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Variability and Heritability of Several Important Traits for Grape Production and Breeding

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Abstract

Yield capacity, quality of grapes and resistance to downy mildew attack remain the important breeding objectives for grape. For these traits were analyzed more than 2200 F_1 hybrids, belonging to eight combinations of wine grape. In each combination cv. Gewürztraminer was used, both as maternal and as paternal genitor, the other genitor being represented by an interspecific selection, rated as highly resistant to diseases (derived from Saint Emilion x Rayon d'or and Seyve-Villard 12-375 x Queen of Vine combinations). The rating of susceptibility to downy mildew in the tested hybrid individuals was performed in natural conditions of infection by visual observation and scored from "0" (no infection on leaves) to "5" (very severe infection), and the scale 1-5 was used for bunch number per hybrid and sugar content in grape must. Obvious differences for analysed traits were noted both among the studied combinations and within the same combination, depending on whether 'Gewürztraminer' has been used as maternal or as paternal genitor. These results suggest possible maternal effects on the phenotypic expression of these traits in grape vine. Variability indices (s%) were high and very high in all combinations (22.1-39.4% for response to *Plasmopara viticola* attack; 24.7-29.7% for bunch number per vine; 32.4-44.0% for sugar content in must, offering a good background for an efficient selection. The characters seem to be polygenically inherited, with high and very high heritability indices in the broad sense. The low values computed for heritability in the narrow sense suggest that except additive effects, epistasis and dominance effects have an important role in the phenotypic expression of vine yield capacity, sugar content of the must and resistance to downy mildew attack.

Keywords: grape, breeding, downy mildew, sugar, bunch, heritability

Introduction

The practical process of obtaining and promoting some wine grape cultivars with resistance to cryptogamic diseases, with agro-productive traits, qualitatively similar or superior to sensitive cultivars regarding the diseases attack still existing in the crop, contributes to the reduction of productivity costs and to the increase of working productivity in vine growing, as well as to the reduction of pollution (Oprea, 1998; Oprea and Moldovan, 1999; Sestras, 2004).

In wine grapes, the producing of downy mildew – *Plasmopara viticola* (B. et C.) Berl. et de T. – resistant cultivars represents an extremely important breeding objective, and at the same time, it maintains its topicality in all centres for grape cultivation worldwide.

Two genetic systems are implied in the inheritance of resistance to downy mildew: a monogenic system, responsible for the emergence of necrosis in stomatal tissues and a polygenic system, which prevents the spread of mycelium in the host-plant's leaves (after Boubals, 1959; Coutinho, 1963, quoted by Einset and Pratt, 1975; Cazaceanu et al., 1982; Moldovan, 1998). The resistant cultivars belonging to European wine grape species - *Vitis vinifera* – possess the monogenic system, being recessive homozygote for the resistance locus (Boubals, 1959). American species and some East-Asian ones possess minor genes for resistance to this disease, so that a part of them have been and are still used in breeding programmes (Boubals, 1956; Husfeld, 1961; Olmo, 1971; Rives, 1979; Potapenko, 1981; He and Wang, 1986; Oprea, 1996; Nikolic, 1997; Patil et al., 1997; Song RunGang et al., 1998; Sestras et al., 2006). A large variability of responses to downy mildew is manifested among *vinifera* cultivars, but Husfeld (1961) noticed that of these, not even the resistant cultivars, used in artificial cross-breeding are capable of giving birth to offspring in a profitable proportion for selection - that represent favourable transgressions (resistant or very resistant vines). In the experiments made by Brown et al. (1999), the general combining capacity of some wine grape combinations (CGC), regarding the offspring response to downy mildew was significantly superior to the specific combining capacity (CSC), so that the authors in question think that, in wine grapes' inherited resistance to downy mildew, the additive effects of genes play the most important role. Brown et al. (1999) noticed that maternal inheritance is not involved in transmitting the resistance to downy mildew.

Glucose and fructose are the predominant sugars in progeny of table grape cultivars; in their berries, there is only trace amounts of sucrose (Huai-Feng et al., 2006; Kitazaki et al., 1998). In Huai-Feng and collaborators' experiment, total sugar content showed additive inheritance and the broad-sense heritability ranged from 0.61 to 0.84. The means of progeny sugar content were lower than mean parent values. This could be explain by the intensity of selection and selection pressure because of the long time to grape cultivation (Sestras, 2004).

Materials and methods

The experiment was conducted at the Wine Research and Development Station Blaj, in the Centre of Transylvania, Romania. More than 2200 F_1 hybrids have been studied on their own roots, resulted from hybridization between Gewürztraminer and various inter-specific selections created in Blaj, from complex inter-specific hybrids. The selections used as genitors have been characterized as showing a good resistance to downy mildew, a trait inherited from their parents: Saint Emilion x Rayon d'or – selections II 125-14 and II 125-15, respectively Seyve-Villard 12-375 x Queen of Vine – selections II 157-3 and II 154-14.

The assessment of the response to downy mildew (*Plasmopara viticola*) has been performed under natural infection environment, in the absence of phytosanitary treatments, every hybrid plant from the selection fields being rated regarding the attack on leaves, on a scale from 0 to 5. The assessment was individually performed, for a period of three consecutive years, in the middle of July, the hybrids being in their 3rd - 4th – 5th year of age (since their obtaining from seeds). The used assessment system has comprised scores corresponding to the following levels of resistance to downy mildew:

0 = no attack;

1 = very low attack (very little and small patches on the leaves);

2 = low attack (small but many patches on the leaves);

3 = medium attack (leaves having medium and many patches or big and rare patches, with greasy aspect due to the appearance and development of fungal fructifications);

4 = severe attack (large, many patches on the leaves, greasy aspect);

5 = very severe attack (greasy leaves with very large and adjacent patches).

The productivity potential of hybrids was analyzed by marks, during two consecutive years, in the 5-6 year age of vines, depending of the bunch number per vine (hybrid):

1 = under 5 bunch per hybrid;

2 = 6-10 bunch per hybrid;

3 = 11-15 bunch per hybrid;

4 = 16-20 bunch per hybrid;

5 = more than 20 bunch per hybrid.

The sugar content of the juice (freshly pressed grapes juice - must) of F_1 hybrids was appreciated in gramme/liter and hybrids were framed in the five classes, using the marks as follows:

1 = under 140 g/l;

2 = 140-160 g/l;

3 = 161-180 g/l;

4 = 181-200 g/l;

5 = over 200 g/l.

For all traits, the scores were calculated as mean value over a three years period, per individual, and then within each hybrid combination, using adequate statistical methods of calculation. A method of variance analysis using the "t" test (Student), was applied, calculating the variability (s%) and heritability indices – in a broad sense (H^2) and in a narrow sense (h^2) for the studied traits (Masiukova, 1979).

In order to prove, as clear as possible, the action of the genetic effects on the analyzed traits, the assessment were differentially performed, by forming groups of hybrids according to their provenience and the type of hybridization used. Thus, the possible maternal effects were assessed from the reciprocal and direct hybridizations and the decomposition of genetic variance for heritability computation was performed in a cyclic hybridization in which Gewürztraminer has participated both as paternal and as maternal tester. The statistical model used was that of half SIB families, suggested by Masiukova (1979).

Results and discussion

Table 1 presents data regarding the total number of hybrids that were analyzed within each hybrid combination and their inclusion into a certain rate of downy mildew response attack.

The number of hybrids used in combinations was between 136 (Gewürztraminer x II 125-15) and 493 (Gewürztraminer x II 154-14), resulting a mean of 286 hybrids per combination.

The hybrids falling into a certain group of downy mildew response, according to the scores obtained, show great differences among the studied combinations. Remarkably, none of the hybrid plants was rated "0" which means that, practically, none of the 2220 individuals prove to be immune to disease. Each variant contained hybrids having different levels of resistance to downy mildew, starting

Table 1 Rates of resistance to downy mildew in F1 wine grape hybrids obtained vfrom different types of combinations with Gewürztraminer

	Hybrid combination	Total number of F_1 analyzed hybrids	Rates of response to downy mildew (scale: 1 = no attack, to 5 = very severe attack)					
			0 (no attack)	1 (very low attack)	2 (low attack)	3 (medium attack)	4 (severe attack)	5 (very severe attack)
1	Gewürztraminer x II 125-15	136	-	4	8	22	90	12
2	II-125-15 x Gewürztraminer	240	-	29	36	91	38	46
3	Gewürztraminer x II 125-14	208	-	8	12	14	114	60
4	II-125-14 x Gewürztraminer	240	-	10	25	34	137	34
5	Gewürztraminer x II 157-3	485	-	10	43	84	260	88
6	II 157-3 x Gewürztraminer	233	-	18	28	75	98	14
7	Gewürztraminer x II 154-14	493	-	12	65	89	229	98
8	II 154-14 x Gewürztraminer	255	-	15	17	18	154	51

with hybrids that had shown no attack whatsoever (very low attack) and ending with very severe attacks.

The hybrids generally falling into middle classes for the bunch number per hybrid and for sugar content in freshly pressed grape juice (tables 2 and 3), but there were individuals in each classes, with differences between the studied combinations.

The mean rates of the downy mildew in F_1 hybrids of each combination are presented in table 4. Table 4 also shows the mean error (s_x), the difference of rates and the significance of those differences comparing the experiment mean, taken as control, and the variability of trait regarding the response of plants to downy mildew, calculated per hybrid combination and experiment.

The best response to downy mildew was noted in the hybrids of variant 2 (II 125-15 x Gewürztraminer), whose mean was 3.15 and showed that this combination has produced the less susceptible to downy mildew offspring, considering the entire experiment.

Comparing the experience mean, considered as control, a low mean of rates for downy mildew has been registered in offspring from crosses II 157-3 x Gewürztraminer. Moreover the analysis of variance by "t" test indicates that of the eight tested combinations, only variants 2 and 6 obtained differences of the medium rates for downy mildew, inferior to the experiment mean and ensured from statistical point of view. As it is shown in table 4, those differences are very significant, negative.

The most sensitive hybrids to *Plasmopara viticola* natural infection have been obtained in the combination Gewürztraminer x II 125-14, in which the mean (3.99) is extremely close to the rate that signifies a very severe attack of downy mildew and which has a very significant difference deviation, comparing with the experience mean.

The offspring from crosses Gewürztraminer x II 157-3 and II 154-14 x Gewürztraminer, whose rates mean was significantly superior to the experiment mean, present susceptibility to disease.

This fact demonstrates that, of the eight hybrid combinations of this experiment, two of them produced offspring less susceptible to downy mildew (variants 2 and 6), three have produced offspring relatively susceptible to downy mildew (variants 3, 8 and 5), and other 3 variants (1, 4 and 7) have had a similar response to the one resulted

Table 2 Rates regarding the bunch number per hybrid at F_1 wine grape hybrids from different types of combinations with Gewürztraminer

Crt. no.	Hybrid combination	Total number of F_1 analyzed hybrids	Rate (mark) according to the bunch number per hybrid (scale 1-5: mark 1 for under five bunch – 5 over 20 bunch)				
			≤ 5 (mark 1)	6-10 (mark 2)	11-15 (mark 3)	16-20 (mark 4)	> 20 (mark 5)
1	Gewürztraminer x II 125-15	136	6	44	66	19	1
2	II-125-15 x Gewürztraminer	240	1	82	128	23	6
3	Gewürztraminer x II 125-14	208	6	77	87	34	4
4	II 125-14 x Gewürztraminer	240	7	36	135	54	8
5	Gewürztraminer x II 157-3	489	13	90	233	118	35
6	II 157-3 x Gewürztraminer	233	3	74	99	48	9
7	Gewürztraminer x II 154-14	493	8	149	235	90	11
8	II 154-14 x Gewürztraminer	255	3	100	113	36	3

Table 3 Rates regarding the number of F_1 wine grape hybrids, including in certain classes for sugar content in freshly pressed grapes juice (must), from different types of combinations with Gewürztraminer

Crt. no.	Hybrid combination	Total number of F_1 analyzed hybrids	Number of hybrids framed into certain classes for sugar content in freshly pressed grapes juice (must):				
			<140 g/l	140-160 g/l	161-180 g/l	181-200 g/l	>200 g/l
1	Gewürztraminer x II 125-15	136	4	8	22	90	12
2	II-125-15 x Gewürztraminer	240	29	36	91	38	46
3	Gewürztraminer x II 125-14	208	8	12	14	114	60
4	II 125-14 x Gewürztraminer	240	10	25	34	137	34
5	Gewürztraminer x II 157-3	485	10	43	84	260	88
6	II 157-3 x Gewürztraminer	233	18	28	75	98	14
7	Gewürztraminer x II 154-14	493	12	65	89	229	98
8	II 154-14 x Gewürztraminer	255	15	17	18	154	51

per entire experiment, as rates mean, without statistical assurance. It is worth mentioning the fact that crosses that have produced offspring with the lowest medium rate of downy mildew (variants 2 and 6), did not show the same response in their reciprocal combination. On the contrary, if variant 2 reciprocal, in the Gewürztraminer x II 125-15 combination, the difference between the rates mean comparing the control is irrelevant, a really spectacular result appears in direct and reciprocal hybridization, between Gewürztraminer and II 157-3 (variants 5 and 6). Thus, the difference between the rates mean of the two variants is too high (0.50 points) and on the other hand, comparing the rates mean per experiment, the rates deviation of the two types of crossing with the same partners is statistically ensured, although in opposite directions. Also, it may be noted that the significant results regarding the studied trait, in variants 3 and 8, are not confirmed in the reciprocals.

The existing differences between F_1 direct and reciprocal wine grape hybrids, regarding their response to downy mildew natural infection could be explained by the possible maternal effects. Obviously, such an assumption suggests that in wine grape genetic resistance to downy mildew, besides the nuclear genetic factors, extra-nuclear genetic factors are involved, too.

Probably, the inherited resistance to downy mildew involves a greater role of cytoplasmatic heredity in case of originally rustic selections than in the case of modern breeds, in this particular situation, than in Gewürztraminer cultivar). The supposition can be proved by observing that, in both experimental instances, the hybrids showing the best response to disease comes from those hybridisations in which the resistance genitors were used as maternal parent (variant 2 and 6).

This hypothesis does not agree with the results of Brown et al. (1999), who have noticed that maternal effects are not involved in the inheritance of resistance to downy mildew in grape.

The variability of hybrids' response to downy mildew may be considered as high in all the analyzed combinations, as well as per entire experiment. The variability index of rates given for downy mildew attack, calculated per entire experiment, is 28.2% and within different combinations the values are comprised between 22.1% (variant 1) and 39.4% (variant 2). It is obvious that the high values of the variability indices prove that, practically, in every experimental combination there are fair chances of iden-

Table 4 Mean rates of downy mildew attack in F_1 hybrid populations of the eight combinations of the experiment

Crt. no.	Hybrid combination	Mean of rates and mean error $x \pm s_x$	Rate differences comparing to experiment mean (±d)	"t" value	Significance of difference	Variability coefficient (s%)
1.	Gewürztraminer x II 125-15	3.72 ± 0.07	+0.06	0.81	-	22.1
2.	II-125-15 x Gewürztraminer	3.15 ± 0.08	-0.51	6.14	ooo	39.4
3.	Gewürztraminer x II 125-14	3.99 ± 0.07	+0.33	4.68	***	23.5
4.	II 125-14 x Gewürztraminer	3.67 ± 0.06	+0.01	0.15	-	26.8
5.	Gewürztraminer x II 157-3	3.77 ± 0.04	+0.11	2.34	*	24.4
6.	II 157-3 x Gewürztraminer	3.27 ± 0.07	-0.39	5.60	ooo	30.9
7.	Gewürztraminer x II 154-14	3.68 ± 0.05	+0.02	0.40	-	27.5
8.	II 154-14 x Gewürztraminer	3.82 ± 0.06	+0.16	2.38	*	26.7
	Experiment mean (Control)	3.66 ± 0.02	-	-	-	28.2

Difference significance: *, **, ***/o, oo, ooo Significant at P<0.05, 0.01 and 0.001 (positive, respectively negative) tifying hybrids with a good response to downy mildew attack.

It is worth mentioning that the highest s% values have been registered in those combinations with individuals less sensitive to disease, and generally the s% values were lower in those combinations in which sensitive plants prevailed.

The percentage of F_1 hybrids framed in a certain rate of downy mildew, in reciprocal and direct hybridization, is represented graphically in figure 1.

From table 5 data, results that the highest bunch number per hybrid was registered in Gewürztraminer x II 157-3 combination (3.15) and II 125-14 x Gewürztraminer (3.08), and the coefficient of variability oscillated between 24.7% (Gewürztraminer x II 125-15) and 29.7% (Gewürztraminer x II 125-14).

The higher content in sugar was registered (table 6) on the berries from progenies belonging to Gewürztraminer x II 157-3 combination (160.7 g/l) and the lowest one from hybridisation between II 125-14 x Gewürztraminer (148.2 g/l). Because there was a large variability for sugar content in must (s% was comprised between 32.4-44.0%), it can be resumed that in each combination it is possible to find hybrids with a rich sugar content in berries, the hybrid populations offering a good background for an efficient selection.

The percentage of F_1 hybrids framed in a certain rate of bunch number per vine and sugar content of berries, in reciprocal and direct hybridization, represented graphically in figure 2 and 3, confirm the previous data.

Moreover, they assert the supposition according to which, transmitting the resistance to downy mildew, the productivity of wine and quality of grapes, expressed by sugar content, imply important genetic effects. Regarding the genetic determinism of these characters, it seems that the cytoplasmatic heredity plays a different role according to the genitors implied in hybridization and traits, but probably for resistance to *Plasmopara viticola* attack the extra-nuclear heritability factors present a greater proportion in rustic genitors than in noble ones.

The way in which the crosses took place, permitted the framing of obtained offspring according to their provenience into a different type of hybridization. And because Gewürztraminer has been crossed both as maternal and paternal genitor, the same four inter-specific selections have produced two cyclic hybridizations (or top cross types).

Figure 4 illustrates F_1 hybrids' distribution into a certain downy mildew attack rate, in the cyclic hybridization in which Gewürztraminer has been used as maternal and as paternal tester.

It is observed that the offspring proportion having the best response to downy mildew (very low attack) is approximately three times higher in the cyclic hybridization in which Gewürztraminer had participated as paternal genitor, comparing to its utilization as maternal genitor (7.4% : 2.6%). Even the plants' proportion that was registered as having a low attack is higher when Gewürztraminer participated as paternal tester than when used as maternal tester (11.0% : 9.7%). In exchange, the use of Gewürztraminer as maternal tester is increasing the hybrids' frequency with

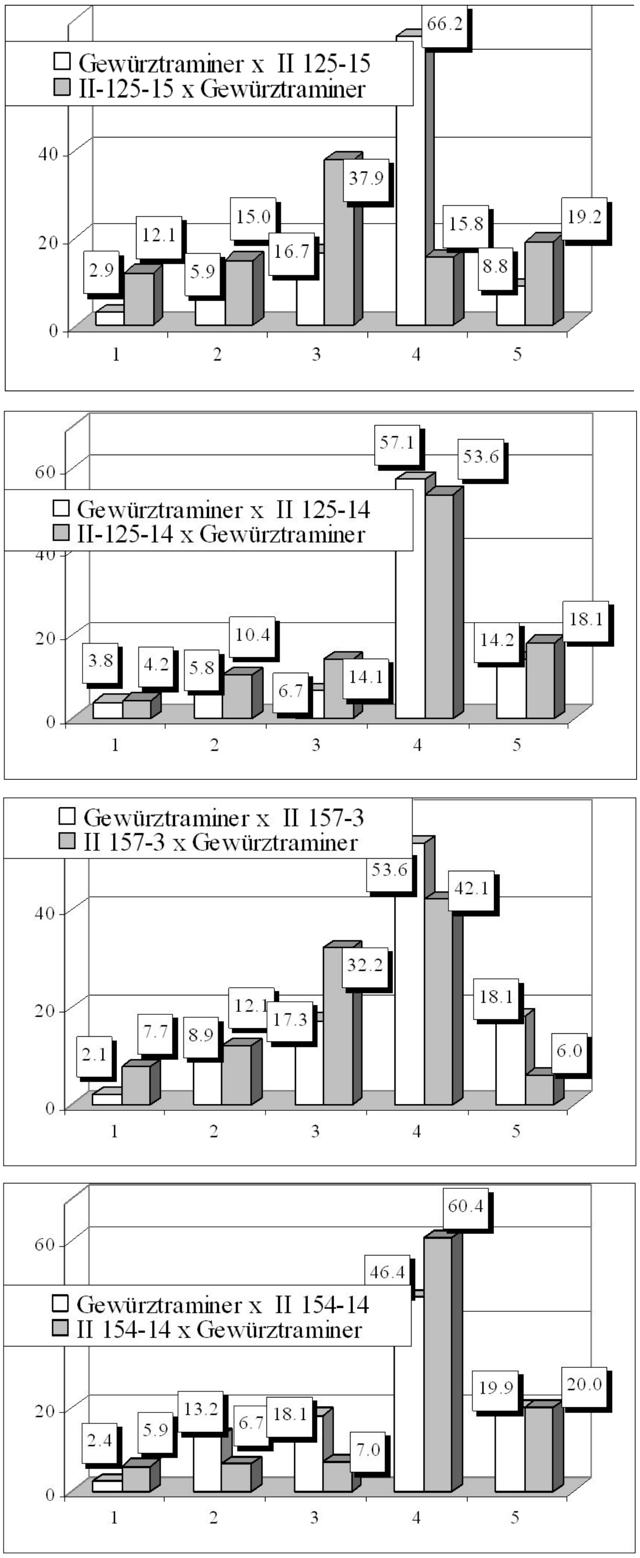

Figure 1 The percentage of F_1 hybrids framed in a certain rate of downy mildew attack (*Plasmopara viticola*) in the direct and reciprocal hybridization from the experiment

Table 5 Mean rates of the bunch number per hybrid in F_1 hybrid populations of the eight combinations of the experiment

Crt. no.	Hybrid combination	Mean of the bunch number per hybrid and mean error $x \pm s_x$	Rate differences comparing to experiment mean (±d)	"t" value	Significance of difference	Variability coefficient (s%)
1	Gewürztraminer x II 125-15	2.74 ± 0.06	- 0.19	3.13	oo	24.7
2	II-125-15 x Gewürztraminer	2.80 ± 0.05	- 0.13	2.63	oo	25.6
3	Gewürztraminer x II 125-14	2.77 ± 0.06	- 0.16	2.68	oo	29.7
4	II 125-14 x Gewürztraminer	3.08 ± 0.05	+ 0.15	2.79	**	25.6
5	Gewürztraminer x II 157-3	3.15 ± 0.04	+ 0.22	5.00	***	28.4
6	II 157-3 x Gewürztraminer	2.94 ± 0.06	+ 0.01	0.17	-	29.0
7	Gewürztraminer x II 154-14	2.89 ± 0.04	- 0.04	1.01	-	27.4
8	II 154-14 x Gewürztraminer	2.75 ± 0.05	- 0.18	3.58	ooo	27.4
	Experiment mean (Control)	2.93 ± 0.02	-	-	-	28.1

Difference significance: *, **, ***/o, oo, ooo Significant at P<0.05, 0.01 and 0.001 (positive, respectively negativ

very severe disease attack (19.5% vs. 15.0% - representing the hybrids with the same attack level as Gewürztraminer used in paternal form).

Considering the hybrids distribution into a certain rate of downy mildew attack, it is obvious that the changes for an efficient selection are much better among the individuals coming from crosses in which Gewürztraminer has participated as paternal genitor. As in these crosses, the plants proportion having a good response to downy mildew is higher, the probability of identifying and choosing elite plants genetic registered with favourable features, is notably increasing.

For bunch number per vine, the F_1 hybrids distribution had a similar allure both in the cyclic hybridization in which Gewürztraminer was used as maternal and as paternal tester (figure 5). This being given, the proportion of hybrids with high marks (4 and 5) in crosses with Gewürztraminer used as mother, suggests that probability to identify progeny with high yield capacity in these combinations is greater than in combinations with rustic genitors used as maternal parents.

The proportion of descendants with higher content of sugar in berries was evidently greater in combination with Gewürztraminer used as maternal genitor (figure 6).

For class with 161-180 g/l sugar, 40.1% progenies were included, belonging to Gewürztraminer as mother, compared with 32.0% for hybrids results by cyclic hybridization in which Gewürztraminer was used as father. The rate remains similar for the next classes: 181-200 g/l (20.9%:15.4%) and more than 200 g/l (3.2%:2.6%).

In accordance with F1 hybrids distribution into certain classes for sugar content, the probability to identify descendants with higher content is expanded in family combinations in which Gewürztraminer participated as mother genitor.

The inheritance of analyzed traits was assessed as polygenic on the ground that, firstly the presented experimental data and previously discussed information proved that offspring hybridization has not produced plants with total resistance (immune) to disease even if each combination included resistant-to-disease genitors. At the same time, in every family (the hybrid population), the individuals

Table 6 Mean rates of the sugar content (g/l) in freshly pressed grapes juice (must) in F_1 hybrid populations of the eight combinations of the experiment

Crt. no.	Hybrid combination	Mean of rates (g/l) $x \pm s_x$	Rates difference comparing to experiment mean (±g/l)	"t" value		Variability coefficient (s%)
1	Gewürztraminer x II 125-15	156.1 ± 6.7	+ 2.4	1.07	-	33.7
2	II-125-15 x Gewürztraminer	153.6 ± 4.2	- 0.1	0.66	-	32.9
3	Gewürztraminer x II 125-14	154.0 ± 3.8	+ 0.3	0.41	-	38.0
4	II 125-14 x Gewürztraminer	148.2 ± 4.4	- 5.5	4.65	ooo	37.5
5	Gewürztraminer x II 157-3	160.7 ± 3.2	+ 7.0	6.52	***	32.4
6	II 157-3 x Gewürztraminer	152.4 ± 4.0	- 1.3	1.35	-	36.9
7	Gewürztraminer x II 154-14	153.2 ± 3.1	- 0.5	1.50	-	35.0
8	II 154-14 x Gewürztraminer	151.3 ± 3.9	- 2.4	2.18	o	44.0
	Experiment mean (Control)	153.7 ± 2.3	-	-	-	36.3

Difference significance: *, **, ***/o, oo, ooo Significant at P<0.05, 0.01 and 0.001 (positive, respectively negative)

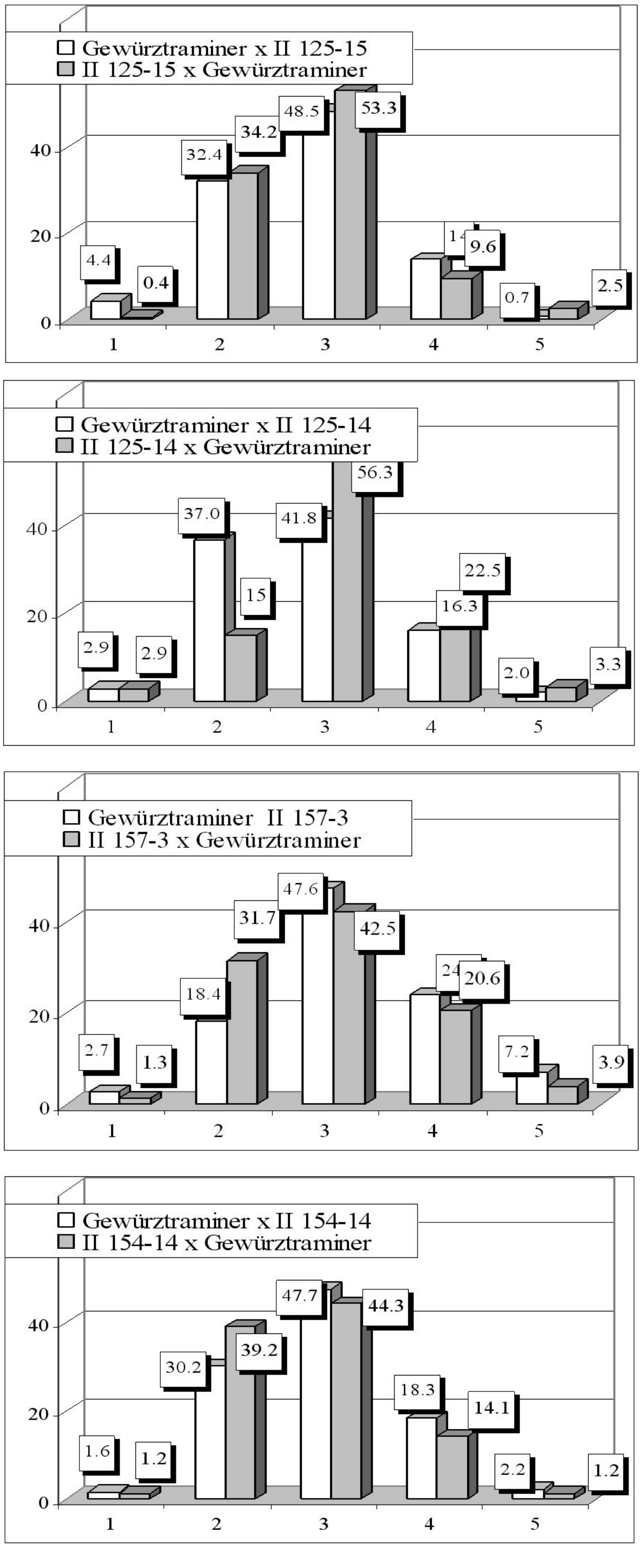

Figure 2 The percentage of F1 hybrids framed in a certain rates for bunch number per vine in the direct and reciprocal hybridization from the experiment

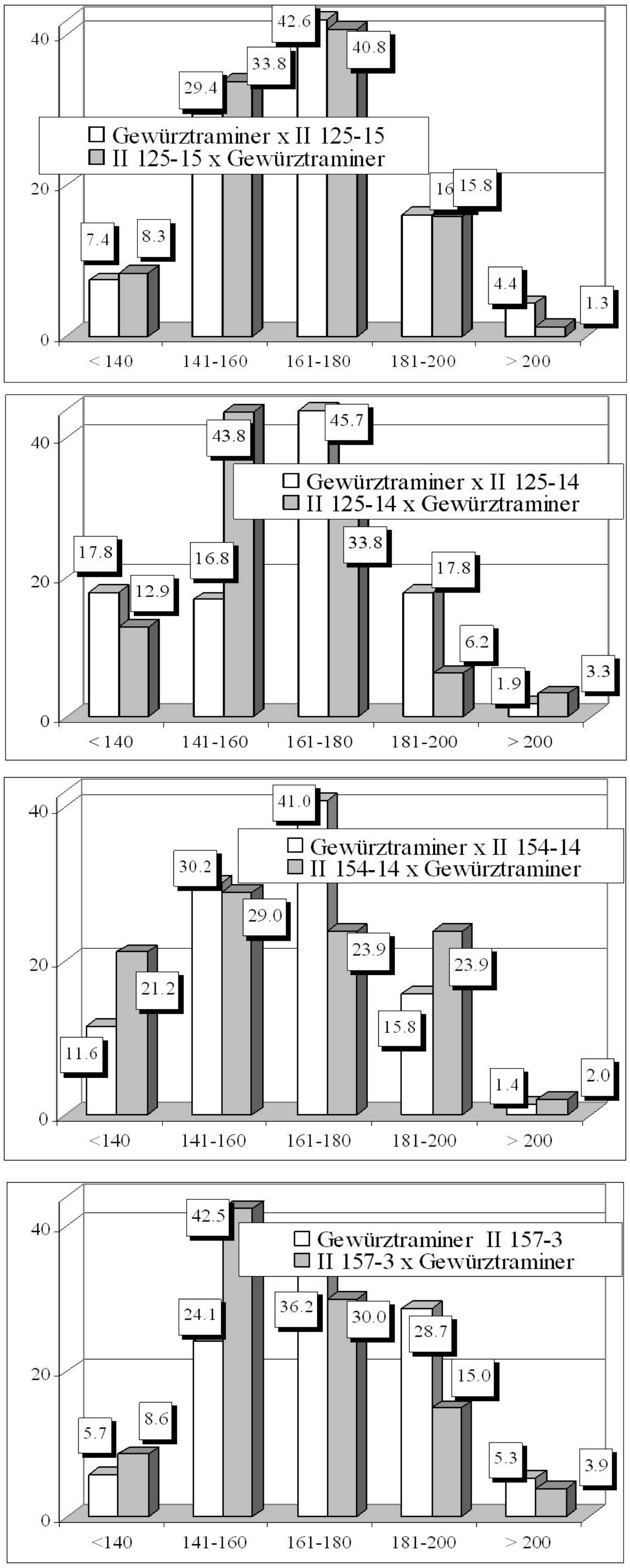

Figure 3 The percentage of F1 hybrids framed in a certain rates for sugar content of the berries in the direct and reciprocal hybridization from the experiment

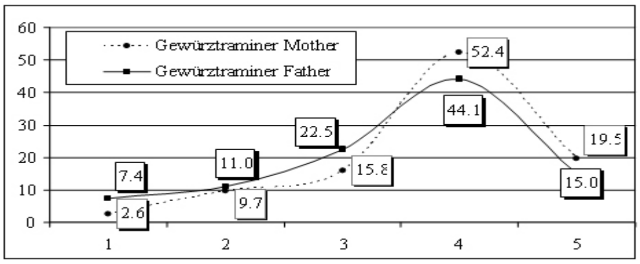

Figure 4 The F_1 hybrids percent distribution into a certain rate of downy mildew attack (1-5), in the cyclic hybridization in which Gewürztraminer was both used as maternal and as paternal tester

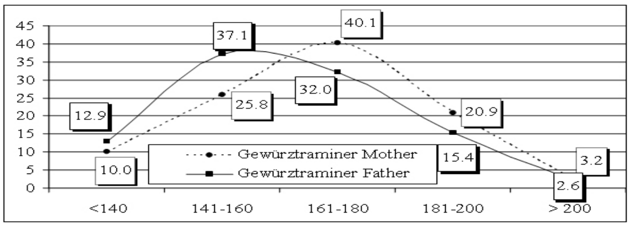

Figure 6 The F_1 hybrids percent distribution into a certain rate for sugar content of berries (g/l), in the cyclic hybridization in which Gewürztraminer was both used as maternal and as paternal tester

distribution considering their response to downy mildew attack, but also for bunch number per vine and sugar content in must, took place according to a specific row of variation for a quantitative trait. Finally, the upper results have been correlated with information from specialty literature, according to which "the resistance to downy mildew is polygenically determined in the hybrids offspring, studied among *vinifera* cultivars and some American cultivars" (Boubals, 1962, quoted by Cazaceanu et al., 1982), and the bunch number per vine and sugar content in the must are poligenically inherited, too (Wei et al., 2003; Sestras, 2004).

The heritability indices in a broad sense (H^2) showed high values in both types of cyclic hybridizations: 0.739 for sugar content and 0.956 for response to downy mildew attack (table 7).

For response to downy mildew attack, the heritability indices in a broad sense (H^2) have high values in both the cyclic hybridization: 0.839 where Gewürztraminer was used as maternal tester and 0.956 when Gewürztraminer was used as paternal tester. In addition, in phenotypic manifestation of other analyzed traits, the genotype has a superior participation rate comparing to other environmental influences.

But the analysis of heritability indices in the narrow sense (h^2), ascertains lower values than indices in broad sense, proving that it is not the additivity which plays the greatest role in the genetic determinism of the traits, but the epistatic and dominant effects. The large differences between (h^2) values in both types of cyclic hybridizations illustrate the notable effect that genitors' position has in achieving an acceptable level of inherited resistance in the

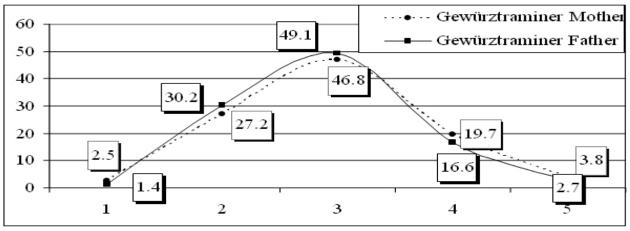

Figure 5 The F1 hybrids percent distribution into a certain rate for bunch number per vine (1-5), in the cyclic hybridization in which Gewürztraminer was both used as maternal and as paternal tester

hybrid combinations, respectively upon expressing resistance to downy mildew in offspring, productivity capacity and sugar content.

The heritability indices in a narrow sense (h^2) have low values in both cyclic hybridizations. For bunch number per vine and sugar content in the must, h^2 values were lower when Gewürztraminer was used as father tester comparing to its use as a maternal tester.

In the cyclic hybridization with Gewürztraminer used as maternal tester, the additivity had a reduced effect in the inheritance of response to downy mildew attack, comparing to the dominance and interaction effects (h^2=0.055). The facts are the opposite when Gewürztraminer is used as paternal tester, in which case h^2 has a remarkable high value (0.316), meaning that in these types of crosses the cumulated effects of homozygote genes ensure a great capacity of transmitting and conserving the desired trait in the offspring.

The enunciated considerations by using the heritability indices values in the two types of cyclic hybridization may have a special importance, both theoretically and practically for grape breeding, even though a certain relativity level still persists regarding the objectivity of obtained information. This relativity is due to the fact that the maternal effects were not taken into consideration in heritability calculation. Besides, apart from the disregard for cytoplasmatic heredity, the model used for variance decomposition is based only on half sib families with one single tester, a fact that reduces its safety and precision.

It is possible that the additivity, together with the epistasis and dominance interactions, play a more important role in the inheritance of resistance to downy mildew in grape offspring when more rustic genitors participate to hybridization as maternal parent, situation in which they show a high capacity of combination for the analysed trait. By using the Gewürztraminer as genitor (a valid assumption for other *vinifera* cultivars, also) offspring resistant to downy mildew attack can be produced, due to the transgressions appearing in the polygenic case. This is not exclusively due to the additivity, but for the antagonic and unequal effects of the alleles, too. The specific combining capacity of Gewürztraminer with interspecific selections in the experiment explains the differences between the

Table 7 The heritability of the analysed traits in the cyclic hybridization with Gewürztraminer cultivar, used as maternal and as paternal tester

Gewürztraminer used as Tester		Heritability coefficient	
Trait	Paternal form	in broad sense (H^2)	in narrow sense (h^2)
Response to downy mildew attack	Maternal	0.839	0.055
	Paternal	0.956	0.316
Bunch number per vine	Maternal	0.941	0.192
	Paternal	0.903	0.130
Sugar content in must	Maternal	0.935	0.167
	Paternal	0.739	0.030

families that have had it as common genitor, either as maternal or paternal parent.

Conclusions

By reciprocal and direct crosses of Gewürztraminer with different interspecific selections, resistant to downy mildew, resulted offspring whose distribution was typical quantitative, regarding the response to *Plasmopara viticola*, but also for bunch number per vine and sugar content of berries.

None of the obtained F_1 hybrids was rated as "0" for downy mildew attack (no attack). Yet, the selection of some plants with much more resistance to downy mildew can be efficient in each family (hybrid population) for the reason that each studied combination contained individuals with low and very low attack, which offers a good selection base from this perspective.

Some of the reciprocal and direct combination contained great differences between the rates mean regarding the hybrids' response to downy mildew, production potential and sugar content of berries, meaning that cytoplasmatic effects are intervening in genetic determinism of the traits. The hybrids with the best response to downy mildew attack have prevailed in those combinations in which the resistance genitor was used as maternal tester. In addition, the number of hybrids with high content of sugar in berries was superior in combinations with Gewürztraminer used as mother.

Even if the participating rate of genotype in the phenotypic manifestation of the analysed traits in F_1 hybrids is considerably great, besides the additivity effects, an important role in trait's inheritance was played by epistasis and dominant effects.

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