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Heritability and correlation studies of certain quantitative traits in table grapes, *Vitis* spp.[1])

by

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Untersuchungen zu Heritabilität und Korrelation quantitativer Merkmale bei Tafeltrauben (*Vitis* spp.)

Zusammenfassung: Bei den Abkömmlingen von *Vitis vinifera* × *V. rotundifolia*-Kreuzungen wurden die Heritabilität von 10 Merkmalen und ihre phänotypischen Korrelationen berechnet; es wurden 46 Familien mit über 1000 Nachkommen bearbeitet, die aus Kreuzungen zwischen 26 Eltern hervorgegangen waren. Messungen der Trauben- und Beerenmerkmale wurden über 4 Jahre (1976—1979) durchgeführt; 1976 wurde auch die allgemeine Wüchsigkeit gemessen. Die Heritabilität wurde aus der Regression zwischen den jahrgangsbereinigten Leistungsmittelwerten der einzelnen Sämlinge und den Mittelwerten ihrer Eltern errechnet. Sie betrug für: Gewicht der Einzeltraube 0,12, Beerendichte der Trauben 0,55, Einzelbeerengewicht 0,49, Festigkeit der Beerenhaut 0,75, Konsistenz des Beerenfleisches 1,04, Mostgewicht 0,34, Mostsäure 0,15, allgemeine Wüchsigkeit 0,10. Die Heritabilität des Traubenertrages je Rebe war praktisch 0 (−0,08). Da — abgesehen von der allgemeinen Wüchsigkeit — die Genauigkeit dieser Berechnungen sehr hoch ist, dürften sie eine verläßliche Prognose der genetisch bedingten Leistungssteigerung erlauben, wenn Sämlinge aufgrund ihrer eigenen Leistungsfähigkeit als Kreuzungseltern selektiert werden. Die zu erwartende Leistung der Nachkommenschaft zufällig gekreuzter hochleistungsfähiger Eltern wurde errechnet. Die Bedeutung der geschilderten genetischen Beziehungen für Züchtungsprogramme und Selektionsverfahren wird diskutiert.

Key words: genetics, selection, statistics, table grape, yield, must quality, growth.

Introduction

For a successful breeding program, the knowledge of genetic variability of desirable characters is very important. The heterozygous nature of the plants is one of the mitigating factors for the success of any breeding program in perennial fruit crops.

Variability in a population is influenced by heredity and environment and the role these two play in this respect bears on the concept of heritability. The heritability of a character is then of importance in being able to predict advances in that character under selection schemes, in establishing an effective breeding system, and in setting up a workable selection index.

Breeding stocks with high heritability for desirable traits can be improved by simple and relatively inexpensive 'mass selection' methods. Progeny tests are unnecessary since superior parents can be discriminated from inferior parents in segregating populations by direct measurements of performance. With high heritability, the breeder is also free to allow selected parents to mate randomly, *inter se*, and need not resort to the expensive techniques of positive and negative assortative matings that are required when overdominance and epistasis have important effects on performance (Falconer 1960).

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[1]) Portion of a thesis submitted by the senior author for the Ph. D. in Genetics.

Table 1

Parental clones and their parentages

Elternklone mit ihrer Abstammung

Parentage	Parental clones	Parentage	Parental clones
Y14-14 × Grenache	e1-78	Queen of Vyds. × Z4-87	37-55F
	e1-93	Z2-86 × Q25-6	41-33F
	e1-100		
	e1-106	Emperor × S95-33	31-30F
Y14-14 × Palomino	e2-40	Gold × Q25-6	31-76F
	e2-82		31-123F
	e2-106	Gold × Z37-13	34-2F
Y14-23 × Red Malaga	e4-72	Z3-7 × Perlette	42-1F
	e4-76	Z2-86 × IP75	40-139F
	e4-93		
	d4-106	Seeded Thompson × Q25-6	38-105F
F2-35 × Y14-16	e5-124	F2-7 × Grenache	P76-36
	e5-133	F2-35 × Seibel 7053	T8-43
	e5-137		
F2-35 × Y14-15	e6-32		

Correlation between different characters is another aspect which should be kept in mind for better planning of selection programs for improving desirable characters.

Only a few studies of heritability have been reported in the grapevine. OLMO (1952) observed strong inbreeding depression in grapes upon self-fertilization, indicating mostly non-additive gene action in characters such as vigor, yield and berry size. We

Table 2

Number of parents, families (crosses), genotypes (offspring) and observations used in heritability estimates

Anzahl der Eltern, Familien (Kreuzungen), Genotypen (Nachkommen) und der den Heritabilitätsberechnungen zugrundeliegenden Beobachtungen

Traits	Parents	Families	Genotypes	Observations
Crop weight	16	28	487	844
Cluster weight	25	43	808	1 339
Cluster compactness	25	43	803	1 028
10-Berry weight	25	43	808	1 335
Skin texture	25	43	799	918
Pulp texture	25	43	799	916
TSS	24	39	730	1 216
Acidity	24	38	721	1 207
General vigor	15	24	462	462

(FIROOZABADY and OLMO 1982) estimated the heritability of root-knot nematode resistance in *Vitis vinifera* × *V. rotundifolia* hybrid derivatives to be 0.39 ± 0.06. The basis of estimation was the linear regression of individual offspring performance on midparent performance.

The present investigation stems mainly from the recent studies on the estimations of heritability obtained in several perennial clonal horticultural species such as sweet cherry (HANSCHE *et al.* 1966), plum and prune (HANSCHE *et al.* 1975), almond (KESTER *et al.* 1977) and grapes (NASSAR 1963; FANIZZA and RADDI 1973; FIROOZABADY and OLMO 1982). The heritabilities obtained have been found to be very useful guides in a cultivar breeding program to ensure relatively rapid improvement of breeding stocks by direct mass selection methods.

The objectives of the present work are to study heritabilities and correlations between vine and fruit characters, including crop weight, cluster weight, cluster compactness, berry weight, berry texture, total soluble solids, acidity of juice, and vine vigor.

Materials and methods

The population studied were vines planted on their own roots in the vineyard of the University of California, Davis. The population consisted of 26 parents and approximately 1000 progeny seedlings from crosses among these parents. Parents were in four series: the e and T series were quasi-F_1 hybrids of *V. vinifera* × *V. rotundifolia* (OLMO 1971) and F and P series were different hybrids of *V. vinifera* grapes (Table 1). Sibs were adjacent in progeny rows.

After 5 years in the seedling blocks (fall 1976), the circumference of the trunks just above ground level was measured to obtain the general vigor of each vine. All of the fruit was harvested from each vine and the total crop was weighed. The weight of 2 of the largest clusters was obtained and their compactness rated as 1 = ragged, 2 = loose, 3 = well-filled, 4 = compact, and 5 = very compact. Then 10 of the largest berries were removed from one cluster and weighed, giving a measure of berry size. Skin and pulp texture were also recorded. Skin texture was classified as 1 = tough or 2 = tender, and pulp texture as 1 = soft, 3 = firm, or 4 = crispy. The fruit sample was crushed and the Balling or total soluble solids (TSS) were determined by using a hand refractometer. Titration with sodium hydroxide to a pink endpoint with phenolphthalein was used for determining total acidity, expressed as tartaric acid in g/100 ml of juice (OLMO 1939).

The above data on fruit traits were obtained from the seedlings and the parents for 4 consecutive seasons, 1976—1979. The cultural practices were the same for all vines over the seasons. The parental population, however, was 3—4 years older than the offspring population and they were all grown in the same vineyard. Their difference with respect to age does not have any effect on any traits with the exception of crop weight.

It is also important to note that in the present studies, since the data were initially collected for other purposes, there was no experimental design with respect to this analysis. Nevertheless, the methods of data collection appear free of bias, and the data appear sufficient in quantity to provide heritability and correlation extimates of reliable accuracy and precision.

To minimize the phenotypic variability of traits due to yearly climatic differences, least squares estimates of year effects were obtained and measurements adjusted accordingly prior to the estimations of heritability and correlation. The statistical procedures for obtaining estimates of year effects are those applicable to the non-orthogonal experiments with unequal numbers of observation within cells and with missing cells. These methods are described in detail by SEARLE and HENDERSON (1961) and their uses have been discussed (HANSCHE *et al.* 1966).

Heritabilities were estimated from the linear regression of year-adjusted offspring performance on the average performance of their parents. Individual offspring performance records were paired with mid-parent performance records being repeated within progenies. In every case performance was based on the weighted mean of observations made in successive years. The use of weighted mean of observations increases the precision of the mid-parent offspring covariance estimate above that expected when estimates are based on only one observation per genotype.

Maximum heritabilities for fruit traits were calculated as

$$h_{max}^2 = \frac{\text{Phenotypic variance — Yearly climatic variance}}{\text{Phenotypic variance}}$$

Phenotypic correlations among traits were estimated in the usual way (after adjustment for year effects).

Results and discussion

1. The effect of variation in yearly climate on discrimination of genetic differences in segregating populations

Yearly differences in climate have a considerable effect on the year-to-year performance of many commercially important traits of tree-fruit crops (HANSCHE *et al.* 1966, 1972 a, 1972 b, 1975). When these effects are large they sharply reduce the confidence that a breeder can place on comparisons among genotypes observed in different years. This is mainly the reason why fruit breeders postpone selection decisions until

Table 3

Least-squares estimates of year effects · See 'Materials and methods' for units of measurements · Numbers of observations are in parentheses

Kleinste Quadrate des Jahrgangseinflusses · Maßeinheiten s. unter „Materials and methods" · Anzahl der Beobachtungen in Klammern

Year	Crop weight	Cluster weight	Cluster compactness	10-Berry weight	Skin texture	Pulp texture	TSS	Acidity
1976	343.854	.691	−.142	−1.176	.010	.006	1.103	−.012
	(523)	(527)	(524)	(525)	(519)	(519)	(513)	(513)
1977	−882.080	−41.549	−.073	−.830	−.001	−.082	−.424	.030
	(279)	(281)	(167)	(280)	(142)	(140)	(274)	(274)
1978	283.739	51.725	.199	1.317	−.029	.140	−.745	−.018
	(307)	(309)	(145)	(308)	(94)	(94)	(300)	(298)
1979	254.486	−10.867	.015	.688	.020	−.064	.065	.000
	(20)	(352)	(304)	(352)	(272)	(272)	(332)	(320)

Fig. 1: Distribution of deviations of observed offspring total soluble solids from those predicted by the regression model. The range of deviation is from −8.77 to +7.28 °Balling.

Verteilung der Abweichungen des bei den Nachkommen beobachteten Mostgewichtes von den mittels Regressionsmodell vorausgesagten Werten. Die Abweichungen bewegen sich im Bereich von −8,77 bis +7,28 °Balling.

measurements have been taken for several years. The effects of yearly differences in climate on some traits of grapes are large; e. g., during the 4 years data were analyzed, the average crop weight of the population ranged about 1226 g/vine (Table 3). The increment of average crop weight in 1977 was 882.08 g (41 %). However, these effects of annual fluctuations in climate need not obscure the distinction of genetic differences in segregating populations. Year effects can be eliminated from comparisons among genotypes observed in different years by applying appropriate statistical techniques (SEARLE and HENDERSON 1961). In the case of grapes, as in other fruit crops the use of such techniques should greatly increase the precision with which genetic differences among seedlings can be discriminated and thus allow an important reduction in the number of years required by the breeder to identify superior genotypes with confidence. Of course, any possible reduction in the number of years required for selection decisions leads not only to major reductions in the per unit cost of genetic improvement, but also to a significant increase in the rate of genetic improvement since selection cycles are shortened.

2. Distributions of deviations observed from predicted regressions

The distributions of deviations observed from predicted regression points (i. e., Fig. 1) are almost symmetric, indicating that it was equally likely to make errors of measurements in higher or lower direction. Consequently, there was not any source of bias with this respect, to reduce the estimates of heritability below the parametric value, i. e., there is no tendency to introduce a spurious curvilinearity to the regression resulting in an underestimate of the proportion of additive genetic variability to phenotypic variability.

3. Means and standard deviations

Estimates of the means and standard deviations of parents and offspring (Table 4) provide both a general quantitative description of these populations and a hint of their

Table 4

Estimates of progeny and mid-parent means, heritabilities, and their standard deviations

Mittelwerte der Nachkommen und der Elternpaare sowie Heritabilität mit Standardabweichungen

Trait	h_{max}^2	Mid-parent		Progeny		h^2	S_h
		Mean	σ	Mean	σ		
Crop weight	0.29	3 416.41	1 485.59	2 168.78	1 444.31	−0.08	0.03
Cluster weight	0.57	313.56	112.09	284.02	145.63	0.12	0.03
Cluster compactness	0.65	2.62	0.25	2.57	0.77	0.55	0.09
10-Berry weight	0.89	25.64	12.51	23.61	10.34	0.49	0.02
Skin texture	0.72	1.17	0.29	1.15	0.35	0.75	0.03
Pulp texture	0.72	1.06	0.08	1.26	0.61	1.04	0.20
TSS	0.55	23.54	1.33	21.31	2.31	0.34	0.05
Acidity	0.62	0.60	0.10	0.81	0.20	0.15	0.06
General vigor		13.99	1.60	12.01	4.17	0.10	0.12

recent history of selection. For example, mean of parental populations for cluster weight is significantly larger than that of their progenies, and the standard deviation of parental population is smaller than that of offspring population. The same is true for the other traits. Therefore, selection, directly or indirectly, has been practiced for higher TSS, lower acidity, larger berry size, well-filled clusters, lower pulp firmness, and more vigorous vines. Estimated means and standard deviations of parental and offspring populations are not much different for skin texture. Thus, no selection probably has been practiced in the past for extreme performance on this trait in the population studied.

4. Heritability and response to selection

Heritability is a measure of the degree to which the performance of progeny can be predicted from that of their parents. Typical relationships between parental and offspring performance (from which heritabilities are calculated) are illustrated in Figs. 2 and 3, where crop weight and TSS of each progeny is plotted against the average value obtained for each pair of parents.

Estimates of heritabilities, means, and their standard deviations are listed in Table 4. All estimates on fruit characters were obtained from data adjusted for year effects. The precision of heritability estimates are high for all traits except vigor, pulp texture and cluster compactness. Heritabilities of pulp texture (1.04) and skin texture (0.75) are very high. Apparently, within this population almost all the variability in year adjusted measurements of these characters can be attributed to the additive effects of genes. Heritabilities of cluster compactness (0.55), berry weight (0.49) and TSS (0.34) are moderately high, heritabilities of cluster weight (0.12), acidity of juice (0.15) and vigor (0.10) are low, and heritability of crop weight is practically 0. Maximum heritabilities in this population are also listed in Table 4. Berry weight has the highest h_{max}^2, indicating that it is the least influenced by environmental factors. In cluster compactness, skin texture and pulp texture h_{max}^2 are approximately equal to or smaller than h^2, indicating little if any non-additive genetic variability is associated with these traits. Berry weight and TSS have significant non-additive genetic variability. Most of the genetic variability in acidity and all the genetic variability, if any, in crop weight are the non-additive types.

The response predictions of the population to selection of parents on the basis of their own performance can be obtained by inserting the estimated heritabilities into response functions such as $R = h^2 i$, where R is the expected response per generation and i is the intensity of selection (FALCONER 1960). Assuming that only 5 % of the seedlings are selected on the basis of superior performance and are allowed to mate randomly, *inter se*, then the expected response and the expected gain are as given in Table 5. No response to selection, nor any gain is expected upon selection of seedlings with the highest crop weight as parents of the next generation, since heritability is practically 0 for this trait. The same is true for general vigor. Although heritability for this trait is not 0, the precision of heritability is so small that no response to selection can be predicted. Therefore, the response to selection for the two traits is not listed in Table 5.

Cluster compactness is influenced by cultural practices, i. e., whatever influences fruit setting. However, in a uniform environment (uniform cultural practices) selection for loose or well-filled cluster based on parental performance is probably an optimal procedure which should produce rapid genetic gain among offspring.

Berry weight is a variety characteristic in the grapevines, yet it varies according to the vigor of vine, water absorption, berry set, girdling, hormonal application (GALET

1979) and daily temperature (KLIEWER 1977). Again in a uniform environment selection for large berries based on parental performance is the optimal method which should produce rapid genetic gain among offspring.

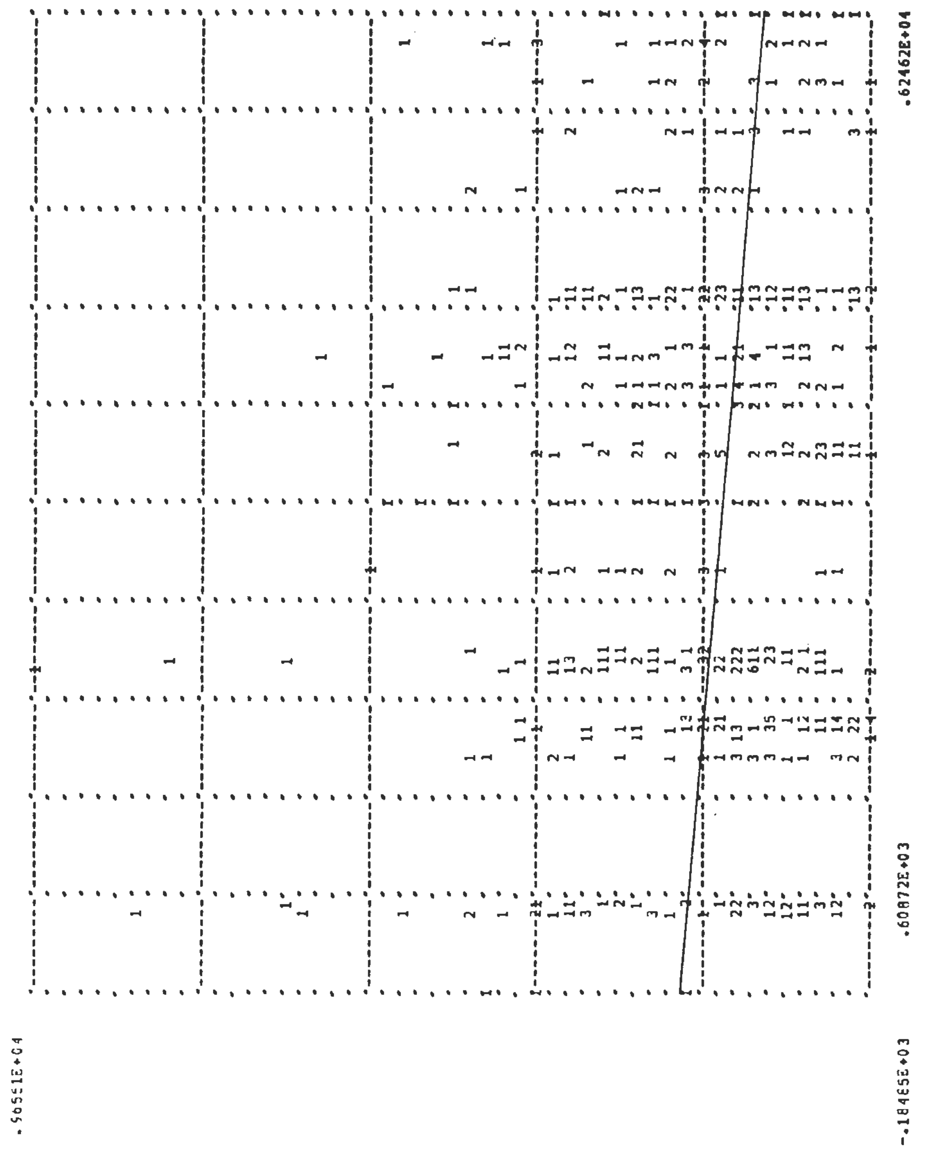

Fig. 2: Heritability of crop weight; each progeny mean plotted against midparent mean. Figures around the regression line are numbers of progeny means plotted against corresponding mid-parent mean.

Heritabilität des Traubenertrages; die Mittelwerte der einzelnen Nachkommen sind jeweils gegen die Mittelwerte ihrer Elternpaare aufgetragen. Die Ziffern über und unter der Regressionsgeraden geben die jeweilige Anzahl der Mittelwerte der Nachkommen an.

Berry textures (i. e., pulp and skin textures) are variety or species characteristics and probably are controlled by simple Mendelian genes, and the environment generally has little influence on the expression of these traits in the grapevine. *V. rotundi-*

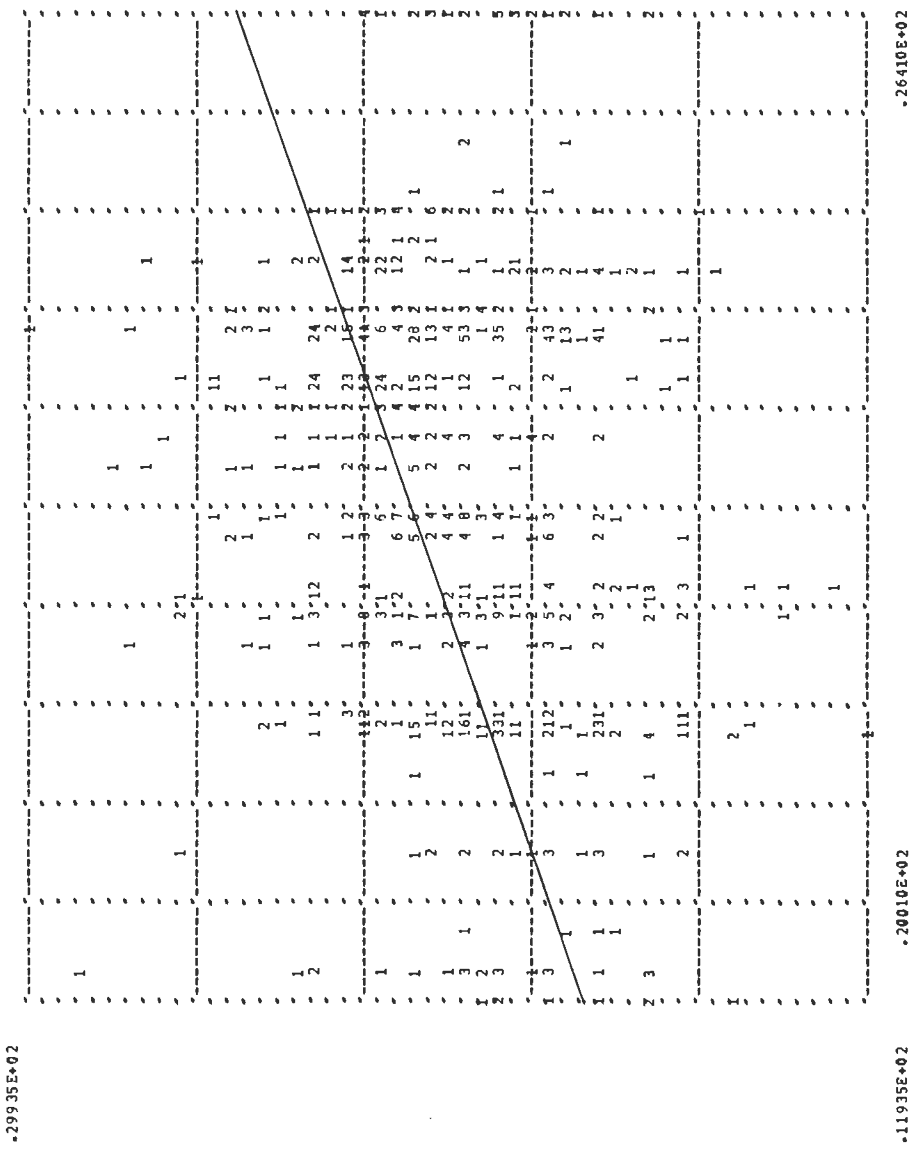

Fig. 3: Heritability of total soluble solids; each progeny mean plotted against mid-parent mean. Figures around the regression line are numbers of progeny means plotted against corresponding mid-parent mean.

Heritabilität des Mostgewichtes; die Mittelwerte der einzelnen Nachkommen sind jeweils gegen die Mittelwerte ihrer Elternpaare aufgetragen. Die Ziffern über und unter der Regressionsgeraden geben die jeweilige Anzahl der Mittelwerte der Nachkommen an.

folia grapes have a tough, thick skin, whereas *V. vinifera* grapes have a tender, thin skin. For improvement of these traits in any direction, simple mass selection is self-evident.

It appears that considerable non-additive genetic variability may be associated with total soluble solids (TSS), since h^2 (0.34) is much less than h_{max}^2 (0.55). Further research is needed to test the validity of this hypothesis. Nevertheless, sufficient additive genetic variability seems to be associated with this trait to indicate selection based upon parental performance after adjustment for yearly climatic effects, would result in reasonable rates of genetic gain in subsequent generations (Table 5).

Table 5

Response to selection · The expected performance of the progeny of randomly mated parents ranked in the upper 5 %[1]) of the progeny generations; $R = h^2 i$

Auswirkungen der Selektion · Die zu erwartende Leistung der Nachkommen zufällig gekreuzter Eltern mit hohem Leistungsniveau (obere 5 % der Sämlingsgenerationen); $R = h^2 i$

Trait	R	Expected gain	$\frac{\text{Expected gain}}{\text{Population mean}} \times 100$
Cluster weight	0.25	36 g	15 %
Cluster compactness	1.13	0.87[2])	34 %
Berry size	1.01	10.5 g/10 berries	44 %
Skin tenderness	1.55	0.55[2])	48 %
Pulp texture	2.06	1.25[2])	100 %
TSS	0.70	1.62[2])	8 %
Acidity	0.31	0.06[2])	8 %

[1]) i = 2.06.
[2]) See 'Materials and methods' for units of measure.

In juice acidity h_{max}^2 (0.62) is much more than h^2 (0.15), indicating that considerable non-additive genetic variability may be associated with this trait also. The measurements for this trait are not very reliable because they vary quickly with the stage of maturity. With such large progenies, no adequate method could be worked out to relate sampling date to stage of maturity. Judgment as to the effectiveness of selection on this trait should be reserved until measurement technique has been improved.

The heritability estimate for cluster weight is low (0.12). But apparently there is a high potential genetic variability for this trait ($h_{max}^2 = 0.57$). It is suggested that increased sample size would give a more meaningful estimate of the actual heritability.

Crop weight has a heritability that is not significantly different from 0. There is apparently no additive genetic variance remaining in this population for this trait; nor is there any indication of large amounts of non-additive genetic variance in this population (Table 4). Thus, the heritability of 0 for crop weight in this population, by itself, precludes the possibility of a reasonable rate of genetic gain, no matter what the genetic basis of inheritance of crop weight may be. It should be noted, however, that crop weight is probably not a critical factor in most grape breeding programs because vines tend to set fruit in considerable excess of that required for commercial production, and removal of excess inflorescences or fruit clusters is sometimes necessary.

The 0 heritability of crop weight in this population could result from one or a combination of the following factors:

1. The breeding stock analyzed is genetically homogeneous with respect to crop weight.
2. The effects of segregating genes on the expression of this trait in this population is entirely epistatic.
3. The effects of random differences in the environment are almost entirely responsible for observed phenotypic differences.

This analysis is not powerful enough to elucidate the cause(s) of 0 heritability estimated for this trait. The appropriate solution to this problem depends primarily on which of the three above mentioned factors is the major cause of the 0 heritability. Some light can be shed on this situation by comparing the means and standard deviations of parents and progenies (Table 4). The mean of mid-parents for crop weight is much higher than that of progenies, indicating that parents were highly selected for this trait. On the other hand, standard deviations (and consequently variances) of parents and progenies are almost equal. These results suggest that the population is homogeneous with respect to this trait. The estimated h_{max}^2 (Table 4) however, indicates the probable existance of some heterogeneity. If so, then the effects of segregating genes on the expression of crop weight is epistatic. This might be the case, as OLMO (1952) has shown the existence of strong inbreeding depression, which is an indication of non-additive gene actions on expression of this trait. The third factor could be examined, if there were data on vines of the same genotype. Then, by comparing the proportion of total variability in this population that arises from both genetic and environmental causes with the proportion of variability arising from differences between propagules (vines of the same genotype), that is variability due to the environment, one could somehow relate the 0 heritability of the crop weight to one or a combination of the three above-mentioned phenomena.

If the epistatic effects of genes are the major cause of 0 heritability, breeding methods other than 'mass selection' methods (those involving inbreeding, tests of specific combining ability and the development of hybrids) would be successful in improving crop weight. If, on the other hand, the 0 heritability of crop weight is due either to genetic homogeneity of this population with respect to this trait, to the effects of random environmental variability, or to some combination of these two phenomena, then no selection procedure or breeding method would be expected to lead to improvement of the trait until the genetic variability of this population is increased and the random effects of environment on crop weight are greatly decreased.

There is considerable evidence that the crop weight of vines in their first 2 years of production is much lower than when the vines are mature. This is probably the main reason for lower mean of crop weight of offspring population than that of parental population (parental population were mature vines). Furthermore, it is likely that the yields of juvenile vines in the first 2 years of production are more subject to environmental variation than are mature vines. This, by itself, could easily account for one of the causes of 0 heritability or low maximum heritability for crop weight. One could eliminate the variability arising from this source by obtaining data on mature vines. This procedure would not only add additional maintenance expense, but would also significantly increase the length of selection cycles by at least 2 years, which is both prohibitively expensive and time consuming. Increasing selection cycles also reduces the rate of genetic improvement per year.

There is an alternative solution to this problem that probably would be both considerably less expensive and quite possibly more effective than a solution that depends upon the reduction of non-genetic variability associated with crop weight. This solution entails selection of traits that presumably are highly correlated with yield and that have moderate to high heritabilities. The crop weight per vine is composed of cluster weight and the number of clusters per vine. ALLEY (personal communication) has shown that cluster number per vine is significantly higher in particular clones than others, and this has been true over the 4 seasons studied. This character must then be highly heritable. Therefore, selection of seedlings as parents on the basis of superior performance of these crop weight determinant traits during their first few seasons of production (and their subsequent random mating *inter se*) should yield rapid genetic improvement. If, as seems apparent, they are highly correlated with yield, this procedure should also affect genetic improvement of yield potential (FALCONER 1960) without adding either to the expense of the breeding program or to the length of selection cycles.

Table 6

Estimates of phenotypic correlations

Phänotypische Korrelationen

No. Trait	1	2	3	4	5	6	7	8
1. Crop weight								
2. Cluster weight	0.61 ± 0.04							
3. Cluster compactness	0.40 ± 0.06	0.42 ± 0.06						
4. 10-Berry weight	0.01	0.26	−0.12					
5. Skin tenderness	− 0.15	0.00	−0.18	0.39 ± 0.06				
6. Pulp firmness	− 0.08	0.10	−0.14	0.49 ± 0.06	0.42			
7. TSS	0.11	− 0.05	0.12	−0.37 ± 0.06	−0.32 ± 0.06	−0.21		
8. Acidity	− 0.06	− 0.09	−0.05	0.02	0.01	−0.04	−0.21	
9. General vigor	0.02	0.07	−0.02	0.10	0.02	0.02	0.01	−0.02

All measurements were previously adjusted for year effects.

95 % confidence intervals about correlation estimates were obtained via Fisher's 'Z' statistic (SNEDECOR and COCHRAN 1967). All confidence intervals are ± 0.07, unless otherwise indicated.

Correlation coefficients considered to be of practical importance by the authors are underlined.

5. Phenotypic correlations

A complete list of estimated phenotypic correlations among the nine traits is presented in Table 6. Those considered to be sufficiently strong to be of practical significance to a breeding program are underlined.

Strong phenotypic correlations among traits probably can be attributed, at least in part, to pleiotropic effects or close linkage among genes affecting different traits. Such phenomena could enhance or inhibit the selection progress of traits depending upon the direction of correlation. Therefore, they should be taken into account by the breeder.

Crop weight and cluster weight have a high positive correlation (0.61 ± 0.04). Heritability for crop weight is 0. If the population is homogeneous with respect to crop weight, then the observed phenotypic correlation between the two traits indicates that environment is exerting a common influence on the traits.

Varieties of *V. rotundifolia* grapes usually have fairly small berries with a tough skin, soft pulp and small loose clusters with few berries. This is the main reason for the observed phenotypic correlations among these traits in the population studied, e. g., skin tenderness and pulp firmness have a high positive correlation, and berry weight has positive correlations with cluster weight, skin tenderness and pulp firmness. These correlations could be useful for the improvement of table grape cultivars that are needed to have well-filled clusters of moderate size and large berries with tender but resistant skin and firm flesh.

The total soluble solids have negative correlations with berry weight, skin tenderness, pulp firmness, and acidity and have a low positive correlation with crop weight.

Vigor also has a low positive correlation with crop weight. There is considerable evidence that, in general, vigorous vines are more productive than the weak vines.

These relations, discussed above, suggest the possibility of taking advantage of relations between characters, considering a scheme of selection for more than one character at the same time, or minimizing the negative influence of negative correlations between characters using a suitable index of selection. The selection index technique provides an objective method whereby the characters are weighed in a systematic manner, and the breeder must apply various weights to different traits as he makes his decisions (HAZEL and LUSH 1942).

Conclusions

The breeder's ability to discriminate superior genotypes in segregating grape populations is seriously hindered by the effects of random fluctuations in annual climate on performance of some traits (Table 3). This variability is probably a common source of selection error and of delayed selection decisions that retard the rate of genetic improvement. Results obtained herein demonstrate that this selection problem in grape breeding stocks can be solved efficiently. Available statistical techniques are sufficiently effective in removing this source of error and thus postponing selection decisions past the 3rd or 4th year that seedlings produce fruits.

Apparently, a considerable portion of the variability in the population remaining after adjustment of measurements for these spurious effects of climate results from segregating genes with additive effects for all traits except crop weight and general vigor (Table 4) (the situation with respect to crop weight remaining, as yet, unclear). Therefore, the straightforward procedure of selecting parents on the basis of their own performance, and their subsequent mating *inter se*, should affect relatively rapid genetic gains (Table 5) for most traits for several generations. Furthermore, the rate of genetic gain for berry weight, cluster weight, TSS, and acidity can probably be increased significantly at a relatively small cost by increasing the sample size for these traits. The heritability of vigor can probably be increased considerably by improving measurement techniques, namely shoot counting.

The high cost of maintenance required to mitigate the random variability in crop weight apparently arising from juvenility renders impracticable the possibility of improving the yield of subsequent generations of this population by selecting parents on the basis of this trait. However, there are other traits that are apparently highly correlated with crop weight (Table 6) and have low to moderate heritabilities. Selection of these traits correlated with yield seems to be an effective and economical means of achieving a reasonable rate of genetic gain in yield. Probably the key traits in this regard are cluster weight and cluster number; and efforts should be made to increase the heritability of cluster weight and to estimate the heritability of cluster number.

Estimates of phenotypic correlations among the traits studied suggest that close linkages among genes affecting these traits or epistatic effects, if they exist, are probably of the sort that should enhance selection progress or may retard it depending upon the direction of selection (Table 6).

In general, the results obtained in this study are similar to those reported for tree fruits and nuts by HANSCHE *et al.* (1966, 1972 a, 1972 b, 1975) and KESTER *et al.* (1977). The studies in perennial fruit trees and grapes have resulted in speculation that the solution for the major problems of breeders of these crops depends on efficient means for discriminating genotypic differences in their breeding stock, and does not depend upon breeding methods that exploit non-additive genetic variability.

Summary

Heritabilities and phenotypic correlations among 10 traits of the grapevine (*Vitis vinifera* × *V. rotundifolia* hybrid derivatives) were estimated from measurements obtained from 46 families, including a total of more than 1000 offspring generated by crosses among 26 parents. Measurements on fruit characters were obtained over a period of 4 years, 1976—1979. (General vigor of the vines was measured in only 1 year, 1976). Prior to this analysis the data on fruit traits were statistically adjusted to mitigate the confounding effects of fluctuating annual climates on estimates of genotypic value. The heritabilities were then estimated by regressing the average performance of each seedling on the average performance of its mid-parent. Heritabilities are 0.12, 0.55, 0.49, 0.75, 1.04, 0.34, 0.15 and 0.10 for cluster weight, cluster compactness, berry weight, skin texture, pulp texture, total soluble solids, acidity of juice and general vigor, respectively. The heritability estimate for crop weight in this population is practically 0 (−0.08). The precision of these estimates is very high, except for that of general vigor. Thus, they should be reliable predictors of the rate of genetic gain attainable in such populations when seedlings are selected as parents on the basis of their own performance. The expected performance of the progeny of randomly mated parents, ranked in the upper 5 % of the progeny generation, were estimated. The implications of these genetic relationships on the effectiveness and efficiency of breeding programs and selection procedures in grapes are discussed.

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