was enough to afford some protection against a mild freeze on April 9, 1977; but did little to prevent damage during a –4.4C (24°F) freeze on May 1, 1978.

Literature Cited

1. Bauer, Mary, C. E. Chaplin, G. W. Schneider, B. J. Barfield, and G. M. White. 1976. Effects of evaporative cooling during dormancy on 'Redhaven' peach wood and fruit bud hardiness. *J. Amer. Soc. Hort. Sci.* 101:452-454.
2. Chaplin, C. E. and G. W. Schneider. 1974. Peach rootstock/scion hardiness effects. *J. Amer. Soc. Hort. Sci.* 99:231-234.
3. Corgan, J. N. and F. B. Widmoyer. 1970. The effects of gibberellic acid on flower differentiation, date of bloom, and flower hardiness of peach. *J. Amer. Soc. Hort. Sci.* 96:54-57.
4. Couvillon, Gary A. and Donald A. Lloyd II. 1978. Summer defoliation effects on peach spring bud development. *HortScience* 13:53-54.
5. Layne, R. E. C., H. O. Jackson, and F. D. Stroud. 1977. Influence of peach seedling rootstocks on defoliation and cold hardiness of peach cultivars. *J. Amer. Soc. Hort. Sci.* 102:89-92.
6. __________ and G. M. Ward. 1978. Rootstock and seasonal influences on carbohydrate levels and cold hardiness of 'Redhaven' peach. *J. Amer. Soc. Hort. Sci.* 103:408-413.
7. __________, G. M. Weaver, H. O. Jackson, and F. Stroud. 1976. Influence of peach seedling rootstocks on growth, yield, and survival of peach scion cultivars. *J. Amer. Soc. Hort. Sci.* 101:568-572.
8. Reeder, B. D. and H. H. Bowen. 1977. Effect of fertilizer applications on bloom delay of peach. *HortScience* 12:411 (Abstr.).
9. Richardson, E. Arlo, Schuyler D. Seeley, and David R. Walker. 1974. A model for estimating the completion of rest for 'Redhaven' and 'Elberta' peach trees. *HortScience* 9:331-332.
10. __________, __________, __________, J. LaMar Anderson, and Gayleen L. Ashcroft. 1975. Pheno-climatography of spring peach bud development. *HortScience* 10:236-237.
11. Stang, Elden J., David C. Ferree, Franklin R. Hall, and Robert A. Spotts. 1978. Overtree misting for bloom delay in 'Golden Delicious' apple. *J. Amer. Soc. Hort. Sci.* 103:82-87.
12. Stembridge, G. E. and J. H. LaRue. 1969. The effect of potassium gibberellate on flower bud development in the Redskin peach. *J. Amer. Soc. Hort. Sci.* 94:492-495.
13. Young, Les D. and Schuyler D. Seeley. 1977. Evaporative cooling of 'Elberta' peaches for bloom delay. *HortScience* 12:411 (Abstr.)

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Inheritance Studies of Seedlessness in Grapes[1]

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Abstract. **More than 10,000 seedlings were studied to elaborate the mode of inheritance of seedlessness in grapes (*Vitis* spp.). Self-pollinations of seeded selections having seedlessness in their parentage gave 0 to 10.7% seedless progeny. Crosses between seeded selections with seedlessness in one or both parents gave similar proportions. Crosses of seeded × seedless selections gave 0-55% seedless. Results were extremely variable, without apparent correlation to normal genetic ratios. Seedlessness appeared to be largely controlled by recessive factors.**

Seedless grapes have been prized for hundreds of years, yet the genetic basis of seedlessness remains obscure. Controlled-breeding work with grapes, primarily for the development of improved seedless cultivars, has resulted in reports on fewer than 10,000 progeny, which gives little genetic information. Seeded × seedless crosses seldom give as many as 50% seedless progeny. Crosses of seeded × seeded result in very few seedless progeny. Inheritance of seedlessness is reported to be extremely variable.

Seedless grapes are of 2 types (11, 19, 20): those which produce seedless progeny in the F_1 generation, as in 'Black Monukka', 'Sultanina' ('Thompson Seedless'), and 'Sultanina Rose'; and those which do not as in 'Concord Seedless', the Corinths, and 'Sultana'. The first type all are stenospermocarpic, fertilization occurs but embryo development fails soon after. The amount of seed development varies from almost none to full-sized, sclerified seeds without embryos. The second type include parthenocarpic cultivars where fruit development occurs without fertilization as in the Corinths and stenospermocarps as in 'Concord Seedless', and 'Sultana'. Stenospermocarpic seedless types may produce some parthenocarpic berries within their fruit clusters (11).

Susa (23) concluded that various grades of seedlessness were possibly caused by various "grades" of embryo abortion.

Gustafson (4) found a higher auxin content in the flower-bud ovaries of the seedless grape cultivars 'Black Monukka' and 'Sultanina' than in the seeded cultivar 'Muscat of Alexandria'.

Recently a difference in the degree of seed development was observed in the 'Flame Seedless' cultivar grown on different rootstocks (unpublished). The following year no differences were observed.

Progeny of crosses range from completely seedless to normally seeded, with various degrees of seed development and intermixtures of types. Consequently, the classification "seeded" or "seedless" is not clear cut. Within each cultivar and under the same conditions, the time of embryo abortion as indicated by amount of seed development is remarkably uniform regardless of pollen type involved. This suggests that seedlessness is caused by a physiological condition.

Mutations from seeded to seedless types have been reported in: 'Geo. Haskells No. 45' (1), 'Chasselas' (1), 'Concord' (19), 'Catawba' (16), 'Emperor' (8), 'Muscat Hamburg' (22), 'Tokay' (2), 'Red Muscadel' (12), and 'Liatiko' (3). Mutations from seedless to seeded have been recorded in 'Panariti' (14), and 'Sultanina' (5).

Seeds or viable embryos have been reported in practically all of the seedless grape cultivars: 'Concord Seedless' (17), the Corinths (11), 'Black Monukka' (13), and 'Sultanina' (7). Thus, the classification seedless includes cultivars in which there is an occasional occurrence of viable seeds. Olmo and Baris (9) classified the seedlessness on dry weight of seeds as well as on the usual visual or sensory perceptions.

Attempts were made as early as 1875 (13, 24) to obtain new

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seedless selections from controlled crosses. In 1921 Stout (17) derived 4 completely seedless seedlings (from seed, not pollen) from 'Concord Seedless'. In 1928 (18) he attempted to obtain seedlessness by intercrossing the seeded F_1 progeny of 'Concord Seedless' "on the general theory of multiple complimentary factors. . ." In 1937 (20) he concluded that seedlessness in 'Sultanina', 'Sultanina Rose', and 'Black Monukka' was apparently controlled by a single dominant factor. This theory was refuted by his later report (21) of a seedless plant among 6 fruiting vines of selfed progeny. The selfed progeny was from a seeded plant so the seedless plant occurred as a result of a recessive factor. His success in obtaining a seedless selection ('Stout Seedless') worthy of introduction from a progeny of 2 fruiting vines is the envy of all grape breeders.

In 1952 Synder and Harmon (15) reported 13.5% seedless progeny from crosses with a seedless variety used as the male parent, and Weinberger and Harmon in 1964 (25) reported on 47 mixed crosses producing nearly 5,000 progeny. They obtained about 8% seedless from crosses of seeded × seedless and less than 1% from seeded × seeded crosses. They concluded that seedlessness was recessive but was not a simple recessive.

In 3 instances of crosses of seeded × seedless, Olmo (9) obtained a good approximation to a ratio of 1 seeded:1seedless, In another cross the ratio was about 3 seeded:1 seedless. He stated that in breeding for seedless grapes a high tendency towards parthenocarpic seedlessness should be combined with stenospermocarpy, but he had no conclusions as to the mode of inheritance.

The present study was set up to investigate the inheritance of seedlessness from (a) self-pollinating vines with seedlessness in their parentage, (b) crossing seeded types with various proportions of seedlessness in their parentage, and (c) crossing seeded × seedless vines with various proportions of seedlessness in the female parent. Table 1 gives parentage of cultivars and selections used in these studies.

Materials and Methods

Seeds obtained from controlled crosses were planted in the greenhouse in January, and the seedlings were transplanted to the field in late April or early May. Fruit records were taken through the fifth growing season. Vines that produced seedless fruits without large stony integuments were recorded as seedless. We noted whether the fruit was parthenocarpic.

Results and Discussion

The crossing of seeded types resulted in a low percentage of seedless progeny, with no apparent correlation to the amount of seedlessness known to be in the parentage (Table 2). Seedlessness ranged from 0 to 11% in the various crosses, including self-pollinations of seeded × seeded. Two F_1 seedlings of a seedless parent, 14-47 and 56-83, and 2 F_2 seedlings of a seedless parent, 15-162 and 85-68.5, gave no seedless progeny when selfed. The two F_1 seedlings, 11-88 and 60-26, gave 9% seedless progeny when selfed.

Nine cross-pollinations of seeded types gave no seedless progeny, and 13 yielded seedless progeny. The recovery of seedless progeny from some crosses of seeded × seeded selections and the lack of it in other crosses and in self pollinations could occur in the case of dominant triplicate complementary factors. This explanation is supported by the work of Patel and Olmo (10), which showed the chromosomes of *Vitis* to occur in 3 genomes, and of Mortensen (6), which showed the resistance to Pierce's Disease was controlled by 3 independently inherited genes. However, 2 self-pollinations of seeded types yielded seedless progeny, which would be impossible if the seedless factor was dominant. Seedlessness must be controlled by recessive factors.

Crosses of seeded × seedless showed great variation (Table 3). With no known seedlessness in the seed parent, the percentage

Table 1. Parentage and seed type of grape varieties and numbered selections used in breeding for seedlessness.

Cultivar or Selection No.	Parentage	Seeded	Seedless
Agadia	?	X	
Almeria	?	X	
Alphonse Lavallee	M. Hamb. × Bl. Hamburg	X	
Bicane	?	X	
Black Hamburg	?	X	
Black Monukka	?		X
Backrose	(Damas Rose × Bl. Monukka) × Al. Lavallee	X	
Calmeria	Almeria OP	X	
Cardinal	Tokay × Alphonse Lavallee	X	
Damas Rose	?	X	
Divizich Early	Probably a U.C. numbered selection		X
Emperor	?	X	
Italia	Bicane × M. Hamburg	X	
Malaga, White	?	X	
Mus. Alexandria	?	X	
Mus. Hamburg	Bl. Hamburg × M. Alexandria	X	
Nunakasia	?	X	
Perlette	Scolokertek kiral. × Sult. marble		X
Queen	M. Hamburg × Sultanina	X	
Scolokertek kiral	?	X	
Sultanina	?		X
Sult. Marble	?		X
Tafafihi Ahmr	?	X	
Thompson (see Sultanina)	?		X
Tokay	?	X	
4-37	M. Alex. × Sultanina		X
4-39	Malaga × Sultanina		X
G4-74	Calmeria × 4-37		X
8-18	M. Alex. × Sultanina		X
11-18	Italia × G4-74	X	
11-160	" × "	X	
14-47	55-10 × 35-126	X	
15-122	Calmeria × Blackrose	X	
15-133	" × "	X	
15-162	" × "	X	
16-80	(Almeria × Emp.) × G4-74	X	
19-153	Blackrose × 64-18		X
20-110	11-88 × G4-74	X	
32-25	60-26 × "	X	
32-68	" × 43-13S		X
32-106	60-26 × 43-13S		X
32-129	" × "		X
32-136	" × "		X
32-139	" × "		X
32-141	" × "		X
32-145	" × "		X
32-155	45-98 × O.P.	X	
32-188	" × "	X	
33-199	11-160 × G4-74		X
35-75	45-98 × 43-13N		X
35-93	" × "	X	
35-106	Blackrose × 35-75	X	
35-126	46-45 × 43-13N		X

(Continued)

Table 1 (Continued)

Cultivar or Selection No.	Parentage	Seeded	Seedless
37-45	Blackrose × 64-18	X	
38-4	Tokay × Alphonse Lavalee[z]	X	
41-125	Blackrose × 43-13N	X	
43-13N	(Malaga × Taf. Ahmr) × 64-18		X
43-13S	(" × .. ..) × "		X
44-121	Queen × Alphonse Lavallee	X	
45-98	[(Agadia × M. Hamb.) × Perlette] OP	X	
46-1	(Agadia × M. Hamb.) × Perlette		X
46-45	(Malaga × Taf. Ahmr) × 8-18	X	
55-10	Calmeria × G4-74	X	
56-83	" × 43-13S	X	
58-22	" × 64-18		X
58-93	" × "		X
60-26	Cardinal × Sultanina	X	
63-88	46-45 × 46-1	X	
64-18	M. Alex. × Sultanina		X
64-80	46-45 × Divizich Early	X	
78-53	Blackrose × 43-13N	X	
78-68	" × "		X
85-68.5	" × Calmeria	X	
100-47	Calmeria × Al. Lavallee	X	
101-120	16-80 × Alphonse Lavallee	X	
103-138	38-4 × 4-39	X	

[z]In California this grape is known as Ribier.

of seedless progeny ranged to about 38%; with seedlessness in the parentage of the seed parent, the seedless percentage ranged to slightly more than 50%, with many progenies in the range of 25-50%. Multiple factors are suggested by the increases in the percentage of seedless progeny with increases in the known amount of seedlessness in the parentage of the seeded parent. The results obtained from crosses of seeded × seedless parents would be possible if controlled by either dominant or recessive factors.

Certain seedless parents, particularly G4-74, 32-139, 32-141, and 43-13S, at times appeared to be prepotent in the production of seedless progeny (Table 3). However, variation was great even when the same cross was made in different years.

Variation was also great when the same seedless pollen parent was used with different seed parents. If seedlessness is a simple recessive, the use of different seedless pollen parents with the same seed parent should result in identical proportions of seedless progeny. This was not the case.

It would also seem that the 2 selections that produced seedless progeny when selfed would more effectively transmit the seedless character when crossed to a seedless parent. This was not the case (Table 3). Selections 11-88 and 60-26, which transmitted seedlessness when selfed, were crossed to the seedless selection 43-13S and gave respectively 18% and 6% seedless progeny. On the other hand, 56-83 and 85-68.5, which failed to transmit seedlessness when selfed, were crossed to the same seedless selection, 43-13S, and gave 29% and 55% seedless progeny. The seedlings 56-83, which gave no seedless progeny when selfed, and 60-26, which gave 9% seedless when selfed, were crossed to the seedless selection 32-145 and gave 47% and 7% seedless progeny.

A possible explanation of the extremely varied and inconsistent transmission of seedlessness is that some embryos in seeds that are genetically "seedless" may abort. Such embryos would have the same genetic constitution as other embryos that produce seedless vines. As adults, genetically seedless vines cannot produce viable seeds and embryos in certain seeds may not even survive past the embryo stage. In this way a part of the seedless progeny would be lost and normal inheritance ratios would not be obtained.

In mature seedless vines, embryo abortion or stenospermocarpy is probably due to genetically induced physiological conditions; the embryos abort regardless of the pollen parent even if the latter is genetically seeded. The loss of embryos due to either genetic or other physiological causes prevents the occurrence of normal genetic ratios.

The data substantiate the conclusion of Weinberger and Harmon (25) that "seedlessness appears to be recessive in nature, though not a simple recessive."

Table 2. Seedlessness resulting from crosses or selfs of seeded grape parents.

A. Self pollinations of selections with established seedlessness in their parentage.			
1. F_1 seedlings of a seedless parent.			
11-88	54	5	9.3
14-47	25	0	0.0
56-83	89	0	0.0
60-26	105	10	9.5
Total	273	15	
2. F_2 seedlings of a seedless parent.			
15-162	41	0	0.0
85-68.5	39	0	0.0
Total	80	0	
B. No known seedlessness in the parentage.			
Calmaria × Alphonse Lavallee[z]	68	0	0.0
Nunakasia[y] × Cardinal	28	3	10.7
" × 100-47	178	3	1.7
Total	274	6	
C. Seedlessness in the seed parent. No known seedlessness in the pollen parent.			
Blackrose × Calamaria	130	2	1.5
" × Cardinal	21	0	0.0
Queen × "	130	3	2.3
15-133 × Alphonse Lavallee[x]	69	1	1.4
" × " "[x]	182	0	0.0
35-106 × " "	62	1	1.6
41-125 × " "	110	4	3.6
101-120 × " "	123	0	0.0
Total	827	11	
D. Seedless in both parents.			
15-133 × 11-88	131	1	0.8
" × 20-110	20	2	10.0
" × 32-25	92	0	0.0
" × 60-26	102	2	2.0
15-162 × 16-80	63	0	0.0
" × 32-25	31	0	0.0
" × 85-68.5	10	0	0.0
32-25 × 15-162	13	0	0.0
45-98 × 11-88	82	3	3.7
" × 32-25	37	1	2.7
" × 60-26	27	2	7.4
Total	608	11	

[z]In California this grape is known as Ribier.

[y]In California this grape is known under the name Kishmishi or Kishmiski (= 'little seedless' in Russian), an obvious misnomer.

[x]These crosses were made in different years.

Table 3. Seedlessness resulting from crosses of seeded x seedless grape parents.

Cross		No. progeny Blossoming	Seedless	% seedless
A. No known seedlessness in the seed parent.				
Calmeria	x G4-74	252	27	10.7
Malaga	x " [z]	181	47	26.0
"	x " [z]	223	84	37.7
"	x 43-13S	27	2	7.4
Tokay	x Black Monukka	71	9	12.7
"	x 43-13S	40	1	2.5
	Total	794	170	
B. Seedlessness in the parentage of the seed parent.				
Blackrose	x 43-13N	70	14	20.0
Queen	x 19-153	196	7	3.6
"	x 68-68	195	4	2.1
11-88	x G4-74[z]	38	13	34.2
"	x " [z]	55	9	16.4
"	x 43-13S	38	7	18.4
15-122	x 58-22	46	0	0.0
"	x 33-199	29	0	0.0
15-133	x "	13	0	0.0
"	x 58-22	138	37	26.8
16-80	x 35-75	264	12	4.5
"	x 43-13S[z]	36	3	8.3
"	x " [z]	468	3	0.6
"	x 64-18	181	4	2.2
32-155	x 43-13S[z]	43	3	7.0
"	x " [z]	76	4	5.3
32-188	x G4-74[z]	50	3	6.0
"	x " [z]	326	126	38.7
"	x 32-139	138	37	26.8
"	x 32-145[z]	80	22	27.5
"	x " [z]	299	108	36.1
"	x 43-13S[z]	12	2	16.7
"	x " [z]	302	74	24.5
"	x " [z]	94	37	39.4
35-93	x 58-93	92	32	34.8
37-45	x G4-74[z]	117	13	11.1
"	x " [z]	198	66	33.3
"	x 32-136	202	65	32.2
"	x 35-75	33	1	3.0
44-121	x 32-106	43	3	7.0
45-98	x Black Monukka	85	24	28.2
"	x 32-139	176	71	40.3
"	x 43-13S	704	225	32.0
56-83	x G4-74	396	167	42.2
"	x 32-68	32	9	28.1
"	x 32-145	462	220	47.6
"	x 35-75	100	12	12.0
"	x 43-13S	55	16	29.1
60-26	x 32-106	226	68	30.1
"	x 32-145	27	2	7.4
"	x 35-75	151	6	4.0
"	x 43-13S[z]	63	7	11.1
"	x " [z]	61	1	1.6
63-88	x 64-18	19	2	10.5
64-80	x 43-13S	59	0	0.0
"	x 64-18	32	3	9.4
78-53	x 32-129	81	24	29.6
"	x 32-141	78	19	24.4
85-68.5	x 35-75	45	3	6.7
"	x 43-13S	20	11	55.0
103-138	x 32-141	103	42	40.8
	Total	6847	1641	

[z]These crosses were made in different years.

Literature Cited

1. Bailey, L. H. 1887. Bud variation. Mich. Agr. Exp. Sta. Annu. Rpt. p. 136-139.
2. Brooks, Reid M. 1964. Register of new fruit and nut varieties. List 19. *Proc. Amer. Soc. Hort. Sci.* 85:708.
3. Galet, P. 1964. Cepages et Vignobles de France. Tome IV: 3033. Montpellier.
4. Gustafson, Felix G. 1939. The cause of natural parthenocarpy. *Amer. J. Bot.* 26:135-138.
5. Krimba, B. 1933. Origine et mutations de la Sultanine. L'Acad. d'Athens. 201-205.
6. Mortensen, John. 1968. The inheritance of resistance to Pierce's Disease in Vitis. *Proc. Amer. Soc. Hort. Sci.* 92:331-337.
7. Oinoue, Yasusi. 1925. Studies on the formation of seedless grapes. *Jap. J. Bot.* 2:57-58.
8. Olmo, H. P. 1940. Somatic mutation in the vinifera grape. III Seedless Emperor. *J. Hered.* 31:211-213.
9. ________ and C. Baris. 1973. Obtention de raisins de table apyrenes. O.I.V. Symposium international sur les raisins de table. Limassol (Chypre) 16-21 Juillet. Paper No. 20, 17 p.
10. Patel, G. I. and H. P. Olmo. 1955. Cytogenetics of Vitis I. The hybrid of V. vinifera x V. rotundifolia. *Amer. J. Bot.* 42:141-159.
11. Pearson, Helen M. 1933. Parthenocarpy and seed abortion in *Vitis vinifera*. *Proc. Amer. Soc. Hort. Sci.* 29:169-175.
12. Perold, A. I. 1927. A treatise on viticulture. Macmillan, London.
13. Ross, Charles. 1875. Crossing the Black Monukka grape. *Gard. Chron.* (n.s.) 3:116.
14. Snyder, Elmer and F. N. Harmon. 1936. Three mutations of Vitis vinifera. *Proc. Amer. Soc. Hort. Sci.* 33:435-436.
15. ________ and ________. 1952. Grape breeding summary. 1923-1951. *Proc. Amer. Soc. Hort. Sci.* 60:243-246.
16. Steuk, William K. 1945. Variations of the Catawba grape. *Bimonthly Bul.* (Ohio Agr. Exp. Sta.) 30(232):31-33.
17. Stout, A. B. 1921. Type of flowers and intersexes in grapes with reference to fruit development. *N. Y. Agr. Exp. Stat. Tech. Bul.* 82.
18. ________. 1928. A new hardy seedless grape. *J. Hered.* 19: 317-323.
19. ________. 1936. Seedlessness in grapes. *N. Y. State Agr. Expt. Sta. Tech. Bul.* 238.
20. ________. 1937. Breeding for hardy seedless grapes. *Proc. Amer. Soc. Hort. Sci.* 34:416-420.
21. ________. 1940. Progress in breeding for seedless grapes. *Proc. Amer. Soc. Hort. Sci.* 37:627-629.
22. Sturtevant, E. Lewis. 1890. Seedless fruits. *Mem. Torrey Bot. Club* 1(4):141-185.
23. Susa, Torasaburo. 1927. Sterility in certain grapes. *Mem. Hort. Soc.* (N. Y.) 3:223-229.
24. Tillery, William. 1875. Crossing the Black Monukka grape. *Gard. Chron.* 3:80.
25. Weinberger, J. H. and F. N. Harmon. 1964. Seedlessness in vinifera grapes. *Proc. Amer. Soc. Hort. Sci.* 85:270-274.