.6 c	1.0 d	72.0 ab

[w] Numbers indicate wilt indices: 0 = shoot fully turgid; 1 = leaf lamina flaccid, stem turgid; 2 = stem bent 0–30 degrees from veritcal; 3 = stem bent 30–60 degrees from vertical; 4 = stem bent 60–90 degrees from vertical; 5 = stem bent ≥90 degrees from vertical (see also Fig. 1). Apple trees were grown as single shoots in the greenhouse. Shoot tips (6 cm long) were excised and placed in amylovorin solution (0.1 mg/ml) in a controlled environment chamber at 26 C, 80% RH, and 19 klux for 10 hr. Four shoots of each cultivar were exposed on each of 2 successive days to amylovorin isolated from ooze produced on *E. amylovora*-infected pear or apple fruits.

[x] Mean percent cortical lesion length following inoculation of trees in the greenhouse (3).

[y] Mean wilt index from tests using amylovorin from apple and pear.

[z] Means (within columns) followed by the same letter do not differ significantly ($P = 0.05$) according to Duncan's new multiple range test.

TABLE 2. Rankings of apple cultivars in order of increasing susceptibility to *Erwinia amylovora* by artificial inoculation and by natural infection

Apple cultivars	Relative susceptibility to fire blight: Artificial inoculation[v]	Natural infection I[w]	II[x]	III[y]
Baldwin	8	7	9	1
Ben Davis	7	3	2	4
Delicious	1	1	5	4
Golden Delicious	3	3	2	10
Grimes Golden	12	6	2	12
Jonathan	12	12	10	11
Macoun	6	8	7	4
McIntosh	5	2	6	1
Rome Beauty	9	11	9	9
Twenty Ounce	14	13	13	14
Wealthy	4	9	10	8
Winesap	2	3	1	3
Yellow Transparent	9	13	13	4
York Imperial	11	10	10	13
Spearman's correlation coefficient (r_s)[z]	...	0.749	0.558	0.598

[v] Derived from greenhouse inoculation test data (3).

[w] Derived from mean of "Northeast" and "Mid-Atlantic" ratings of field susceptibility from a survey of research workers (1).

[x] Derived from ratings of field infection at Blairsville, GA (18).

[y] Derived from ratings of field infection at Carbondale, IL (12).

[z] The correlation coefficient between rank by artificial inoculation and the indicated ranking. For significance, r_s must ≥ 0.532 at $P = 0.05$, and 0.661 at $P = 0.01$.

TABLE 3. Sensitivity of shoot tips of 13 apple cultivars to wilting in amylovorin solution and the susceptibility of vegetative shoots to inoculation with *Erwinia amylovora*

Cultivar	Wilt index[x]	Percent cortical lesion length[y]
Hawaii	5.0 a[z]	22.1 e
Baldwin	4.8 a	90.6 b
Golden Delicious	4.7 a	58.7 cd
Twenty Ounce	4.3 ab	99.9 a
Delicious	3.8 abc	33.8 de
Rhode Island Greening	3.8 abc	93.5 ab
Jonathan	3.5 abc	79.2 bc
Niagara	3.3 abc	63.9 c
Rome Beauty	2.5 bcd	63.6 c
Britemac	2.3 cd	1.5 f
McIntosh	1.5 d	61.7 cd
Idared	1.3 d	76.9 bc
Northern Spy	1.0 d	68.1 c

[x] Numbers indicate wilt indices: 0 = shoot fully turgid; 1 = leaf lamina flaccid, stem turgid; 2 = stem bent 0–30 degrees from vertical; 3 = stem bent 30–60 degrees from vertical; 4 = stem bent 60–90 degrees from vertical; 5 = stem bent ≥90 degrees from vertical (see also Fig. 1). Apple trees were grown as single shoots in the greenhouse. Shoot tips (6-cm long) were excised and placed in amylovorin solution (0.1 mg/ml) which had been isolated from ooze produced on *Erwinia amylovora*-infected immature pear fruits. Four shoots of each cultivar (three of Golden Delicious) were exposed to amylovorin in a controlled environment chamber for 12 hr at 26 C, 80% RH and 19 klux.

[y] Mean percent cortical lesion length following inoculation of trees in the greenhouse (3).

[z] Mean (within columns) followed by the same letter do not differ significantly ($P = 0.05$) according to Duncan's new multiple range test.

either a linear correlation coefficient ($r = 0.064$) or Spearman's rank correlation test ($r_s = 0.028$).

Factors affecting the sensitivity of shoots to amylovorin-induced wilting. Both shoot flexibility and shoot transpiration rate were related to the sensitivity of cotoneaster shoots to amylovorin-induced wilting. A highly significant ($P = 0.01$) negative correlation ($r = -0.658$) was observed between the flexibility of 42 cotoneaster shoots and the time elapsed before wilting occurred (Fig. 4). When both shoot flexibility and transpiration rate were determined in a sample of 24 shoots in 1.0 mg of amylovorin per milliliter, transpiration rate was a significant component ($P = 0.05$) and flexibility a highly significant component ($P = 0.01$) in the equation:

$$Y = 355 - 33.2\ X_1 - 7.95\ X_2$$

in which Y is the time (min) required for wilting, X_1 is the flexibility rating (cm), and X_2 is the transpiration rate (milligrams of water per cm^2 per hr).

The sensitivity of apple shoots to amylovorin-induced wilting also was related to shoot flexibility. There was a significant ($P = 0.05$) negative correlation ($r = -0.567$) between shoot flexibility and wilt index 12 hr after placing 15 Rome Beauty shoots in amylovorin solution. Total shoot length ranged from a mean of 16 cm for Rome Beauty shoots which had grown for 2 wk to 46 cm for those that had grown for 9 wk.

The flexibility of shoots of the 13 cultivars tested in the second experiment was significantly correlated ($P = 0.05$, $r = -0.317$) to their wilt indices. However, adjustment of the wilt indices of the cultivars in Table 1 and Table 3 for difference in flexibility by covariance analysis (17) did not increase the correlation coefficient between sensitivity to amylovorin and susceptibility to the pathogen. Thus, differences in shoot flexibility among cultivars would conceal any possible correlation between the inherent sensitivity of those cultivars to amylovorin and their susceptibility to *E. amylovora*.

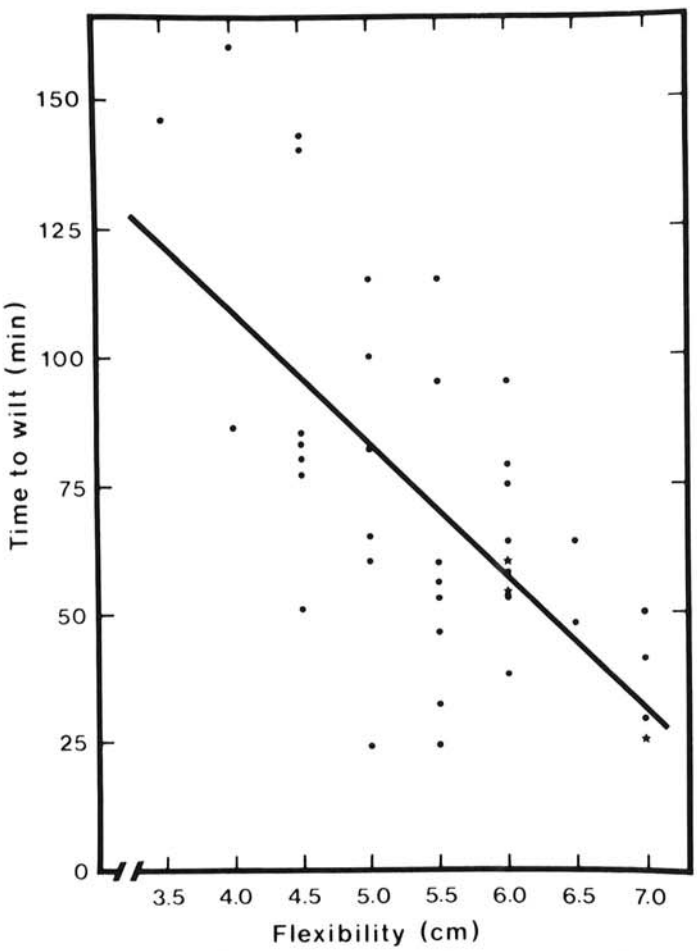

Fig. 4. The relationship between shoot flexibility and time required for wilting of *Cotoneaster pannosa* shoots in 1.0 mg/ml amylovorin solutions. The line represents the best-fit linear regression model for the data points. Flexibility was determined gravimetrically as illustrated in Fig. 2. Time to wilt was defined as the time required for shoot apices to bend 90 degrees from normal. Stars represent two observations.

DISCUSSION

These data indicate clearly that amylovorin lacks host-specificity and cannot be used for screening apple cultivars for fire blight resistance as had been suggested previously (5,10,11). Although varietal differences in sensitivity to amylovorin were apparent among apple cultivars used in these studies (Table 1 and Table 3), these differences were not correlated with the susceptibility of the same cultivars to vegetative shoot infection by *E. amylovora* after artificial inoculation.

Artificial inoculation data cannot be compared directly with observations of the incidence and severity of natural infections, which depend on many uncontrolled factors, but the following analysis indicates that they agree well with field observations. Fourteen apple cultivars used in artificial inoculation tests conducted in the greenhouse (3) were also used in three sets of field observations (Table 2). There was a highly significant positive correlation ($P = 0.01$) between the ranking of the cultivars by artificial inoculation and by a survey of research and extension workers (1). Also, there were significant positive correlations ($P = 0.05$) between the rankings by artificial inoculation and by field infection ratings made in Illinois (12) and Georgia (18). Similarly, Quamme (14) found significant positive correlations between susceptibility ratings of pear cultivars by artificial inoculation and by natural infection. Thus, it is legitimate to regard quantitative data from artificial inoculation as indicative of fire blight susceptibility in the field, and they can be used for comparison with amylovorin wilt indices.

The wilt assay used in these studies was cumbersome and difficult to quantify. In spite of great efforts taken to ensure uniformity of shoots of each cultivar, and the use of a quantitative measure of wilting, substantial differences were apparent in the rate of wilting of cotoneaster shoots and the degree of wilting of apple shoots. In addition, the relative ranking of two apple cultivars, Rome Beauty and Golden Delicious, based on wilt indices, differed in the two tests. These differences may have resulted from somewhat different greenhouse growing conditions for the plants included in the two tests that were done 4 mo apart. A more direct measure of shoot water-conducting capacity such as the transpiration rate of excised shoots in amylovorin versus that in water (19), may have resulted in greater precision. However, one of the objectives of these studies was to test the validity of the simple shoot wilt assay used by previous workers (10).

The lack of significant correlations between the sensitivity of apple cultivars to amylovorin in shoot wilt assays and susceptibility of the cultivars to *E. amylovora* precludes the use of amylovorin to assess varietal susceptibility. There is now no alternative method for evaluating host response to *E. amylovora* other than using data from natural infection or artificial inoculation (4).

The differential sensitivity of apple and pear cultivars to amylovorin reported here and previously (5,7,10,11) may be related more closely to differences in the water conducting systems of the cultivars than to differences in the inherent susceptibility to *E. amylovora*. These differences may be reflected in the flexibility of shoots, which was shown to be negatively correlated with wilt indices. These conclusions are supported by our earlier studies that demonstrated that amylovorin induces wilting of cotoneaster shoots by restricting water movement. No direct effect of the polysaccharide on susceptible host tissues was observed. By contrast, the wilting of cotoneaster shoots infected by *E. amylovora* appeared to result from a loss of membrane semipermeability (16).

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