Variation Within and Among *Vitis* spp. for Foliar Resistance to the Powdery Mildew Pathogen *Erysiphe necator*

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Abstract

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To complement existing control strategies, grape growers desire cultivars with resistance to powdery mildew caused by *Erysiphe necator*. Numerous disease resistance screens of diverse *Vitis* germplasm have been conducted previously to identify powdery mildew resistance but ratings of named cultivars were inconsistent and identities of resistant individuals in wild species were not typically provided. In the current study, controlled inoculations of a single isolate were made onto detached leaves from 1,025 *Vitis* accessions. The results were compared with natural epidemics in two vineyards: the cold-hardy *Vitis* spp. repository in Geneva, NY, in 2007–08, and a replicated vineyard of 89 *Vitis* accessions in Fredonia, NY in 2006–08. Of the genotypes screened using both natural infection and single-isolate inoculation, 33% were resistant to a single isolate but susceptible to diverse isolates in either or both vineyards, possibly due to race-specific resistance. This was exemplified by selection of *E. necator* genotypes virulent to *Vitis labrusca* in the Fredonia, NY vineyard, which is surrounded by

production of the interspecific *labrusca* hybrids Concord and Niagara. Otherwise, there was good correlation of ratings between the vineyard and single-isolate ratings ($r = 0.55$ to 0.56) and between Geneva and Fredonia vineyard ratings ($r = 0.75$). No accession rated in all three screens was immune from infection. Although individual accessions of *V. aestivalis*, *V. palmata*, *Vitis* × *doaniana*, and *Ampelopsis brevipedunculata* were resistant in Geneva and Fredonia, each well-represented species had notable intraspecific variation in resistance. For 129 interspecific hybrids in this and previous studies, ratings infrequently corresponded among previous studies (39%) and between the current and previous studies (17 to 46%). However, three cultivars (Cayuga White, Diana, and Mars) were consistently rated as resistant across four independent studies. The results underscore the importance of uniform testing in multiple environments and the need for strategies for the development of cultivars with durable resistance.

The powdery mildew pathogen *Erysiphe necator* (syn. *Uncinula necator*) infects green tissues of *Vitis* spp. everywhere grapevines are grown. Although comprising many of the highest quality grape cultivars, nearly all *Vitis vinifera* genotypes are susceptible to *E. necator*. As a result, growers rely on fungicides and cultural controls to manage powdery mildew on *V. vinifera*. *E. necator* is widely accepted to have originated on wild vines in eastern and central North America, and early researchers noted that wild North American *Vitis* spp. were significantly more resistant to powdery mildew than the European grape *V. vinifera* (12). As a result, grape breeders in the 1800s attempted to introduce genetic resistance from North American *Vitis* spp. into French cultivars, resulting in many *Vitis* interspecific “French-American” hybrids, such as Vignoles and Baco noir.

A major effort to isolate powdery mildew resistance genes and incorporate them into improved cultivars is currently being made by grape breeders and geneticists (1–5,9,11,13,14,26). The most common approach is a pseudo-backcross introgression of resistance from wild accessions into a series of *V. vinifera* recurrent parents known for high fruit quality (16). To this end, an array of genotypes representing dozens of cultivars and *Vitis* spp. has been

characterized for resistance to *E. necator* (6–8,15,17–19,21,24,25). However, most such projects involve uncharacterized populations of the pathogen with isolate presence and frequencies that may be quite different from year to year or from location to location. Further, generalizations are often made about the relative resistance or susceptibility of a species without regard to the variation of resistance within a species.

As a result, relative to more precisely characterized pathosystems such as barley powdery mildew, little is known about *E. necator* race structure, and only one study has directly demonstrated race specificity using diverse *E. necator* isolates (10). Nevertheless, anecdotal evidence for race specificity is more widely cited in *Vitis* spp., as described in a prior review by Roy and Ramming (19), and examples of conflicting ratings abound. For instance, the *Vitis* interspecific hybrid cv. Vidal blanc is reported to be highly resistant to powdery mildew in Germany (21), and yet is highly susceptible to powdery mildew in New York (27). The inconsistency of relative susceptibility is also temporal. For example, in New York vineyards, Dutchess was reported to be uninfected in 1945 (22) and moderately susceptible in 1987 (27), whereas Missouri Riesling was slightly infected (22) and extremely susceptible (27). Although these observations could be due to differential responses of resistance genes, thus far, only the *Run1* and *Ren1* loci of resistance gene analogues from *V. rotundifolia* and *V. vinifera*, respectively, have been directly associated with powdery mildew resistance in *Vitis* spp. (2,3).

All green tissues of *Vitis* spp. (berries, pedicels, rachises, shoots, leaves, and buds) can be infected by *E. necator*. Further, additional *Vitaceae* species can be infected by some isolates of *E. necator* (10). Still, resistant individuals have been identified even in the most susceptible *Vitis* spp. (3). Some of these resistance sources are tissue specific but most confer a similar level of resistance in all green tissues (7). Although the fungus can overwinter as mycelia in dormant buds in warmer climates, only ascospores in cleistothecia survive the winter in colder climates. A bipolar heterothallic

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mating system is required for cleistothecial initiation. The outcrossing necessary for surviving cold winters helps the pathogen overcome disease management strategies, with successful isolates rapidly propagated by polycyclic conidial infections, typically every 10 to 14 days.

Genetic resources for breeding for resistance and other traits are maintained by several international grapevine germplasm repositories and, in the United States, two United States Department of Agriculture–Agricultural Research Service (USDA-ARS) locations maintain a combined total of over 4,100 *Vitis* accessions (23). This material, freely available worldwide, has been widely used by grape breeders around the world and is maintained for future generations, providing a long-term reference population and genetic resource. Cold-sensitive species are among the major holdings at the National Clonal Germplasm Repository near Davis, CA, whereas the cold-hardy species, breeding lines, and interspecific hybrid cultivars are maintained at the Plant Genetic Resources Unit (PGRU) in Geneva, NY.

The objectives of this study were to characterize the variation in foliar resistance to powdery mildew within and among cold hardy *Vitis* spp. and to identify candidate accessions for race-specific resistance in the genus *Vitis*. This is the first comprehensive screen of the PGRU cold-hardy *Vitis* spp. collection for powdery mildew resistance.

Materials and Methods

Natural infection in Geneva, NY. Grapevines in the PGRU grape collection are maintained in the field as own-rooted vines at the McCarthy South vineyard, Geneva, NY. Each accession is represented by two adjacent, replicate, own-rooted vines planted with 1.8-m within-row spacing, cane pruned, and trained to the Umbrella Kniffin system using a three-wire trellis. Each accession has a unique plant introduction (PI) number listed in the USDA-ARS Germplasm Resources Information Network (GRIN) database (23). PI is linked with additional information related to that accession (<http://www.ars-grin.gov/npgs/index.html>), including species classification, which is presented here without revision. GRIN categorizes interspecific hybrids of *V. labrusca* and *V. vinifera* within either *V. labrusca* or *Vitis* hybrid.

The vineyard contains two blocks: the I1 block consists of clonally propagated cultivars, breeding lines, and wild species; and the W2 block consists of open-pollinated seedling populations collected from wild vines. Each year, standard production practices were followed for the Finger Lakes region, with vines being sprayed on a chemical rotation at 2-week intervals for the management of powdery mildew, downy mildew, and insects until mid-August, following which time late-season powdery mildew epidemics occurred. Chemicals applied included Rally, Captan, Pro-Phyt, Rubigan, Penncozeb, and Quintec. Disease ratings were recorded on 15 October 2007 and 24 September 2008, as described below.

Natural infection in Fredonia, NY. Eighty-nine accessions from 14 *Vitis* spp. and 35 interspecific hybrids were selected for vegetative propagation from the PGRU cold-hardy grape collec-

tion. Two- and three-year-old own-rooted grapevines were planted in an experimental vineyard at the Cornell Vineyard Lab in Fredonia, NY, in June 2005 with 1.8-m spacing between vines and in a randomized complete block design with five blocks. Standard production practices for insect, deer, and weed control were followed, but no fungicides were applied in 2006, 2007, and 2008. Disease severity ratings were recorded on 3 October 2006, 8 October 2007, and 22 September 2008. Disease severity was assessed in the vineyard by rating coverage on the adaxial surface of the most heavily infected leaf on a vine. Coverage was rated as the percentage of leaf area with powdery mildew mycelia in 10% increments and recorded on a 0-to-10 scale (0 = no visible mycelia and 10 = 100% coverage).

Detached-leaf single-isolate inoculations. Detached-leaf inoculations were completed during June to August 2006. A single-spored isolate of *E. necator* (isolate 10-18) was obtained from a Chardonnay plant in Dresden, NY (10 km south of Geneva, NY) in 2003. A single camel hair affixed to a Pasteur pipette was used to transfer a single conidial chain to a susceptible leaf, viewed under $\times 20$ magnification, and thereafter maintained by bulk transfer. Isolation, amplification, and maintenance of the isolate were done using surface-sterilized, detached leaves of Chardonnay seedlings maintained in 1% water agar petri dishes. For surface sterilization, leaves were submersed into calcium hypochlorite at 0.88 g liter⁻¹ for 2 min with agitation and then washed three times in sterile distilled water for at least 1 min each. To ensure use of a single isolate for this screen, in April 2006, a single conidial chain of isolate 10-18 was transferred. Fourteen days after transfer, a single conidial chain from the resulting colony was transferred to another sterile, detached leaf. The resulting colony, isolate 10-18-1, was amplified to produce inoculum for the germplasm screen. For inoculum increase, leaves with sporulating colonies were shaken in 40 ml of distilled water with 0.001% Tween 20 (Sigma-Aldrich, St. Louis) to form a spore suspension. The spore concentration was quantified with a hemacytometer and adjusted to approximately 10⁵ conidia/ml, and approximately 0.5 ml of the suspension was applied to susceptible detached leaves using a portable paint sprayer (Preval, Coal City, IL).

Leaves for the screen were collected from the McCarthy South vineyard described above. Twelve days after each biweekly fungicide spray application, replicate leaves were collected for the experiment, with tissue collection initiating a biweekly routine of protocols, until leaves from each accession were collected at least once for screening. In 2006, 1,025 accessions were inoculated using isolate 10-18-1. For each accession, resistance was characterized on the northern vine only of each pair, except when that vine was missing or damaged, in which case the other replicate vine was sampled. Two shoots were arbitrarily selected, and replicates of the fourth-youngest expanded leaf from each shoot were removed and placed into a flexible plastic compact disc (CD) sleeve labeled with the accession number. Each CD sleeve had nine holes punched into it to facilitate wetting during subsequent leaf sterilization and washing. Leaves were collected early in the day before air temperatures reached 29°C, placed over ice within 15 min

Table 1. Index used in the current study for rating powdery mildew sporulation at $\times 20$ magnification for detached *Vitis* leaves inoculated with *Erysiphe necator* isolate 10-18

Rating	Description
0	No conidiophores
1	Conidiophores without conidia
2	Two dozen conidiophores averaging one or fewer conidia each
3	Two dozen conidiophores averaging two to three conidia
4	Two to four dozen conidiophores averaging two to three conidia or two dozen conidiophores averaging four conidia
5	Densely packed conidiophores averaging two conidia or loosely spaced averaging three to four conidia
6	Densely packed conidiophores averaging three to four conidia
7	More than four dozen conidiophores averaging at least four conidia
8	More than four dozen conidiophores averaging at least five conidia
9	Densely packed lawn of conidiophores averaging more than five conidia
10	The entire colony is packed with conidial chains of six or more conidia

of collection, and maintained at 4 to 8°C until further sample processing within 24 h.

Leaves in CD sleeves were submersed into calcium hypochlorite at 0.88 g liter⁻¹ for 2 min with agitation and then washed three times in sterile distilled water for 5 min each. The leaves were removed from each CD sleeve and plated adaxial side up onto 100-by-15-mm petri dishes containing 18 ml of 1% water agar amended with natamycin (Haorui Pharma-Chem, Edison, NJ) at 0.01 g liter⁻¹. Each petri dish was prelabeled to track the accession, shoot replicate, and leaf age. Residual water was evaporated by removing the petri dish cover in a sterile laminar flow hood.

After preparation of a complete batch, inoculation was conducted using isolate 10-18-1. Spore suspensions were made as described above, and their concentration was adjusted to 5 × 10⁴ conidia ml⁻¹. Leaves were inoculated using a Preval sprayer and then placed in a 20 ± 2°C growth chamber with a 12-h photoperiod. Detached leaves were inspected for powdery mildew coverage and sporulation at 21 days post inoculation. Coverage was rated on the 0-to-10 scale described above, and sporulation for the most heavily sporulating colony on each leaf was rated on a 0-to-10 scale described in Table 1.

Data analysis. Analyses of variance (ANOVAs) were completed using SPSS 12 (Chicago). Correlation, descriptive statistics, Tukey's multiple comparisons, and hierarchical clustering analyses were completed using JMP 7.0.1 (SAS Institute, Cary, NC). Predictors included year, location, species, and leaf age with the random variable PI number for each accession and the response variables coverage or sporulation. ANOVA was used to compare "species" as a predictor. For cross-study comparisons, ratings were categorized as resistant, moderate, or susceptible as described in table footnotes. Ratings corresponded when an accession was rated in the same category in two studies. Correspondence was expressed as a percentage of the total comparisons made.

Results

Natural infection in Geneva, NY. In all, 1,009 *Vitis* accessions were rated for late-season powdery mildew severity in Geneva, NY. The mean severity was 5.2 in 2007 and 4.3 in 2008, with a range of

0 to 10 in each year. Species varied in their relative susceptibility. No infection was observed on accessions of *V. rotundifolia*, *Vitis* × *doaniana*, and *Ampelopsis brevipedunculata* (Table 2). The highest natural severity in Geneva was observed across accessions of *V. pseudoreticulata*, *V. vinifera*, and *V. coignetiae*.

Variation was also partitioned within species and between years. The intra- and interspecific variation in powdery mildew resistance for accessions of all well-represented species rated in the Geneva vineyard, using the same y-axis scale for each species, is depicted in Figure 1. Within-species variation was evident in all species represented by eight or more accessions (Fig. 1) as well as in *V. palmata* (five accessions) and *Vitis* × *champinii* (five accessions). Although all species had susceptible accessions, some had a greater proportion of accessions resistant to natural infection (e.g., *V. amurensis*) than did other species (e.g., *V. acerifolia*). To assess year-to-year variability, mean severity ratings for each accession were compared between 2007 and 2008, and 765 of the 926 accessions (83%) screened in both years had similar ratings (i.e., within 30% coverage). A majority (67%) of this discrepancy was due to higher severity in 2007, the year with higher mean severity.

Natural infection in Fredonia, NY. In total, 89 *Vitis* accessions were rated for natural powdery mildew severity in the vineyard. The overall mean severity was 5.2 in 2006, 4.6 in 2007, and 5.0 in 2008, with a range of 0 to 10 in each year. Species varied in their relative susceptibility (Table 2). Only PI 588271 (*V. riparia*) was completely free from infection in multiple years. The highest natural severity was observed across accessions of *Vitis* × *andersonii*, *V. labrusca*, and interspecific hybrids.

Variation was also partitioned within species and among years. Within-species variation was evident in *V. aestivalis*, *V. amurensis*, and *V. rupestris* (Table 3). To assess year-to-year variability, mean severity ratings for each accession were compared among the three years at Fredonia, and 305 of the 345 (88%) comparisons within accession between years had similar ratings (i.e., within 30% coverage). Surprisingly, most of this between-year disparity (68%) occurred due to lower disease severity in 2006, even though that was the year with the highest overall disease severity.

Table 2. Variation in *Erysiphe necator* colony coverage among *Vitaceae* spp. in natural vineyard infections and single-isolate detached leaf inoculations^y

<i>Vitaceae</i> spp. ^z	Geneva			Fredonia			Single-isolate inoculation		
	Cvg	Range	No.	Cvg	Range	No.	Cvg	Range	No.
<i>Vitis pseudoreticulata</i>	9.3 abc	8–10	2	ND	...	...	0.0 abcde	0–0	2
<i>V. vinifera</i>	7.8 a	0–10	22	ND	...	...	6.1 abc	0–10	22
<i>V. coignetiae</i>	6.3 abcd	4–8	6	4.2 abcd	0–9	1	6.7 a	0–9	6
<i>Vitis</i> hybrid	5.5 b	0–10	726	6.1 a	0–10	25	2.4 bcd	0–10	738
<i>Vitis</i> × <i>andersonii</i>	5.3 abcd	4–7	1	5.8 abcd	3–8	1	0.0 abcde	0–0	1
<i>Vitis</i> spp.	5.0 abcd	0–10	10	8.8 a	1–10	8	4.6 ab	0–10	11
<i>V. acerifolia</i>	4.4 bcd	0–9	13	4.9 abcd	2–9	5	0.7 cde	0–9	13
<i>Vitis</i> × <i>novae-angliae</i>	4.0 abcd	1–7	1	4.2 abcd	0–9	1	0.0 abcde	0–0	1
<i>V. vulpina</i>	3.5 bcd	0–8	13	4.0 d	3–5	1	3.5 bcde	0–7	13
<i>V. aestivalis</i>	3.1 bcd	0–8	8	4.0 bcd	0–10	3	0.8 bcde	0–3	8
<i>V. cinerea</i>	2.7 cd	0–8	31	2.8 d	0–5	4	0.1 e	0–2	32
<i>V. riparia</i>	2.7 cd	0–10	70	4.1 d	0–10	18	0.9 de	0–9	72
<i>V. amurensis</i>	2.4 cd	0–10	15	2.8 cd	0–9	2	0.5 de	0–6	15
<i>V. labrusca</i>	2.4 cd	0–10	44	5.5 abc	0–10	8	3.2 abcd	0–10	44
<i>V. rupestris</i>	2.2 cd	0–9	29	3.6 bcd	0–9	8	0.7 de	0–8	29
<i>Vitis</i> × <i>champinii</i>	1.8 bcd	0–7	5	ND	...	...	0.4 bcde	0–3	5
<i>V. palmata</i>	1.2 cd	0–6	5	2.3 d	0–8	2	1.3 abcde	0–6	5
<i>V. piasezkii</i>	0.3 bcd	0–1	2	ND	...	...	4.7 abcde	0–8	2
<i>Ampelopsis brevipedunculata</i>	0.0 abcd	0–0	1	1.3 d	0–5	1	6.5 abcde	3–10	1
<i>V. rotundifolia</i>	0.0 d	0–0	4	ND	...	...	0.0 bcde	0–0	4
<i>Vitis</i> × <i>doaniana</i>	0.0 abcd	0–0	1	1.1 d	0–7	1	0.0 abcde	0–0	1
Mean	4.9	...	...	4.8	...	...	2.3	...	...
Sum	...	...	1,009	...	...	89	...	...	1,025

^y Cvg = mean coverage (0 = 0%, 1 = 1 to 10%...10 = 100%), calculated by averaging all rated leaves for that category, based on natural infection of the most heavily infected leaf per vine in Geneva (2007–08) and Fredonia (2006–08) or on single-isolate inoculations with isolate 10-18-1 on detached leaves in 2006. Groupings with the same letter were not significantly different in Tukey's multiple comparisons analysis at $\alpha = 0.05$. Range = range of mean rating of each accession in a given species; No. = number of accessions rated; ND = no data, due to the vine not being planted.

^z Species listed for each accession, provided in the Germplasm Resources Information Network database (<http://www.ars-grin.gov/npgs/index.html>), sorted by Geneva coverage. *Vitis* interspecific hybrids are listed as *Vitis* hybrid. Unclassified species are listed as *Vitis* spp.

Detached-leaf single-isolate inoculations. The species with the highest mean severity across all tested accessions were *V. coignetiae*, *A. brevipedunculata*, and *V. vinifera* for coverage on the fourth leaf (Table 2). No infection was observed on accessions of five underrepresented species, and accessions of *V. cinerea* were typically resistant (Table 2). Within-species variation was pronounced in all species represented by eight or more accessions (Fig. 1) as well as in *V. palmata* (five accessions).

Correlation of natural and single-isolate powdery mildew severity. In all, 89 genotypes were tested for powdery mildew severity using both natural infection at two locations in New York State and single-isolate inoculation of detached leaves (Table 3). Thirty-two (33%) were resistant to single-isolate inoculation but at least moderately susceptible (mean vineyard severity ≥ 5) to naturally occurring isolates in at least one vineyard (Table 3). Of these 32 accessions, 5 (16%) plus 2 additional *V. labrusca* accessions had significantly less powdery mildew coverage in

Fig. 1. Powdery mildew coverage of well-represented *Vitis* spp. by accession following single-isolate inoculation of detached leaves or natural infection in the Geneva, NY repository vineyard. Along the x-axis, each accession has a filled bar depicting coverage of detached leaves next to an open bar depicting coverage in the vineyard. Due to the large number of interspecific hybrid accessions presented here ($n = 726$), the open bars are not visibly distinct from filled bars. Accessions are sorted from left to right based on coverage in the vineyard. The same 0-to-10 scale is used for all y-axes to enable cross-species comparisons. Interspecific hybrids and taxonomic species with eight or more rated accessions are depicted.

Geneva than in Fredonia (Table 3). The remaining accessions had moderate correlation between coverage on detached leaves and the mean vineyard rating for both Geneva ($r = 0.55$) and Fredonia ($r = 0.56$), and good correlation between Geneva and Fredonia ($r = 0.75$).

Correlation analysis was also conducted, including all data collected in these studies (Table 4). For detached leaf ratings, coverage was highly correlated with sporulation ($r = 0.91$; Table 4). Although there were strong correlations within location between years and moderately strong correlations between locations, detached-leaf ratings were not significantly correlated with field ratings (Table 4).

Cross-study comparison of ratings. For 129 interspecific hybrids previously screened for resistance and categorized as resistant, moderate, or susceptible, ratings infrequently corresponded among the previous studies (39%), between the previous studies and single-isolate inoculations (46%), between previous studies and current Geneva vineyard ratings (41%), and between previous studies and current Fredonia vineyard ratings (17%). As examples of the lack of concordance, named cultivars rated in at least two studies are summarized in Tables 5 and 6. Only three cultivars (Cayuga White, Diana, and Mars) with data from four independent studies were resistant in all four studies (Tables 5 and 6). For five accessions of wild species previously rated resistant (20), ratings

Table 3. Foliar powdery mildew coverage on accessions of *Vitis* spp. showing relative consistency of responses across pathogen sources

PI ^x	Accession name ^y	Vitaceae spp. ^z	Mean coverage (SD) ^w		
			Geneva	Fredonia	Single isolate
588592		<i>Ampelopsis brevipedunculata</i>	1.0 (n/a)	1.3 (1.9)	0
588442	GVIT780	<i>Vitis acerifolia</i>	0	3.9 (1.4)	0
588458		<i>V. acerifolia</i>	4.0 (n/a)	5.6 (2.1)	0*
588459		<i>V. acerifolia</i>	0.0 (n/a)	3.7 (2.1)	0
588459		<i>V. acerifolia</i>	0.0 (n/a)	3.8 (2.4)	0
588459		<i>V. acerifolia</i>	0.0 (n/a)*	5.6 (2.6)	0*
237621	Jaeger	<i>V. aestivalis</i>	6.5 (2.1)	7.8 (1.7)	0*
483130	Rem NE 4	<i>V. aestivalis</i>	1.5 (0.7)	0.9 (2.6)	0.8 (1.5)
483137	Rem 46-77	<i>V. aestivalis</i>	4.5 (0.7)	1.8 (2.3)	0
588382		<i>V. amurensis</i>	5.0 (7.1)	0.4 (0.7)	0*
588629		<i>V. amurensis</i>	6.5 (0.7)	3.3 (2.9)	0*
588634		<i>V. amurensis</i>	4.0 (0.0)	4.3 (3.1)	3.0 (4.2)
588186	Ill 58	<i>V. cinerea</i>	6.0 (n/a)	2.6 (1.8)	0*
588220	B 55	<i>V. cinerea</i>	4.0 (1.4)	2.8 (1.1)	0
588222	C-66-7	<i>V. cinerea</i>	3.0 (1.4)	2.8 (1.3)	0
588447		<i>V. cinerea</i>	4.0 (n/a)	1.7 (2.1)	0
588451		<i>V. coignetiae</i>	3.0 (n/a)	3.6 (2.5)	0
588128	Vergennes	<i>V. labrusca</i>	0*	5.9 (1.8)	0*
588145	GBC 12	<i>V. labrusca</i>	2.0 (2.8)	5.2 (1.8)	0*
588165	Alba	<i>V. labrusca</i>	0	3.0 (1.7)	0
588173	GBC 2	<i>V. labrusca</i>	1.5 (0.7)	4.9 (1.5)	3.5 (0.7)
588277	Jersey Muscat	<i>V. labrusca</i>	0.5 (0.7)	5.3 (1.4)	0*
588307	Champagne	<i>V. labrusca</i>	0.5 (0.7)*	5.5 (2.1)	5.5 (4.9)
588583	Grem-4	<i>V. labrusca</i>	6.0 (1.4)	5.7 (2.2)	8.5 (2.1)
588658	Lutie	<i>V. labrusca</i>	5.5 (0.7)	6.4 (1.6)	0*
594349	Alexander	<i>V. labrusca</i>	0	4.5 (2.0)	3.3 (5.8)
588201	GVIT239	<i>V. palmata</i>	1.5 (2.1)	3.3 (2.9)	1.5 (3.0)
588233	Cache 8	<i>V. palmata</i>	0.5 (0.7)	0.5 (0.8)	0
313922	Tarnau	<i>V. riparia</i>	3.0 (1.4)	3.2 (1.7)	0
495622		<i>V. riparia</i>	9.0 (0.0)	4.9 (3.2)	3.0 (4.2)
588054		<i>V. riparia</i>	2.5 (0.7)	5.1 (1.4)	3.5 (4.9)
588259	37	<i>V. riparia</i>	1.0 (n/a)	2.5 (2.5)	0
588262	89	<i>V. riparia</i>	1.5 (2.1)	3.3 (1.6)	0
588435	2F	<i>V. riparia</i>	5.5 (2.1)	4.2 (2.2)	0*
588438	GVIT774	<i>V. riparia</i>	1.5 (0.7)	1.9 (1.2)	0
588439	GVIT775	<i>V. riparia</i>	5.5 (3.5)	4.7 (2.5)	0*
588440		<i>V. riparia</i>	1.5 (2.1)	1.8 (1.8)	0
588450		<i>V. riparia</i>	5.0 (n/a)	5.7 (0.6)	0*
588453		<i>V. riparia</i>	0.0 (n/a)	2.6 (1.7)	0
588483	Rem NE 21	<i>V. riparia</i>	1.0 (1.4)	3.9 (2.8)	0
588565	Grem	<i>V. riparia</i>	7.5 (2.1)	4.4 (3.3)	0*
588587		<i>V. riparia</i>	0.0 (n/a)*	5.1 (1.9)	0*
588588		<i>V. riparia</i>	4.0 (n/a)	4.3 (2.2)	0
588590		<i>V. riparia</i>	0.0 (n/a)	3.3 (1.6)	0
588710		<i>V. riparia</i>	3.0 (n/a)	4.2 (2.5)	0
588710		<i>V. riparia</i>	3.0 (n/a)	5.2 (1.8)	0*

(continued on next page)

^w Mean and standard deviation (SD) of powdery mildew coverage (0 = 0%, 1 = 1–10%...10 = 100%), calculated by averaging all rated leaves for that category, based on natural infection of the most heavily infected leaf per vine in Geneva (2007–08) and Fredonia (2006–08) or on single-isolate inoculations with isolate 10-18-1 on detached leaves in 2006. Symbols: 0 indicates accessions with no infection observed across all replicates and n/a indicates the SD for unreplicated observations in the Geneva vineyard. Bold entries with an asterisk are resistant ratings when natural infection in one or both vineyards averaged at least five categories more susceptible; for detached leaves, due to lower average colonization, these are only highlighted when no infection was observed across all replicates.

^x PI = plant introduction number, a unique identifier for each accession in the Germplasm Resources Information Network (GRIN) database, where PI is linked with additional information related to that accession (<http://www.ars-grin.gov/npgs/index.html>). Lines with the same PI number (e.g., *V. acerifolia* 588459) are open-pollinated seedlings from the same mother vine.

^y Name listed for each accession, provided in the GRIN database. Accessions of wild species with GVIT numbers listed here were rated by Staudt (20) as resistant.

^z Species listed for each accession, provided in the GRIN database. *Vitis* interspecific hybrids are listed as *Vitis* hybrid. Unclassified species are listed as *Vitis* spp.

confirmed resistance in some screens (Table 3, accessions with GVIT numbers).

Discussion

Around the world, *Vitis* germplasm repositories provide an excellent resource for identifying and introgressing new sources of resistance. However, stringent pest management practices are typically followed until fruit harvest, limiting the approaches to obtaining resistance data that fully correspond with field ratings. In addition, field ratings for a given accession often vary from one study to another. Here, three approaches were applied for screening diverse accessions of cold-hardy *Vitis* spp. for resistance to *E. necator*—natural, late-season epidemics in the repository, natural infection in an unsprayed and replicated experimental vineyard, and single-isolate inoculations on detached leaves.

Our results support previous findings documenting the presence of race-specific resistance to *E. necator* (10), and suggest that race specificity could be widespread among resistant *Vitis* accessions.

Table 3. (continued from preceding page)

PI ^x	Accession name ^y	<i>Vitaceae</i> spp. ^z	Mean coverage (SD) ^w		
			Geneva	Fredonia	Single isolate
594344	Zumbrunnen	<i>V. riparia</i>	4.0 (1.4)	5.2 (2.3)	2.0 (2.8)
588146	R-66-4	<i>V. rupestris</i>	0*	5.3 (2.9)	0*
588160	B 38	<i>V. rupestris</i>	3.8 (4.6)	4.4 (1.1)	0
588223	R-65-43	<i>V. rupestris</i>	3.0 (2.8)	3.6 (2.5)	0
588224	R-65-44	<i>V. rupestris</i>	0.5 (0.7)	2.5 (1.4)	2.5 (0.7)
588335		<i>V. rupestris</i>	0	2.1 (1.8)	0
588454		<i>V. rupestris</i>	0.0 (n/a)	2.6 (1.9)	1.5 (2.1)
588454		<i>V. rupestris</i>	9.0 (n/a)	2.6 (1.6)*	0*
588454		<i>V. rupestris</i>	10.0 (n/a)	5.8 (3.7)	0*
588133	GBC 5	<i>V. vulpina</i>	5.0 (2.8)	3.9 (3.2)	1.5 (3.0)
588679		<i>V. vulpina</i>	7.0 (0.0)	1.1 (2.2)*	0*
588392		<i>Vitis</i> × <i>andersonii</i>	5.3 (2.5)	5.8 (1.7)	0*
588149	GVIT165	<i>Vitis</i> × <i>doaniana</i>	0	1.1 (2.2)	0
588257		<i>Vitis</i> × <i>novae-angliae</i>	4.0 (4.2)	4.2 (2.7)	0
588421		<i>V. yenshanensis</i>	10.0 (n/a)	8.9 (1.5)	3.0 (0.0)
588421		<i>V. yenshanensis</i>	10.0 (n/a)	9.2 (0.7)	1.5 (2.1)
588421		<i>V. yenshanensis</i>	10.0 (n/a)	9.6 (0.7)	5.0 (5.8)
588421		<i>V. yenshanensis</i>	10.0 (n/a)	9.6 (1.1)	5.0 (5.8)
588422		<i>V. yenshanensis</i>	5.0 (n/a)	8.2 (1.6)	0*
588422		<i>V. yenshanensis</i>	10.0 (n/a)	9.3 (0.8)	0.5 (1.0)
588650		<i>V. yenshanensis</i>	10.0 (n/a)	8.4 (1.6)	1.0 (1.4)
157518	Villard Blanc	<i>Vitis</i> hybrid	9.5 (0.7)	8.6 (1.5)	1.0 (2.0)
175494	Cascade	<i>Vitis</i> hybrid	4.5 (2.1)	9.0 (2.9)	0*
181481	Vignoles (Ravat 51)	<i>Vitis</i> hybrid	6.5 (2.1)	6.8 (1.6)	0.4 (0.9)
181642	Bertille Seyve 872	<i>Vitis</i> hybrid	8.5 (0.7)	9.6 (0.5)	1.0 (1.4)
279899	Kober 5BB	<i>Vitis</i> hybrid	2.0 (n/a)	3.4 (1.9)	0.5 (0.7)
588070	Catawba	<i>Vitis</i> hybrid	3.0 (2.8)	4.4 (2.8)	0
588077	Concord	<i>Vitis</i> hybrid	7.5 (0.7)	7.2 (2.1)	1.5 (2.1)
588078	Delaware	<i>Vitis</i> hybrid	8.0 (1.4)	6.2 (1.5)	0.8 (1.5)
588094	J.S. 23.416	<i>Vitis</i> hybrid	8.0 (1.4)	4.7 (2.2)	0*
588095	Himrod	<i>Vitis</i> hybrid	8.0 (0.0)	7.6 (1.5)	0*
588107	Marechal Foch	<i>Vitis</i> hybrid	6.0 (2.8)	8.1 (1.3)	0.5 (1.0)
588111	Golden Muscat	<i>Vitis</i> hybrid	6.5 (2.1)	6.3 (1.5)	0.1 (1.2)
588113	Steuben	<i>Vitis</i> hybrid	7.0 (2.8)	7.7 (1.2)	0*
588180	M.G. 101-14	<i>Vitis</i> hybrid	7.0 (2.8)	5.4 (2.4)	8.5 (2.1)
588196	Mills	<i>Vitis</i> hybrid	3.0 (0.0)	4.4 (1.8)	0
588234	Jaeger 70	<i>Vitis</i> hybrid	5.0 (0.0)	4.3 (2.3)	2.0 (2.8)
588279	Goethe	<i>Vitis</i> hybrid	8.5 (0.7)	8.9 (1.3)	0*
588303	Clinton	<i>Vitis</i> hybrid	7.0 (n/a)	6.6 (2.6)	0*
588315	Noah	<i>Vitis</i> hybrid	3.5 (0.7)	4.9 (2.8)	0
588319	Diana	<i>Vitis</i> hybrid	2.0 (2.8)	2.9 (1.4)	0.2 (0.4)
588327	Ill 547-1	<i>Vitis</i> hybrid	0.0 (n/a)	1.8 (2.2)	0
588397		<i>Vitis</i> hybrid	3.0 (n/a)*	8.2 (1.3)	0*
588405		<i>Vitis</i> hybrid	4.0 (n/a)	4.5 (3.0)	0
588419		<i>Vitis</i> hybrid	4.5 (0.7)	3.7 (1.4)	2.5 (3.5)
588488	NY 65.592.1	<i>Vitis</i> hybrid	2.0 (2.8)	6.1 (2.8)	0.8 (1.5)
588623	Taylor	<i>Vitis</i> hybrid	2.5 (2.1)	6.0 (1.7)	3.0 (0.0)
588627	7623	<i>Vitis</i> hybrid	6.8 (3.2)	7.3 (1.5)	7.0 (4.2)
588693	Ivan	<i>Vitis</i> hybrid	8.5 (0.7)	9.2 (1.0)	0*
594334	Baco noir (Baco 1)	<i>Vitis</i> hybrid	7.0 (1.4)	7.2 (1.8)	0*
594346	Karmrajut	<i>Vitis</i> hybrid	9.5 (0.7)	9.0 (2.2)	0*
Overall	...	...	4.2 (3.3)	5.0 (3.0)	2.7 (1.3)

Table 4. Correlation analysis of powdery mildew ratings following natural infection or single-isolate inoculations^z

Variable 1	Variable 2	Correlation (R)
Leaf sporulation	Leaf coverage	0.914
2008 Fredonia	2007 Fredonia	0.781
2008 Fredonia	2006 Fredonia	0.707
2007 Fredonia	2006 Fredonia	0.706
2008 Geneva	2007 Geneva	0.626
2008 Fredonia	2007 Geneva	0.554
2008 Fredonia	2008 Geneva	0.520
2007 Fredonia	2008 Geneva	0.452
2007 Fredonia	2007 Geneva	0.401
2006 Fredonia	2008 Geneva	0.347
2006 Fredonia	2007 Geneva	0.314

^z Based on powdery mildew coverage following natural infections in Geneva (2007 and 2008) or Fredonia (2006, 2007, and 2008) vineyards, or coverage or sporulation for detached leaves inoculated with a single isolate. Statistically nonsignificant comparisons with *P* values greater than 0.1 are not shown. Comparisons listed here were significant with *P* values less than 0.006.

Of the subset of accessions screened with all three approaches, many (33%) were resistant to the single isolate but susceptible in at least one of the vineyards, which could be due to a number of factors, including race specificity, environment, or inoculation protocol. Several accessions (9%) had differential responses between vineyards. For the remaining accessions, there was a reasonably good correlation between single isolate coverage on older leaves and vineyard ratings ($r = 0.55$ to 0.56). Given that one-third of the accessions resistant to a single isolate were susceptible in vineyards, and that accessions susceptible to artificial inoculation were frequently resistant in the vineyard (Fig. 1), there is little to be gained from artificial inoculation with a single isolate in a breeding selection program. However, for isolating, tracking, and pyramiding individual race-specific resistance genes, controlled inoculations with characterized isolates would be highly advantageous.

Nearly all *V. labrusca* accessions were resistant in Geneva, NY but susceptible in Fredonia, NY (Table 3). This is noteworthy because Fredonia (200 km from Geneva) is a center of production for Concord and Niagara, two interspecific hybrids with disease resistance introgressed from *V. labrusca*. This suggests that even within geographic regions, selection could occur for host adaptation, or virulence, on a local scale. This observation fits with findings of Gadoury and Pearson (10), who inoculated the labrusca hybrid Catawba with 46 *E. necator* isolates; their results revealed a differential ability to infect (qualitative) and colonize (quantitative) Catawba leaves (10), which could explain local selection for virulence.

A number of previous studies have screened diverse germplasm for resistance to grape powdery mildew, including studies focused primarily on interspecific hybrids, wild species, or both. In most of

Table 5. Powdery mildew resistance ratings for accessions of *Vitis* interspecific hybrids rated in Eibach (7) and in the current study

Plant ID ^y	PI ^y	Eibach ^z	Cadle-Davidson ^x	
			Geneva/Fredonia	Single isolate
Agawam	588211	S	S	S
Alden	588102	R	M	...
Alwood	588081	R	M	R
Atoka	588551	M	S	...
Baco noir (Baco 1)	594334	M	S/S	R
Bailey Alicante	588361	S	M	M
Bath	597101	R	M	S
Bertille Seyve 3408	597146	R	S	...
Bertille Seyve 4825	181646	M	M	R
Beta	588148	R	S	R
Bianca	597287	R	S	S
Black Eagle	597206	M	S	S
Bluestar	597211	R	M	R
Brighton	597201	M	R	...
Bronx Seedless	588126	S	S	...
Burdin 4672	597160	M	S	R
Canada Muscat	588080	R	M	...
Canadice (NY 45625)	588096	M	R	R
Cascade (Seibel 13.053)	175494	S	R/S	R
Century 1	597264	S	S	S
Chambourcin (J.S. 26.205)	588075	M	S	R
Chancellor (Seibel 7053)	588072	R	S	R
Chelois (Seibel 10.878)	588071	R	R	...
Colobel (Seibel 8357)	588062	R	S	R
Couderc Noir (Couderc 7120)	597143	R	M	...
Croton	597207	R	S	M
De Chaunac (Seibel 9549)	371984	M	S	R
Diana	588319	R	R/R	R
Dunkirk	597171	M	M	M
Florental (Burdin 7705)	256487	R	M	R
Glenora (NY 35814)	597100	M	R	...
Goff	597107	S	M	M
Golden Muscat	588111	M	M/M	M
Hanover	597113	R	M	...
Hector	597132	R	R	...
Herbert	588150	S	S	R
Himrod	588095	R	S/S	...
Interlaken	597241	S	S	...
Iona	588193	R	R	R
Joannes Seyve 23.416	588094	R	S/M	R
Karmrajut	594346	S	S	...
Lady Patricia	588089	R	S	M
Lakemont	588383	M	S	...
Landot 1678	597142	R	S	R
Leon Millot (Kuhlmann 194-2)	588112	S	M	R

(continued on next page)

^x Data from the current study. All interspecific hybrids shown here were rated in Geneva and, for the few that were rated in Fredonia, ratings are listed as "Geneva/Fredonia". For natural infection, ratings were categorized: below 3.5 = resistant (R); 3.5 to 5.4 = moderate (M); 5.5 or greater = susceptible (S); and no data = Single-isolate ratings were categorized based on the mean of all rated leaves as follows: below 2 = R; 2 to 5.4 = M; 5.5 or greater = S; and no data =

^y PI = Plant Introduction number, a unique identifier for each accession in the Germplasm Resources Information Network database, where PI is linked with additional information related to that accession, including a Plant ID (<http://www.ars-grin.gov/npgs/index.html>). A PI number has not yet been assigned to Roucaneuf (GVIT 1676).

^z Eibach (7) rated coverage of necrosis and mycelia from 1991 to 1993 on naturally infected vines in Geilweilerhof, Germany and reported the maximum degree of infection on a 1-to-9 scale. Here, ratings were categorized: 1 to 3 = R, 4 to 5 = M, 6 to 8 = S, and no data =

the studies involving wild species, a single accession was used to represent each wild species, and the identity of that accession was not provided, eliminating the possibility of cross-study comparisons. However, Staudt (20) screened leaf discs of multiple accessions per species, identified intraspecific variation, and provided identification for some of the accessions tested, allowing rating comparisons with the current data set. Although ratings of individual accessions corresponded well between that study and the current study (Table 3, accessions with GVIT numbers), species with only susceptible accessions in Staudt (20) frequently had some resistant accessions in the current study. For nearly all of the 135 cultivars screened in this and previous studies, ratings infrequently corresponded among previous studies (39%) and between the current and previous studies (17 to 46%). Among cultivars rated in the United States and elsewhere, Athens, Campbell Early, Cayuga

White, Diana, Iona, and Mars were the only cultivars consistently rated resistant in at least three studies, even though most of the cultivars listed (75%) were resistant in at least one study.

In the current study, extensive effort was spent precisely phenotyping sporulation under the microscope for thousands of leaves. However, coverage and sporulation were highly correlated ($r = 0.91$ to 0.92), suggesting that the effort required for rating sporulation provided little additional information.

Here, we showed that, whereas some *Vitis* spp. are, on average, more resistant than others, nearly all *Vitis* spp. have both resistant and susceptible accessions, and we provided additional evidence suggesting that pathogen genotype may affect resistance phenotype. In addition, for grape breeding programs interested in broad-spectrum resistance, the lack of correspondence between powdery mildew resistance screens highlights the importance of confirming

Table 5. (continued from preceding page)

Plant ID ^y	PI ^x	Eibach ^z	Cadle-Davidson ^x	
			Geneva/Fredonia	Single isolate
Marechal Joffre (Kuhlmann 187-1)	588254	R	M	M
Missouri Riesling	588285	R	S	M
Naples	597205	R	S	R
Noah	588315	M	M/M	R
Norwood	597263	R	S	...
Oberlin 604	279509	M	R	R
Othello	588310	R	S	M
Plantet (Seibel 5455)	588179	R	S	R
Price	588105	R	M	...
Ravat Blanc (Ravat 6)	588522	M	S	S
Reliance	597233	R	S	R
Romulus	597095	M	S	S
Roucaneuf	n/a	R	S	...
Schuyler	588099	R	S	R
Seibel 11.342	163512	R	S	M
Seibel 15.051	187218	M	M	...
Seibel 880	588314	R	S	R
Seneca	588076	S	M	...
Seyval (Seyve-Villard 5.276)	588309	R	M	R
Seyve-Villard 10.271	181605	R	R	...
Seyve-Villard 12.303	597138	R	S	...
Seyve-Villard 12.347	597272	R	S	R
Seyve-Villard 15.151	181624	R	M	...
Seyve-Villard 23.512	181639	S	S	R
Seyve-Villard 26.166	597290	M	M	...
Seyve-Villard 28-86	597288	R	S	M
Seyve-Villard 34.211	588702	M	S	...
Seyve-Villard 5.247	181603	R	M	R
Sheridan	588171	S	M	R
Sovereign Charter	588469	R	...	S
Sovereign Coronation	588086	M	S	M
Sovereign Noir	588471	R	M	R
Sovereign Rose	588470	R	R	S
Sovereign Tiara	588468	S	S	M
Stepnyak	594345	R	R	S
Stout Seedless	597204	S	S	M
Suffolk Red	597242	R	S	M
Taylor	588623	M	R/M	M
Telegraph	597099	M	R	M
Totmur (Baco 2-16)	188597	R	S	M
Valerien (Seyve-Villard 23.410)	181632	M	S	S
Valiant	588266	S	R	R
Vanessa Seedless	588288	M	S	M
Veeblanc	597181	S	S	R
Ventura	588066	R	R	S
Venus	597243	M	M	M
Vergennes (<i>V. labrusca</i>)	588128	R	R/M	R
Vignoles (Ravat 51)	181481	R	S/S	R
Vincent	588108	S	S	...
Vinered	588093	S	R	S
Vivant	597231	M	S	...
Watkins (NY7588)	588695	R	S	R
Wayne	597122	M	R	S
Westfield	588131	M	M	M
Yates	588114	M	S	S

Table 6. Powdery mildew resistance ratings for named cultivars of *Vitis* spp. screened in at least two studies¹

Plant ID ^w	PI ^w	Cadle-Davidson ^u			Eibach ^v		Roy ^x	Suit ^y	Other ^z
		Geneva	Fredonia	Single	1994	1989			
Athens	588158	R	...	R	...	...	...	...	R
AxRno. 1	588092	R	...	R	...	...	M	...	...
Bacchus	588297	M	...	R	...	...	S	...	...
Baco blanc	312797	S	...	...	M	R	...	...	...
Baroque	588326	M	...	M	...	...	R	...	...
Campbell Early	588122	R	...	...	R	...	...	...	R
Castel 19.637	188582	S	...	R	...	R	...	...	...
Catawba	588070	M	M	R	R	...	M	M	R
Cayuga White	588079	R	...	R	R	...	R	...	...
Clinton	588303	...	S	R	...	...	R	R	...
Concord	588077	S	S	R	M	...	M	S	R
Delaware	588078	S	S	M	M	...	M	R	...
Dutchess	588109	M	...	S	R	...	M	R	...
Elvira	588298	R	...	...	R	...	M	R	...
Fredonia	597098	M	...	S	...	...	M	M	...
Isabella	588207	R	M	...	S	...	...	...	R
Ives	588110	R	...	M	...	...	R	R	...
Marechal Foch	588107	M	S	R	R	R	...	...	Var
Mars	597234	R	...	R	R	...	R	...	...
Niabell	597275	S	...	...	...	...	R	...	...
Niagara	588106	S	R	S	M	...	M	M	R
Riesling (white)	588673	S	...	...	...	S	M	...	S
Rkaziteli	588177	M	...	...	...	...	R	...	R
Rosette	588290	S	...	...	M	...	S	...	...
Steuben	588113	M	...	...	M	...	R	...	...
Vidal Blanc (Vidal 256)	200684	R	...	M	R	R	...	...	...
Villard blanc	157518	S	S	...	R	...	...	...	M
Villard noir	588291	S	...	M	R	...	...	...	M

¹ For all studies, ... denotes no data.

^u Data from the current study. For natural infection, ratings were categorized: below 3.5 = resistant (R), 3.5 to 5.4 = moderate (M), and 5.5 or greater = susceptible (S). Single-isolate (Single) ratings were categorized based on the mean of all rated leaves as follows: below 2 = R, 2 to 5.4 = M, and 5.5 or greater = S.

^v Eibach (7) rated coverage of necrosis and mycelia from 1991 to 1993 on naturally infected vines in Geilweilerhof, Germany and reported the maximum degree of infection on a 1-to-9 scale. Here, ratings were categorized: 1 to 3 = R, 4 to 5 = M, and 6 to 9 = S. Eibach et al. (8) used an inverse scale to rate inoculated leaves, here categorized as 1 to 3 = S, 4 to 5 = M, and 6 to 9 = R.

^w PI = Plant Introduction number, a unique identifier for each accession in the Germplasm Resources Information Network database, where PI is linked with additional information related to that accession, including a Plant ID (<http://www.ars-grin.gov/npgs/index.html>).

^x Roy and Ramming (19) reviewed the literature and categorized resistance into five classes: significantly resistant (R), moderately resistant and two intermediate classes (M), and significantly susceptible (S).

^y Suit (22) rated natural infections in grower vineyards across New York State from 1940 to 1944, and provided ratings on relative susceptibility. Ratings were categorized here as follows: 0 = R, + = M, and +++ = S.

^z Patil et al. (15) reported summaries of natural infections occurring in a vineyard in Hol (Pune), Maharashtra, India from 1982 to 1988. Only R accessions were reported, including Athens, Catawba, Concord, Isabella, and Rkaziteli. Doster and Schatnorst (6) inoculated cuttings in a growth chamber and monitored latent period at 20°C. Cultivars that did not allow sporulation within the nine day duration of the experiment are listed here as R, including Concord and Niagara. Stein et al. (21) evaluated resistance to powdery mildew on artificially inoculated leaves and leaf discs from the vineyard or greenhouse and ranked cultivars from most susceptible to most resistant. Riesling was consistently among the six most susceptible (S), and Marechal Foch was variable (Var), being among the six most resistant or the six intermediate, depending on experiment. Peros et al. (18) inoculated detached leaves with conidial droplets and measured incidence of infection and colony diameter by leaf age. Villard blanc and Villard noir were intermediate (M) in susceptibility relative to S (Cabernet Sauvignon) and R (Jacquez) checks. Wan et al. (24) evaluated resistance to natural infections in a vineyard in Yangling, Shaanxi, China, from 2001 to 2003, identifying individuals as highly resistant, resistant (R; Campbell Early), susceptible, and highly susceptible.

resistance across multiple geographic regions with the use of uniform testing procedures. In most cases, when considering cultivar development and release, the possible threat of virulent isolates justifies the pyramiding of multiple resistance genes and the use of complementary control tactics to protect resistance gene efficacy.

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