Vitis 6, 129—135 (1967)

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Inheritance of Flower Type in Some Grape Varieties (Vitis vinifera L.)

by

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Introduction

Cultivated grape varieties of *Vitis vinifera* L. usually have hermaphrodite flowers, only a small number have functionally female flowers. No commercial varieties, however, posses functionally male flowers only. Because of the fact that the flowers can influence the yield of some grape varieties considerably, most of the previous research work had been devoted to determine and describe the flower type of cultivated grape clones. Less work has been published concerning inheritance of flower type in grape varieties.

According to the available literature, Hedrick and Anthony (1915) were the first who tried to explain the way of inheritance of flower type in grape varieties. By selfing the varieties with hermaphrodite flowers they produced seedlings with either hermaphrodite or female flowers. The appearance of male flowers in the progenies was associated with the use of one of the parent with male flowers. Hedrick and Anthony's interpretation of their experimental results were criticized by Rasmusson (1916) and Valleau (1916).

A genetical scheme of inheritance of flower type — Müller-Thurgau and Kobel (1924) — is based on two pairs of genetical factors which control flower types. These two factors are able to recombine, thus, no linkage exists. By their recombinations it is possible to get even assexual individuals, i. e. without male and female sexual organs. Furthermore, according to the same scheme, crossing varieties with hermaphrodite flowers, it is expected to receive seedlings with male flowers only. As far as we know, none of these gene combinations have been found in progenies. Therefore, the hypothesis of Müller-Thurgau and Kobel cannot be accepted.

Negrul (1936) proposed a monofactorial inheritance of flower type in grape varieties. He presented evidence that varieties with female flowers are homozygous for this character.

The most comprehensive work relating to the inheritance of flower types in grape was published by Oberle (1938). On the basis of 613 combinations of crossings and of 103 populations obtained by selfing, the hermaphrodite varieties of *Vitis vinifera* L. were either homozygous or heterozygous, whereas varieties with female flowers were homozygous. His interpretation is that the flowers in grape are controlled by two pairs of genetical factors, located on the same chromosome and linked.

Breider and Scheu (1938) presented the scheme of inheritance of flower type in grape on the basis of the sex chromosome x and y.

The purpose of this paper is to present results of crosses in the course of our grape breeding program which show the genotype of some grape varieties for a given flower type and the way of inheritance. Studies of the genetic constitution are both of practical and theoretical importance. From the practical point of view, this knowledge could be of great value in planning improvement of grape varieties. From

the theoretical point of view, this would be an important contribution in the understanding of the mechanism of sex inheritance in higher plants.

Material and methods

The varieties used as parents were grown in a collection of the Centre for grape breeding at the Fruit Growing and Viticulture Experimental Station „Radmilovac" in Vinca. The technique of crossing, the harvest of hybrid seeds and the production of hybrid seedlings followed the common procedure in breeding of grape varieties as described in detail by Olmo (1955). The flower type of the seedlings was determined by the degree of development of pistils and stamens.

As was indicated by Dorzey (1914), Baranov (cited by Levadoux 1946), Levadoux (1946), Avramov (1956) and others, varieties with functionally female flowers have stamens which are completely reflexed with short filaments. In varieties with hermaphrodite flowers, filaments are not bent downwards and anthers are located at the same level as the stigmatic surface of the pistil. It is well known that, within the same flower cluster, one can find all three types of flowers inclusive intermediate ones (Levadoux 1946). In such cases seedlings with mixed flower types were classified according to the predominant types of flowers.

If, however, functionality of pollen could not be established by visual ovservations, pollen was tested for germination capacity, according to Avramov (1955).

Results

1. Flower types in seedlings obtained by self-pollination of some grape varieties with functionally hermaphrodite flowers.

The results obtained after selfing varieties with hermaphrodite flowers are summarized in table 1. Out of eleven varieties which were self-pollinated, ten produced two kinds of seedlings, i. e. seedlings with hermaphrodite or female flowers.

Table 1

Type of flowers in seedlings obtained by self-pollination of some varieties with hermaphrodite flowers

Number of variety	Variety	Total number of seedlings	Hermaphrodite		Female		χ^2
			Number	Percent	Number	Percent	
1.	Muscat Hamburg	102	85	83,3	17	16,6	3,77
2.	Chasselas buvie	27	19	70,3	8	29,7	0,30
3.	Pearl of Csaba	23	18	78,2	5	21,8	0,12
4.	Italia	6	5	83,3	1	16,7	—
5.	Queen of the vineyards	3	3	100,0	—	—	—
6.	Merlo	69	46	66,6	23	33,4	2,56
7.	Beli Medenac	35	30	85,7	5	14,3	2,13
8.	Bagrina	21	16	76,1	5	23,9	0,14
9.	Semillon	35	24	62,8	11	37,2	0,76
10.	Pinot noir	32	22	68,7	10	31,3	0,66
11.	Prokupac	8	6	75,0	2	25,0	—

Table 2

Varieties with hermaphrodite flowers which after crossing produce seedlings with hermaphrodite flowers only

Number of combination	Parents	Number of seedlings		
		Total	Hermaphrodite Number	Percent
1.	Muscat Hamburg × Žilavka	124	124	100,00
2.	Muscat Hamburg × Datier (Afuzali)	95	95	100,00
3.	Muscat Hamburg × Smederevka	85	85	100,00
4.	Muscat Hamburg × Queen of the vineyards	38	38	100,00
5.	Smederevka × Datier (Afuz-ali)	11	11	100,00
6.	Chasselas buvie × Volovsko oko	9	9	100,00
7.	Prokupac × Traminer red	11	11	100,00
8.	Volovsko oko × Portuguese blue	20	20	100,00
9.	Volovsko oko × Muscat Otonel	14	14	100,00
10.	Smederevka × Muscat Otonel	27	27	100,00
11.	Volovsko oko × Chasselas white	13	13	100,00
12.	Chasselas white × Queen of the vineyards	9	9	100,00

The progeny of the variety Queen of the Vineyards, however, had hermaphrodite flowers only. In a population of 361 seedlings obtained by self-pollination, no seedlings with male flowers could be detected. Thus, the ratio of seedlings with hermaphrodite and female flowers in each individual population was approximately 3 : 1. In order to establish the nature of deviation of the exact 3 : 1 ratio, χ-square values have been calculated; none of them are significant.

2. Flower type in seedlings obtained by crossing varieties with hermaphrodite flowers.

The combinations of such crossings, which resulted in seedlings with hermaphrodite flowers, have been summarized in table 2. No seedlings with female or male

Table 3

Varieties with hermaphrodite flowers which after crossing produce seedlings with hermaphrodite and female flowers

Number of combination	Parents	Number of seedlings					χ^2
		Total	Hermaphrodite Number	Percent	Female Number	Percent	
1.	Muscat Hamburg × Chasselas buvie	14	13	92,86	1	7,14	—
2.	Chasselas buvie × Italia	22	18	81,81	4	18,19	—
3.	Chasselas buvie × Muscat Hamburg	15	14	93,33	1	6,67	—
4.	Prokupac crni × Point noir	86	60	69,77	26	30,23	1,25
5.	Prokupac crni × Gamay	54	45	83,33	9	16,67	—
6.	Pinot noir × Prokupac crni	29	22	75,86	7	24,14	—
7.	Šljiva × Volovsko oko	24	22	91,60	2	8,40	—
8.	Šljiva × Chasselas buvie	13	11	84,60	2	15,40	—

Table 4

The flower sex of seedlings after crossing varieties with female and hermaphrodite flowers

Number of combination	Parents	Number of seedlings				
		Total	Hermaphrodite		Female	
			Number	Percent	Number	Percent
1.	Drenak Crveni × Chasselas buvie	11	8	72,7	3	27,3
2.	Drenak crveni × Italian Riesling	47	43	91,4	4	8,6
3.	Čauš × Chasselas white	20	14	70,0	6	30,0
4.	Čauš × Prokupac	11	10	90,9	1	9,1

flowers were found in any of these populations. Table 3 presents the results of crossing varieties with hermaphrodite flowers which produce two types of seedlings, namely seedlings with hermaphrodite and seedlings with female flowers. More than 70 percent of the seedlings have hermaphrodite flowers. In five combinations, this percentage is even over 90. In this group of crosses no seedlings with male flowers were found.

Due to the small number of seedlings obtained with female flowers, only combination number 4 is tested by χ-square test. Deviation from 3 : 1 ratio in cross number 4 is non significant. Genetical analysis of these data and the relation to the data in table 1 will be given later in this paper.

3. Flower type in seedlings obtained by crossing varieties with functionally heraphrodite flowers.

The results of these crossings are given in table 4. It is evident that the progeny consisted of seedlings with hermaphrodite or female flowers. As in the above mentioned combinations of crossings, here also no seedlings with male flowers were obtained. The ratio of seedlings with hermaphrodite and female flowers varies. Here again, as in table 3, the seedlings with female flowers are in lower percentage than those with hermaphrodite flowers.

Genetical Analysis and Discussion

From the results in table 1 it is evident that nearly all varieties of *Vitis vinifera* L. with hermaphrodite flowers tested are heterozygous for those genetical factors which control hermaphroditism. These results are in agreement with the data presented by HEDRICK and ANTHONY (1915), MÜLLER-THURGAU and KOBEL (1924), NEGRUL (1936), OBERLE (1938) and LEVADOUX (1950), who considered that only a small number of varieties with hermaphrodite flowers are homozygous for hermaphroditism. HEDRICK and ANTHONY (1915), OBERLE (1938) and OLMO (1955) reported that Muscat Hamburg is homozygous for hermaphroditism. Our results, however, show that this variety is to be considered as heterozygous. This disagreement may result from the possibility that, with regard to the flower type, genotypic different clones of Muscat Hamburg exist.

Considering the number of genetical factors which establish flower type, the calculated values of χ-square on the basis of a theoretical ratio of 3 : 1 show, that

a monogenic nature of inheritance is in question, i. e. one pair of factors determine flower type.

MÜLLER-THURGAU and KOBEL (1924), OBERLE (1938) worked out in detail a model by which the flower type of grape varieties depends on two genetic factors. However, their data do not present an experimental evidence. If we designate the factor for production of female flowers with S^f and the factor for hermaphroditism with S^h, the genotype of the varieties tested by selfing are $S^f F^h$. In this formula S^f is recessive to S^h. The recessiveness of a factor which controls female flowers was already established by NEGRUL (1935), HEDRICK and ANTHONY (1915) and OBERLE (1938).

If we proceed on the same line and consider the result of table 2, we come to the conclusion that the varieties Žilavka, Datier, Smederevka, and Queen of the Vineyards are homozygous for hermaphroditism, i. e. $S^h S^h$. By crossing with Muscat Hamburg which is genetically $S^h S^f$ (table 1), only seedlings with hermaphrodite flowers were obtained. This can be presented by the following scheme:

$$S^h S^h \times S^h S^f \rightarrow S^h S^h + S^h S^f.$$

Therefore, all seedlings of the progeny have phenotypically hermaphrodite flowers. On the other hand, if the mentioned varieties were heterozygous, one could expect a population of individuals with female flowers, i. e.

$$S^h S^f \times S^h S^f \rightarrow S^h S^h + S^h S^f + S^f S^f$$

where phenotypically 75 percent of the seedlings develop hermaphrodite flowers and 25 percent female flowers. The combinations of crossing numbers 1 through 4 in table 2 support the first scheme.

In a similar way it can be shown that the variety Volovsko Oko is homozygous for hermaphroditism, i. e. $S^h S^h$. From table 1 we have seen that the genotypical composition of Chasselas Buvie is $S^h S^f$. Crossing this variety with Volovsko Oko (number 6, table 2), only seedlings with hermaphrodite flowers were obtained. However, crossing Šljiva with Chasselas Buvie (combination 8, table 3) gives seedlings with female flowers also, indicating the heterozygous nature of Šljiva, i. e. $S^h S^f$.

Since Prokupac is heterozygous, i. e. $S^h S^f$ (table 1), we may conclude that Traminer due to crossing number 7, table 2, is homozygous, i. e. $S^h S^h$. Likewise, crossing number 5, table 3 indicates the heterozygoty of Gamay ($S^h S^f$).

The genotypical composition of Muscat Otonel cannot be established from crossings number 9 and 10, table 2, since this variety has been crossed only with the varieties which seem to be homozygous. On the other hand, these crossings give evidence to the homozygous character of the varieties Volovsko Oko and Smederevka. The same holds true for variety Portugizac.

Considering the results of the crossings with the variety Chasselas White, it can be seen that this variety is heterozygous, i. e. $S^h S^f$. The experiments of NEGRUL (1936), OBERLE (1938) and LEVADOUX (1950) reveal that varieties with functionally female flowers are homozygous, i. e. $S^f S^f$. By crossing variety Čauš, which is $S^f S^f$ with Chasselas White (cross number 3, table 4), both seedlings with hermaphrodite and female flowers were obtained:

$$S^f S^f \times S^h S^f \rightarrow S^h S^f + S^f S^f.$$

Similarly, Crveni Drenak with the allels $S^f S^f$, when crossed with Italian Riesling (combination 2, table 4), gives a progeny with hermaphrodite and female flowers. That means that Italian Riesling is heterozygous, i. e. $S^h S^f$.

The results of crossing number 7, table 3, are not in agreement with the above mentioned explanations. Regarding the presented data and their interpretation, it would not be expected to have in the progeny of combination 7 individuals with

female flowers, since Volovsko Oko has a genotypical composition of $S^h S^h$. Since Šljiva is heterozygous (combination 8, table 3), the appearance of seedlings with female flowers can only be explained by contamination with pollen from heterozygous hermaphrodite varieties.

The numerical ratios of seedlings with hermaphrodite and female flowers correspond to a monofactorial scheme of inheritance (table 1). However, in table 3, where a 3 : 1 ratio is to be expected, the percentage of seedlings with female flowers is considerably lower than 25 percent. As varieties with functionally female flowers are homozygous ($S^f S^f$), one would expect in the progenies of the crossings of table 4, 50% with hermaphrodite and 50% with female flowers. Here also, seedlings with female flowers are less represented. This phenomenon may be explained by a relatively small population of seedlings in each crossing, by the action of a great number of lethal and semi-lethal factors in some clones of Vitis vinifera, which may disturb the ratio, and the existence of genetic modifiers, which alter the expression of a main genetical factor. In the present phase of research it is difficult to establish the reason of these deviations. It is interesting to note that, if there exists any deviation from an expected ratio of sexes in a progeny, usually heterogametic sex appears in deficit (WESTERGARD 1958). Our results, however, reveal, that obviously homogametic female sex is in deficit.

Summary

This paper presents the results and genetical analysis of crossing grape varieties *Vitis vinifera* L. with regard to the inheritance of flower type. From the results obtained, following conclusions could be drawn:

1. The flower type (hermaphrodite and female) in grape varieties *Vitis vinifera* L. is controlled by two allels. The genetic factor for female flower is designated by S^f and the factor for hermaphroditism by S^h. Factor S^f is recessive to S^h.
2. Varieties with hermaphrodite flower type are either homozygous ($S^h S^h$) or heterozygous ($S^h S^f$) for hermaphroditism. Out of 20 tested varieties with hermaphrodite flowers, 14 were heterozygous and 6 homozygous. The following varieties are homozygous: Datier, Smederevka, Queen of the Vineyards, Volovsko Oko, Traminer Red and Zilavka. Heterozygous varieties are: Muscat Hamburg, Chasselas Buvie, Pearl of Csaba, Chasselas White, Italia, Italian Riesling, Merlo, Beli Medenac, Bagrina, Semillon, Pinot Noir, Prokupac, Šljiva, Muscat Otonel.
3. Varieties with functionally female flowers are probably homozygous, i. e. $S^f S^f$. These are: Čauš and Crveni Drenak. In all combinations of crossings, seedlings having homogametic flower type were in deficit.
4. Considering the improvement of grape varieties it is suggested to use hermaphrodite varieties of the genetic constitution $S^h S^h$.

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Eingegangen am 29. 6. 1966

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