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Department of Viticulture and Enology, University of California, Davis, USA

Studies on sex conversion in male Vitis vinifera L. (sylvestris) [1]

by

S. S. Negi[2]) and H. P. Olmo[3])

Introduction

There are three main flower sex types of *Vitis vinifera* L.: (1) "functionally staminate" or "female sterile" (A in Fig. 1) in which the upright stamens with viable pollen grains are well developed, but the pistil is only rudimentary, without stigma and style and with only a very small ovary containing incompletely developed ovules. Such flowers are usually called "males" and they do not produce fruit; (2) "functionally pistillate" or "male sterile" (B in Fig. 1) in which the pistil is well developed and functional, but the stamens are reflexed, having abundant pollen grains without germ-pores and hence non-functional. Such flowers are usually called "females" and are self-sterile; however, with proper cross pollination and fertilization fruits develop from such flowers and contain one or more normal seeds; (3) "functionally hermaphroditic" (C in Fig. 1) in which the five erect stamens have functional pollen grains and there is a well developed functional pistil. Such flowers are usually called "perfect" and are self-fruitful. All flower types are, however, morphologically hermaphroditic as they have a full complement of stamens and a pistil.

The native vines of *V. vinifera (sylvestris* form) are dioecious whereas most of the cultivated varieties *(sativa* form) are hermaphroditic and self-fruitful (Rathay 1888—1889, Bailey 1934, Negrul 1936, Levadoux 1946). Normally only one type of flower is found on an individual vine. However, in rare instances, the pistils of some flowers on male vines develop to the point that the flowers are functionally hermaphroditic and upon pollination and fertilization develop into seeded berries (Baranov and Rajkova 1929). This appearance of some functionally hermaphroditic flowers and mature seeded berries on male vines may be defined as a natural sex conversion from functionally male to functionally hermaphroditic flowers. Sex conversion in grapevines was first observed by Rathay (1888—1889) and has since been reported in one degree or another in practically all well known species of *Vitis*. The most recent citations are those of Bethmann (1939) and Levadoux (1946).

Most botanists agree that *V. vinifera* L. is indigenous to the region between and to the south of the Black and Caspian seas (Vavilov 1951, Winkler 1962). In 1948, a seed sample was collected from indigenous vines of *V. vinifera* L. *(sylvestris)* growing in a forested area of northweastern Iran. Progeny grown from these seeds in the University of California vineyard at Davis produced both male and female vines in an approximate ratio of 1 : 1. One of the male vines numbered 030-44 on rare oc-

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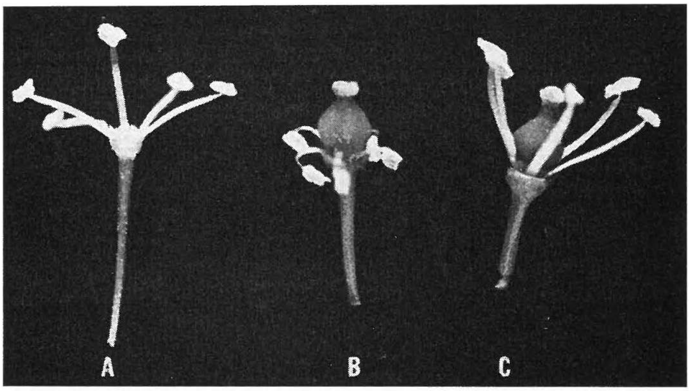
[2]) Geneticist (grapes), Institute of Horticultural Research, 255 Upper Palace Orchards, Bangalore 6, Mysore, India.

[3]) Professor of Viticulture, Dept. of Viticulture and Enology, University of California, Davis, Calif.



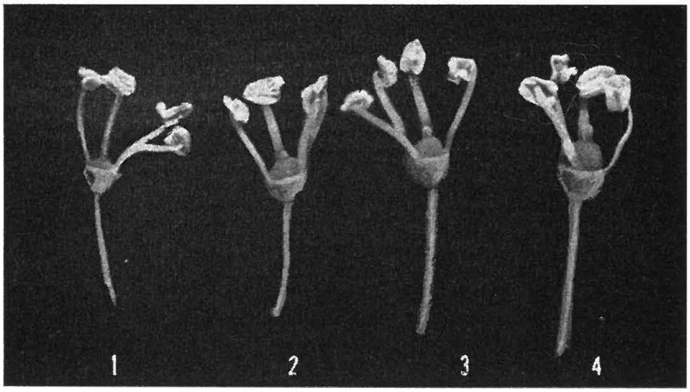


Fig. 1: Main types of individual grape flowers: A, functionally staminate or male; B, functionally pistillate or female; and C, functionally hermaphroditic or perfect, ×5.
Fig. 2: Flower types on *V. vinifera* male vines classified arbitrarily: 1—3, functionally male; 4, functionally hermaphroditic, ×5.

casions showed natural sex conversion by producing a few functionally hermaphroditic flowers and mature seeded berries.

The present investigation was conducted to study the frequency of natural sex conversion in vegetatively propagated vines of the male seedling 030-44 and to determine the influence of vegetative selection for high fruitfulness on the frequency of sex conversion.

Materials and Methods

First unselected vegetative propagation of the seedling 030-44:

The original seedling 030-44 was propagated by budding it on Ganzin 1 rootstock in 1958. The buds taken were selected at random. Thirty one mature vines were available for study in 1964.

Second vegetative propagation selected for high fruitfulness:

In 1961, a second vegetative propagation was made from some vines of the first vegetative propagation of 033-44. Buds were selected, however, from the most fruitful canes that had been marked in 1960. One or two buds from each cane were grafted on Ganzin 1 rootstock (see column 2 in Table 2). Thirty mature vines were available for study in 1967.

Classification of flower types:

The flowers on male vines were arbitrarily classified into 4 types as shown in Figure 2. (1) The pistil is very small and is almost hidden by the nectaries. Neither stigma nor style is conspicuous. Megaspore mother cells differentiate in the ovules, but they may or may not divide. It is a functionally male flower. (2) This type is structurally intermediate between types 1 and 4. The pistil has a small stigma and a short style. Megasporogenesis is normal in that reduction division and a linear tetrad result. A very small embryo sac is formed in some ovules. The megaspore does not divide further and the flower remains functionally male. (3) This type is also morphologically intermediate between (1) and (4), but the pistil is larger than in (2). Reduction division and tetrad formation occur normally and a small embryo sac is formed in many ovules. Degeneration occurs between the 2- and 4-nucleate stage of the embryo sac; hence, the flower is functionally male. The pistil in (4) is well developed with a functional stigma, but it is structurally smaller than in the female (B in Fig. 1) or hermaphroditic (C in Fig. 1) flowers of cultivated varieties. The ovules have complete embryo sacs with normal egg apparatus and polar nuclei. Thus, it is a functionally hermaphroditic flower.

Percentages of seeded berry set and fruitful clusters on male vines:

The frequency of natural sex conversion in a male vine was finally measured by the % seeded berry set. At bloom, the total clusters on a male vine were counted and the position of each was recorded. The flowers in ten clusters at each insertion point (the basal one numbered one) were counted and the average number per cluster per position was calculated. The total number of flowers on a vine was then calculated. At harvest, the total fruitful clusters on a vine was counted. If there were only a few fruiting clusters on the vine, the total seeded berries were counted. When a large number of clusters had berries, the total weight of the mature berries*) was taken first. The weight of a random sample of 20 mature berries was determined and from this the total number of mature berries on the vine was calculated. The % natural seeded berry set per vine was determined by

$$\frac{\text{total mature seeded berries}}{\text{total flowers}} \times 100$$

and the percent fruitful clusters was determined by

$$\frac{\text{total fruitful clusters at harvest}}{\text{total clusters at bloom}} \times 100.$$

Similarly, the total number of normal seeds was determined by actual count when the number of mature berries was small. If a large number of berries matured, the normal seeds in a random sample of 100 mature berries were counted. The average number of normal seeds per berry was calculated by dividing the total number of normal seeds by the total number of mature berries.

Results and Discussion

First vegetative propagation:

Data on flower types, fruitfulness and average number of normal seeds per berry of 31 vines of the first vegetative propagation were obtained in 1967 and 1968

*) In general no mature parthenocarpic berries were observed to develop on male vines.

and are presented in Table 1. In 1967, 90.3% of the vines produced a few functionally hermaphroditic flowers (type 4) and mature seeded berries, while in 1968 only 64.5% of them showed this phenomenon. There was a very close correlation between the number of hermaphroditic flowers present and % seeded berry set. The vines which had a few hermaphroditic flowers had predominantly flowers of types 1, 2 and 3 described previously. Those which did not have hermaphroditic flowers had predominantly types 1 and 2 and a few type 3 flowers. The percentages of fruitful clusters and seeded berry set varied from vine to vine in the same season and in the same vine between seasons. Certain isolated shoots and clusters were found to

Table 1

Flower types, fruitfulness, and average number of normal seeds per berry of 31 vines of first vegetative propagation of the male seedling 030-44

Vine	Flower types 1967 Majority	Flower types 1967 Minority	Flower types 1968 Majority	Flower types 1968 Minority	Fruitful clusters, % 1967	Fruitful clusters, % 1968	Seeded berry set % 1967	Seeded berry set % 1968	Normal seeds per berry avg. 1967	Normal seeds per berry avg. 1968
M5:1	1,2,3	4	1,2	3	13.5	0.0	0.42	0.00	1.06	—
M5:3	1,2,3	4	1,2	3	2.4	0.0	0.09	0.00	0.83	—
M5:5	1,2,3	4	1,2,3	4	18.5	6.9	0.63	0.31	0.98	1.03
M5:7	1,2,3	4	1,2,3	4	12.0	1.8	0.50	0.17	1.00	1.02
M5:9	1,2,3	4	1,2,3	4	14.8	13.6	0.51	0.66	0.82	1.04
M5:11	1,2,3	4	1,2,3	4	10.6	7.0	0.33	0.25	1.01	1.04
M5:13	1,2,3	4	1,2,3	4	24.6	9.6	1.65	0.24	0.98	1.00
M5:15	1,2,3	4	1,2,3	4	22.4	12.5	0.71	1.07	1.01	1.03
M5:17	1,2,3	4	1,2	3	8.6	0.0	0.42	0.00	0.92	—
M5:19	1,2,3	4	1,2,3	4	21.8	1.7	0.48	0.06	1.03	1.08
M5:21	1,2,3	4	1,2,3	4	24.0	1.5	0.37	0.42	0.99	1.22
M5:23	1,2,3	4	1,2	3	4.4	0.0	0.02	0.00	1.00	—
M5:25	1,2,3	4	1,2,3	4	8.3	8.9	0.22	0.28	0.90	1.18
M5:29	1,2,3	4	1,2,3	4	22.4	5.7	0.69	0.25	1.21	1.09
M5:31	1,2,3	4	1,2	3	3.5	0.0	0.37	0.00	1.09	—
M5:33	1,2,3	4	1,2,3	4	13.7	3.4	0.70	0.15	1.00	1.14
M5:35	1,2,3	4	1,2	3	8.0	0.0	0.14	0.00	0.90	—
M5:37	1,2,3	4	1,2	3	5.1	0.0	0.01	0.00	0.89	—
M5:39	1,2,3	4	1,2,3	4	6.8	5.7	0.67	0.16	1.03	0.89
M5:40	1,2	3	1,2,3	4	0.0	1.6	0.00	0.03	—	1.00
M5:43	1,2,3	4	1,2,3	4	5.3	1.6	0.05	0.04	0.90	1.25
M5:45	1,2	3	1,2,3	4	0.0	3.6	0.00	0.06	—	1.01
M5:47	1,2	3	1,2,3	4	0.0	1.7	0.00	0.03	0.92	1.04
M5:49	1,2,3	4	1,2,3	4	13.6	1.8	0.38	0.17	1.12	1.00
M5:51	1,2,3	4	1,2,3	4	17.3	2.0	0.78	0.17	0.72	1.00
M5:53	1,2,3	4	1,2	3	2.1	0.0	0.01	0.00	1.00	—
M5:55	1,2,3	4	1,2,3	4	9.6	1.6	0.01	0.01	0.93	1.00
M5:58	1,2,3	4	1,2,3	4	5.0	3.1	0.10	0.04	1.11	0.78
M5:59	1,2,3	4	1,2	3	5.1	0.0	0.22	0.00	1.05	—
M5:61	1,2,3	4	1,2	3	11.7	0.0	0.42	0.00	0.98	—
M5:64	1,2,3	4	1,2	3	13.1	0.0	0.38	0.00	1.11	—

Table 2

Flower types, fruitfulness and average number of normal seeds per berry of 30 vines of second vegetative propagation selected for high fruitfulness from some vines of the first vegetative propagation of 030-44

First vegetative propagation		Second vegetative propagation	Flower types				Fruitful clusters %		Seeded berry set %		Normal seeds berry avg.	
			1967		1968							
Vine	Cane	Vine	Majority	Minority	Majority	Minority	1967	1968	1967	1968	1967	1968
M5:7	1	Y53:2	1,2,3	4	1,2,3	4	6.1	1.9	0.08	0.09	0.83	0.87
M5:9	2	Y53:3	1,2	3	1,2,3	4	0.0	2.9	0.00	0.09	—	1.36
	2	Y53:4	1,2	3	1,2,3	4	0.0	8.4	0.00	0.65	—	1.07
	3	Y53:5	1,2,3	4	1,2,3	4	2.2	7.6	0.21	0.45	1.46	1.20
	3	Y53:6	1,2,3	4	1,2,3	4	1.4	9.4	0.01	0.69	1.00	0.88
	4	Y53:7	1,2	3	1,2,3	4	0.0	7.2	0.00	0.23	—	1.07
	4	Y53:8	1,2,3	4	1,2,3	4	2.3	3.8	0.01	0.20	1.00	1.00
	5	Y53:9	1,2,3	4	1,2,3	4	3.3	12.2	0.02	0.11	1.00	0.90
	5	Y53:10	1,2,3	4	1,2,3	4	2.8	8.7	0.17	0.82	1.09	1.38
	6	Y53:12	1,2,3	4	1,2	3	7.5	0.0	0.25	0.00	1.00	—
	7	Y53:13	1,2,3	4	1,2,3	4	4.0	4.9	0.02	0.54	0.80	1.03
M5:11	10	Y53:17	1,2,3	4	1,2,3	4	8.4	6.0	0.38	1.11	0.76	1.14
	10	Y53:18	1,2,3	4	1,2,3	4	3.1	3.6	0.02	0.41	1.00	1.19
M5:13	12	Y53:19	1,2,3	4	1,2,3	4	5.0	9.3	0.09	0.94	1.08	1.26
	12	Y53:20	1,2,3	4	1,2,3	4	4.0	8.2	0.05	1.06	0.80	1.08
	13	Y53:22	1,2,3	4	1,2,3	4	6.1	4.9	0.07	0.54	1.10	1.44
	14	Y53:24	1,2,3	4	1,2,3	4	5.0	4.8	0.25	0.27	1.26	1.13
M5:15	15	Y53:25	1,2,3	4	1,2,3	4	4.6	3.6	0.16	0.12	1.12	0.83
	16	Y53:27	1,2	3	1,2,3	4	0.0	13.3	0.00	0.85	—	1.19
	16	Y53:28	1,2,3	4	1,2,3	4	4.2	7.7	0.12	0.19	1.05	1.32
	17	Y53:29	1,2,3	4	1,2,3	4	2.6	7.0	0.04	0.37	1.00	1.24
	17	Y53:30	1,2,3	4	1,2,3	4	5.4	5.3	0.08	0.16	1.07	0.97
M5:19	18	Y53:31	1,2,3	4	1,2,3	4	2.0	14.5	0.02	1.35	0.88	1.23
M5:21	19	Y53:34	1,2,3	4	1,2,3	4	7.1	25.7	0.15	1.72	1.05	1.32
M5:25	22	Y53:37	1,2	3	1,2,3	4	0.0	4.3	0.00	0.20	—	1.11
	22	Y53:38	1,2,3	4	1,2,3	4	5.4	16.4	0.16	1.33	1.02	0.87
	23	Y53:39	1,2,3	4	1,2,3	4	4.5	7.4	0.06	0.59	0.88	1.06
M5:29	24	Y53:41	1,2,3	4	1,2,3	4	6.4	20.9	0.11	1.59	0.97	1.15
M5:39	26	Y53:43	1,2	3	1,2,3	4	0.0	6.2	0.00	0.89	—	1.35
M5:55	27	Y53:45	1,2,3	4	1,2,3	4	2.6	1.5	0.06	0.15	1.11	0.94

produce a larger number of converted flowers and mature seeded berries than others on the same vine. In 1967, the range of fruitful clusters varied from 0.0 to 24.6% and seeded berry set from 0.00 to 1.65%. Comparable values for 1968 were 0.0 to 13.6 and 0.00 to 1.07, respectively. The average normal seeds per berry ranged from 0.72 to 1.21 in 1967 and from 0.78 to 1.25 in 1968.

These data suggest a great influence of environment, both local and seasonal, on the frequency of sex conversion. Mutation could also be a factor in sex conversion. The influence of certain external conditions on sex conversion in male vines of *Vitis* has been mentioned by several authors (Negrul 1936, Breider and Scheu 1938, Bethmann 1939, Levadoux 1946, Kozma 1955, Barrett 1966). Levadoux (1946) re-

Table 3

Percent seeded berry set on some vines of the first unselected vegetative propagation of the seedling 030-44 versus those of the second selected for high fruitfulness from vines of the first propagation

	First vegetative propagation			Second vegetative propagation		
	Vine	Seeded berry set, % 1967	Seeded berry set, % 1968	Vine	Seeded berry set, % 1967	Seeded berry set, % 1968
	M5:7	0.50	0.17	Y53:2	0.08	0.09
	M5:9	0.51	0.66	Y53:3	0.00	0.09
				Y53:4	0.00	0.65
				Y53:5	0.21	0.45
				Y53:6	0.01	0.69
				Y53:7	0.00	0.23
				Y53:8	0.01	0.20
				Y53:9	0.02	0.11
				Y53:10	0.17	0.82
				Y53:12	0.25	0.00
				Y53:13	0.02	0.54
Mean % Seeded berry set		0.51	0.66		0.07	0.49
	M5:11	0.33	0.25	Y53:17	0.38	1.11
				Y53:18	0.02	0.41
Mean % seeded berry set		0.33	0.25		0.25	0.79
	M5:13	1.65	0.24	Y53:19	0.09	0.94
				Y53:20	0.05	1.06
				Y53:22	0.07	0.54
				Y53:24	0.25	0.27
Mean % seeded berry set		1.65	0.24		0.11	0.67
	M5:15	0.71	1.07	Y53:25	0.16	0.12
				Y53:27	0.00	0.85
				Y53:28	0.12	0.19
				Y53:29	0.04	0.37
				Y53:30	0.08	0.16
Mean % seeded berry set		0.71	1.07		0.09	0.34
	M5:19	0.48	0.06	Y53:31	0.02	1.35
	M5:21	0.37	0.42	Y53:34	0.15	1.12
	M5:25	0.22	0.28	Y53:37	0.00	0.20
				Y53:38	0.16	1.33
				Y53:39	0.06	0.59
Mean % seeded berry set		0.22	0.28		0.07	0.76
	M5:29	0.69	0.25	Y53:41	0.11	1.59
	M5:39	0.67	0.16	Y53:43	0.00	0.89
	M5:55	0.01	0.01	Y53:45	0.06	0.15

ported that sex conversion was more pronounced on the vigorous shoots that grew after severe pruning of a male plant of *V. rupestris* Géant. This association was not apparent in the vines of 030-44.

Second vegetative propagation:

Data on flower types, fruitfulness and average number of normal seeds per berry of 30 vines of the second vegetative propagation are presented in Table 2. None of these vines was true hermaphroditic. In 1967, 80.0% and in 1968, 96.7% of all vines had a few functionally hermaphroditic flowers that produced mature seeded berries. As in the first vegetative propagation, buds of the second generation produced vines with the same correlation in range of flower types. Unfruitful vines had flowers mainly of types 1 and 2 with a small number of type 3. The percentages of fruitful clusters and seeded berry set ranged from 0.0 to 8.4 and from 0.00 to 0.38, respectively, in 1967, and from 0.0 to 25.7 and from 0.00 to 1.72, respectively, in 1968. The range of average normal seeds per berry was from 0.76 to 1.46 in 1967 and from 0.83 to 1.44 in 1968. Thus, the influence of environment, both local and seasonal, on sex conversion was indicated in these vines also.

A comparison of the percentages of seeded berry set on some vines of the first vegetative propagation with those of the second (Table 3) shows that the differences are negligible. Thus, vegetative selection within the clone was ineffective in increasing the number of hermaphroditic flowers and subsequent fruitfulness. Sex conversion is thus sporadic and is not due to somatic mutation or any vegetative syndrome within the vine that responds to selection.

Summary

The appearance of functionally hermaphroditic flowers and mature seeded berries on otherwise male vines was defined as a natural sex conversion from functionally male to functionally hermaphroditic flowers. Sex conversion was investigated in vegetatively propagated vines of the wild male *V. vinifera* clone 030-44 derived from a seed sample collected in Iran.

Frequency of sex conversion varied markedly among inflorescences on the same vine, among vines side by side, and from season to season, which implicated the effect of environment, both local and seasonal.

Studies on vegetative selection for high fruitfulness revealed that sex conversion was not due to somatic mutation or any vegetative syndrome within the vine.

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Prof. Dr. H. P. Olmo
Dept. of Viticulture and Enology
Univ. of California
Davis, Calif.
USA