Empty-seededness in Varieties of *Vitis vinifera*

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In germinating seed from many vinifera grape varieties during the past three years, marked varietal differences were noted. Thus the seed of Chaouch, an important table grape in Turkey, Greece and the Crimea, seldom produced more than three or four per cent of seedlings. At the other extreme were Muscat of Alexandria and Emperor, which often produced an 80 per cent seedling stand. Differences of seed treatment before germination, such as altering the duration and temperature of stratification, failed to give good seedling stands with varieties that had regularly shown poor germination.

Of approximately 20 varieties investigated that showed low seed viability, all were exceptional in that a large number of the mature seeds were "empty." Of the seeds saved for planting, two classes were segregated, namely, those that floated on water and those that did not. The seeds that floated have been designated "empty"; but examination of the seed lumen always revealed some shriveled tissue, occupying a variable portion of the cavity. In addition many, if not all, seeded varieties produced ovules that aborted at various stages of development. These early-abortive ovules lacked bony seed coats and seldom approximated the size of a fully matured seed. This phenomenon does not form a part of the present discussion, although it may be correlated with empty-seededness, at least in some varieties.

Plant breeders and others who propagate the vine from seed recognize that hollow seeds rarely germinate and often eliminate such seed. Viala and Ravaz (3) advocated separation and selection by placing the seed in water and noted that "bad seeds float, good seeds sink to the bottom." Beach (1) in 1903 noted a correspondence between the specific gravity of the seeds and the germination and vigor of the seedlings in the American hybrids Empire State and Canada. In the former variety no germination occurred with seeds of less specific gravity than 1.045 and only weak germination below 1.065. The data were fragmentary. Empty seeds rarely germinate. In 1932, of 304 seeds of Ribier that floated in water, none germinated, whereas the seed that sunk gave from 62 to 86 per cent germination. That poor germination of many vinfera varieties is largely attributable to the presence of seeds with degenerated contents is further substantiated by the data of Table I. The varieties are arranged in increasing order of viability. The samples with a high proportion of empty seeds are those that are poorly viable. A few seeds of the variety Chaouch, even though light enough to float in water, are capable of germination. In planting seeds of such a variety it would be unwise to discard those that floated.

The questions of interest center about the factors responsible for empty-seededness. Data collected at this station by Professor F. T. Bioletti in 1930 and by Dr. Helen Pearson in 1931 and 1932 have been incorporated in Table II to supplement records of the author. During the 1933 and 1934 seasons, samples of three to four clusters were taken at random from several vines, not always in the same location in the vineyard. The seeds were extracted by hand, washed, and

TABLE I—Germination Percentages of a Number of Vinifera Varieties and the Corresponding Percentages of Empty Seeds in the Sample

Variety	Year	Percentage of Empty Seeds	Percentage Germination
Chaouch	1931	99.2	2.0
	1932	99.2	4.2
Burgrave	1931	66.8	2.2
Damas Rose	1931	66.7	14.8
Dattier	1932	65.6	16.5
Tokay	1932	50.5	34.5
Ribier	1931	47.3	40.4
Diamond Jubilee	1932	36.7	53.0
Olivette blanche	1932	32.1	56.3
Rambola	1931	12.0	58.5
Hunisa	1931	12.6	59.1
Molinera	1932	23.6	65.7
Muscat Blowers	1932	6.0	68.6
Emperor	1932	16.9	69.0
Muscat of Alexandria	1932	5.7	84.5

dried at room temperature. The total number of seeds in each sample varied from 200 to 1,200. The 1930 and 1931 collections were made without the present study in mind, so that the size of the samples was small. In addition, some seeds were obtained from cross-pollinated ovaries, on bagged clusters. It will be noted that the per cent of empty seeds is considerably higher in such cases. Of three lots of Tokay seed collected in 1932, the one secured from bagged clusters had approximately 50 per cent of empty seeds. Two other samples of 1,200 seeds each; from unbagged clusters, gave about 30 per cent, an indication that conditions within the bags, possibly higher temperature, markedly increased the number of seeds classified as empty.

The variety Chaouch consistently produced empty seeds over the 5-year period. The average was 99.5 per cent. Dattier produced over

TABLE II—Percentages of Empty Seeds in Some Vinifera Varieties During Different Seasons

Variety	Percentage of Empty Seeds					
	1930	1931	1932	1933	1934	Average
Chaouch	99.2	99.2	100.0*	100.0	99.0	99.5
Dattier	—	—	65.6*	52.9	54.8	57.8
Diamond Jubilee	26.0	—	36.7*	—	30.6	31.1
Emperor	0.0	—	16.9*	—	1.6	6.2
Hunisa	—	9.0	5.9	12.6	29.1	14.1
Madresfield Court	15.0	8.2	7.8	15.2	8.9	11.0
Molinera	—	—	23.6 28.8	28.3	8.6	22.3
Muscat of Alexandria	3.0	—	5.7	7.3	6.7	5.7
Muscat Blowers	7.0	—	6.0	7.0	3.5	5.9
Olivette blanche	—	—	32.1	47.9	31.2	37.1
Ribier	22.0	47.3*	29.3	32.0	41.9	34.5
Tokay	—	67.6*	50.5* 30.2 31.2	—	22.9	40.5

*From cross-pollinated ovaries of bagged clusters.

50 per cent of empty seeds, whereas Muscat of Alexandria, Muscat Blowers, and Emperor yielded a very high proportion of sound seed. The other varieties listed were more or less intermediate. In most cases the results from year to year were of the same magnitude; but some marked fluctuations appeared that were not easily explained. The variety Molinera, for example, with 28 per cent of empty seeds in 1933, had approximately 9 per cent in 1934. This would indicate that environmental factors may be very important in certain seasons, so that the ratio of empty seeds, even though hereditarily determined, may be modified considerably by climate, amount of crop, etc. It seems illogical, however, to attribute the significant differences found between varieties to other than hereditary factors. Progeny grown from the cross Hunisa x Muscat of Alexandria produced a very high proportion of sound seed, whereas most selfed seedlings of the Burgrave, a variety with many empty seeds, exhibited the phenomenon of empty-seededness to a high degree.

Most of the hybrids between Vinifera and other species produced seed that was highly viable, and in general few first-generation hybrids were characterized by the production of a large number of empty seeds. This relationship is illustrated graphically in Fig. 1. Data on the number of empty seeds have been obtained for 243 varieties of *Vitis vinifera* and for 70 varieties which are hybrids between Vinifera and an American species, usually *V. labrusca.* About 40 per cent of the total number of vinifera varieties studied have 10 per cent or less of empty seeds, whereas approximately 58 per cent of the interspecific hybrids fall in this category. Most of the data have been kindly furnished by Professor F. T. Bioletti. The hereditary factor or factors that determine empty-seededness are apparently of a recessive nature, so that in general seeds from F_1 hybrids are more viable than those of the Vinifera parent. This postulate may not necessarily follow from the trend shown in Fig. 1, since the greater number of hybrid varieties having sound seeds may be attributable to the frequent employment of Vinifera parents of high seed viability.

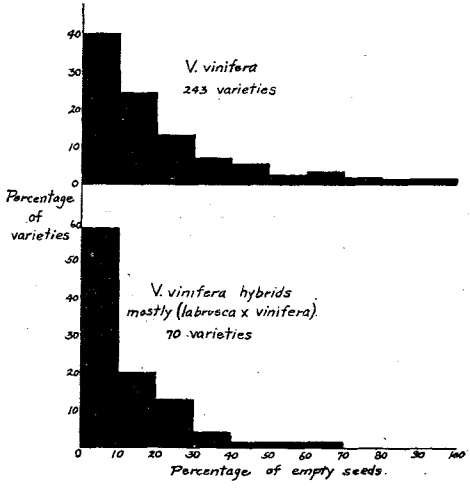

FIG. 1. Varieties of *Vitis vinifera* and its hybrids in relation to the percentages of empty seeds which they produce.

Seeds classified as empty were usually recognizable by an abnormal coloring of the seed coats. The empty seeds of Chaouch were very dark brown, some almost black, whereas

those of Olivette blanche and Diamond Jubilee were often tinged with green, signifying an incomplete maturation of the testa. Seeds that were empty in highly pigmented varieties, such as Ribier, were frequently reddish and stained-looking. Many seeds with degenerated contents and classified as empty were smaller than the normal seed of the variety. This was more likely to be the case in varieties that varied greatly in seed size, such as Molinara and Dattier. In such cases the abortion occurred earlier in development, but not early enough to prevent the formation of bony seed coats.

In the mature Vitis seed the fatty endosperm makes up the bulk of the internal tissue, being snugly enclosed by the folded seed coats. The undeveloped embryo is very small and spindle-shaped, embedded in the endosperm at the micropylar end of the seed. It is seldom more than 1 or 2 millimeters in length. Dissection of "empty" seeds always indicates the previous formation of endosperm tissue, which now appears shriveled and degenerated. In many seeds the remnants of the internal tissue may be desiccated, leaving the seed completely hollow. Embryos have been dissected from some empty seeds, but whether they are always present has not been determined.

The pollen parent exerts no influence in altering the percentage of empty seeds. Chaouch has been repeatedly pollinated with Muscat of Alexandria and Black Corinth pollen, but the percentage of empty seeds is the same as if the ovules were self-pollinated. Empty-seededness is therefore determined by the maternal parent. This is an interesting parallel to the case reported by Tukey (2) in the sweet cherry, where the early-ripening varieties, characterized by embryo abortion, fail to produce viable seed even though pollen of a late variety is used. On the other hand, he finds that pollen of an early variety, used on a late variety, results in normal seed development. From such evidence Tukey has formed the opinion that the production of non-viable seed is not genetic, but is a problem of nutrition and physiology. To say that nutrition and physiology are responsible does not exclude a genetic basis for embryo abortion. The literature is replete with reports of nutritional disturbances that have been shown to be inherited. There is danger of discouraging breeders who are attempting to obtain earlier varieties of cherry by maintaining that the phenomenon of early-ripening is non-genetic. That Tukey believes this is an inherited phenomenon is supported by his statement: "By culturing an embryo from an early-ripening type upon which another early-ripening variety had been used as the male parent, the chances would be increased of securing a new individual with a combination of genes for early-ripening from both male and female parent."

The genetic constitution of the embryo and endosperm may be quite unlike that of the maternal parent that is nourishing them. Consider the cross previously mentioned, when pollen of the Muscat of Alexandria is used to fertilize Chaouch ovules. If we admit that empty-seededness is inherent, then factors for normal seed development are contributed by the pollen of Muscat, whereas factors for abortion are transmitted through Chaouch ovules. With this introduction of genetic factors tending toward normal seed development,

we should sometimes expect the development of embryo and endosperm to proceed to maturity; but such is not the case. "Empty-seededness" is therefore manifested regardless of the genetic constitution of embryo and endosperm. The cause of the abortion is to be sought in maternal tissue; the abortion itself is only secondary.

This same concept may apply to embryo abortion in early-ripening cherry varieties. The cessation in growth of the embryo is a result of disturbances originating in maternal tissues. Although these disturbances may be nutritional in nature, as Tukey (2) has suggested, they are genetically controlled by the mother plant.

Summary

The poor germination of many Vinifera grape varieties may be largely attributed to empty-seededness. Seeds classified as "empty" by their flotation in water rarely germinate. The internal tissue of "empty" seeds consists largely of remnants of the fatty endosperm that have degenerated and left the seeds more or less hollow. Records obtained over a 4-year period for a number of varieties indicate that the phenomenon of empty-seededness is hereditary, although its expression may be modified considerably by environmental conditions. A comparative study of Vinifera varieties and their hybrids suggests that the phenomenon is inherited as a recessive factor complex. The expression of empty-seededness is the same whether the ovaries are cross or self-fertilized. This fact suggests that the cause of empty-seededness is maternal and exterior to the developing zygotes. This concept may also apply to embryo abortion in the sweet cherry, as reported by Tukey (2).

Literature Cited

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