Evaluation of Host Resistance to Botrytis Bunch Rot in *Vitis* spp. and Its Correlation with Botrytis Leaf Spot

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Additional index words. disease resistance, cultivar evaluation, *Botrytis cinerea*, grape

Abstract. *Botrytis cinerea*, the causal agent of Botrytis bunch rot and gray mold, is the number one postharvest disease of fresh grapes in the United States. Fungicide applications are used to manage the disease, but fungicide-resistant isolates are common and postharvest losses occur annually. Host resistance is needed for long-term management of the disease. Sources of resistance in grape have been identified, but often have poor fruit quality. In this study, 27 grape lines (cultigens and species), including high fruit-quality *Vitis vinifera*, were evaluated for fruit and leaf susceptibility to two isolates of *B. cinerea*. No significant differences in virulence or pathogenicity were detected between the two isolates, but differences in disease incidence were evident among lines in leaves and berries. Most *V. vinifera* cultivars evaluated had high disease incidence in berries, whereas complex hybrids, *Vitis aestivalis* and *Vitis arizonica*, had low- to moderate disease incidence. Two *V. vinifera* breeding lines had moderate susceptibility (<50% disease) to Botrytis bunch rot when inoculated with either isolate. Only one *V. vinifera* line had little (<5%) to no berry or leaf disease when inoculated with either isolate. Moderate resistance (10% to 25%) was detected in *Vitis* spp., and a single *V. vinifera* line. Correlations were examined among soluble solids, leaf susceptibility, and fruit susceptibility. No correlations between soluble solids and disease susceptibility (leaves or berries) were identified, but moderate correlations between leaf and berry susceptibility were observed. Moderate resistance to Botrytis bunch rot and leaf spot were detected in *Vitis* breeding lines, suggesting these may be useful for developing grape cultivars with high fruit quality and resistance to *B. cinerea*.

Botrytis cinerea is a generalist necrotrophic fungus capable of infecting more than 200 species of plants (Droby and Lichter, 2007). In *Vitis* spp., *B. cinerea* can incite bunch rot, also known as gray mold, in addition to cane and leaf spot. Annual losses caused by *Botrytis* can range from 10% to 44% (pre- and postharvest), with most loss occurring postharvest (Droby and Lichter, 2007; Reglinski et al., 2010). Disease management requires regular applications of fungicides to minimize reductions in yield and quality, in addition to cultural practices, such as canopy thinning. Heavy use of fungicides has contributed to the development of resistance in

Botrytis in vineyards around the world (Hahn, 2014; Panebianco et al., 2015; Rupp et al., 2017). Chemical rotation or reducing the number of applications can slow, but not prevent, the development of resistant individuals. *Botrytis*-resistant grape cultivars are needed to complement chemical practices to develop a comprehensive management system.

Botrytis-resistant cultivars are presently unavailable for many fruit, ornamental, and vegetable growers (Bestfleisch et al., 2015; Reisch et al., 2014; Smith et al., 2014). The same genome plasticity that contributes to rapid development of fungicide resistance likely requires a multilayer system for the host to maintain *Botrytis* resistance. *Vitis vinifera*, the cultivated grape species grown for its high-quality berries, is highly susceptible to *Botrytis*. Resistance to *Botrytis* has been identified in closely related *Vitis* spp., including *Vitis labrusca*, *Vitis lincecumii*, and *Vitis rotundifolia*. These species are important sources of resistance to various abiotic and biotic stresses, but lack desirable fruit quality characteristics found in *V. vinifera*.

Studies have evaluated physical, chemical, morphological, and genetic components contributing to *Botrytis* resistance in *Vitis* (Deytieux-Belleau et al., 2009; Gabler et al., 2003; Herzog et al., 2015; Kulakiotu et al., 2004; Renault et al., 2000; Trotel-Aziz et al., 2006). Gabler et al. (2003) determined that the number of surface pores on berries

was negatively correlated with resistance. In contrast, cuticle and wax content, as well as the number and thickness of epidermal and hypodermal cell layers were weakly positively correlated with resistance. This is consistent with later work that found *Botrytis* resistance to be associated with thicker skins and high levels of epicuticular waxes, both of which are undesirable characteristics for commercial cultivars (Deytieux-Belleau et al., 2009; Herzog et al., 2015). Other evidence has suggested that aromatic volatiles produced by *V. labrusca* accessions reduce pathogenicity and spore production of *B. cinerea* (Kulakiotu et al., 2004). Although resistant materials have been identified, accessions that harbor resistance often have poor fruit quality or flavors that are not commercially desirable.

Besides potential linkage with poor commercial traits, host resistance can be further complicated by isolate- or tissue-specific interactions. Isolate-specific or line-by-isolate interactions have been reported in some, but not all, *B. cinerea*-host systems (Rowe and Kliebenstein, 2008; Zhang et al., 2016). The diverse arsenal of virulence factors produced by *Botrytis* make it likely that resistance in grape would be a function of isolate-specific and general resistance components similar to those observed in *Arabidopsis* and tomato (Finkers et al., 2007; Rowe and Kliebenstein, 2008). Previous laboratory-based studies have evaluated *Vitis* spp. against single or mixed isolates, neglecting potential isolate-specific interactions or responses by the host.

Tissue-specific resistance has not been reported in other *Botrytis*-host systems, but is an important consideration when breeding. The use of leaf evaluations as an early indicator of fruit susceptibility could be useful for evaluating perennial crops with a long generation time, such as grape. In strawberry, leaf disk evaluations were found to have a high correlation with field susceptibility to *Botrytis*-induced fruit rot (Olcott-Reid et al., 1993). No studies to date have looked at relationships between *Botrytis* bunch rot and leaf spot in grape. However, gene expression varied between leaf and berry tissue when inoculated with *B. cinerea*, which may indicate tissue-specific response in grape (Bézier et al., 2002).

Although previous studies have identified sources of resistance and physiochemical factors associated with resistance, information is needed on tissue and isolate-specific resistance in grape. Here, research objectives were to 1) determine the isolate-specific susceptibility of grape accessions, including high-quality *V. vinifera*, to two isolates of *Botrytis* 2) and evaluate the correlation among susceptibility of grape berries and leaves and soluble solids between two *Botrytis* isolates.

Materials and Methods

Plant material and isolates. Twenty-seven lines (cultivars and breeding lines), and species maintained at the USDA ARS

Received for publication 26 Oct. 2017. Accepted for publication 15 Dec. 2017.

We thank Cameron Saunders, Marcos Alvarez, and Jeff DeLong for technical assistance, and Chang Lin Xiao for providing the *Botrytis cinerea* isolate (449) from grape.

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San Joaquin Valley Agricultural Science Center (SJVASC), were evaluated for resistance to *B. cinerea* (Table 1). Two isolates of *B. cinerea*, 16-23 and 449, collected from California were used in this study. Isolate 16-23 was collected from apricot in 2016. Isolate 449 (collected in 2012 from grape) was donated courtesy of Dr. C.L. Xiao (USDA ARS SJVASC). Before the experiment, ‘Scarlet Royal’ berries were surface disinfested with a 10% bleach solution (0.2625% sodium hypochlorite) for 5 min, rinsed with reverse osmosis (RO) water, and placed into a humidity chamber. The berries were wounded and inoculated with an individual isolate to ensure virulence of each isolate before cultivar evaluations. The pathogen was reisolated from diseased ‘Scarlet Royal’ berries onto 1/2 strength potato dextrose agar (PDA) (BD Diagnostics/Difco Laboratories, Inc., Sparks, MD) and used for subsequent inoculations. The isolates were maintained in the laboratory on 1/2 strength PDA under constant light at 25 °C on 100-mm petri dishes (Thermo Fisher Scientific Inc., Waltham, MA).

Inoculations. Grape clusters (soluble solid content $\geq 14\%$ with the exception of PS08-108) were harvested from the vineyard and stored in a cold room (4 °C) until evaluation. Individual berries without blemishes were cut from the rachis of each cultivar, leaving the pedicel attached. Berries were surface

disinfested with a 10% bleach solution for 5 min and rinsed with RO water. Unwounded berries were placed onto metal racks and placed in metal bins inside of clear plastic bags. A thin layer of water was added to the bottom of each metal bin to maintain humidity to promote infection. Spore suspensions for each isolate were made from 7- to 12-d-old colonies. For each plate, 6 mL of sterile H₂O were added and spores were gently dislodged using a cell spreader. The resulting suspension was filtered through six layers of sterile cheesecloth. Spore concentration was calculated with a hemacytometer and suspensions were diluted to 1×10^5 spores/mL. The resulting suspensions or water controls were applied to grape berries using a misting spray bottle until berry surface was covered with droplets. Berries were maintained in the laboratory at 25 °C. Berries were evaluated 5 d after inoculation for symptoms and signs. Ten individual grapes were used for each replication, with three replication evaluated per isolate per cultivar. Disease score was expressed as the percentage of berries showing symptoms or signs of bunch rot in each replication. About 20% of berries were used for isolations on 1/2 strength PDA to confirm the presence of the pathogen. The experiment, performed twice (Run 1 and Run 2), was a completely randomized design and blocked by treatment. Secondary contamination from *Rhizopus* was prevalent in some

cultigens, and those experimental runs with high *Rhizopus* incidence were removed from analyses.

Lines evaluated for fruit resistance were also evaluated using leaf assays to determine correlations between fruit and foliar resistance. Immature grape leaves of a similar age and size (about the S4 stage) were collected from field-grown vines and returned to the laboratory (Chitwood et al., 2016). Leaves were immersed for 30 s in a 10% bleach solution, rinsed in RO water, and air-dried. Leaves were placed onto damp paper towels on a screen rack in aluminum trays containing a thin layer of water. Spore suspensions of isolates 449 and 16-23 were made from 10- to 12-d-old cultures as described previously. Spore suspensions or water controls were applied to the surface of each leaf using a misting spray bottle. Trays with leaves were placed into sealed plastic bags to maintain humidity. Leaves were maintained in the laboratory at 25 °C and evaluated 7 d postinoculation for signs of *B. cinerea*. Three individual leaves were used for each replication, with two replications evaluated per isolate per cultivar. Disease score was expressed as the percentage of leaves showing signs of *B. cinerea*. About 66% of symptomatic and asymptomatic leaves were used for isolations onto 1/2 strength PDA to confirm the presence or absence of the pathogen. The experiment, performed twice,

Table 1. Mean berry and leaf disease incidence for *Vitis* lines inoculated with one of two isolates of *Botrytis cinerea* (16-23 and 449) on berries and leaves in laboratory studies.

Identifier ^a	Species ^b	Soluble solids (%) ^c	Berry disease incidence				Leaf disease incidence	
			16-23		449		16-23	449
8909-15	<i>V. ariz</i> × <i>V. rup</i>	22.5 ^w	0.2	0.17	0.13	0.13	0.17	0.17
A61-61	<i>V. vin</i>	21.3	0.53	0.67	0.07	0.03	0.44	0.67
B32-94	<i>V. vin</i>	16.3	0.23	0.23	0	0.1	0.08	0
B52-72	<i>V. vin</i>	18.6	0.93	—	0.86	—	0.33	0.5
Flame Seedless	<i>V. vin</i>	15.3	0.47 ^v	0.73	0.3	0.47	0.33	0.58
PS08-108	<i>V. vin</i>	13.9	0.37	0.33	0.27	0.2	0.83	0.4
RW Munson	hybrid (<i>V. lab</i> , <i>V. vin</i> , <i>lin</i>)	22.3	0.13	0	0.2	0.03	0.25	0.08
Scarlet Royal	<i>V. vin</i>	20.7	0.3	0.1	0.3	0.57	0.67	0.5
Strawberry Grape	<i>V. lab</i> × <i>V. vin</i>	22.6	0	0.03	0	0	0.08	0
Summer Royal	<i>V. vin</i>	20.5	0.97	0.67	0.77	0.45	0.89	0.89
Sweet Scarlet	<i>V. vin</i>	21	0.77	0.8	0.65	0.8	0.17	0.25
Tamiami	<i>V. aes</i>	18	0.84	0.8	0.87	0.8	0.67	0.83
Tampa	hybrid (<i>V. aes</i> , <i>V. vin</i> , <i>V. lab</i>)	19.8	0.93	0.57	0.97	0.4	0.5	0.42
Thompson Seedless	<i>V. vin</i>	19.5	0.97	0.8	0.67	0.67	0.83	0.75
USDA1	<i>V. vin</i>	21.1	0.63	1	0.57	0.87	0.75	0.92
USDA2	<i>V. vin</i>	21.6	0.53	0.97	— ^u	0.8	0.75	0.67
USDA3	<i>V. vin</i>	20.1	0.15	—	0.03	0.07	0.17	0.17
USDA4	<i>V. vin</i>	18.5	0.6	0.7	0.27	0.63	—	—
USDA5	<i>V. vin</i>	22.5	0.6	0.53	0.13	0.03	0.17	0.33
USDA6	<i>V. vin</i>	18.9	0.57	0.43	0.53	0.3	0.5	0.33
USDA7	<i>V. vin</i>	20.1	0.87	0.67	0.4	0.6	0.33	0.58
USDA8	<i>V. vin</i>	21.2	0.83	0.73	0.87	1	1	0.89
USDA9	<i>V. vin</i>	19.8	0.7	0.57	0.47	0.3	0.83	0.67
Valley Pearl	<i>V. vin</i>	17.3	0.97	1	0.9	1	1	0.92
Y308-311-06	<i>V. vin</i>	16.7	0.93	0.6	0.3	0.37	0.58	0.83
Y511-167-12	<i>V. vin</i> × <i>V. cin</i>	14.8	0.56	0.37	0.43	—	0.33	0.42
Y514-110-11	<i>V. vin</i>	16	0.03	0.13	0.39	0.3	0.08	0.25

^aGrape (*Vitis*) germplasm identifier.

^bSpecies for each grape accession evaluated, *V. vin* = *Vitis vinifera*; *V. aes* = *Vitis aestivalis*; *V. lin* = *Vitis lincedumii*; *V. lab* = *Vitis labrusca*; *V. cin* = *Vitis cinerea*; *V. rup* = *Vitis rupestris*; *V. ariz* = *Vitis arizonica*; hybrid = interspecific hybrid among the listed species.

^cBerry soluble solids measured at harvest based on a 50-berry sample.

^wSoluble solid content was calculated based on the average of 10 individual berries.

^vColumn 1 indicates mean berry disease incidence values (0–1) for experimental run 1 and column 2 represents the second run of the experiment for isolates 16-23 and 449 for both berries and leaves.

^u“—” indicates missing value.

was a completely randomized design and blocked by treatment.

Percent soluble solids (brix) were calculated using a 50-berry sample, pureed using an electric blender, filtering the resulting slurry using a strainer. Soluble solids were measured with a Refracto 30GS portable refractometer (Mettler Toledo, Columbus, OH), except where otherwise noted. For the remaining samples, where fruit numbers were limited, percent soluble solids were calculated as the average for 10 individual berries using a hand refractometer (Refracto 30GS).

Data analyses. Incidence for each replication was calculated based on the observed symptoms and signs. Lines were described as Resistant (<10%), Moderately Resistant (10% to 25%), Moderately Susceptible (25% to 50%), or Susceptible (>50%) disease incidence. Data were analyzed using analysis of variance implemented in SAS statistical software (SAS Institute, Inc., Cary, NC). Significance of line, isolate, experimental run, and all interactions were tested using PROC GLIMMIX and significance determined using least significant difference; multiple testing adjustment was made using the simulate option. Correlations among soluble solids, leaf disease, and berry disease were calculated using Pearson's correlation coefficient using PROC CORR implemented within SAS.

Results

Berries. For grape berries, no significant differences ($P = 0.05$) in disease incidence were detected between the two experimental runs; however, interactions between line, treatment, and replications were significant ($P < 0.001$). Signs and symptoms observed included brown spots or sunken lesions, surface mycelial growth, and *Botrytis*-induced "slip skin" (Fig. 1). The *Botrytis* isolates from apricot (16-23) and grape (449) were not significantly different ($P = 0.05$) in virulence. However, significant differences were detected among treatments, grape lines and line-by-isolate interactions in experimental runs 1 and 2 ($P < 0.0001$). Grape cultivar Strawberry Grape and breeding line 8909-15 were consistently the most resistant lines evaluated for both isolates, with disease incidence $\leq 15\%$ (Table 1). However, *Vitis* hybrid breeding lines B32-94 and Y308-311-06, as well as Tamiami (*V. aestivalis*), were moderately resistant and moderately susceptible, respectively, to both isolates. Isolate-specific responses, moderate resistance to 449 but not isolate 16-23, were observed in breeding selections PS08-108 and USDA4. Cultivar Valley Pearl and breeding selection USDA1 were among the most susceptible lines across both isolates evaluated.

Leaves. Line and treatment were both highly significant ($P < 0.0001$) and a significant line-by-isolate interaction ($P = 0.0012$) was observed when evaluating grape leaves. Experimental run and all its subsequent interactions were not significant ($P = 0.05$). No

Fig. 1. Left to right, resistant, moderately resistant, and susceptible grape cultivars 7 or 5 d after inoculation with *Botrytis cinerea* on leaves (A) and berries (B), respectively.

significant differences were detected in disease incidence between the two isolates ($P > 0.05$). Lines 'Strawberry Grape', B32-94, 8909-15, 'RW Munson', 'Sweet Scarlet', 'Tampa', and 'Tamiami' all had low disease incidence ($\leq 25\%$). Breeding line USDA7 and cultivar Valley Pearl had highest susceptibility ($\geq 70\%$ disease incidence) to both isolates evaluated. No differential response (resistant vs. susceptible) was observed for any of the grape lines evaluated with the two isolates evaluated.

Correlations. No correlations ($P = 0.05$) were observed between disease susceptibility (berries or leaves) and soluble solids for either of the isolates evaluated. Leaf and berry disease had a small, but significant positive correlation for both isolate 16-23 (Run 1: $P = 0.0001$, $r^2 = 0.443$; Run 2: $P = 0.0272$, $r^2 = 0.312$) and 449 (Run 1: $P < 0.0001$, $r^2 = 0.547$; Run 2: $P = 0.0077$, $r^2 = 0.384$) when experimental runs were evaluated individually or combined (16-23: $P < 0.001$, $r^2 = 0.382$; 449: $P < 0.0001$, $r^2 = 0.4611$).

Discussion

Grey mold incited by *B. cinerea* is the most important postharvest disease of fresh grapes and requires intensive chemical management to minimize crop losses (Droby and Lichter, 2007; Gabler and Smilanick, 2001). Resistant cultivars, a staple for integrated management systems, are unavailable for fresh market table grapes. Previous studies have identified host resistance in wild *Vitis* species and legacy cultivars, but no "seedless" cultivars or breeding lines with favorable fruit quality and disease resistance have been reported.

'Strawberry Grape' or 'Isabella', found to be resistant to *Botrytis* in previous studies, was resistant to both *Botrytis* isolates used in this study, confirming its suitability as a source of resistance (Gabler et al., 2003; Kulakiotu et al., 2004). As with other *V. labrusca*-derived lines, 'Strawberry Grape' has poor fruit quality such as small, soft, seeded berries and clusters, as well as a sensitivity to sulfur, making it undesirable for breeding commercial cultivars. Moderately resistant lines 'RW Munson' and '8909-15' were resistant to one, but not both isolates evaluated. Line 8909-15 is a small-fruited *V. arizonica* $\times$ *V. vinifera* hybrid, whereas 'RW Munson' is a complex interspecific hybrid which includes *V. labrusca* in the background. Both 'RW Munson' and 8909-15 are seeded and have poor fruit quality; however, 8909-15 is a hybrid from a major source of Pierce's disease resistance routinely used in breeding programs (Krivaneck et al., 2005, 2006). High fruit-quality *V. vinifera*-derived breeding lines also showed moderate resistance to one or more isolates of *B. cinerea*. Only one *V. vinifera* cultivar (Scarlet Royal) evaluated in this study had reduced susceptibility to both isolates of *B. cinerea* compared with the other *V. vinifera* cultivars evaluated. However, breeding lines with moderate- to high fruit quality and disease resistance were identified making them potential sources for breeding resistant cultivars.

In this study, line-by-isolate interactions were detected among some, but not all, moderately resistant cultivars. This is consistent with other pathosystems where *Botrytis* resistance was found to be controlled by both general and isolate-specific factors. However,

most of the accessions evaluated were either resistant or moderately resistant to both isolates evaluated, or susceptible to both. This suggests that although multiple genes likely contribute to *Botrytis* resistance, stacking multiple genes into a single individual may not be a major consideration when breeding for resistant cultivars. This is in contrast to studies in tomato, *Arabidopsis*, and *Brassica rapa*, where large isolate-specific differences in resistance were observed (Corwin et al., 2016; Rowe and Kliebenstein, 2008). Future studies will need to evaluate additional isolates to determine the extent to which isolate-specific interactions should be considered when breeding resistant grapes.

Tissue-specific resistance was not observed in this study. In grape, disease incidence-based leaf assays were able to distinguish between resistant and susceptible grape berries, but were less accurate at distinguishing moderately resistant berries from susceptible berries. This could be in part due to the greater variability in leaf susceptibility observed within cultivars, similar to previous work with *Vitis* species (Wan et al., 2015). Despite this variability, incidence-based seedling leaf assays may have some use for early fruit disease susceptibility evaluations. This is similar to results from strawberry (Olcott-Reid et al., 1993). Whereas strawberry leaf assays had a strong correlation with field fruit susceptibility though, grape leaves had a moderate to low positive correlation with fruit susceptibility (Olcott-Reid et al., 1993). Leaf evaluations may be useful as an early approximation of berry susceptibility, but further work will be needed to determine if laboratory resistance translates to field resistance in grape.

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