Variation Within and Between *Vitis* spp. for Foliar Resistance to the Downy Mildew Pathogen *Plasmopara viticola*

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ABSTRACT

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To complement existing control strategies, grape growers in humid climates desire cultivars with resistance to downy mildew caused by *Plasmopara viticola*. Numerous disease resistance screens of diverse *Vitis* germplasm have been conducted previously to identify downy mildew resistance; however, ratings of named cultivars were inconsistent and identities of resistant individuals in wild species were not typically provided. Inconsistencies among previous studies could be due to race-specific resistance. In the current study, controlled inoculations of two single isolates onto two leaf ages of 883 *Vitis* accessions were used and these results compared with natural infection in a fivefold replicated vineyard of 80 *Vitis* accessions in 2006 and 2007. Of the accessions rated in both assays, 16.2% were resistant to a single isolate but susceptible in the vineyard. Otherwise, there was good correlation of ratings between the field assay and the rating of older leaves ($r = 0.62$ to 0.71). Five accessions from *Vitis cinerea*, *V. labrusca*, and *Vitis × champinii* averaged zero severity in both vineyard years, yet some individuals of *V. cinerea* and *V. labrusca* were moderately or highly susceptible in the field. Similarly, although significant differences in mean severity separated *V. vinifera*, *Vitis* hybrid, *V. riparia*, and *V. labrusca* for single-isolate inoculations (from susceptible to resistant), notable intraspecific variation was identified for all well-represented species. Resistant individuals were identified in most species with the prominent exceptions of *V. vinifera* and *V. acerifolia*. Single-isolate, detached-leaf resistance ratings in 2006 corresponded well (94.6%) to 2007 ratings using a separate isolate collected from the same vineyard. Categorizing the ratings for this and previous studies, ratings infrequently corresponded among previous studies (31.9%) as well as between previous studies and the current single-isolate (34.9%) or vineyard (46.4%) ratings. These results highlight important factors for downy mildew resistance screens: leaf age, pathogen genotype, and host species and accession. The results further underscore the importance to breeders of uniform testing in multiple environments.

Vitis vinifera grapevines are highly susceptible to downy mildew caused by the host-specific oomycete *Plasmopara viticola*. In humid climates like New York, where the unchecked pathogen will defoliate vines and destroy young fruit clusters, growers depend upon multiple fungicide applications for disease management. However, management of *P. viticola* by fungicides is tenuous, because the pathogen has repeatedly overcome a broad range of previously effective fungicides (9). To complement chemical disease control (31) and predictive models (13), disease-resistant interspecific hybrids have been developed to combine disease resistance with the production of high-quality fruit (1). Molecular markers associated with

some downy mildew resistance genes have been identified to facilitate additional introgression of resistance (7,8,17,30).

Numerous germplasm screens have been conducted in *Vitis* spp. to identify accessions resistant to downy mildew (3,5,6,18–20,23,25,26,29). In those studies that screened multiple accessions per species, variation in resistance was identified not only between but also sometimes within species (10,26,29). In spite of these findings, *Vitis* spp. are often generalized as being more or less resistant without characterizing the resistance of accessions within each species (5,6,18,19,21,25). Some cultivars were screened in multiple studies and their resistance ratings frequently failed to match. For example, *Vitis* hybrid ‘Athens’ was rated resistant (19), moderately susceptible (5), and susceptible (3,25), and *Vitis* hybrid ‘Isabella’ was rated resistant (3,19), moderately resistant (6), moderately susceptible (5), and susceptible (25). These results highlight the need to control environment and pathogen source in grape downy mildew resistance screens and to ensure cultivar identity. However, one cultivar, *Vitis* hybrid ‘Concord,’ was consistently resistant (6,19) or moderately

resistant (3) across studies and, thus, appears to have durable, broad-spectrum resistance.

Given the long lifespan of grapevines in commercial vineyards and the high cost of their establishment, durable disease resistance is a desirable trait for cultivars. Race-specific resistance has been shown in other host-specific downy mildew pathosystems, including lettuce (32), *Arabidopsis* (11), and sunflower (24), and this form of resistance has been shown to be overcome by virulent isolates in each pathosystem. Although race-specific resistance has not previously been demonstrated in *Vitis* spp., isolates of *P. viticola* vary in their quantitative virulence on different cultivars of *Vitis* (12).

Novel sources and mechanisms of disease resistance can be found among the genetically diverse accessions maintained by grapevine germplasm repositories (22). There are a number of repositories around the world 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. *V. vinifera* and cold-sensitive species are among the major holdings at the National Clonal Germplasm Repository near Davis, CA, whereas the cold-hardy species are maintained at the Plant Genetic Resources Unit (PGRU) in Geneva, NY.

One limitation of screening for disease resistance in a *Vitis* germplasm repository is that the accessions are maintained as living grapevines, and the health status of the vines is critical to their long-term preservation. Therefore, screening for resistance in the repository vineyard is not routinely possible. In this study, two methods were tested for screening diverse accessions of *Vitis* spp. for resistance to downy mildew. In the first, a subset of the cold-hardy germplasm collection was vegetatively propagated, established in a vineyard, and natural epidemics of downy mildew were allowed to progress. In the second screen, leaves were directly collected from the germplasm repository, surface sterilized, and inoculated in petri dishes using a single isolate.

MATERIALS AND METHODS

Plant material for natural infection in the vineyard. In all, 80 accessions from 14 *Vitis* spp. and 35 interspecific hybrids were selected for vegetative propagation

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Table 1. Downy mildew severity on accessions of *Vitis* species for natural infections in 2006 and 2007 and for two developmental stages of detached leaves inoculated with a single isolate

PI ^w	Accession name ^x	<i>Vitis</i> spp. ^y	Average disease severity ^v			
			2006 Vineyard	2007 Vineyard	Younger leaf	Older leaf
588442		<i>V. acerifolia</i>	6	3	0	5
237621	Jaeger	<i>V. aestivalis</i>	3	4	5	4
483130	Rem NE 4	<i>V. aestivalis</i>	4	5	0	7
483137	Rem 46-77	<i>V. aestivalis</i>	0	1	0	2
588382		<i>V. amurensis</i>	2	0	nd	nd
588629		<i>V. amurensis</i>	2	0	nd	0
588634		<i>V. amurensis</i>	4	0	nd	0
588186	Ill 58	<i>V. cinerea</i>	3	1	0	0
588210	B 65-7	<i>V. cinerea</i>	2	0	nd	8
588220	B 55	<i>V. cinerea</i>	0	0	0	0
588222	C-66-7	<i>V. cinerea</i>	0	0	0	0
N/A	44-53M	<i>Vitis</i> hybrid	1	3	2	2
N/A	Schwarzmann	<i>Vitis</i> hybrid	3	7	2	4
157518	Villard Blanc (Seyve-Villard 12.375)	<i>Vitis</i> hybrid	0	1	nd	nd
175494	Cascade (Seibel 13.053)	<i>Vitis</i> hybrid	5	6	2	1*
181481	Vignoles (Ravat 51)	<i>Vitis</i> hybrid	6	8	7	7
181642	Bertille Seyve 872	<i>Vitis</i> hybrid	2	7	6	5
279899	Kober 5BB	<i>Vitis</i> hybrid	4	5	2	2
313922	Tarnau	<i>Vitis</i> hybrid	0	5	0	3
588070	Catawba	<i>Vitis</i> hybrid	6	3	0*	0*
588078	Delaware	<i>Vitis</i> hybrid	7	9	0*	0*
588094	Joannes Seyve 23.416	<i>Vitis</i> hybrid	3	9	2	4
588095	Himrod	<i>Vitis</i> hybrid	6	7	nd	4
588107	Marechal Foch (Kuhlmann 188-2)	<i>Vitis</i> hybrid	5	3	5	3
588111	Golden Muscat	<i>Vitis</i> hybrid	5	6	4	5
588113	Steuben	<i>Vitis</i> hybrid	7	3	nd	6
588180	Millardet et de Grasset 101-14	<i>Vitis</i> hybrid	3	2	2	3
588196	Mills	<i>Vitis</i> hybrid	7	5	0*	0*
588207	Isabella	<i>Vitis</i> hybrid	6	4	nd	nd
588234	Jaeger 70	<i>Vitis</i> hybrid	3	2	nd	nd
588279	Goethe	<i>Vitis</i> hybrid	5	8	nd	nd
588303	Clinton	<i>Vitis</i> hybrid	0	6	nd	6
588315	Noah	<i>Vitis</i> hybrid	4	5	0	7
588319	Diana	<i>Vitis</i> hybrid	5	4	0	3
588327	Ill 547-1	<i>Vitis</i> hybrid	3	1	0	0
588397		<i>Vitis</i> hybrid	4	2	3	3
588405		<i>Vitis</i> hybrid	4	7	4	3
588419		<i>Vitis</i> hybrid	4	3	0*	0*
588488	NY 65.592.1	<i>Vitis</i> hybrid	0	4	7	4
588623	Taylor	<i>Vitis</i> hybrid	6	10	0	5
588627	7623	<i>Vitis</i> hybrid	6	8	0	4
588693	Ivan	<i>Vitis</i> hybrid	6	5	1	6
594334	Baco Noir (Baco 1)	<i>Vitis</i> hybrid	8	8	8	4
594336	Seibel 29	<i>Vitis</i> hybrid	7	6	5	3
594346	Karmrajut	<i>Vitis</i> hybrid	nd	9	3	7
594349	Alexander	<i>Vitis</i> hybrid	4	7	0*	1*
588128	Vergennes	<i>V. labrusca</i>	6	6	2	1*
588145	GBC 12	<i>V. labrusca</i>	0	0	0	0
588165	Alba	<i>V. labrusca</i>	2	0	0	0
588173	GBC 2	<i>V. labrusca</i>	2	1	0	0
588277	Jersey Muscat	<i>V. labrusca</i>	0	0	0	1
588307	Champagne	<i>V. labrusca</i>	2	0	0	0
588583	Grem-4	<i>V. labrusca</i>	2	0	nd	0
588658	Lutie	<i>V. labrusca</i>	2	1	nd	3
588201	...	<i>V. palmata</i>	3	1	1	3
588233	Cache 8	<i>V. palmata</i>	2	1	1	1
588054	Iowa 7	<i>V. riparia</i>	1	4	1	4
588259	37	<i>V. riparia</i>	6	4	0*	0*
588262	89	<i>V. riparia</i>	5	6	0	4
588435	2F	<i>V. riparia</i>	6	3	1*	0*
588438	...	<i>V. riparia</i>	4	1	0	1

(continued on next page)

^v Average severity of downy mildew across all replicates was rated in 2006 and 2007 for each accession naturally infected in the vineyard, and in 2006 and 2007 for each accession artificially inoculated with two isolates for younger and older leaves. Older leaves were the fourth fully expanded leaf in each year whereas younger leaves were the second fully-expanded leaf in 2006 only; nd = not determined due to all replicate leaves dying prior to disease ratings and * denotes instances of low severity on detached leaves where that same accession was susceptible to natural inoculum.

^w 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>). N/A: Schwarzmann and 44-53M do not have PI numbers and are not distributed by ARS-PGRU but are widely available as commercial rootstocks.

^x Name listed for each accession, provided in the GRIN database.

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

^z Overall averages were calculated based on ratings for each leaf rated.

Table 1. (continued from preceding page)

PI ^w	Accession name ^x	Vitis spp. ^y	Average disease severity ^z			
			2006 Vineyard	2007 Vineyard	Younger leaf	Older leaf
588439	...	<i>V. riparia</i>	2	2	0	3
588440	...	<i>V. riparia</i>	4	1	0	2
588483	Rem NE 21	<i>V. riparia</i>	3	6	0	3
588565	Grem	<i>V. riparia</i>	1	3	1	2
594344	Zumbrunnen	<i>V. riparia</i>	3	4	0	3
594348	C-166-043	<i>V. romanetii</i>	0	10	nd	1*
588146	R-66-4	<i>V. rupestris</i>	1	2	0	2
588160	B 38	<i>V. rupestris</i>	nd	2	0	1
588223	R-65-43	<i>V. rupestris</i>	0	1	0	4
588224	R-65-44	<i>V. rupestris</i>	2	1	0	3
588335	...	<i>V. rupestris</i>	3	2	7	6
588454	...	<i>V. rupestris</i>	4	6	nd	0*
588133	GBC 5	<i>V. vulpina</i>	4	4	3	5
588142	GBC 28	<i>V. vulpina</i>	0	1	1	4
588679	...	<i>V. vulpina</i>	1	0	1	1
588392	...	<i>Vitis</i> × <i>andersonii</i>	2	3	0	5
588371	...	<i>Vitis</i> × <i>champinii</i>	0	0	nd	nd
588149	...	<i>Vitis</i> × <i>doaniana</i>	2	0	0	3
588257	...	<i>Vitis</i> × <i>novae-angliae</i>	7	6	0	3
Overall averages ^z	...	...	3.2	3.5	1.4	2.2

from the USDA-ARS, PGRU cold-hardy grape collection. Two- and three-year-old, own-rooted grapevines were planted in an experimental vineyard in Fredonia, NY, in June 2005 with 1.8-m spacing between vines and with five replicate blocks in a randomized complete block design. Standard production practices for insect, deer, and weed control were followed but no fungicides were applied in 2006 and 2007.

Plant material for single-isolate inoculation of detached leaves. Grapevines in the USDA-ARS, 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 using a three-wire trellis, cane-pruned and trained to the Umbrella Kniffin system. Each accession has a unique plant introduction (PI) number listed in the USDA-ARS Germplasm Resources Information Network (GRIN) database (28). Each year, standard production practices were followed for the Finger Lakes region, with vines being sprayed at 2-week intervals for the management of downy mildew and powdery mildew.

Downy mildew isolation. *P. viticola* isolates Pv05-01 and Pv07-03 were isolated from a prebloom cluster of *Vitis* hybrid 'Chancellor' collected in June 2005 and 2007, respectively, at the Robbins farm, Geneva, NY. Sporulation was induced from the epinastic cluster by incubating it overnight in a moist chamber. A single sporangioaphore branch was transferred by forceps to a 10- μ l water droplet on the abaxial surface of a surface-sterilized, detached leaf of a *V. vinifera* 'Riesling' seedling placed on 1% water agar. A single sporangioaphore branch from the resulting lesion was again transferred to produce each isolate. Inoculum was

subsequently maintained on leaves of Riesling or *V. vinifera* 'Chardonnay' seedlings by bulk transfer every 6 to 14 days. Sporangia were collected from the leaf surface by spraying with distilled water and collecting the spore suspension in a vessel. The suspension was adjusted to 5×10^4 sporangia/ml and sprayed onto surface-sterilized, detached leaves.

Leaf collection for single-isolate inoculations. Twelve days after each bi-weekly fungicide spray application, replicate leaves were collected for the experiment, with tissue collection initiating a biweekly routine of protocols. In 2006, 883 accessions were inoculated with Pv05-01 and, in 2007, a subset of 205 accessions was inoculated with Pv07-03 to confirm results. 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 second and fourth fully expanded leaves (2006) or the fourth leaf (2007) from each shoot were removed, stacked in a standard order, 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 of collection, and maintained at 4 to 8°C until further sample processing within 24 h.

Surface sterilization, plating, and inoculation. Leaves in CD sleeves were submersed into calcium hypochlorite at 0.88 g/liter 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, still in their

original stacking order, and plated abaxial 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. Each petri dish was prelabeled to track the accession, shoot replicate, and leaf age. Residual water was removed from each leaf surface using a sterile Kimwipe (Kimberly Clark, Dallas).

After preparation of a complete batch, inoculation was conducted using isolate Pv05-01 or Pv07-03. Spore suspensions were made as described above and concentration adjusted to 5×10^4 sporangia/ml. Leaves were inoculated by bulk transfer, then placed into a dark $20 \pm 2^\circ\text{C}$ growth chamber overnight. The leaf surface was once again dried with a sterile Kimwipe and petri dishes were placed in a $20 \pm 2^\circ\text{C}$ growth chamber with a 12-h photoperiod.

Downy mildew disease ratings and statistical analyses. Detached leaves were inspected at up to $\times 10$ magnification for downy mildew sporulation at 9 days post inoculation. Sporulation was rated based on the percentage of leaf area with visible sporangia in 10% increments and recorded on a 0-to-10 scale, where 0 = no visible sporangia and 10 = 100% coverage. For field ratings, disease severity was rated based on the most heavily sporulating leaf for a given vine, which was typically within 0.5 m of the ground, using the same 0-to-10 scale. Correlation coefficients for accessions tested in the vineyard and fourth-leaf, single-isolate assays were calculated for disease severity using Mini-tab 15 (State College, PA). Tukey's multiple comparisons analysis was used to compare relative susceptibility of species for the fourth-leaf, single-isolate severity data, based on a mixed model in JMP 7 (SAS Institute, Cary, NC). Predictors included "year" and "species," with the ran-

dom variable “PI” for each accession and the response variable “severity.” Species represented by more than three accessions were included in the model. To compare younger and older leaves, a mixed model

with the same response variable and predictors was used in addition to the predictor “leaf age,” and each predictor was significant at $P < 0.0001$ in both models. For cross-study comparisons, ratings were

categorized as resistant (R), moderate (M), or susceptible (S). Ratings corresponded when an accession was rated in the exact same category in two studies. Correspondence was expressed as a percentage of the total comparisons made.

Fig. 1. Correlation of downy mildew severity ratings, comparing single isolate inoculations (x-axis) to natural infection in a vineyard (y-axis). Twelve of the accessions were resistant (average severity <1.5) to the single-isolate inoculation but at least moderately susceptible (average severity ≥ 2.5) to naturally occurring isolates in the vineyard and are plotted separately (gray square). A single accession of *Vitis cinerea* (PI 588210) was highly resistant in the vineyard but susceptible to detached-leaf inoculation (open triangle). The R^2 value and regression formula with forced-zero intercept are based on the remaining data points (filled rhombus).

RESULTS

Variation in natural downy mildew severity within and between *Vitis* spp. Eighty *Vitis* accessions were rated for natural downy mildew severity in a no-spray vineyard. The average severity in 2006 was 3.2, with a range of 0 to 8; in 2007, it was 3.5, with a range of 0 to 10. The frequency of escapes (no disease on an entire susceptible vine) was estimated. Of the moderately susceptible and susceptible accessions (average severity ≥ 2.5), no sporulating downy mildew was detected for 44 of 326 (13.5%) replicate vines.

Species varied in their relative susceptibility. The lowest natural severity was observed across accessions of *V. cinerea* and in *Vitis* $\times$ *champinii* (Table 1), which is thought to be a natural hybrid of *V. rupestris* and *V. candicans*. Only three accessions (PI 588220, 588222, and 588371), two of *V. cinerea* and one of *Vitis* $\times$ *champinii*, were completely free from downy mildew sporulation on all vines in both years; in addition, two accessions of *V. labrusca* (PI 588145 and 588277) averaged zero severity in both years. The highest natural severity was observed across

Table 2. Variation in resistance to downy mildew within and between *Vitis* spp., as quantified by inoculation of detached leaves with a single isolate of *Plasmopara viticola*^a

<i>Vitis</i> spp. ^w	Younger leaves ^a			Older leaves ^v		
	Avg. severity ^x	Range ^y	No. rated ^z	Avg. severity ^x	Range ^y	No. rated ^z
<i>V. vinifera</i>	4.7	1.5–8.0	13	5.5 a	0.0–6.5	17
<i>Vitis</i> $\times$ <i>andersonii</i>	0.0	0.0–0.0	1	4.5 –	4.5–4.5	1
<i>Vitis</i> hybrid	2.1	0.0–9.3	565	3.3 b	0.0–9.0	617
<i>V. acerifolia</i>	1.3	0.0–5.0	11	3.3 bc	0.5–5.0	12
<i>Vitis</i> $\times$ <i>doaniana</i>	0.0	0.0–0.0	1	3.0 –	3.0–3.0	1
<i>Vitis</i> $\times$ <i>novae-angliae</i>	0.0	0.0–0.0	1	3.0 –	3.0–3.0	1
<i>V. piasezkii</i>	3.0	1.0–5.0	2	2.8 –	1.5–4.0	2
<i>V. riparia</i>	0.9	0.0–6.5	61	2.5 c	0.0–7.0	61
<i>Vitis</i> spp.	1.5	0.0–5.5	18	2.4 c	0.0–6.5	24
<i>V. rupestris</i>	1.9	0.0–7.0	27	2.3 cd	0.0–5.5	27
<i>V. palmata</i>	0.7	0.0–2.0	5	2.0 bcd	0.0–3.5	5
<i>Vitis</i> $\times$ <i>champinii</i>	1.8	0.0–3.0	3	2.0 –	0.0–4.0	3
<i>V. aestivalis</i>	0.7	0.0–4.5	8	1.5 cd	0.0–6.5	8
<i>Ampelopsis</i>	1.0	1.0–1.0	1	1.5 –	1.5–1.5	1
<i>V. vulpina</i>	1.0	0.0–4.0	14	1.4 cd	0.0–5.0	14
<i>V. amurensis</i>	1.5	0.0–7.0	11	1.1 cd	0.0–5.0	12
<i>V. coignetiae</i>	0.0	0.0–0.0	4	1.1 bcd	0.0–5.5	5
<i>V. cinerea</i>	0.1	0.0–1.5	28	0.8 d	0.0–7.5	30
<i>V. labrusca</i>	0.3	0.0–8.5	40	0.5 d	0.0–5.5	42
Grand total	1.8	0.0–9.3	814	2.9	0.0–9.0	883

^a Species are listed in order of decreasing severity ratings on older leaves. For fourth-leaf data, Tukey’s multiple comparisons analysis was used; groupings with the same letter were not significantly different at $\alpha = 0.05$. Species represented by three or fewer accessions were not included in the analysis and are denoted by –.

^b Includes the second fully expanded leaf in 2006.

^c Includes the fourth fully expanded leaf in 2006 and 2007.

^d Species listed for each accession, provided in the Germplasm Resources Information Network database (<http://www.ars-grin.gov/npgs/index.html>). *Vitis* interspecific hybrids are listed as *Vitis* hybrid. One accession of *Ampelopsis brevipedunculata*, a relative of *Vitis* in the Vitaceae, was included in the study.

^e Average disease severity, calculated by averaging all rated leaves for that category.

^f Range of average severity of each accession in a given species.

^g Number of accessions rated. The discrepancy between numbers rated for younger and older leaves is due to higher mortality of younger leaves in petri dishes.

accessions of interspecific hybrids as well as in *V. acerifolia* and in *Vitis* × *novae-angliae*, considered to be the spontaneous hybrid of *V. labrusca* and *V. riparia*. Three interspecific hybrids (PI 588078, 588623, and 594334) were consistently susceptible, with leaf samples of every vine in both years rated 5 or higher.

Variation was also partitioned within species and between years. Within species, variation was pronounced in all species represented by five or more accessions (*V. labrusca*, *V. riparia*, and *V. rupestris*) as well as in *V. aestivalis* (three accessions) and *V. vulpina* (three accessions) (Table 1). To assess year-to-year variability, average severity ratings for each accession were compared between 2006 and 2007, and 68 of the 78 accessions screened in both years had similar ratings (within three gradations). In all cases but two, this between-year disparity occurred due to higher disease severity in 2007.

Correlation of natural and single-isolate, detached-leaf downy mildew severity. Eighty accessions were tested for downy mildew severity using both natural infection and inoculation of detached leaves. For six of the accessions, all detached-leaf replicates died before rating; leaves of these accessions died on the water agar media whether inoculated or not. Of the remaining 74 accessions, 12 (16.2%) were resistant (average single-isolate severity <1.5) to the single-isolate inoculation but at least moderately susceptible (average vineyard severity ≥2.5) to naturally occurring isolates in the vineyard (Table 1; Fig. 1). The remaining accessions

had moderate correlation between disease severity on younger detached leaves and the average vineyard rating across both years ($r = 0.37$) and good correlation between disease severity on older detached leaves and the average vineyard rating across both years ($r = 0.62$). One accession (*V. cinerea*, PI 588210) was highly resistant in the vineyard (average severity = 0.7) but susceptible to detached-leaf inoculation (average severity = 7.5); removal of this outlier resulted in a correlation of $r = 0.71$.

For the same 74 accessions, the frequency of escapes (no disease on susceptible accessions) was estimated for the fourth leaf. Of the moderately susceptible accessions (average severity ≥1.5 in the single isolate screen), 17 of 115 (14.8%) inoculated leaves had no sporulating downy mildew. Therefore, these estimates suggest that a susceptible accession could escape infection on two replicate leaves, but likely at rates less than approximately

2.2% (0.148×0.148); with four replicate leaves, approximately 1 in every 2,000 susceptible accessions would escape infection.

Variation in single-isolate downy mildew severity within and between *Vitis* spp. Detached-leaf screening was repeated in 2007 with a new isolate for a subset of arbitrarily selected accessions to assess reproducibility of results. Ratings were consistent (within three gradations) with those from 2006 for 194 of 205 (94.6%) accessions. All discrepancies resulted from higher disease severity ratings in 2006. The frequency of escapes for the fourth leaf on all moderately susceptible accessions was 171 of 1,222 (14.0%), similar to the escape frequency calculated for the correlation subset above (14.8%).

The species with the highest average severity across all tested accessions was *V. vinifera* whereas the lowest severity was observed across accessions of *V. labrusca*, *V. cinerea*, and *V. coignetiae* (Table 2). *V. vinifera*, *Vitis* hybrid, *V. riparia*, and *V.*

Table 3. Number of resistant accessions identified within species for this study (C-D) and Staudt and Kassemeyer (26)

Species	Proportion of accessions resistant (resistant/total)	
	Staudt ^y	C-D ^z
<i>Vitis acerifolia</i>	0/10	0/11
<i>V. aestivalis</i>	0/13	5/8
<i>V. amurensis</i>	0/2	5/11
<i>Vitis</i> × <i>champinii</i>	0/5	1/3
<i>V. cinerea</i>	3/7	21/28
<i>Vitis</i> × <i>doaniana</i>	1/5	0/1
<i>V. palmata</i>	1/5	2/5
<i>V. riparia</i>	1/2	14/61
<i>V. rupestris</i>	0/3	9/27
<i>V. vulpina</i>	0/9	9/14
<i>Vitis</i> hybrid	0/8	119/565

^y As provided in Table 1 of Staudt and Kassemeyer (26), with *V. solonis* being grouped with *V. acerifolia* and *V. rubra* with *V. palmata* here. Sevenfold replicated leaf discs were inoculated with a population (H. H. Kassemeyer, *personal communication*) of *Plasmopara viticola* collected in Freiburg, Germany. Resistant accessions, defined by the lack of sporangioophores at 5 days post inoculation, were listed.

^z Data from the current study, based on average disease severity for accessions inoculated with a single-isolate. Any accession with severity <1.5 on both second and fourth fully expanded leaves was categorized as resistant.

Fig. 2. Downy mildew severity for well-represented species by accession and leaf age. For each accession along the x-axis, filled bars representing younger leaves (second fully expanded leaf in 2006) are coupled with open bars representing older leaves (fourth fully expanded leaf in 2006 and 2007). Accessions are sorted from left to right based on disease severity of older leaves. Interspecific hybrids and taxonomic species with eight or more rated accessions are depicted here.

labrusca anchored four significantly different categories, ranging from most susceptible to most resistant, respectively (Table 2). However, significant within-species variation was observed for most species (Table 3). For example, some accessions of *V. vinifera* repeatedly had low disease severity with little or no sporulation, and some accessions of *V. labrusca* and *V. cinerea* were highly susceptible, with some of the most severe sporulation observed (Table 2; Fig. 2). In fact, with the exception of *V. vinifera* and *V. acerifolia*, for each the 14 species with at least three accessions screened there were accessions that had no sporulation on any replicate leaves (Fig. 2). Therefore, *V. labrusca* and *V. cinerea* had the lowest average disease severity of the species not only because they comprised resistant accessions but also because most of the accessions in these species were resistant (Table 2).

Age-related resistance. Two ages of leaves were rated in the single-isolate resistance screen in petri dishes. In 2006, second fully expanded leaves frequently died (379 of 2,052) prior to downy mildew rating compared with fourth leaves (44 of 2,052). Because of high mortality of the second leaf in petri dishes, only fourth fully expanded leaves were inoculated in

2007. On average across all accessions tested, the increased susceptibility of older leaves (average severity = 2.9) relative to younger leaves (1.8) was highly significant ($P < 0.0001$; Table 2). This was exemplified by *V. acerifolia*, *V. cinerea*, *V. hybrid*, and *V. riparia*. Once again, however, this generalization was not true for all accessions, some of which appeared to have more susceptible younger leaves (e.g., PI 588488 and 588334; Table 1).

Cross-study comparison of ratings. For 64 named cultivars and 25 accessions of wild species previously screened for resistance and categorized as resistant, moderate, or susceptible, ratings infrequently corresponded among the previous studies (31.9%), between the previous studies and single-isolate inoculations (34.9%), between previous studies and current vineyard ratings (46.4%), and between previous studies and all current data (37.3%). As examples of the lack of concordance, named cultivars rated in at least three studies are summarized in Table 4, and data for all accessions of wild species tested in multiple studies are provided in Table 5.

DISCUSSION

Around the world, *Vitis* germplasm repositories provide an excellent resource for

identifying and introgressing new sources of resistance. However, aside from allowing epidemics to develop in the repository and compromise grapevine health and survival, there are no simple approaches to screening for resistance that fully correspond with field ratings. In addition, field ratings for a given accession often vary from one study to another. Here, two approaches were applied for screening diverse accessions of cold-hardy *Vitis* spp. for resistance to grape downy mildew: natural infection in a replicated, experimental vineyard and single-isolate inoculations on detached leaves. Of the subset that was screened with both approaches, several accessions (16.2%) were resistant to the single isolate but susceptible in the vineyard. For the remaining accessions, there was a reasonably good correlation between single-isolate inoculations of older leaves and vineyard ratings ($r = 0.62$ to 0.71). This suggests that preliminary screens to identify resistant accessions could be conducted on detached leaves and these results subsequently confirmed in more natural conditions.

A number of studies have tested and applied various strategies for quantifying resistance to *P. viticola*, including dual-culturing of the pathogen with in vitro

Table 4. Downy mildew resistance ratings for named cultivars of *Vitis* species screened in at least three studies

Cultivar	PI ^s	C-D ^t	Brown ^u	Datar ^v	Demaree ^w	Patil ^x	Sohi ^y	Wan ^z
Concord	588077	R/–	M	...	R	R	...	...
Lomanto	588172	R/–	M	...	S	...	...	...
Westfield	588131	R/–	M	M	...	...	M	...
Athens	588158	R/–	S	M	...	R	S	...
Catawba	588070	R/S	...	...	S	R	...	...
Lutie	588658	M/R	R	...	R	...	...	...
Diamond	588120	M/–	M	...	R	...	...	...
Ontario	588074	M/–	M	...	S	...	...	...
Cottage	588576	M/–	R	...	R	...	...	...
Ives	588110	M/–	M	...	M	...	...	...
Clinton	588303	S/M	M	...	R	...	...	...
Brighton	597201	S/–	M	...	S	...	...	...
America	588119	S/–	M	...	R	...	...	...
Suelter	588256	S/–	M	...	R	...	...	...
Loretto	588659	S/–	R	...	R	...	...	...
Manito	588302	S/–	S	...	R	...	...	...
Captivator	588159	S/–	S	...	S	...	...	...
St. George	588331	S/–	...	...	...	R	R	...
Goethe	588279	–/S	M	M	M	R	...	...
Isabella	588207	–/S	R	M	M	R	S	...
Campbell Early	588122	...	M	...	S	...	...	R

^s 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 (<http://www.ars-grin.gov/npgs/index.html>).

^t Data from the current study (C-D = Cadle-Davidson), with the rating of the fourth detached leaf given first and that for natural infection listed second. Ratings were categorized for detached leaves as follows: less than 1.5 = resistant (R); from 1.5 to 3.4 = moderate (M); 3.5 or greater = susceptible (S); and no data = –. For natural infection, ratings were categorized as follows: less than 2.5 = R; from 2.5 to 4.4 = M; 4.5 or greater = S; and no data = –.

^u Brown et al. (3) provided ratings of resistant (R), moderately resistant (M), and susceptible (S) from natural infection in a fourfold replicated vineyard in Clarksville, AR. Data were presented for 2 years; here, the more susceptible rating of the 2 years is provided.

^v Datar (5) inoculated grapevines in a fivefold replicated vineyard in Parbhani, Maharashtra, India from 1979 to 1981 and identified resistant (R) and moderately susceptible (M) individuals.

^w Demaree et al. (6) allowed natural infection to occur in a vineyard in Washington, D.C. in 1937 and provided ratings on percent coverage of sporulation. Ratings were categorized as follows: 10% or less = resistant (R), 15–30% = moderate (M), and more than 30% = susceptible (S).

^x Patil et al. (18,19) reported summaries of natural infections occurring in a vineyard in Hol (Pune), Maharashtra, India from 1982 to 1988. Only resistant (R) accessions were reported.

^y Sohi and Sridhar (25) in Hessarghatta, Mysore, India in 1969 observed natural infection on up to 20 vines per accession and summarized ratings as resistant (R), moderately susceptible (M), susceptible (S), and highly susceptible (S).

^z Wan et al. (29) evaluated resistance to natural infections in a vineyard in Yangling, Shaanxi, China, from 2001 to 2003, identifying individuals as highly resistant, resistant (R), susceptible, and highly susceptible.

plantlets (2), inoculation of single-node cuttings (16), or inoculation of detached leaf discs (4,27). One detailed study compared artificial inoculation of leaf discs or greenhouse plants with natural infections in a nursery vineyard, using ratings for sporulation, chlorosis, and necrosis (4). Sporulation ratings of leaf discs and vineyard plants correlated well ($r = 0.47$ to 0.67), similar to the current study. In addition, sporulation following artificial inoculations (leaf discs or greenhouse) correlated better with all vineyard ratings than necrosis or chlorosis did (4). Another study confirmed the correlation of leaf disc ratings with those in the vineyard or greenhouse but cited higher disease severity for leaf discs of some resistant accessions (27).

A number of previous studies have screened diverse germplasm for resistance to grapevine downy mildew, including studies focused primarily on interspecific hybrids (5,6), wild species (10,26), or both (3,18,19). In most of 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 and Kassemeyer (26) screened leaf discs of multiple accessions per species, identified intraspecific variation, and provided identification for some of the accessions tested, enabling ratings comparisons with the current data set. In both that study and the current study, no resistance was identified in *V. acerifolia*, and resistant accessions were most frequently identified in *V. cinerea*. For nearly all of the 89 cultivars screened in this and previous studies, ratings infrequently corresponded among previous studies (31.9%) and between the current and previous studies (37.3%). For cultivars rated in the United States and abroad, *Vitis* hybrid Concord remains the only cultivar consistently resistant (6,19) or moderately resistant (3), suggesting a broad-spectrum, durable foliar resistance rarely found in cultivated *Vitis* spp.

For the remaining accessions, the effect of pathogen source on resistance ratings could reflect genetic variation in *P. viticola* for overcoming race-specific resistance, which is indirectly supported by data in the current study. Of the 74 accessions (16.2%) rated for both natural and single-isolate resistance, 12 were resistant to single-isolate inoculation but at least moderately susceptible to naturally occurring, virulent isolates in the vineyard (Table 1; Fig. 1). An individual detached leaf could have no disease severity either by being resistant or by randomly failed inoculation (an escape). Individuals at least moderately susceptible did escape infection in the detached-leaf screen on 14.8% of inoculated leaves. At this escape rate, detached leaves would randomly escape infection on two, three, or four leaves with a frequency

of 2.0, 0.32, or 0.04%, respectively. These 12 accessions with putative race-specific resistance were rated on an average of 2.9 replicate leaves; thus, the lack of disease severity in these individuals was much more likely due to resistance against the single isolates screened rather than escapes.

One accession of *V. cinerea* (PI 588210) was highly resistant in the vineyard (average severity = 0.7) but susceptible to detached-leaf inoculation (average severity = 7.5). Hydrophobic leaf hairs of *V. cinerea* and other wild species reduce access of water droplets harboring downy mildew sporangia to stomatal infection sites (14). Although the identity of accessions used in

that study was not provided, when the leaf hair defense was overcome by addition of a detergent, other resistance factors prevented colonization in *V. cinerea* (15). Secondary resistance factors were similarly present in an accession of *V. labrusca* but not in accessions of *V. davidii* or *Vitis* × *doaniana*, which were susceptible when detergents were used to bypass leaf hairs (15). If the physical force of our spray inoculation of detached leaves allowed the sporangia to bypass leaf hairs, this suggests that PI 588210 and moderately susceptible *Vitis* × *doaniana* PI 588149 lack additional resistance factors present in other accessions of *V. cinerea* and *V. labrusca* in Table 1. These results imply that

Table 5. Downy mildew resistance ratings for accessions of wild *Vitis* spp. screened in multiple locations

Species, PI ^w	Accession name ^x	Previous study ^y	Previous rating	Cadle-Davidson ^z
<i>Vitis acerifolia</i>				
318684	...	Brown	M	S/–
588378	...	Brown	M	M/–
588144	...	Staudt	R	S/–
<i>Vitis</i> × <i>andersonii</i>				
588392	...	Brown	M	S/M
<i>Vitis</i> × <i>champinii</i>				
483190	...	Brown	R	M/–
<i>V. cinerea</i>				
588205		Brown	M	S/–
588134	Ill 45	Staudt	R	R/–
588154	B 9	Staudt	R	R/–
588217	B 27	Staudt	R	R/–
597232	Ill 23	Staudt	R	R/–
<i>Vitis</i> × <i>doaniana</i>				
588149	...	Brown	S	M/R
588149	...	Staudt	R	M/R
<i>V. labrusca</i>				
588182	GBC 17	Brown	M	R/–
483133	Rem NE 19	Staudt	R	R/–
<i>V. palmata</i>				
588201	...	Brown	M	M/R
588201	...	Staudt	R	M/R
588155	RU-66-10	Staudt	R	S/–
<i>V. riparia</i>				
588262	89	Brown	S	S/S
483181	Rem NE 22	Staudt	R	S/–
<i>V. rupestris</i>				
588160	B 38	Brown	S	R/R
<i>V. thunbergii</i>				
588452	...	Brown	R	–/R
<i>Vitis</i> sp.				
588282	...	Brown	R	M/–
<i>V. vulpina</i>				
483184	Rem 29-77	Staudt	R	R/–
<i>V. yenshanensis</i>				
588421	...	Brown	S	S/S

^wPI = 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>). Two accessions (588149 and 588201) were rated in all three studies.

^xName listed for each accession, provided in the GRIN database.

^yBrown et al. (3) provided ratings of resistant (R), moderately resistant (M), and susceptible (S) from natural infection in a fourfold replicated vineyard in Clarksville, AR. Data were presented for 2 years; here, the more susceptible rating of the 2 years is provided. Staudt and Kassemeyer (26) inoculated sevenfold replicated leaf discs with a population (H. H. Kassemeyer, *personal communication*) of *Plasmopara viticola* collected in Freiburg, Germany and listed resistant (R) accessions, defined by the lack of sporangioophores at 4 days post inoculation.

^zData from the current study with the rating of the fourth detached leaf given first and that for natural infection listed second. Ratings were categorized for detached leaves as follows: less than 1.5 = resistant (R), from 1.5 to 3.4 = moderate (M), 3.5 or greater = susceptible (S), and no data = –. For natural infection, ratings were categorized as follows: less than 2.5 = R, from 2.5 to 4.4 = M, 4.5 or greater = S, and no data = –.

other accessions of these species susceptible to single-isolate inoculations may be resistant to natural infection in the vineyard.

Data from the current study highlight important factors for downy mildew resistance screens: the fourth fully expanded leaf corresponds well with vineyard ratings; pathogen genotype may affect resistance phenotype; and, although some *Vitis* spp. may be more resistant than others on average, most *Vitis* spp. have both resistant and susceptible accessions. In addition, for grape breeding programs interested in broad-spectrum resistance, the lack of correspondence between downy mildew resistance screens highlights the importance of confirming resistance across multiple geographic regions with the use of uniform testing procedures.

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