The Epidemiology of Powdery Mildew on Concord Grapes

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ABSTRACT

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Vitis labruscana 'Concord' is a grape cultivar widely grown in the United States for processing into juice and other grape products. Concord grapes are sporadically but sometimes severely damaged by the grape powdery mildew pathogen, *Uncinula necator*. Although the foliage is often reported to be moderately resistant to powdery mildew, severe fruit infection occurs in some years. We observed the seasonal development of powdery mildew on leaves, rachises, and berries of unsprayed Concord grapevines. Inoculations of flower and fruit clusters revealed a brief period of berry susceptibility and a protracted period of rachis susceptibility. The rachis remained highly susceptible to infection, and the severity of rachis infection increased throughout the growing season until the rachis formed a periderm shortly before harvest. In contrast, berries were nearly immune to infection within 2 weeks after fruit set. Rachis and berry infections were detected before the disease was observed on foliage, and the incidence of rachis and berry infection often exceeded disease incidence observed on foliage until after fruit acquired substantial

ontogenic resistance. Excellent control of fruit infection, and adequate control of leaf infection, was achieved by two fungicide applications targeted at the peak period of fruit susceptibility. Although Concord is thought to be moderately resistant to powdery mildew, the rachis is highly susceptible, and may be the avenue by which prebloom infections make their way onto the developing fruit. Late-season infection of the rachis neither spread to the fruit, nor did it cause fruit to drop prematurely, and may be of little economic consequence on fruit destined for processing. Although fruit of *V. vinifera* cultivars have been reported to remain susceptible to infection until berry sugar levels reach 8 to 15%, Concord fruit become nearly immune to infection nearly 6 weeks before this stage of development. Because powdery mildew does not become conspicuous on foliage until late summer, it is generally regarded as a late-season problem on Concord grapes, and previous management programs have reflected this belief. However, the greatest contribution to control of fruit infection is due to fungicides applied during the peak period of fruit susceptibility, from bloom until shortly after fruit set, long before the disease is observed on foliage.

Additional keywords: disease management, Oidium, ontogenic resistance.

Powdery mildew is the most widespread and destructive disease of grapevines worldwide. Much of what is known of the damage caused by the pathogen, *Uncinula necator*, comes from studies of the disease on cultivars of the European grape, *Vitis vinifera*, which bears leaves and fruit that are highly susceptible to this disease (20). Concord grapes are of the species *V. labruscana*, which is native to North America, and are generally thought to be more resistant to powdery mildew than cultivars of *V. vinifera* (20). Concord grapes are widely planted throughout the states of New York, Pennsylvania, Ohio, Michigan, and Washington for processing into unf fermented juice and other products. Despite their widespread culture and the routine use of fungicides to suppress powdery mildew on this cultivar, management of powdery mildew on Concord grapes has largely evolved by trial and error rather than through systematic study of pathogen development, host development, and disease progress. Many of the assumptions under which we operate when controlling powdery mildew on Concord are based upon research on *V. vinifera* cultivars, and have not been shown to be valid for Concord. In *V. vinifera* cultivars, (i) early leaf infection is assumed to provide a pool of inoculum for later fruit infection (20), (ii) a protracted period of fruit susceptibility lasting until fruit sugar levels reach 8 to 15% is assumed (20,21), and (iii) there is, therefore, an assumed need for season-long fungicidal suppression of powdery mildew to preserve the health of the canopy and protect fruit from infection (20,21). Our preliminary studies have indicated that some, and perhaps all, of

these assumptions are invalid in the case of Concord grapevines (14,17). Further, previous studies of berry susceptibility have used only detached fruit (2,4), which may not accurately represent expression of resistance in rapidly differentiating berries. Presently, we report our more recent findings on (i) the seasonal development of powdery mildew on Concord under vineyard conditions; (ii) when fruit on such vines are most susceptible to infection; (iii) the differential susceptibility of fruit and rachises over time; and (iv) how fungicides can be deployed in a manner consistent with the risk of crop loss from powdery mildew.

MATERIALS AND METHODS

Seasonal development of powdery mildew on leaves and fruit of unsprayed vines. The seasonal development of powdery mildew on leaves and fruit was studied in a 12-ha Concord vineyard in Westfield, NY, from 1987 to 1989 (12). The vines were trained to a top-wire cordon system and were hedge-pruned. Between-vine spacing was 2.4 m, and between-row spacing was 2.7 m. Within the vineyard, three plots (10 rows wide by 12 vines long) were arbitrarily selected for assessments and were not treated with fungicides. Beginning at 15 cm of shoot growth, and at 7- to 21-day intervals thereafter, the incidence and severity of powdery mildew was assessed on 10 shoots per vine, on 10 vines in each of the three plots. The number of infected leaves per shoot, as well as the proportion of the leaf surface colonized, was recorded. The percentage of the cluster surface infected was estimated and recorded for all clusters born on the shoots selected for the foliar disease assessments.

Ontogenic resistance in Concord fruit. In order to definitively measure the effects of infection by *U. necator* at precise stages of fruit development in the vineyard, it was necessary to produce clus-

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ters that were both disease-free and free of an effective fungicide residue. This was accomplished by spraying vines with the locally systemic fungicide myclobutanil (Nova 40 WP) at 112 g/ha at 2-week intervals from 20 cm of shoot growth until veraison (start of berry ripening), and covering selected fruit clusters with small polyethylene bags immediately before the spray applications. The bags were removed within 1 h after each spray application. The possibility that an effective level of myclobutanil was present on the bagged clusters following spraying was assessed in a preliminary experiment in 1994 conducted in a 20-year-old planting of Concord vines at the New York State Agricultural Experiment Station in Geneva. The vines were Umbrella-Kniffen trained and cane-pruned. At the prebloom stage of cluster development, 24 h after the fungicide application, clusters that had been bagged on both sprayed and unsprayed vines were inoculated with *U. necator* as follows. Conidia were harvested from 14-day-old mildew colonies on *V. vinifera* seedlings by shaking infected leaves in 50 ml of distilled water containing 0.05% (vol/vol) Tween 20. The concentration of the suspension was adjusted to a concentration of 10^5 conidia per ml, and was applied within 30 min of its preparation. The conidial suspension was applied with a hand-held atomizer (Preval Model 268, Precision Valve Corp., Yonkers, NY) until droplets of suspension were visible on the cluster. Five clusters per vine were inoculated, and treatments were replicated on three vines. The percentage of the cluster surface infected was assessed 4 weeks after inoculation. This preliminary experiment was repeated at the fruit-set stage of cluster development in 1994.

For the purpose of assessing ontogenic resistance in 1994, clusters protected from fungicide residues by bagging as previously described were inoculated at four stages of cluster development in the above vineyard: immediate prebloom, fruit set, 6-mm-diameter fruit, and 10- to 13-mm-diameter fruit. Clusters to be inoculated were examined on the day of inoculation with a $\times 14$ hand lens to confirm the absence of preexisting powdery mildew colonies, and five clusters per vine on three replicate vines per treatment were inoculated as described previously. Responses recorded included the percentage of the cluster surface infected and the percentage of the rachis surface infected, assessed at 14- to 21-day intervals until harvest. The experiment was repeated in 1995.

In both 1994 and 1995, accumulation of soluble solids in berries was monitored by collecting the two apical berries from each of two clusters per vine on five randomly selected vines in the experimental vineyard. The berries were crushed with a mortar and pestle, and the soluble-solid level of the juice was determined with a hand-held temperature compensating refractometer. Soluble-solid levels were assessed at approximately 10-day intervals from the time fruit were 6 mm in diameter until harvest.

Management trials. A disease management trial was established at a commercial Concord vineyard in Westfield, NY, in 1994. The overall goal of the trial was to evaluate the comparative efficacy of a minimal number of fungicide applications targeted at

the peak susceptibility of fruit to powdery mildew, which was assumed to be centered on bloom, but of unknown duration. The vines were trained to a top-wire cordon system, and were hedge-pruned. Between-vine spacing was 2.4 m, and between-row spacing was 2.7 m. Treatments consisted of zero, one, and four fungicide sprays in 1994 and 1995, and zero, one, two, and four fungicide sprays in 1996 and 1997. The selection of fungicides and the timing of the applications are given in Table 1.

Plots consisting of nine rows of 12 vines were arranged within the vineyard in a randomized complete block design with three replications. The incidence and severity of powdery mildew were assessed in early September of each year of the trial. Other major grape diseases (e.g., black rot [*Guignardia bidwellii*], downy mildew [*Plasmopara viticola*], and Phomopsis cane and leaf spot and fruit rot [*Phomopsis viticola*]) were assessed similarly. The percentage of the cluster surface infected by each pathogen was estimated visually for 10 clusters on each of 10 vines selected from the center five rows of each replicated plot. Loss of grapes due to dropping ahead of the mechanical harvester was assessed by counting the berries contained in an 18.5-cm² frame tossed to 10 locations directly under the trellis wire in each plot. Fallen fruit within the frame were counted immediately before and immediately after passage of the mechanical harvester through each plot.

At harvest, two apical berries were collected from approximately five clusters per vine, for each of 10 vines per replicated plot. The berry samples were crushed as described previously, and juice-soluble solids was measured with a hand-held temperature compensating refractometer.

RESULTS

Seasonal development of powdery mildew. Approximately 2 weeks after bloom in 1987 to 1989, the incidence of powdery mildew was significantly ($P = 0.01$) and substantially higher on fruit clusters than on foliage (Fig. 1). Foliar mildew was not detected or remained at trace levels for several weeks after bloom (Fig. 2). Thereafter, the incidence of foliar mildew increased rapidly, reaching approximately 40 to 60% by late August in each year of the study (Fig. 2A). In contrast, incidence of powdery mildew on fruit clusters, although initially higher than on foliage, did not increase significantly after it was first detected, approximately 2 weeks after bloom (Fig. 2B). The slope coefficients of linear regressions of the incidence of cluster infection against time, between 2-weeks postbloom and harvest, were not significantly different from zero at $P = 0.10$.

Fig. 1. Incidence of fruit cluster and leaf infection on Concord grapevines by *Uncinula necator* at Westfield, NY. Vines were within a managed commercial vineyard, but were not treated with fungicides. Disease was assessed 2 weeks after bloom in each year of the study. Bars represent one standard error of the mean.

TABLE 1. Timing of fungicide applications in disease management trials on Concord grapes, Westfield, NY, 1994 to 1997

Treatment	Timing of fungicide application ^w			
	4-cm shoots ^x	10 to 14 days after 4-cm shoots ^x	First bloom ^y	10 to 14 days after first bloom ^z
1-spray	—	—	+	—
2-spray	—	—	+	+
4-spray	+	+	+	+
Control	—	—	—	—

^w + and — indicate that a spray was or was not included, respectively, at the indicated time as part of the treatment.

^x Material applied was myclobutanil at 112 g/ha (Nova 40WP).

^y Materials applied were myclobutanil at 112 g/ha + metalaxyl at 224 g/ha + mancozeb at 2.16 kg/ha (Ridomil MZ).

^z Materials applied were myclobutanil at 112 g/ha + metalaxyl at 224 g/ha + copper hydroxide at 1.34 kg/ha (Ridomil Copper).

The severity of powdery mildew on foliage ranged from approximately 10 to 55% of the leaf surface infected by late August of 1987 to 1989 (Fig. 3A), and appeared to increase rapidly once disease incidence (Fig. 2A) exceeded trace levels in midsummer. As in the case of disease incidence on fruit clusters, disease severity on fruit clusters did not increase significantly after 2-weeks postbloom (Fig. 3B). The slope coefficients of linear regressions of the severity of cluster infection between 2-weeks postbloom and harvest were not significantly different from zero at $P = 0.10$.

Mildew colonies on the upper leaf surface were easily found in vineyard assessments of disease (Fig. 4A). Colonization of the lower leaf surface resulted in the production of a yellowed or chlorotic spot visible from the upper surface (Fig. 4B). However, the mildew colony itself was obscured by the dense growth of trichomes on the lower leaf surface (Fig. 4C), which gave the surface a whitish cast and thereby obscured the presence of the mildew colony to the naked eye. The presence of the pathogen itself could only be confirmed in the vineyard by examination of the lower leaf surface with a $\times 14$ hand lens, or in the laboratory at higher magnifications (Fig. 4D).

Ontogenic resistance in Concord fruit. There was no effective residue of myclobutanil on clusters that were bagged during fungicide applications. Four weeks after inoculation of clusters at prebloom, there was no significant ($P = 0.05$, Student's t test) difference in the severity of powdery mildew that developed on clusters that were bagged during spraying (25.9%, SE = 2.61) versus clusters that were inoculated on unsprayed control vines (22.1%, SE = 3.04). Similarly, there was no significant difference between the severity of mildew that developed 4 weeks after inoculation on sprayed (35.4%, SE = 4.33) versus unsprayed (38.2%, SE = 3.22) vines when the experiment was repeated at fruit set.

In the experiments to assess the development of ontogenic resistance, berries on clusters inoculated at prebloom or 2 weeks later at fruit set became severely diseased by harvest (Fig. 5). However, clusters inoculated 2 weeks after fruit set, when berries were approximately 6 mm in diameter, or later in development remained relatively mildew-free (Fig. 5). Berries were nearly immune to infection by the time they reached 6 mm in diameter, a time when fruit-soluble solids were at a basal (nonsugar) level of approximately 4% (Fig. 6). Accumulation of a soluble-solids level of approximately 8% did not occur until nearly 45 days after fruit were nearly immune to infection in both 1994 and 1995 (Figs. 5 and 6).

In sharp contrast to the berries, the rachis appeared to remain susceptible throughout its development and, once inoculated, disease severity progressed linearly (Fig. 7). The severity of rachis infection was higher in 1994 than in 1995 (Fig. 7). Nearly the entire rachis was colonized on clusters inoculated at prebloom or fruit set (Fig. 7A and B), but the percentage of the rachis that was colonized reached relatively high levels by day 220 to 240, even when inoculation was delayed until later stages of fruit development (Fig. 7C and D) or when unsprayed and uninoculated controls (Fig. 7E) became diseased from background levels of inoculum within the vineyard.

Infections of the calyptra were rarely observed, were nonsporulating, were not observed to grow from the calyptra to the pedicel, and appeared to be shed with the calyptra (Fig. 4E) at anthesis. However, after anthesis, colonies on the pedicel rapidly grew to colonize the wall of the fertilized ovary (Fig. 4F). Growth from the pedicel onto the shoulder of the developing immature berry often resulted in colonization of 30 to 50% of the berry surface

Fig. 2. Incidence of powdery mildew (*Uncinula necator*) on **A**, leaves and **B**, fruit clusters of Concord grapevines at Westfield, NY. Vines were within a commercial vineyard, but were not treated with fungicides. Vines bloomed between day 165 and 170, and fruit soluble solid levels (brix) reached 4.5 to 5.0% between day 195 and 200 in each year of the study.

Fig. 3. Severity of powdery mildew (*Uncinula necator*) on **A**, leaves and **B**, fruit clusters of Concord grapevines at Westfield, NY. Vines were within a commercial vineyard, but were not treated with fungicides. Vines bloomed between day 165 and 170, and fruit soluble solid levels (brix) reached 4.5 to 5.0% between day 195 and 200 in each year of the study.

Fig. 4. Signs and symptoms of powdery mildew on Concord grapevine. **A**, Typical powdery mildew colony (arrow) on upper surface of Concord leaf. **B**, Typical chlorotic spot (arrow) on upper leaf epidermis near tip of leaf midvein subtended by a powdery mildew colony on the lower leaf surface. **C**, Lower surface of Concord leaf showing whitish cast due to dense trichomes. **D**, Powdery mildew colony sporulating on lower leaf surface (arrow) of Concord amongst trichomes. **E**, Prebloom and post-anthesis flowers of Concord grapevine. **F**, Colonization of the pedicel showing sporulation on pedicel and spread to the wall of the fertilized ovary (arrow) 72 h postanthesis. **G**, Colonization of berry shoulder 10 days after fruit set resulting from infection of the rachis at prebloom. Note sharp demarcation between colony and uncolonized tissue due to acquisition of ontogenic resistance during colony expansion. **H**, Rachis colonization without berry infection resulting from infection of the rachis after development of ontogenic resistance in berries.

before colony expansion was halted by ontogenic resistance (Fig. 4G). The acquisition of ontogenic resistance during colony expansion often resulted in a sharp demarcation between colonized and healthy tissue on the surface of infected berries (Fig. 4G). Colonization of the rachis after the development of ontogenic resistance in berries resulted in clusters with severe rachis infection, but little visible colonization of the fruit (Fig. 4H).

Management trials. Between 19.7 and 95.3% of the unsprayed fruit clusters developed powdery mildew, with 4.4 to 42.3% of the

Fig. 5. Severity of cluster infection at harvest on Concord grapes inoculated at different stages of fruit development with conidia of *Uncinula necator*. Bars represent one standard error of the mean.

Fig. 6. Accumulation of soluble solids in Concord grapes in A, 1994, and B, 1995.

Fig. 7. Seasonal development of powdery mildew on rachises of Concord grapevines inoculated with a conidial suspension of *Uncinula necator* at A, prebloom, B, fruit set, C, 6-mm-diameter fruit, D, 10- to 13-mm-diameter fruit, and E, uninoculated check, in 1994 and 1995.

cluster surface infected depending on the year (Table 2). A single application of the fungicide myclobutanil applied at first bloom significantly and substantially decreased both the incidence and severity of powdery mildew on fruit in all 4 years of the study (Table 2). The two-spray treatment that was evaluated only in the last 2 years of the study provided suppression of powdery mildew on fruit and early-season foliar powdery mildew, which was equivalent to a program that incorporated two additional, earlier fungicide applications (Table 2). Programs that included sprays at first bloom and 10 to 14 days later provided significantly better control of foliar mildew at veraison than the treatment consisting of a single spray at bloom. However, severity of powdery mildew on foliage at harvest did not differ significantly among treatments in any year of the study (Table 2). Soluble-solid levels in fruit were significantly higher at harvest when vines received the two- or four-spray treatments than on those receiving the one-spray treatments or on unsprayed vines (Table 2). There was no significant difference in soluble-solid levels in fruit from vines that received the one-spray treatment compared with unsprayed vines (Table 2).

Even on unsprayed vines, downy mildew was not detected in the vineyard in any year except 1996, when its incidence reached 43% on unsprayed clusters (Table 2). All spray treatments provided significant but equivalent suppression of downy mildew on fruit in 1996 (Table 2). Black rot was not detected in the vineyard until 1997, when the incidence on unsprayed clusters reached 16% (Table 2). The incidence and severity of black rot on fruit were significantly reduced by all fungicide treatments compared with the unsprayed vines in 1997 (Table 2), although severity was significantly higher when the postbloom spray was omitted (Table 2).

In 1994, vines that received four fungicide sprays dropped significantly less fruit before harvest than vines that were unsprayed or received one spray, but lost more fruit during the actual harvest operation than either treatment (Table 3). The total amount of unharvested fruit in 1994 was far higher among all treatments than in any other year of the study, primarily due to winds in excess of 60 km/h during a thunderstorm 1 week before harvest. From 1995 to 1997, there was no significant impact of spraying upon dropping of fruit either before or during harvesting operations (Table 3).

DISCUSSION

Seasonal development of powdery mildew. Despite the predominance of foliar tissue with respect to target area for infection

during all phases of vine growth, we found powdery mildew colonies earlier in the growing season and at a substantially higher frequency on fruit clusters than on leaves. Colonies on the first-formed leaves supposedly provide a pool of inoculum for the later-developing clusters (20). However, it is difficult to reconcile the extremely low incidence of disease on foliage at bloom with the relatively high incidence of infection on clusters if the former serves as an important source of infection for the latter. Although powdery mildew colonies were difficult to see with the naked eye on the lower surface of Concord leaves, which are extremely hairy, colonies on the lower leaf surface were usually accompanied by an easily detected yellow or chlorotic spot on the upper surface (Fig. 4B). Thus, unless the mildew colonies were exclusively on the lower leaf surface and unaccompanied by any symptoms on the upper leaf surface, the preponderance of fruit cluster infection relative to foliar infection measured at fruit set should be accurate, despite their inverse ratios of tissue availability for infection.

Ascospores released from cleistothecia that have overwintered on the bark of the vine constitute the primary inoculum for grape powdery mildew in New York, and in many regions with similar climates (3,9,18,19,24). The ascospores are released and dispersed in the vineyard air during rain events of 2.5 mm or more between the stages of bud break and shortly after fruit set (10,11,13). The prebloom cluster of Concord grapes has a cross-sectional area of less than 3 cm². An immature, expanding (and presumably mildew-susceptible) Concord leaf could present a cross-sectional area of 30 cm² or more, depending upon its orientation relative to an airborne spore's trajectory. The area of mature, fully expanded leaves can exceed 200 cm². Most shoots on Concord vines bear two fruit clusters but produce up to 15 leaves during the period of ascospore release. Although some previous studies have reported on the development of ontogenic resistance in grapevine leaves (23), or on the relative susceptibility of leaves of various *Vitis* spp. and cultivars (1,5), little is known of the relative susceptibility of leaves, rachises, and fruit within a cultivar. Our results indicate that the comparatively high susceptibility of clusters on Concord grapevines can have a profound influence on how epidemics develop; indeed, even such basic aspects as which tissues serve as sources of infection for later disease development can be affected. Although we did observe some prebloom leaf infection in Concord, it appears that mildewed clusters may serve as a source of infection for leaves, rather than the converse.

The incidence and severity of foliar infection increased substantially beginning 20 to 35 days after bloom on unsprayed vines, and

TABLE 2. Incidence and severity of powdery mildew (*Uncinula necator*), downy mildew (*Plasmopara viticola*), and black rot (*Guignardia bidwellii*) on Concord grapevines at Westfield, NY, 1994 to 1997^z

		Fruit						Leaf surface with powdery mildew (%)		Fruit-soluble solids (%)
		Powdery mildew		Downy mildew		Black rot				
Year	Treatment	Incidence	Severity	Incidence	Severity	Incidence	Severity	Veraison	Harvest	
1994	1-spray	12.0 a	0.9 a	0.0 a	0.0 a	0.0 a	0.0 a	12.7 a	50.6 a	16.6 a
	4-spray	2.3 b	0.1 b	0.0 a	0.0 a	0.0 a	0.0 a	2.1 b	50.7 a	17.0 b
	Unsprayed	19.7 c	4.4 c	0.0 a	0.0 a	0.0 a	0.0 a	19.8 a	57.6 a	16.4 a
1995	1-spray	67.8 a	8.1 a	0.0 a	0.0 a	0.0 a	0.0 a	14.1 a	53.9 a	16.1 a
	4-spray	12.2 b	0.4 b	0.0 a	0.0 a	0.0 a	0.0 a	4.4 b	40.2 a	16.8 b
	Unsprayed	91.1 c	34.6 c	0.0 a	0.0 a	0.0 a	0.0 a	18.0 a	49.2 a	16.0 a
1996	1-spray	91.0 a	15.9 a	10.0 a	1.7 a	0.0 a	0.0 a	18.8 a	58.0 a	15.3 a
	2-spray	57.0 b	5.6 b	11.1 a	0.6 a	0.0 a	0.0 a	6.5 b	53.2 a	16.1 b
	4-spray	56.3 b	4.4 b	9.0 a	0.6 a	0.0 a	0.0 a	5.5 b	55.9 a	16.1 b
	Unsprayed	95.3 a	42.3 c	43.0 b	5.8 b	0.0 a	0.0 a	22.4 a	63.6 a	14.9 a
1997	1-spray	31.7 a	6.1 a	0.0 a	0.0 a	3.3 a	2.1 a	11.3 a	42.0 a	16.4 a
	2-spray	21.3 b	3.7 b	0.0 a	0.0 a	3.3 a	0.8 b	6.5 b	46.4 a	16.9 b
	4-spray	18.0 b	2.1 b	0.0 a	0.0 a	0.7 b	0.3 b	5.4 b	48.5 a	16.8 b
	Unsprayed	43.7 c	24.9 c	0.0 a	0.0 a	16.0 c	7.0 c	15.7 a	43.1 a	16.3 a

^z The incidence (percentage of clusters with berry infection) and severity (percentage of the cluster surface infected) of powdery mildew, downy mildew, and black rot was assessed in early September of each year of the trial. The percentage of the leaf surface colonized by powdery mildew was assessed at veraison and at harvest. Fruit soluble solids were assessed at harvest using a refractometer. Within a year, means in a column followed by the same letter are not significantly different at *P* = 0.05 according to Duncan's multiple range test.

foliar disease continued to increase linearly until harvest from 1987 to 1989 (Figs. 2 and 3). The same was not true of fruit infection, which failed to increase significantly in either incidence or severity beyond 20 days after bloom (Figs. 2 and 3). The conspicuous nature of powdery mildew on Concord foliage in the later stages of the epidemic may account for the reputation of powdery mildew as a late-season problem on Concord grapevines. However, the incidence and severity of fruit infection are apparently determined by events early in the epidemic.

Our research was conducted exclusively in upper New York State, where growing seasons are typified by moderate temperatures and rainfall, the latter of which is, in most years, evenly distributed through the growing season. Concord grapes are grown in more arid regions, under irrigation, and in locations with relatively hot summer weather, e.g., eastern Washington State. There may be more limited opportunities for ascospore infection during the critical period of fruit susceptibility in such regions. Thus, the sporadic appearance of severe fruit infection that we observed in New York due to the temporal distribution and abundance of rainfall relative to fruit development could be exacerbated by the scarcity of rain for ascospore release in arid regions. However, overhead or under-vine sprinkler irrigation in arid regions could easily supply sufficient moisture for ascospore release, as it does in some areas of South Australia, where vines may receive three applications of 30 to 50 mm of water during a 21-day period immediately before bloom (18). Although it is impractical to withhold water from drought-stressed vines to manage powdery mildew, drip irrigation would be preferable to lower the risk of releasing ascospores when the fruit are most susceptible to infection.

High summer temperatures coupled with aridity would almost certainly have a deleterious impact on the increase of disease severity on both foliage and the rachis. Low relative humidity decreases germinability of conidia (4). Temperatures above 35°C will actually kill portions of mildew colonies on foliage (1,4,18, 20). It is uncertain whether similar mortality would occur on the rachis, due to its sheltered location within the canopy. However, because we found no evidence of foliar infection acting as a

source of inoculum for fruit in upper New York State, where weather is most favorable for its development, it seems unlikely that this fundamental relationship (or lack thereof) would be altered in regions where circumstances are less favorable for foliar disease. With respect to the epidemiology of powdery mildew on Concord grapevines, the principal differences between upper New York State and hotter, dryer regions, therefore, appear to be quantitative rather than qualitative.

Ontogenic resistance in Concord fruit. The period of susceptibility of Concord fruit was surprisingly brief, and contrasted sharply with what is reported in the literature for various cultivars of *V. vinifera* (20,21). Only fruit inoculated within 2 weeks after bloom developed severe disease (Fig. 5) and those inoculated 3-weeks postbloom, when fruit were approximately 6 mm in diameter, were nearly immune to infection. Whereas the duration of this critical period could be modified by warmer or cooler temperatures, it is unlikely that it would vary by more than a few days between years, or within the range of cultivation of Concord grapevines.

Development of ontogenic resistance was not associated with sugar accumulation as fruit matured, but occurred long before sugar accumulation ever began (Figs. 5 and 6). In fact, fruit were nearly immune to infection approximately 45 days before fruit-soluble solids reached 8% and nearly 80 days before soluble solids reached 15% (Figs. 5 and 6). The aforementioned levels of soluble solids are widely reported as being either coincidentally or functionally related to the development of ontogenic resistance in grape berries (20–22), and contribute to the concept of a protracted period of fruit susceptibility lasting two or more months, and a gradual acquisition of ontogenic resistance. In contrast, we found that Concord fruit progress from highly susceptible to highly resistant organs in as little as 10 days. The anatomical and molecular basis of this rapid change in susceptibility is the subject of continued research (6–8).

The relatively brief period of fruit susceptibility may partially explain the sporadic nature of severe fruit infection in Concord grapevines. Previous studies in New York have indicated that severe fruit infection in grapevine is associated with frequent and intense rainfall, specifically the occurrence of multiple ascospore infection periods (2.5-mm rainfall and temperatures above 10°C) between the prebloom and fruit set stages of cluster development (12,15,16). Our most recent findings on ontogenic resistance in fruit illustrate one mechanism by which rain events during a relatively brief period, early in fruit development, could play a critical role in determining the severity of fruit infection several months later.

In contrast to the berries, the rachis of Concord appears to remain susceptible to infection throughout its development, and is the avenue by which prebloom infections make their way onto the epidermis of the immature berry. Before bloom, the ovary of the grapevine flower is covered by the fused petals, forming a cap (calyptra) that is shed during bloom (Fig. 4E). Prebloom infection of the ovary wall is thus prevented, and infections of the cap are shed during bloom. However, prebloom infections on the rachis can spread rapidly from the berry stem to the immature berry once anthesis has occurred (Fig. 4F). Once it has spread to the shoulder of the developing berry, the mildew colony has only 10 to 14 days to expand before its development is halted by ontogenic resistance in the fruit. Eventually, the spread of rachis infection is halted by the development of periderm in portions of the rachis, effectively killing the mildew colony.

Management trials. The management trials illustrated the degree to which a limited number of fungicide applications, targeting the peak period of fruit susceptibility, could contribute to the overall control of fruit infection. The one-spray treatment was probably inadequate for commercial grape production. Although it significantly suppressed powdery mildew on fruit in each of the 4 years of the study, the severity on fruit in 1996 exceeded that

TABLE 3. Preharvest and harvest drop of berries from Concord grapevines at Westfield, NY, 1994 to 1997

Year	Treatment ^x	Dropped berries (kg/ha) ^y			Value of unharvested fruit (\$/ha) ^z
		Preharvest	Harvest	Total	
1994	1-spray	434.1 a	394.6 a	828.7 a	219.28 a
	4-spray	288.0 b	449.8 b	737.8 b	195.22 b
	Unsprayed	493.1 a	382.8 a	875.9 a	231.75 a
1995	1-spray	55.2 a	90.5 a	145.7 a	38.55 a
	4-spray	53.9 a	74.8 a	128.7 a	34.05 a
	Unsprayed	54.4 a	117.6 a	172.0 a	45.52 a
1996	1-spray	73.1 a	63.2 a	136.3 a	36.08 a
	2-spray	85.4 a	56.5 a	141.9 a	37.54 a
	4-spray	89.2 a	50.1 a	139.3 a	36.86 a
	Unsprayed	87.9 a	81.2 a	169.1 a	44.73 a
1997	1-spray	78.6 a	50.5 a	129.1 a	34.17 a
	2-spray	67.5 a	69.3 a	136.8 a	36.19 a
	4-spray	81.1 a	50.6 a	131.7 a	34.84 a
	Unsprayed	75.2 a	67.9 a	143.1 a	37.88 a

^x Material plus labor cost of treatments was assumed to be \$126.10/ha, \$252.20/ha, and \$381.24/ha for the 1-spray, 2-spray, and 4-spray treatments, respectively.

^y Dropped fruit within a 18.5-cm² frame directly under the trellis at 10 locations per plot were counted immediately before and immediately after mechanical harvesting of plots. Fallen berries were assumed to be uniformly distributed in a 30 cm wide band under the trellis, with 3,700 lineal meter of row per hectare. Within a year, means in a column followed by the same letter are not significantly different at *P* = 0.05 according to Duncan's multiple range test.

^z Cost of unharvested fruit was determined assuming a value of \$26.46 per 100 kg. Within a year, means in a column followed by the same letter are not significantly different at *P* = 0.05 according to Duncan's multiple range test.

which would be accepted by most grape processors. Furthermore, in all 4 years of the study, the one-spray treatment allowed a level of leaf infection that resulted in a significant reduction in fruit-soluble solids at harvest, an effect that is likely to be magnified by increased crop loads (16).

The two-spray treatment, which more completely spanned the period of fruit susceptibility to powdery mildew, provided a degree of disease suppression that was equivalent to a treatment incorporating two additional, earlier sprays, without the reduction of fruit-soluble solids seen in the one-spray treatment. The equivalent fruit-soluble solids reflected the equivalent control of foliar mildew provided by the two treatments at veraison (Table 2). This contrasted with the one-spray treatment, in which foliar mildew increased to levels equivalent to unsprayed vines by veraison (Table 2). Downy mildew and black rot were only observed in 1996 and 1997, respectively. Both diseases were well controlled on fruit by one or two sprays beginning at bloom. We anticipate that the two-spray treatment would provide even better control of fruit infection in warmer and drier climates, due to the decreased risk of fruit infection and the unfavorable effect of high summer temperatures on development of powdery mildew on foliage (1,4, 18,20).

The dropping of fruit during mechanical harvesting operations was related to the intensity of the spray program and the level of powdery mildew in only 1 year of the study (Table 3), and this effect may have been confounded by severe winds near harvest. In this year, the increased cost of even a minimal spray program exceeded the value of the increased yield in the sprayed versus unsprayed treatments (Table 3). Severe powdery mildew on the rachis has been presumed to result in berries dropping ahead of the mechanical harvester (T. Davenport, National Grape Cooperative, *personal communication*). We found little evidence to support this presumption. Indeed, on unsprayed vines in 3 of 4 years there was no significant relationship between the severity of powdery mildew and loss of fruit during harvesting.

Previous disease management recommendations for powdery mildew on Concord have sometimes reflected the perception that it is a late-season problem, and have both delayed fungicide applications beyond prebloom, and extended fungicide applications late into the growing season. However, our research has demonstrated that the level of fruit infection is determined early in the epidemic. The disease is most efficiently managed by targeting a limited number of fungicide applications at the peak period of fruit susceptibility, rather than a protracted program of multiple fungicide applications, without adequate protection when it is most critically needed.

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