

# Inheritance of Downy Mildew Resistance in Table Grapes

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**ADDITIONAL INDEX WORDS.** disease resistance, *Vitis* sp., plant breeding, combining ability, heritability, *Plasmopara viticola*

**ABSTRACT.** A study was conducted to determine how resistance to downy mildew [*Plasmopara viticola* (Bert. & Curt.) Berl. & de Toni] is inherited in germplasm (*Vitis vinifera* L., *V. labrusca* L., *V. rupestris* Scheele, and *V. riparia* Michx.) used for breeding table grapes. Crosses, including reciprocals, among parents possessing different levels of downy mildew resistance were evaluated in 1994 and 1995. The proportion of foliar tissue with sporulation, chlorosis, or necrosis was used to measure resistance. All genotypes were rated for these characters on two separate dates in 1994 and 1995. Hypersensitive flecking was also evaluated in the 1995 seedlings to determine its relationship with downy mildew resistance. Crosses with at least one resistant parent had a larger number of resistant offspring than crosses between two susceptible parents. General combining ability (GCA) effects were highly significant for 1994 and 1995. Specific combining ability effects were significant, but were relatively small compared to GCA, suggesting additive gene action was a primary influence on downy mildew resistance. Heritability estimates for sporulation, chlorosis, and necrosis were the highest at the second rating in 1994 (0.88, 0.74, and 0.57, respectively) and 1995 (0.50, 0.60, and 0.60, respectively). Reciprocal crosses indicated that maternal inheritance did not influence downy mildew resistance. A small percentage of progeny with hypersensitive flecking were identified from the germplasm. Seedlings with the flecking characteristic tended to have lower sporulation, chlorosis, and necrosis ratings earlier in the growing season.

Downy mildew of grape (*Vitis* L.), caused by *Plasmopara viticola* (Berk. & Curt.) Berl. & de Toni, can develop and spread rapidly on susceptible grapevines (Emmett et al., 1992). A major concern with downy mildew is that infected leaves can prematurely senesce, causing a reduction in energy reserves that can lead to winter injury and vine death. Because of the destructive nature of downy mildew, grape breeders are actively trying to enhance resistance to downy mildew in their breeding material. Interspecific crosses have been made primarily between resistant American hybrids and *Vitis* species and susceptible European *V. vinifera* cultivars to increase downy mildew resistance in high quality wine grapes (Alleweldt, 1980; Avramov et al., 1980; Becker and Zimmermann, 1978; Coutinho, 1982; Csizmazia, 1978; Doazan, 1980; Doazan and Kim, 1978; Eibach et al., 1989). There are no reports, however, on the mechanism of resistance to downy mildew in table grape germplasm.

Resistance to downy mildew at the stomatal level is considered to be controlled by a single dominant gene, but inter- and intracellular development of the mycelia are controlled by multiple genes (Boubals, 1959; Denzer et al., 1995). Results from interspecific (Avramov et al., 1980; Borgo et al., 1989) and intraspecific (Coutinho, 1982; Rives, 1979) crosses have shown that resistance to downy mildew can also be quantitatively expressed in seedling

populations. A single dominant gene was found to control resistance in an interspecific cross (Avramov et al., 1980), as well as in a seedling population derived from *V. yenshanensis* nomen nudum (Eibach et al., 1989). Downy mildew resistance was found to be maternally inherited in certain seedling populations (Becker and Zimmermann, 1978; Doazan and Kim, 1978).

Recurrent selection (Filippenko and Shtin, 1978) and backcrossing (Becker and Zimmermann, 1978) have been used effectively to improve downy mildew resistance by selecting resistant seedlings with good fruit characteristics as parents for succeeding generations. Eibach et al. (1989) determined from 26 interspecific crosses that downy mildew resistance had a narrow sense heritability of 0.26 to 0.39, and a broad sense heritability of 0.83 to 0.94. This indicates that resistance can be selected with little environmental influence.

Necrotic flecks are symptomatic of hypersensitive responses in many incompatible fungus-plant interactions (Goodman and Novacky, 1994). Such reactions have been observed on leaves of resistant genotypes inoculated with downy mildew (Boubals, 1959; Denzer et al., 1995). Little is known of how grape cells are genetically able to express a hypersensitive response to downy mildew. Therefore, the following study was conducted to determine how downy mildew resistance is inherited in germplasm composed of different amounts of *V. vinifera*, *V. labrusca*, *V. rupestris*, and *V. riparia* used for breeding table grapes.

## Materials and Methods

**PLANT MATERIALS.** Grape germplasm was selected from the collection at the University of Arkansas Fruit Substation, Clarksville, Ark. Parents were field screened from 1991 through 1994 to determine their level of downy mildew resistance. The germplasm selected for this study was composed of different

Received for publication 4 May 1998. Accepted for publication 18 Feb. 1999. Published with the approval of the director of the Arkansas Agricultural Experiment Station as manuscript no. 98028. The cost of publishing this paper was defrayed in part by the payment of page charges. Under postal regulations, this paper therefore must be hereby marked *advertisement* solely to indicate this fact.

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amounts of *V. labrusca* (6% to 88%), *V. vinifera* (12% to 88%), and *V. rupestris* or *V. riparia* (0% to 12%). Crosses were made in all possible combinations among resistant and susceptible selections at the Fruit Substation. There were 25 crosses made in 1993, including 10 reciprocals. Only 21 of the 25 crosses produced seeds. In 1994, 15 additional crosses were made, including 1 reciprocal cross. Of the 15 crosses, 8 crosses produced seeds.

At harvest, seeds were extracted, thoroughly rinsed with tap water, treated with Captan (3 $\alpha$ ,4,7,7-tetrahydro-2-[trichloromethyl]thio]-1*H*-isodole-1,3(2*H*)-dione), and stratified at least 4 months in moist sphagnum moss in the dark at 4 °C. Seeds were sown in Sunshine mix no. 1 (Hummerts, St. Louis) in plastic flats and allowed to germinate and grow for 4 to 5 weeks. Seedlings at the first or second true leaf stage were transplanted to peat pots (4.4  $\times$  10<sup>-4</sup> L) containing potting soil amended with Osmocote 18N-7.9P-14.9K (Hummerts, St. Louis) fertilizer at 100 g/60 L of compressed potting soil. After 1 Mar., Peters 20N-8.8P-16.6K (Hummerts, St. Louis) liquid fertilizer at a concentration of 300 ppm was applied every 2 weeks until seedlings were transplanted to the vineyard to enhance their growth. The number of seedlings in each population ranged from 8 to 220 and the average population size was  $\approx$ 112 seedlings.

Parents were propagated from hardwood cuttings three nodes long,  $\approx$ 10 mm in diameter, and were placed in a greenhouse mist bed containing perlite until leaves and root systems developed. Rooted cuttings were potted in the same manner as the seedlings, but were placed back under the mist system for 14 d to condition them to the new soil environment. Seedlings and rooted cuttings were grown in the greenhouse until plants reached the fifth or sixth leaf stage. All plants were acclimated to the outdoors by reducing greenhouse temperatures. Grapes were transplanted to a vineyard in May after nights remained above 10 °C.

**VINEYARD PLANTING AND MAINTENANCE.** Grapevines were planted 0.3 m apart within rows on trellises spaced 3.0 m apart with a bilateral-cordon training system. Perennial ryegrass (*Lolium perenne* L.) and tall fescue (*Festuca arundinacea* Schreb.) mixture was sown to establish and maintain a perennial grass strip between vineyard rows. Experimental design was a randomized complete block with 12 and 10 replications of crosses planted in the 1994 and 1995 seedling trials, respectively. One plant of a parent was planted in each replication. Vineyard maintenance included an application of Surflan (3,5-dinitro-*N*<sup>4</sup>,*N*<sup>4</sup>-dipropylsulfanilamide), fertilizer (13N-5.7P-10.8K, 13.6 kg N per acre) applied following transplanting, and drip irrigation applied to avoid drought stress. Fungicides and insecticides were not applied.

**DISEASE EVALUATIONS.** Seedlings and parents were exposed to endogenous sources of downy mildew in the vineyard. Plants were evaluated for resistance to downy mildew by rating sporulation, chlorosis, and necrosis on all leaves of each plant. Seedlings established in 1995 were also rated as hypersensitive flecking (+) or nonflecking (-) to determine if this character was associated with resistance. Disease ratings were made on a scale of 0 to 5: 0 = no sign, no symptoms; 1 = >0% to 10%; 2 = >10% to 30%; 3 = >30% to 60%; 4 = >60% to 80%; and 5 = >80% to 100% of the total leaf surface area affected on each plant. Plants were rated as follows: 0 to 1 = resistant; 2 = moderately resistant; 3 = susceptible; and 4 or 5 = highly susceptible. Ratings were made on 1 Aug. and 2 Sept. 1994 and 25 July and 30 Sept. 1995.

**DATA ANALYSES.** Data were analyzed by the GLM and mixed procedures in SAS (SAS Institute, 1996). The fixed terms in the model included the block classification factor and individual terms for the general combining ability (GCA) effect of each parent, specific combining ability (SCA) effect of each cross, and the reciprocal effect which is the difference between the two populations

of the same cross. The GCA and SCA effects were determined using the Experimental Method III by Griffing (1956), and parents were considered a fixed set. The random terms in the model were those for the block  $\times$  population interaction and the residual errors, the latter reflecting variation among plants within the same population and block of the randomized block design. Data for 1995 downy mildew ratings were analyzed similarly except that the crosses were insufficient to permit inclusion of the SCA effects. For this analysis, GCA effects are only interpretable as GCA effects for the complete diallel if all SCA effects are zero. Without this condition, GCA effects are specific to the particular crosses included. Estimate of heritabilities for sporulation, chlorosis, and necrosis were determined using SAS, with progeny of each cross regressed on midparent. No analysis of coancestry was conducted, because insufficient downy mildew ratings were available on grandparents.

## Results

There was wide variation sporulation, chlorosis, and necrosis ratings among the 1994 and 1995 seedling populations. Seedlings

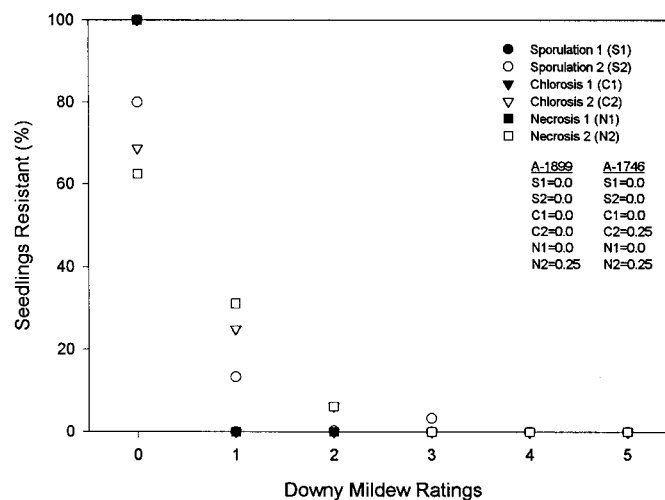


Fig. 1. Seedlings in population A-1899  $\times$  A-1746 (resistant  $\times$  resistant) exhibiting resistance to downy mildew. Ratings based on a scale of 0 to 5,  $\geq$ 80% leaf area affected. Rating 1 = 1 Aug., rating 2 = 2 Sept.

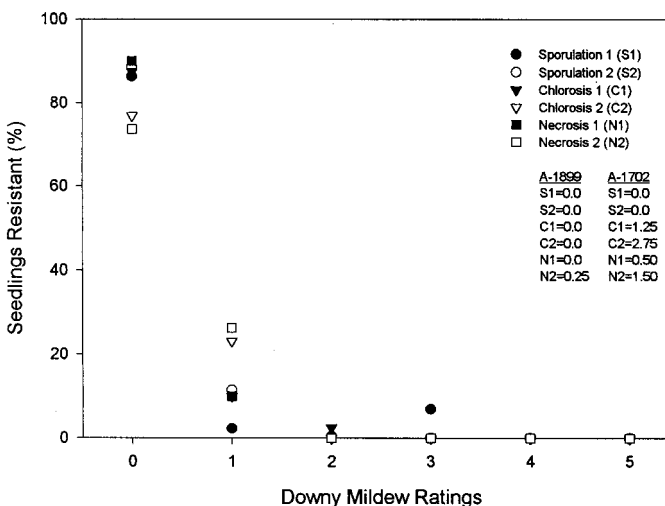


Fig. 2. Seedlings in population A-1899  $\times$  A-1702 (resistant  $\times$  susceptible) exhibiting resistance to downy mildew. Ratings based on a scale of 0 to 5,  $\geq$ 80% leaf area affected. Rating 1 = 1 Aug., rating 2 = 2 Sept.

within resistant x resistant populations had a narrow range of variability. For example, a large number of the seedlings produced from the cross A-1899 x A-1746 were found resistant to sporulation, chlorosis, and necrosis on 1 Aug. and 2 Sept. (Fig. 1). Also, most grape seedlings produced from a resistant x susceptible parents (e.g., A-1899 x A-1702) were rated resistant to downy mildew (Fig. 2). Seedlings produced from cross A-1746 x

A-1702 (resistant x susceptible) did, however, show more variability in sporulation, chlorosis, and necrosis (Fig. 3) than did the A-1899 x A-1702 seedlings (Fig. 2). The seedlings produced from crosses of two susceptible parents (e.g. A-1046 x A-1702) showed wide variation in sporulation, chlorosis, and necrosis at the first and second rating (Fig. 4). In most cases, populations derived from two susceptible parents had significantly higher ratings for sporulation, chlorosis, and necrosis than populations with at least one resistant parent.

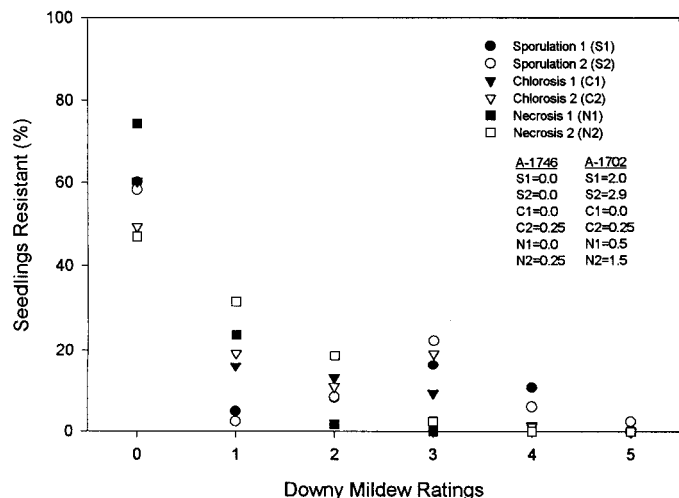


Fig. 3. Seedlings in population A-1746 x A-1702 (resistant x susceptible) exhibiting resistance to downy mildew. Ratings based on a scale of 0 to 5, 5 ≥ 80% leaf area affected. Rating 1 = 1 Aug., rating 2 = 2 Sept.

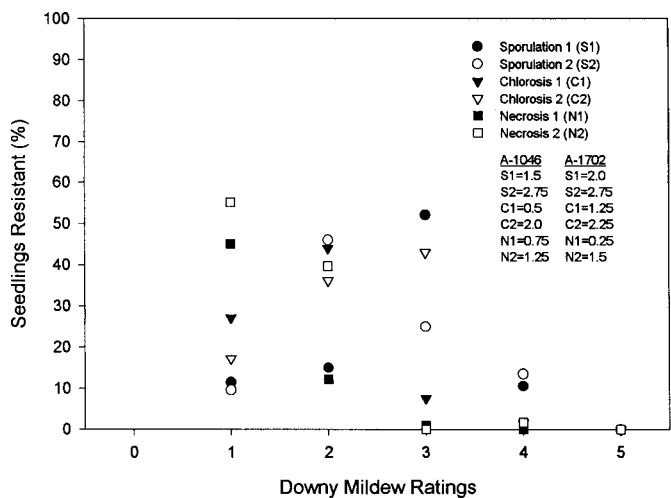


Fig. 4. Seedlings in population A-1046 x A-1702 (susceptible x susceptible) exhibiting resistance to downy mildew. Ratings based on a scale of 0 to 5, 5 ≥ 80% leaf area affected. Rating 1 = 1 Aug., rating 2 = 2 Sept.

**MATERNAL EFFECTS.** Populations produced from reciprocal crosses were compared at both ratings to determine if there were any maternal effects on downy mildew resistance (Table 1). Of the 1994 reciprocal crosses, only 10 had a sufficient number of seedlings to evaluate. Reciprocal crosses, A-1746 x A-1702 and A-1702 x A-1746, were significantly different in sporulation and chlorosis on 1 Aug. When A-1746 was used as a maternal parent, sporulation and chlorosis ratings were significantly higher. There was a significantly higher amount of chlorosis found in population A-1702 x A-1850 than in A-1850 x A-1702 on 1 Aug. No significant differences were found, however, between reciprocal populations on 2 Sept. In 1995, reciprocal crosses A-1046 x A-1702 and A-1702 x A-1046 were compared and sporulation, chlorosis, and necrosis ratings were significantly higher 25 July and 30 Sept. when A-1702 was the maternal parent (Table 2). Evaluations of this same reciprocal cross in 1994 found no significant maternal effect for all three parameters.

**GCA AND SCA.** Diallel analysis of the 1994 seedling populations was used to determine the nature of inheritance for downy mildew resistance. The GCA estimates were significant at the first and second rating (Table 1), indicating that additive effects were primarily responsible for downy mildew resistance in the 1994 seedling populations. Resistant selections had significant ( $P = 0.0001$ ) negative estimates for sporulation, chlorosis, and necrosis at both ratings, and in most cases susceptible parents had significant ( $P \leq 0.05$ ) positive estimates (data not shown). Comparisons among observed versus predicted GCA estimates for sporulation indicated that downy mildew resistance could be predicted by using the GCA estimates for the first (Fig. 5) and second (Fig. 6) rating. The mean parental value versus observed mean of cross for chlorosis and necrosis GCA estimates were comparable to the data shown for sporulation.

Seedlings derived from each of the susceptible parents generally had mean values for sporulation, chlorosis, and necrosis that were greater than the overall progeny mean. SCA effects were significant for chlorosis and necrosis at rating two and sporulation and chlorosis at rating two in 1994. Seven crosses showed significant SCA effects for sporulation, chlorosis or necrosis on 1 Aug. However, only five crosses had significant SCA estimates for sporulation, chlorosis, or necrosis at the second rating.

The GCA effects were significant for the 1995 seedling trial, which indicated, as in the 1994 seedling populations, that resis-

Table 1. Results of analysis of variance of general combining ability (GCA) and specific combining ability (SCA) and reciprocal crosses for sporulation (S), chlorosis (C), and necrosis (N) ratings in the 1994 seedlings at the first (1) and second (2) rating.

Source	df	S1	C1	N1	S2	C2	N2
Replication	11	3.7	3.0	0.8	3.9	1.5	1.3
GCA	5	122.5**	43.7**	13.4**	107.1**	60.9**	17.6**
SCA	9	15.8**	6.1**	1.2**	6.1**	3.6**	1.0
Reciprocal	5	3.6	2.1*	0.3	0.7	0.6	0.4
Error	197(192) <sup>z</sup>	1.8	0.9	0.5	1.5	1.0	0.7

<sup>z</sup>df for rating 1 (rating 2).

\*\*Significant F test at  $P \leq 0.05$  or 0.01, respectively.

Table 2. Results of analysis of variance of general combining ability (GCA) and reciprocal crosses for sporulation (S), chlorosis (C), and necrosis (N) ratings in the 1995 seedlings at the first (1) and second (2) rating.

Source	df	S1	C1	N1	S2	C2	N2
Rep	9	7.3	7.2	12.1	12.5	2.2	2.4
GCA	6	76.0**	47.9**	49.1**	33.0**	37.8**	42.3**
Reciprocal	1	48.3**	21.9**	28.0**	5.1*	5.7*	5.8*
Error	63(60) <sup>z</sup>	2.6	1.8	1.9	1.2	1.1	1.1

<sup>z</sup>df for rating 1 (rating 2).

\*,\*\*Significant F test at  $P \leq 0.05$  or 0.01, respectively.

tance to downy mildew is primarily a result of additive variance (Table 2). When comparing GCA estimates for susceptible parents in 1994 and 1995 trials, downy mildew estimates were significantly increased in 1995. Resistant parents had significantly lower amounts of sporulation, chlorosis, and necrosis.

**HERITABILITY ESTIMATE.** Heritabilities for sporulation, chlorosis, and necrosis were estimated for the 1994 seedling populations for the first and second ratings. On 1 Aug., sporulation, chlorosis, and necrosis had  $h^2$  estimates of 0.59, 0.43, and 0.32, respectively. Heritability estimates ( $h^2$ ) of sporulation, chlorosis, and necrosis (0.88, 0.74, and 0.57, respectively) were considerably higher on 2 Sept., which indicates that selection for resistance for these traits would be more effective during this time of the growing season. Heritability estimates in 1995 for sporulation, chlorosis, and necrosis of 0.36, 0.40, and 0.49, respectively, were low on 25 July and increased considerably (0.50, 0.60, and 0.60, respectively) by 30 Sept. Heritability estimates were also higher at the second rating in the 1994 seedling trial. Overall, the  $h^2$  estimates for the second rating in 1995 were lower compared with estimates in 1994.

**HYPERSENSITIVE FLECKING EVALUATION.** Seedlings were compared within each population in which parents exhibited the flecking character in 1995 (Fig. 7). In general, plants with flecking had significantly ( $P \leq 0.001$ ) less downy mildew in this study than plants that did not exhibit flecking.

Population MB-35 had the highest percentage of seedlings exhibiting hypersensitive flecking on 30 July, and also had significantly less downy mildew than most of the other populations. Hypersensitive flecking appeared to be related to the amount of sporulation more than the amount of either chlorosis or necrosis. Plants that had hypersensitive flecks were less likely to develop sporulation early in the season. Of the populations with hypersensitive flecking plants, fewer seedlings showed this type of response on 30 Sept. than on 25 July (Fig. 7). This may have been because disease development was confounded with the flecking symptom.

The highest percentage of flecking progeny was found in population MB-41 on 25 July, which also had the most resistant offspring (50%) in 1995. Sporulation, chlorosis, and necrosis ratings for MB-41 were significantly ( $P \leq 0.05$ ) lower on 25 July than all other populations, except for necrosis ratings of MB-42. There were no seedlings in MB-42 that exhibited hypersensitive flecking (Fig. 7), however, this population had the second highest percentage (10%) of resistant progeny. Remaining populations had <5% resistant seedlings.

Parental genotypes which showed flecking symptoms, developed considerably less sporulation and chlorosis than parents that did not express hypersensitive flecking. Selection A-1046 was found to have hypersensitive flecking, but still manifested downy mildew at an epidemic proportion by the end of summer. There was some indication of a maternal inheritance regarding hypersensitive flecking. Evaluations of the reciprocal crosses A-1046 x

A-1702 and A-1702 x A-1046 indicated that sporulation, chlorosis, and necrosis were significantly reduced at the first and second rating in progeny in which A-1046 was the maternal parent.

## Discussion

This study suggests that by crossing two parents with high levels of downy mildew resistance there will be a large number of the progeny that will be resistant as well. However, when a resistant parent was crossed with a susceptible parent, there were generally fewer resistant seedlings produced compared with seed-

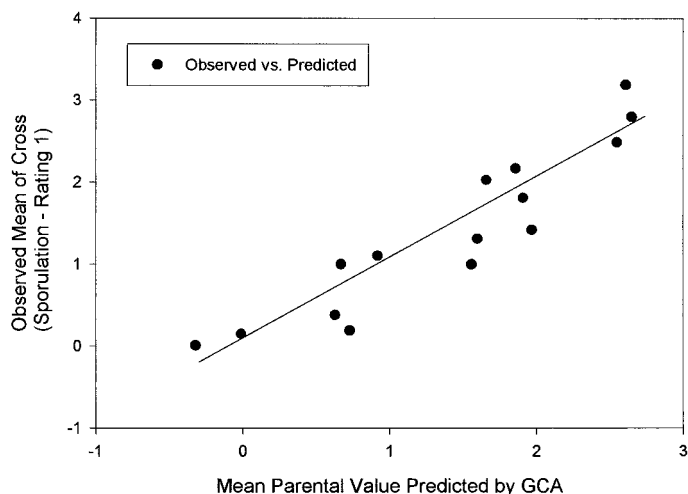


Fig. 5. General combining ability effects for downy mildew sporulation in the 1994 seedling populations for 1 Aug.

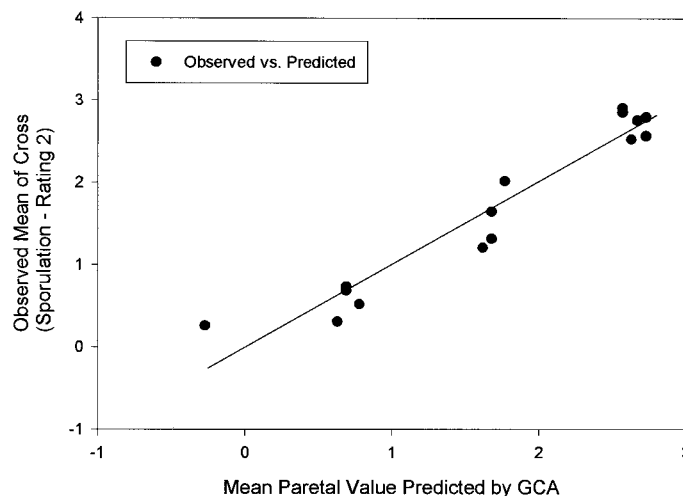


Fig. 6. General combining ability estimates for downy mildew sporulation in the 1994 seedling populations for 2 Sept.

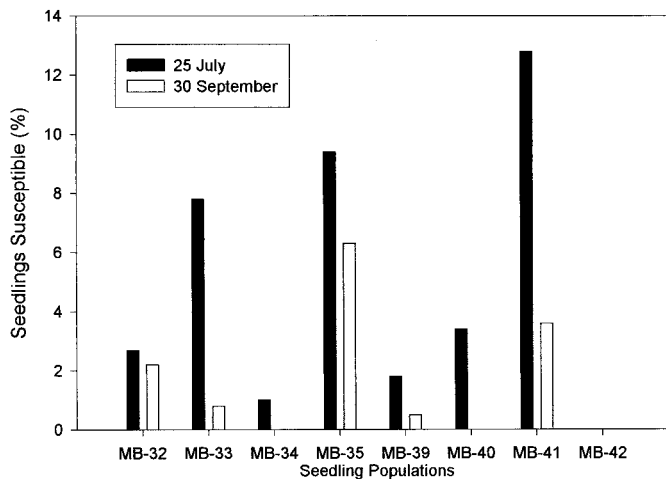


Fig. 7. Percentage of seedlings in populations showing hypersensitive flecking.

lings produced from two resistant parents. Sporulation, chlorosis, and necrosis of downy mildew are most probably controlled quantitatively. Significant GCA effects for each of the three factors in 1994 and 1995 indicated that downy mildew resistance was primarily additive gene action. The mean parental values, predicted by GCA estimates, provided a good indication of what the actual mean population value would be for downy mildew resistance. SCA, although found to be significant during the earlier rating, does not appear to be significant later in the season. Thus, probably little or no intra- and/or interallelic gene action exists for downy mildew resistance in this germplasm. Boubals (1959) and Denzer et al. (1995) determined from studying downy mildew resistance in wine grapes (primarily composed of *V. vinifera*) that resistance appears to have two types of genetic effects, a single gene for initial penetration, and multiple genes controlling inter- and intracellular development of mycelia. Additional crosses should be made to determine if there is indeed a single gene for downy mildew resistance in table grape germplasm, which would help expedite developing cultivars that have resistance.

Since the GCA estimates were significant, additive gene action was considered to be the most important genetic influence on resistance to downy mildew. Narrow sense heritability ( $h^2 = V_A/V_P$ ) can be used to estimate the magnitude of additive effects (Falconer, 1981). Heritability estimates for sporulation, chlorosis, and necrosis obtained from both trials were considerably higher than those found by Eibach et al. (1989). Heritability ( $h^2$ ) estimates for sporulation, chlorosis, and necrosis were considerably higher later in the season than the  $h^2$  estimates at the first rating each year. Since  $h^2$  estimates were highest in September, selection among families for downy mildew resistance would be more effective later in the growing season. Heritability estimates in this study are based on the offspring in each population being regressed onto the midparent values. Heritability estimates may be biased upward in each trial if there was a genotype  $\times$  year interaction contributing to the estimate of additive variance, because the downy mildew ratings were taken only 1 year for each seedling population and parents evaluated over 2 years.

Downy mildew can infect developing green tissue throughout the growing season, but generally does not become epidemic until late July through September. Seedlings should be evaluated for resistance during late summer when downy mildew became fully expressed. If selections for resistance to downy mildew are made too early, there is a greater chance of rating a seedling as resistant

when it is actually susceptible. With high  $h^2$ , a grape breeder could more accurately determine which germplasm possessed genes for resistance to downy mildew and thus be able to select breeding material that would better enhance downy mildew resistance in succeeding generations.

Heritability of a character depends on the population from which the parents are selected and the environment in which the selection is made for the character. The parents in this study had, for the most part, diverse genetic backgrounds. There were instances, however, where seedlings had related grandparents. Although the parents were rated at the same location prior to crossing, downy mildew ratings were taken under different environmental conditions each year. By rating each parent for downy mildew over 4 years before making the crosses, adequate information was available to develop a crossing plan.

Although maternal inheritance of downy mildew resistance was observed in certain reciprocal crosses, it was not found to be as important as reported in other studies (Becker and Zimmermann, 1978; Doazan and Kim, 1978). Given the small number of reciprocal crosses evaluated in this study, additional reciprocal crosses between highly resistant and susceptible parents would be required to adequately assess maternal influences.

This research has shown that hypersensitive flecking reaction in table grape may be associated with the amount of downy mildew found in grapevines. Sporulation, chlorosis, and necrosis would often be delayed in plants expressing hypersensitive flecking. The significant reduction in the amount of sporulation on the flecking plants indicated they were able to resist initial infection or provided an extended latent period compared to plants that did not express hypersensitive flecks. A hypersensitive response may provide enough protection to delay the expression of downy mildew and thus reduce the number of fungicide applications needed during the growing season.

To determine whether hypersensitive flecking is important in downy mildew resistance in grape, additional crosses are needed between parents that express and do not express this trait. The hypersensitive reaction, if involved in resistance, may not have prevented downy mildew development under the high levels of secondary inoculum in the fungicide-free vineyard. Hypersensitive reactions have been observed on resistant grapes and were thought to be controlled by a single gene at the stomatal level (Boubals, 1959; Denzer et al., 1995). Further genetic studies are needed to determine if downy mildew was indeed responsible for the hypersensitive reactions observed on the plants, and if so, how the hypersensitive flecking character is genetically controlled in grape germplasm.

Results with the table grape germplasm used in this study were comparable to previous studies on enhancing downy mildew resistance in wine grapes (Avramov et al., 1980; Borgo et al., 1989; Coutinho, 1982; Rives, 1979). Wine grape breeding programs have effectively incorporated genes for resistance to downy mildew from American *Vitis* species (e.g., *V. rupestris*, *V. riparia*) into the European *vinifera* cultivars, while maintaining wine quality. Table grape breeding programs in the eastern United States have also been successful in combining genes from *V. vinifera* with other *Vitis* spp., primarily *V. labrusca*, to develop varieties with good fruit quality and disease resistance. Plant material used in this study, composed primarily of *V. vinifera*, generally had poor downy mildew resistance. There were some cases where plant material with a large component of *V. vinifera* had good resistance, however, those plants had either *V. rupestris* or *V. riparia* in their background, which probably was the source of downy mildew resistance. Genes for resistance have been

incorporated successfully into table grape germplasm from different sources. Plant material should be evaluated for resistance in conjunction with good horticultural characteristics (e.g., fruit quality, vigor, yield) to assure maximum potential of cultivars developed.

#### Literature Cited

- Alleweldt, G. 1980. The breeding of fungus-resistant grapevine varieties, p. 242–250. In: Proc. 3rd Intl. Symp. Grape Breeding. Dept. Viticult. Enol., Univ. Calif., Davis.
- Avramov, L., M. Babovic, M. Jovanovic, and M. Ruzevic. 1980. Breeding *Plasmopara*-resistant varieties in *Vitis*, p. 302–307. In: Proc. 3rd Intl. Symp. Grape Breeding. Dept. Viticult. Enol., Univ. Calif., Davis.
- Becker, N.J. and H. Zimmermann. 1978. Breeding of yield varieties resistant to downy mildew, p. 209–214. In: Grapevine Genetics and Breeding, II. Symp. Intl. Sur l'Amelioration de la Vigne, Bordeaux, France, June 1977, INRA, Paris.
- Borgo, M., S. Cancellier, and A. Costacurta. 1989. Protection integree de la vigne avec l'amelioration genetique par croisement, p. 297–301. In: Proc. Influence Environmental Factors on Control of Grape Pests, Diseases, and Weeds. EC Experts Group, Thessaloniki, Greece, 6–8 Oct. 1987.
- Boubals, D. 1959. Contribution a l'etude des causes de la resistance des Vitacees au Mildiou de la Vigne et de leur mode de transmission hereditaire. Ann. Amelior. Plantes 9:5–233.
- Coutinho, M.P. 1982. A resistencia da videira ao mildiou: Evolucao dum trabalho. Garcia de Orta, Ser. Est. Agron., Lisboa 9:229–236.
- Csizmazia, J. 1978. Selection pour la resistance au mildiou: Resultats obtenus en Hongrie, p. 235–241. In: 2nd Intl. Symp. Grapevine Breeding, Bordeaux, France, 14–18 June, 1977.
- Denzer, H., G. Staudt, and E. Schlosser. 1995. Host settlement of *Plasmopara viticola* on different susceptible hosts. *Vitis* 34:45–49.
- Doazan, J.P. 1980. The selection of grapevine genotypes resistant to fungus diseases and their use under field conditions, p. 324–331. In: Proc. 3rd Intl. Symp. Grape Breeding. Dept. Viticult. Enol., Univ. Calif., Davis.
- Doazan, J.P. and S.K. Kim. 1978. Recherche de genotypes resistants au mildou dans des croisements interspecifics, p. 243–249. In: Grapevine genetics and breeding, II Symposium International Sur L'amelioration de la Vigne, Bordeaux, France, June 1977, Paris.
- Eibach, R., H. Diehl, and G. Alleweldt. 1989. Untersuchungen zur vererbung von Resistenzeigenschaften bei Reben gegen *Oidium tuckeri*, *Plasmopara viticola*, und *Botrytis cinerea*. *Vitis* 28:209–228.
- Emmett, R.W., T.J. Wicks, and P.A. Magarey. 1992. Downy mildew of grapes, p. 90–128. In: J. Kumar, H.S. Chaube, U.S. Singh, and A.N. Mukhopadhyay (eds.). vol. 3. Diseases of fruit crops—Plant diseases of international importance. Prentice Hall, Englewood Cliffs, N.J.
- Falconer, D.S. 1981. Introduction to quantitative genetics. Wiley, New York.
- Filippenko, M. and L.T. Shtin. 1978. Ways of increasing the degree of mildew resistance in grapes. *Genetika* 14:1968–1874 (English translation).
- Goodman, R.N. and A.J. Novacky. 1994. The hypersensitive reaction in plants to pathogens—A resistance phenomenon. Amer. Phytopathol. Press, St. Paul, Minn.
- Griffing, B. 1956. Concept of general and specific combining ability in relation to diallel crossing systems. *Austral. J. Biol. Sci.* 9:463–493.
- Rives, M. 1979. Selection pour la resistance au mildou dans l'espece *Vitis vinifera*: Utilisation du concept de relation hote-pathogene polygenique-stable et de l'interpretation polygenique de l'heredite des caracteres quantitatifs. *Bul. Soc. Bot. France* 126, Actual Bot. 4:45–49.
- SAS Institute, Inc. 1996. SAS/STAT software: Changes and enhancements through release 6.11. SAS Inst., Cary, N.C.