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Inheritance of downy mildew (*Plasmopara viticola*) and anthracnose (*Sphaceloma ampelinum*) resistance in grapevines

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ABSTRACT. Downy mildew (*Plasmopara viticola*) and anthracnose (*Sphaceloma ampelinum*) are two of the major diseases of most grapevine (*Vitis vinifera* L.) cultivars grown in Thailand. Therefore, breeding grapevines for improved downy mildew and anthracnose resistance is crucial. Factorial crosses were made between three downy mildew and/or anthracnose resistant lines ('NY88.0517.01', 'NY65.0550.04', and 'NY65.0551.05'; male parents) and two or three susceptible cultivars of *V. vinifera* ('Black Queen', 'Carolina Black Rose', and/or 'Italia'; female parents). F_1 hybrid seedlings were evaluated for downy mildew and anthracnose resistance using a detached/excised leaf assay. For both diseases, the general combining ability (GCA) variance among male parents was significant, while the variance of GCA among females and the specific combining ability (SCA) variance were not significant, indicating the prevalence of additive over non-additive gene actions. The estimated narrow sense heritabilities of downy mildew and anthracnose resistance were 55.6 and 79.2%, respectively, suggesting that downy mildew/anthracnose resistance gene(s) were highly heritable. The 'Carolina Black Rose x NY65.0550.04' cross combination is recommended for future use.

Key words: Combining ability; *Elsinoe ampelina*; Heritability; Scab; *Vitis* spp

INTRODUCTION

Downy mildew caused by *Plasmopara viticola* (Berk. & M.A. Curtis) Berl. & de Toni is responsible for viticulturally significant economic losses of grape production, especially in Thailand. The quality of table grapes may decrease as a result of downy mildew, since only 25-50% of the sugar remains in the infected berries (Agrios, 1997). Although *Vitis vinifera* L. is highly susceptible to several diseases, including downy mildew, many American and Asian *Vitis* species are reported to be resistant to *P. viticola*. *V. rupestris* and *V. amurensis* are moderately resistant, whereas *V. cinerea*, *V. riparia*, *V. rubra*, *V. candicans* and *V. rotundifolia* are highly resistant (Boubals, 1959; Langcake and Lovell, 1980; He and Wang, 1986; Eibach et al., 1989; Alleweldt et al., 1990). Eibach et al. (1989) estimated the narrow sense and broad sense heritabilities for downy mildew resistance to be 0.26-0.39 and 0.83-0.94, respectively. These results indicated that the resistance characteristics were only slightly influenced by the environment. In addition, maternal inheritance of downy mildew resistance was not found to be important (Becker and Zimmermann, 1978; Doazan and Kim, 1978; Brown et al., 1999b).

Anthracnose, or scab as it is referred to by Thai pathologists, caused by the fungus *Sphaceloma ampelinum* de Bary (teleomorph *Elsinoe ampelina* Shear), is a destructive disease of grapevines grown in humid and warm climates, especially the European grapevine (*V. vinifera*) cultivars that are widely cultivated in Thailand. The disease could cause as high as 50% crop losses in a season (CAB International, 2000). Therefore, a grapevine cultivar that is highly resistant to anthracnose is greatly needed for efficient and environmentally friendly grapevine production in Thailand. Fennell (1948) reported that moderate resistance to scab could be found in the majority of wild tropical grape species. Similarly, Mortensen (1981) and Patil et al. (1990) reported the sources of resistance to anthracnose in *V. simpsoni*, *V. aestivalis*, *V. champini*, *V. rupestris*, *V. smalliana*, *V. shuttleworthii*, *V. labrusca*, *V. rotundifolia*, *V. tiliaefolia, V. vulpina*, and *V. munsoniana*. Genetic resources for anthracnose resistance were also found in several Asiatic and Chinese *Vitis* species, including *V. amurensis*, *V. quinquangularis*, *V. romanetii*, *V. adstricta*, *V. pseudoreticulata*, *V. piazezkii*, *V. davidii*, *V. davidii* var. *cyanocarpa*, *V. liubanensis*, *V. qinlingensis*, *V. bashanica*, *V. yeshanensis*, *V. hancockii*, *V. coignetiae*, and *V. thunbergii* (Lu, 1997; Li et al., 2008; Tian et al., 2008). However, to the best of our knowledge, there has been no report on gene action analysis of anthracnose resistance in grapevines.

In Thailand, the main cultivars for table grapes are 'White Malaga' and 'Cardinal'. Other cultivars such as 'Carolina Black Rose', 'Early Muscat', 'Italia', and 'Black Queen' are also cultivated in Thailand because of their high fruit quality (Nilnond, 2001). However, these cultivars are susceptible to downy mildew and anthracnose. Several applications of fungicides are usually needed to provide protection. Therefore, many grape breeding programs seek to develop new disease resistant cultivars by combining the disease resistant characteristics from the American and Asian species with the high fruit quality of *V. vinifera*. Selection of the best parents, crosses, and breeding strategies, which are crucial for all breeding programs, could be facilitated by the estimation of general combining ability (GCA) and specific combining ability (SCA) effects through gene action analysis (Dabholkar, 1992). Moreover, the relative contribution of additive variance and the influence of the environment on inherited characteristics can be estimated by heritability analysis. High narrow sense heritability values indicate that desirable characters are likely to be achieved with great success in a breeding program. To estimate the types and relative importance of genetic variation in a specified population, different mating systems may be used, including the North Carolina (NC) design I, II, and III mating systems reported by Comstock and Robinson (1952).

The objective of this study was to determine the GCA, SCA, and heritabilities of downy mildew and anthracnose resistance of grapevines using the NC design II mating system.

MATERIAL AND METHODS

Plant materials

A 3 x 3 NC II mating design, consisting of three potentially resistant male parents, 'NY88.0517.01', 'NY65.0550.04', and 'NY65.0551.05', and three female parents with high fruit quality but susceptibility to downy mildew and anthracnose, including 'Black Queen', 'Carolina Black Rose', and 'Italia', was used to generate F_1 hybrids for inheritance analysis of downy mildew resistance. However, for anthracnose inheritance analysis, a 3 x 2 NC II mating design, consisting of the same three male parents, but with only two female parents, 'Black Queen' and 'Carolina Black Rose', was used to generate F_1 hybrids. The male parents, which were the complex interspecific hybrids, 'NY88.0517.01' [Joannes Seyve 23.416 x (*V. rupestris* x *V. cinerea*)], 'NY65.0550.04' {[Jaeger 70 (*V. rupestris* x *V. lincecumii*) x Victoria's Choice] x (Seyve Villard 23-18 selfed)}, and 'NY65.0551.05' {[Jaeger 70 (*V. rupestris* x *V. lincecumii*) x Victoria's Choice] x Lady Patricia (S.14664 x S.V. 20-365)}, were obtained from the grape breeding program of the New York State Agricultural Experiment Station (NYSAES), Cornell University (Geneva, NY, USA). These genotypes had variable levels of genetic composition from several American species such as *V. cinerea*, *V. riparia*, *V. rupestris*, *V. labrusca*, and *V. lincecumii*, along with *V. vinifera* in their pedigrees. They were selected based on field observations for downy mildew and/or anthracnose resistance.

Nine crosses were performed at the Suranaree University of Technology (SUT) Farm, Nakhon Ratchasima, Thailand, following Reisch and Pratt (1996). The seedlings of F_1 hybrids were grown in a greenhouse in 24 cm diameter x 20 cm deep plastic pots in a soil mix (peat moss, soil, burnt rice-chaff, perlite, vermiculite, and sand in a 1:1:1/2:1:1:3/4 ratio by volume) with one plant per pot. The plants were managed for diseases by spraying once every 2 weeks with 2 g/L mancozeb (manganese-zinc ethylene bis [dithiocarbamate]) for downy mildew and 0.6 g/L triadimefon [1-(4-chlorophenoxy)-3,3-dimethyl-1-(1H-1,2,4-triazol-1-yl) butanone] for rust and anthracnose. Plants were fertilized with 10 mL/L 11-8-6 foliar fertilizer every 2 weeks, and stable manure was applied every 2 months. The fungicides were exempt for 1 month prior to inoculation.

Downy mildew resistance evaluation

Eighty-five F_1 hybrids (14 'Black Queen x NY88.0517.01', 6 'Black Queen x NY65.0550.04', 15 'Black Queen x NY65.0551.05', 10 'Carolina Black Rose x NY88.0517.01', 8 'Carolina Black Rose x NY65.0550.04', 13 'Carolina Black Rose x NY65.0551.05', 6 'Italia x NY88.0517.01', 7 'Italia x NY65.0550.04', and 6 'Italia x NY65.0551.05') and 6 parents were evaluated for resistance to downy mildew by the detached leaf assay described by Mahanil (2007). The number of total spores per leaf was counted and converted to number of spores/25 cm^2 leaf area according to Mahanil (2007). Resistance was classified based on spore production: 0, 0-5 spores/25 cm^2 (highly resistant); 1, 6-10 spores/25 cm^2 (resistant); 2, 11-15 spores/25 cm^2 (moderate or intermediate); 3, 16-25 spores/25 cm^2 (moderately susceptible); 4, 26-40 spores/25 cm^2 (susceptible); 5, ≥ 40 spores/25 cm^2 (highly susceptible) (Gadoury DM, personal communication). The mean disease reaction value of each hybrid was used for statistical analysis.

Anthracnose resistance evaluation

Eighty-five F_1 hybrids (16 'Black Queen x NY88.0517.01', 11 'Black Queen x NY65.0550.04', 22 'Black Queen x NY65.0551.05', 11 'Carolina Black Rose x NY88.0517.01', 9 'Carolina Black Rose x NY65.0550.04', and 16 'Carolina Black Rose x NY65.0551.05') and five parents were assessed for anthracnose resistance by the excised leaf assay described by Tharapreuksapong et al. (2009). One representative fungal isolate from Nakhon Ratchasima (Nk4-1) was used for the analysis. The disease severity was estimated by lesion scoring. A scale of 1 to 5 based on lesion numbers per inoculated droplet was used: 1, 0-6 lesions (highly resistant); 2, 7-25 lesions (resistant); 3, 26-50 lesions (moderate or intermediate); 4, 51-100 lesions (susceptible); 5, ≥ 100 lesions (highly susceptible). The mean disease severity value of each hybrid was used for statistical analysis.

Statistical analysis

Using transformed data $X' = (X + 1)^{1/2}$ and a completely randomized design (CRD) model with 4-10 replications, analysis of variance (ANOVA) for disease reaction of parents and hybrids was performed using SPSS version 14.0 (Levesque and SPSS Inc., 2006). Combining ability was estimated and analyzed with the NC II mating system according to Comstock and Robinson (1952). Narrow sense heritability was calculated as follows: Heritability (%) = $[\sigma^2_A/(\sigma^2_A + \sigma^2_D + \sigma^2_E)] \times 100$.

RESULTS AND DISCUSSION

Downy mildew resistance

The downy mildew disease reaction data from F_1 hybrids and their parents were analyzed and mean squares from the analysis of variance of the disease reaction are presented in

Table 1. Highly significant differences in mean disease ratings among grapevine genotypes were obtained (P < 0.01). The contrasted comparison of hybrids *vs* parents was highly significant at P < 0.01. Highly significant differences among parents (P < 0.01) and among hybrids (P < 0.01) indicated high genetic variability within each group.

Table 1. Mean squares from analysis of variance for downy mildew disease reaction of parents and hybrids.

Sources	d.f.	SS	MS	F (test)
Treatments	14	13.90	0.99	6.21**
Parents *vs* hybrids	1	1.21	1.21	7.56**
Parents	5	7.24	1.45	9.05**
Hybrids	8	5.45	0.68	4.26**
Error	102	16.28	0.16	
Total	116	30.18		

**P < 0.01; CV (%) = 21.06.

Among the female parents, 'Black Queen' was highly susceptible. The number of spores in 'Black Queen' was as high as 178.5 spores/25 cm^2 leaf area (disease score 4.2), while the highest number of spores in 'Carolina Black Rose' (disease score 3.6) and 'Italia' (disease score 3.9) were only 86.3 and 90.0 spores/25 cm^2 leaf area, respectively. Moreover, the field observations also showed that 'Black Queen' was the most susceptible cultivar among female parents, suggesting that the disease resistance evaluation by the detached leaf assay correlated with field observations. Similarly, Brown et al. (1999a) found a high correlation of disease ratings based on downy mildew sporulation among leaf disk assays, greenhouse evaluations, and field observations. Eibach et al. (1989) also reported that leaf disk evaluation was significantly correlated with field results (r = 0.98).

All male parents ['NY88.0517.01' (disease score 0.5), 'NY65.0551.05' (disease score 0.5), and 'NY65.0550.04' (disease score 1.0)] showed downy mildew resistance. The progenies of all resistant x susceptible crosses showed variation in downy mildew resistance ranging from highly resistant (disease score = 0) to highly susceptible (disease score = 5). Resistance levels of the F_1 hybrids classified into three groups: resistance (disease scores = 0 and 1), moderate (disease scores = 2 and 3), and susceptible (disease scores = 4 and 5). This showed that the majority of the seedlings were susceptible (52.9%), and the remaining 28.2% were resistant, while 18.9% were moderate. At least half of the seedlings from most crosses were susceptible, suggesting that the gene(s) controlling downy mildew resistance in the resistant parents were in a heterozygous condition. 'Carolina Black Rose x NY 65.0550.04' appears to be the best candidate parental combination for the development of downy mildew resistant hybrids because it gave the highest number of resistant seedlings (75.0%).

The combining ability analysis mean squares for GCA and SCA effects are presented in Table 2. Differences among the hybrids were highly significant (P < 0.01). The mean square for GCA of males was larger than that of females, indicating greater genetic diversity among the male parents. These results were not unexpected since the male parents represent genotypes with accumulation of resistance gene(s), whereas the female parents are cultivars with susceptibility gene(s). The data indicated that the GCA effect was significant for males (P < 0.01) but not females. The interaction between male and female effects provides a measure of the SCA effect. The source of variation was not significant for this effect (P > 0.05). These results indicated that additive gene effects were important for downy mildew resistance in these populations.

Table 2. Mean squares from analysis of variance for general (GCA) and specific (SCA) combining ability of downy mildew resistance.

Sources	d.f.	SS	MS	F (test)
Hybrids	8	5.45	0.68	3.37**
GCA (females)	2	0.26	0.13	0.64^{ns}
GCA (males)	2	3.53	1.77	8.74**
SCA	4	1.66	0.42	2.05^{ns}
Error	76	15.36	0.20	
Total	84	20.81		

*P < 0.05; ^{ns}P > 0.05; CV (%) = 18.09.

The relative importance of the mean squares for GCA and SCA were 13.6:1, 4.2:1, and 0.3:1 for GCA (males):GCA (females), GCA (males):SCA, and GCA (females):SCA, respectively. These results indicated the predominance of additive genetic effects over other types of gene action and that the male parents used in this experiment contributed more additive gene effects to the inheritance of this trait than did female parents (Griffing, 1956; Lu and Myers, 2011). The estimated narrow sense heritability for downy mildew resistance was 55.6%. The high percentage of heritability may result from the prevalent additive gene action over the non-additive gene action, along with relatively low environmental effects. Similarly, Brown et al. (1999b) also reported high heritability (88.0%) of this character, along with additive genetic effects.

Due to the fact that the mean squares of the GCA were significant, the GCA effect was calculated from means of the disease reaction in each parent, and results are presented in Table 3. The downy mildew rating score of zero represented high resistance, and the rating score of 5 represented high susceptibility. Therefore, negative values of GCA and SCA effects indicated contributions toward resistance against downy mildew, while positive values indicated susceptibility. The potential to transmit the disease resistance characteristic from the parents to the progenies is suggested by a negative GCA effect. Therefore, 'NY65.0551.05', which showed positive GCA effects, is not desirable. The significantly negative GCA effects of 'NY88.0517.01' and 'NY65.0550.04' (-0.46 and -0.37, respectively; Table 3), suggested that these genotypes might be effective parents in breeding for downy mildew resistance. On the other hand, the GCA effects of the female parents were not significantly different. 'Black Queen', which was determined to be the most susceptible female parent, also showed a positive GCA effect, while 'Carolina Black Rose' and 'Italia' showed negative GCA effects (Table 3). 'Carolina Black Rose' was found to be the most effective female parent. Its progenies showed high germination rates, seedling survival, and vegetative growth. In addition, the highest number of resistant seedlings (36.7%) was obtained when 'Carolina Black Rose' was used as the female parent.

Anthracnose resistance

The anthracnose disease severity data from F_1 hybrids and their parents were analyzed and mean squares from the analysis of variance are shown in Table 4. Highly significant differences in mean lesion scores were found among grapevine genotypes (P < 0.01). The contrasted comparison between parents and hybrids was not significant (P > 0.05). However, highly significant differences were found among parents and among hybrids (P < 0.01), demonstrating the high genetic variability within each group.

Table 3. Estimates of general combining ability (GCA) effects for downy mildew disease reaction on 6 parental genotypes.

Parents	GCA
NY88.0517.01	-0.46 **
NY65.0550.04	-0.37 **
NY65.0551.05	0.84
Black Queen	0.26
Carolina Black Rose	-0.11
Italia	-0.13

**P < 0.01.

Table 4. Mean squares from analysis of variance for anthracnose disease reaction of parents and hybrids.

Sources	d.f.	SS	MS	F (test)
Treatments	10	7.57	0.76	11.65**
Parents *vs* hybrids	1	0.03	0.03	0.46^{ns}
Parents	4	6.27	1.57	24.12**
Hybrids	5	1.27	0.25	3.91**
Error	117	7.64	0.07	
Total	127	15.21		

**P < 0.01; ^{ns}P > 0.05; CV (%) = 11.94.

Between female parents, 'Black Queen' showed a higher lesion score than 'Carolina Black Rose' (4.6 and 3.9, respectively). This result is in agreement with field observations, in which 'Black Queen' was observed to be consistently more susceptible than 'Carolina Black Rose' across different years of field evaluations (Poolsawat et al., 2012). The only male parent with a substantially low lesion score was 'NY65.0550.04' (1.0), whereas the others ('NY88.0517.01' and 'NY65.0551.05') exhibited lesion scores comparable to susceptible female parents under high disease pressure in an excised leaf assay (4.0 and 4.7, respectively). It is interesting to note that 'NY65.0550.04' may inherit the downy mildew and anthracnose resistance gene(s) from its wild *Vitis* progenitors, such as *V. riparia*, *V. rupestris*, *V. labrusca*, and/or *V. lincecumii*.

Reaction of F_1 hybrids from all crosses to anthracnose varied considerably from highly resistant (1.0) to highly susceptible (5.0). Resistance levels were classified into three groups: resistance (lesion scores = 1 and 2), moderate (lesion score = 3), and susceptible (lesion scores = 4 and 5). Although the majority of F_1 hybrids were susceptible (51.6%), resistant (27.1%) and moderate (21.3%) F_1 hybrids, which may be useful for future breeding programs, were also identified. Among the six crosses, the cross between 'Carolina Black Rose', a less susceptible female parent, and 'NY65.0550.04', the most resistant male parent, had the highest proportion of resistant seedlings (44.4%). Therefore, this is potentially the best parental combination for the development of anthracnose-resistant hybrids. Similarly, this cross combination is also the best for producing downy mildew-resistant hybrids. Recently, we found three resistance gene analog (RGA)-single-strand conformation polymorphism (SSCP) markers that were associated with downy mildew and anthracnose resistance in crosses using 'NY65.0550.04' as a resistance source. These markers could be used to accelerate the selection process for improved downy mildew and anthracnose resistance, particularly in the 'Carolina Black Rose x NY65.0550.04' cross in future breeding programs (Tantasawat et al., 2012).

Combining ability analysis mean squares for GCA effects of males and females as well as SCA effects in six crosses after inoculation with isolate Nk4-1 are presented in Table

5. Highly significant differences (P < 0.01) in GCA effects for males were indicated, but no GCA effect was observed for females. The source of variation was not significant for the interaction between male and female effects, suggesting that the SCA effect was not evident. The relative importance of the mean squares for GCA and SCA were 25.5:1, 4.3:1, and 0.2:1 for GCA (males):GCA (females), GCA (males):SCA, and GCA (females):SCA, respectively. Similar to results of downy mildew resistance, these results indicated the predominance of additive genetic effects over other types of gene action, and that the male parents used in this experiment contributed more additive gene effects to the inheritance of anthracnose resistance than female parents. The narrow sense heritability for anthracnose resistance was estimated at 79.2%. The high heritability may reflect the prevalence of additive gene action over non-additive gene action, as well as relatively low environmental effects. This is in agreement with a previous report by Mortensen (1981), which showed that anthracnose susceptibility/resistance was controlled by only three genes, two dominant genes (An_1 and An_2) for susceptibility, and one dominant gene (An_3) for resistance.

Table 5. Mean squares from analysis of variance for general (GCA) and specific (SCA) combining ability of anthracnose resistance.

Sources	d.f.	SS	MS	F (test)
Hybrids	5	1.27	0.25	2.88*
GCA (females)	1	0.02	0.02	0.17^{ns}
GCA (males)	2	1.02	0.51	5.78**
SCA	2	0.24	0.12	1.33^{ns}
Error	79	6.95	0.09	
Total	84	8.22		

*P < 0.05; **P < 0.01; ^{ns}P > 0.05; CV (%) = 13.86.

The GCA effects were calculated from means of the anthracnose disease reaction in each parent (Table 6). Because the anthracnose lesion score of 1 represented high resistance and the score of 5 represented high susceptibility, negative values of GCA effects demonstrated contribution toward the resistance against anthracnose, while positive values indicated susceptibility. The highest negative and the most highly significant GCA value was observed for ‘NY65.0550.04’. Therefore, it should possess a high frequency of anthracnose resistance gene(s) and should be an effective parent for genetic improvement of grapevines for anthracnose resistance. On the contrary, ‘NY65.0551.05’ and ‘Black Queen’ showed positive GCA effects for the disease response to Nk4-1. In particular, ‘NY65.0551.05’, which possessed the largest positive GCA effect, should not be used to improve anthracnose resistance.

Table 6. Estimates of general combining ability (GCA) effects for anthracnose disease reaction on 5 parental genotypes.

Parents	GCA
NY88.0517.01	-0.12
NY65.0550.04	-0.43**
NY65.0551.05	0.55
Black Queen	0.03
Carolina Black Rose	-0.04

**P < 0.01.

Our results provided evidence for the prevalence of additive over non-additive gene actions for downy mildew and anthracnose resistance in grapevines. This was supported by the high narrow sense heritability of downy mildew and anthracnose resistance (55.6 and 79.2%, respectively), which implied high potential achievement in grapevine breeding for resistance to both diseases. The 'Carolina Black Rose x NY65.0550.04' cross is recommended for future improvement of downy mildew and anthracnose resistance.

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