INHERITANCE STUDIES WITH THE TROPICAL GRAPE

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THIS paper is the first report on the development of a promising new class of fruits — the tropical and subtropical vineyard grapes. It is a résumé of genetic, physiological and pathological observations made during a period of twelve years on a group of wild tropical species of grapes previously little known or completely unknown to horticulture.

The tropical grapes are genetically and taxonomically distinct from temperate zone species. Many of the problems experienced in their horticultural improvement have proved to be peculiar to their climatic and specific background, though much that is learned in regard to them is applicable to grape improvement in general.

Little is known regarding genetics of the genus *Vitis,* which is difficult to study because of its polygamo-dioecious heterozygous constitution. The many small chromosomes, the wide range of variability in character expression, frequent natural hybridity, and a long time-interval between generations, present numerous problems. Even in the temperate zone, the grape breeder must contend with many special problems. In working with the tropical species the complexities are increased by numerous physiological specializations which characterize the parent species.

It has been necessary to employ in our studies species adapted to widely different climates. The tropical species have furnished the necessary adaptability, and the temperate-zone cultivated varieties have been the source of high fruit qualities. That is to say, the parents used heretofore in making crosses were either strictly temperate, or, as with oranges, avocadoes, etc., wholly tropical or subtropical in their adaptation. The extensive hybridization of tropical and temperate species, which has been the basis of the present project, seems never to have been undertaken before.

The Tropical Species

Though all of the "tropical" species listed below are not found within strictly tropical latitudes, they are indigenous to essentially tropical climates and their reactions are tropical.

The most widely distributed and commonly known tropical species is *Vitis tiliaefolia* H. B. (*V. caribaea*), the "Agras" or "Uva Silvestre" of the jungles of Central and South America. This species is indigenous to medium and low elevations from Cuba and Mexico south to the Equator. Its "basswood"-like leaves make it easy to recognize. The species is exceedingly prolific of large and compound clusters; the small acid berries are of very poor quality. Despite this, it has been a valuable parent in breeding some of our promising new horticultural varieties.

The Callosa grape (*Vitis shuttleworthii* House) is known to occur wild only in the swamps in the southern half of the Florida peninsula. The vines are vigorous, healthy and prolific. Its small dark green leaves are typically white- or tan-felted beneath. Its fruit clusters are small and compact; the large, maroon to dark red berries often measure above three-fourths of an inch in diameter. In dessert quality it varies from fair to poor. The wild vines of this species used in these experiments were collected in extreme southern Florida.

Another species, extensively em-

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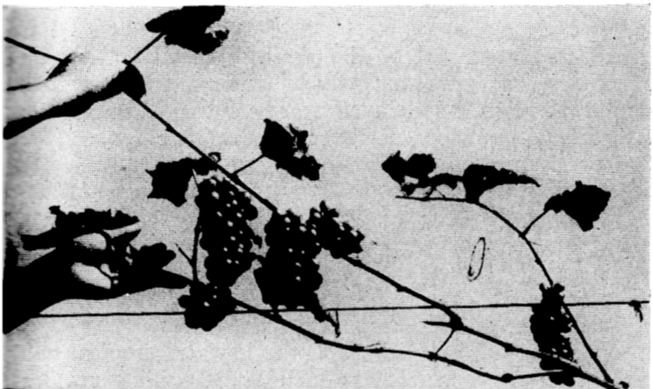


ECOLOGICAL QUANDARY

Figure 8

Vine of the North American cultivated variety Golden Muscat in premature dormancy and with immature fruit. Note the short weak canes.

PROMISING HYBRID

Figure 9

Vine of one of the new hybrid tropical selections with ripe fruit and ample healthy foliage.

GROWTH-SCHEDULE UPSET

Figure 10

An illustration of prolonged dormancy affecting all but the terminal buds. "Bull-canes" are in the making and only a slight fruit crop is in prospect. This adverse reaction to a tropical environment is a heritage from the temperate climate parent.

LUXURIANT ADAPTED GROWTH

Figure 11

Normal and equal growth from many buds is shown by *Vitis shuttleworthii,* one of the wild tropical species.

ployed in this breeding project, is the rare and little known *Vitis gigas* Fen., a new species recently discovered along the Atlantic coast of southern Florida. Indications are that this may have been a comparatively recent immigrant from the Bahamas where a similar grape is reported to occur. The vines are strong and vigorous, producing large sharply lobed leaves with acute or attenuate apexes. They are thinly tan-felted beneath.

Fruit clusters of this species are usually large and well compounded, having medium small (11 to 14 mm.) good quality black berries with bloom. The species seems to prefer strand locations and dry slightly alkaline soils.

Two subtropical forms of the Aestivales series of species, *V. rufotomentosa* and *V. smalliana,* have likewise been used, though to a lesser extent than the three first mentioned.

Climatic Influence on Growth and Dormancy

Perhaps the most important physiological maladjustments encountered in hybridizing temperate climate horticultural varieties, such as Concord, Tokay or Beacon, with a tropical* species (*V. shuttleworthii* or *V. tiliaefolia*) were those connected with the normal growth and rest cycles. These apparently result from the individual or combined action of temperature, of humidity of air or soil, or perhaps of photoperiodism—especially during the dormant season.

Practically all of the European and North American grapes have a low temperature requirement for the rest period. With some this is so pronounced as to inhibit spring growth when winter temperatures do not fall far enough. With others, as the varieties Niagara, Isabella, Golden Muscat and similar hybrids with *vinifera,* as well as with certain southern types of the *vinifera* species, this phenomenon may be evidenced by abnormal and delayed spring foliation from fully dormant canes. Weak early growths of poor color, or activation of only a few dormant buds, with subsequent development of abnormally large "bull canes," may give additional evidence of insufficient chilling. The yield under these conditions is usually small and of mediocre or poor quality.

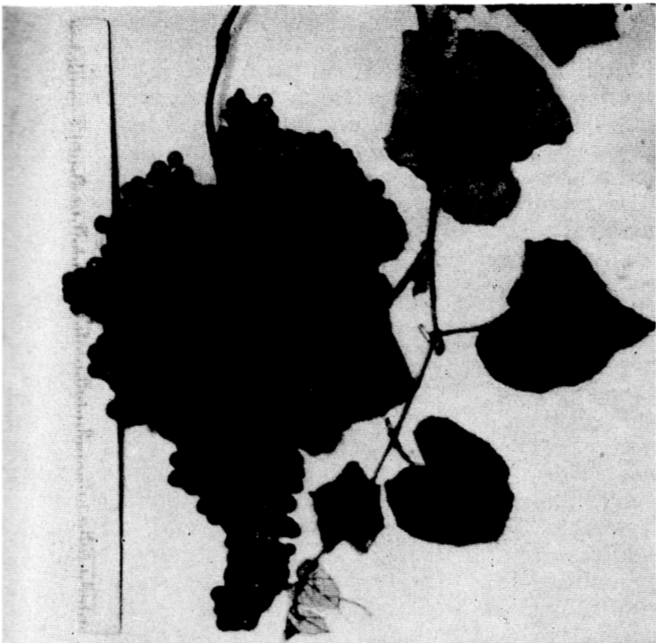
By contrast, the lowland tropical wild species have little or no chilling requirement, as would be expected in view of their environment.

In temperate climates the important function of starch hydrolysis in dormant tissues is aided by cold weather.[2] In the warmer regions, where chilling does not occur, this transformation must be accomplished in other ways which the tropical species are normally adapted to do. For this reason, more than any other, we must resort to the wild tropical species as a foundation for warm climate viticulture.

When the temperate climate varieties such as Niagara, Concord, Isabella, the Munson hybrids, or even most *vinifera* varieties, were planted in the humid tropical climate of lowland Costa Rica (latitude 10 degrees North; elevation 1,900 ft.) or even in southern Florida, the first season's growth was by no means normal. Most of the temperate North American sorts produced mature leaves and canes in an abnormally brief time after budding, lapsing into dormancy usually in the very middle of the growing season. Our observations strongly indicate that this is due, in part at least, to photoperiodic influences. In any case, two or more prunings a year have been necessary to keep the plants even partially in harmony with the seasons.

When lowland tropical species, having

*In this project the dividing-line between tropical and temperate conditions has been determined mainly by temperature. In latitudes 25° - 30° N., the southern edge of the temperate zone has been determined by the following criteria: occasional (once in five years) extreme minimum temperature not lower than 27° F.; typical annual minimum not lower than 32° F.; mean temperature during winter or dormant season not lower than 65° F.; mean minimum temperature during growth season not lower than 70° F. Where temperatures are above this and the latitude less, the climate would be considered as subtropical or tropical; if temperatures range lower, and latitude higher, the climate would be considered temperate.



LARGE CLUSTER—SMALL BERRIES

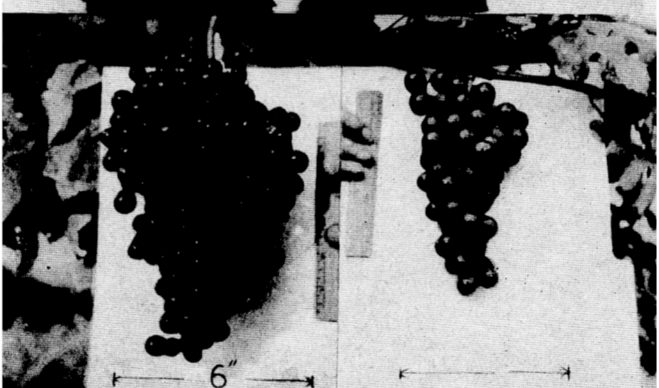
Figure 12

The large compound cluster and small berries of *Vitis tiliaefolia,* a native of tropical America. The rule is one foot long. This species has been a valuable source of adapted genes in the production of superior hybrids.

DISEASE RESISTANCE FROM OVERSEAS

Figure 13

An illustration of the inheritance of disease resistance in a hybrid. The leaves on the left are badly attacked by leaf-spot. They are from native American types. The resistant foliage at right is from hybrids of these species with *V. vinifera* from Europe.



SUPERIOR SELECTIONS

Figure 14

The large compound cluster and medium size grapes (left) were produced by a complex hybrid combining genes from several tropical species and the Malaga-Pense variety of *Vitis vinifera.* These large and tasty grapes (right) are a rare and desirable combination of genetic factors in a complex hybrid. Fruit size, quality and flavor closely resemble the European grape, while vine adaptability and foliage is mostly that of the wild tropical species.

no chilling requirement and well adjusted to short-day periods, were hybridized with temperate climate species, various complications arose. With few exceptions, the poor adaptability of the temperate climate parents to tropical environments has been at least partially dominant in first generation progeny. In most cases, it has been necessary to cross these partially adjusted F_1 hybrids back on the wild tropical species in order to attain a satisfactory degree of adaptability. It has been difficult to attain at the same time high fruit quality.

In a population of 1,300 F_2 and double cross progeny, all with tropical × temperate parentage, there was no clear-cut segregation with respect to chilling requirement or general adaptability. This might indicate that these differences are conditioned by complex, multiple-gene heredity. The percentage of individuals that showed adaptability equal to that of the tropical parent species was so small and hard to classify that no definite conclusions were suggested regarding the number of genes involved.

When these F_1 hybrids were crossed back to the tropical species, not more than ten per cent of the progeny has equalled the tropical parent in adaptability to warm dormant periods. It is understood, of course, that in such complex quantitative expressions many indirect and possibly interacting factors may be concerned. It is possible, also, that such modifying circumstances as variation in soil, atmosphere and reaction to disease may be involved. The selection of strains having good adaptability with even mediocre quality fruit has been the most difficult aspect of the entire project.

Disease Resistance

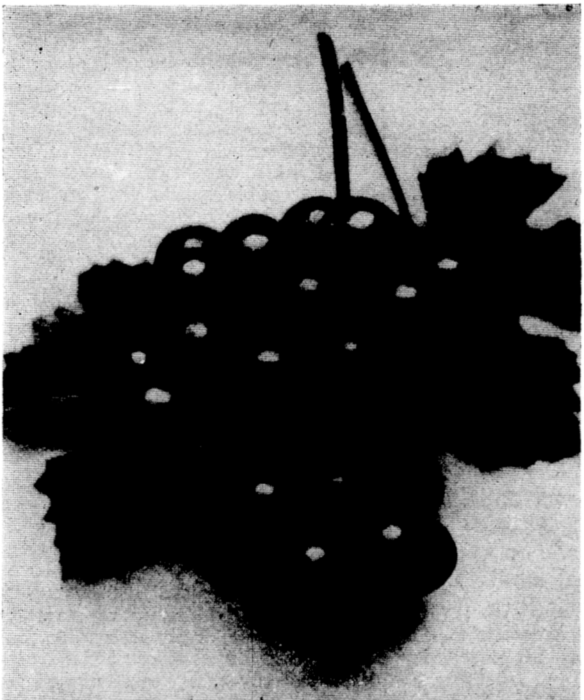
Freedom from disease is a condition usually difficult to attain. Often it is correlated with various climatic and physiological influences such as temperature, humidity and perhaps even with photoperiodism as it effects the maturity of tissue cells. Results of our experiments have indicated that premature defoliation of North American grapes in the tropics is often as much the result of early cell senility as of direct fungus attack.

Four important vine diseases of the tropics, downy mildew, rust, anthracose and *Cercospora* leaf-spot, with several others of minor consequence, have been studied for twelve years of the author's experiments in Costa Rica, Puerto Rico, and southern Florida. No correlations in resistance involving any two of these diseases could be found. A wild species or a hybrid variety may have good resistance to any one, two, or three of the

TABLE I.—Species of pronounced importance to warm climate viticulture and their pertinent characteristics. 0=completely susceptible or unsatisfactory. 10=completely resistant or satisfactory.

	Resistance to					Adaptability to		
	Rust	Anthracnose	Downy† mildew A	Downy† mildew B	Alternaria leaf-spot	Warm dormant season	Wet Soils	Dry Soils
Tropical Species								
V. shuttleworthii, House	9	8	6	9	9	10	10	7
V. simpsoni, Munson	9-10	7	8	9	8	10	10	5
V. tiliaefolia, H. & B.	9-10	7	8	9	9	10	10	6
V. gigas, Fennell	6	10	7	9	7	9	7	9
V. rufotomentosa, Small	6	10	8	9	7	8	6	9
V. smalliana, Bailey	6	10	8	9	7	8	6	8
**V. munsoniana*, Simpson	10	7	10	10	7	9-10	9	9
**V. popenoei*, Fennell	10	6	10	10	8	10	9	5
Temperate Species								
V. labrusca, L.	3	10	8	7	4	1	6	4
V. vinifera, L.	0-2	0-3	0-9	0-2	4-8	0-5	3	8
V. bourquina, Mun	5	8	5	5	4-5	3	4	7
V. lincecumii, Buckley	4	8	8	8	4	2	4	8
V. champini, Planch	4	7	8	9	3	3	3	9
**V. rotundifolia*, Michx	10	8	10	10	6	3	7	6

*Sub-genus muscadinia
†A—resistant in young growth; B—resistant in mature growth.



HORTICULTURAL VICTORY

Figure 15

Superior strain selected from *Vitis shuttleworthii.* Grapes average seven-eighths of an inch in diameter.

EXTREME FECUNDITY

Figure 16

An F_1 hybrid of *Vitis tiliaefolia* $\times$ *V. vinifera* at Turrialba, Costa Rica. These plants are resistant to the important diseases and are very sturdy, with large crops of fruit.

QUANTITY AND QUALITY

Figure 17

A derivative of the selection shown in Figure 9 crossed with a wild hybrid from southern Florida. This plant has three-fourths tropical parentage involving at least three species. Fruit from this vine is shown in Figure 14 (right).

pathogens and complete susceptibility to all the others. Or in rare cases it may possess pronounced resistance to all of them. Studies[3] in the United States have likewise shown this in part. In our new tropical varieties resistance to each pathogen has had to be obtained separately, and usually from a different specific source. No linkages of resistance to one disease with susceptibility to another have been experienced.

Table I lists the known *Vitis* species of greatest promise to tropical grape development, together with ratings for their relative resistance to the most destructive fungi. Their adaptability to warm dormant seasons and to wet and dry soils is likewise indicated.

The ratings in Table I are made on a basis of 0 to 10 for the principal modifying influences at Turrialba, Costa Rica, and at Miami, Florida. 0 would indicate the extreme in susceptibility or poor adaptability, and any rating below 2 would be too poor for survival; 4, roughly, forms the dividing line in relation to satisfactory behavior, any rating below this figure being viewed as entirely unsatisfactory. To be considered as satisfactory for growth and production of fruit under humid tropical conditions a species should have no rating below the level of 6. Those rating six or higher in all categories have proven to be entirely satisfactory.

Notes on Disease Resistance

Rust

The fungus known as grape rust (*Physopella vitis* [Thuem.] Arth.) is one of the most destructive vine diseases of the American tropics. In our Institute vineyard where some leaves persist on the vines throughout the year, this fungus remains almost perpetually in the uredinal stage.

Varieties derived mostly from *Vitis labrusca, V. vinifera, V. aestivalis,* or nearly any of the temperate species, have been most susceptible to *Physopella.* On the other hand, three species of the tropical group, *V. tiliaefolia, V. simpsoni* and *V. shuttleworthii*, have been consistently almost immune to it. Breeding experiments conducted by the author have shown that the first two species transmit resistance as a dominant to mature progeny and that it is controlled by relatively few genes. This situation appears to parallel the mature plant resistance to *Puccinia* in wheat.[1]

When *V. tiliaefolia* was hybridized with *V. vinifera,* which appears to be homozygous for susceptibility, all resultant mature F_1 progeny have been practically immune. When these rust-free F_1 plants were again crossed with moderately susceptible species, 24 from a total population of 38 have been relatively free of the fungus in mature specimens.

From a population of 28 F_1 progeny of *V. simpsoni,* × *V. rufotomentosa* and × *V. shuttleworthii,* all mature plants have shown virtual immunity. Inheritance in the F_2 generation in this case has not been studied. When the muscadines, *V. popenoei* and *V. munsoniana* were crossed with Euvitis varieties homozygous for rust susceptibility, all F_1 progeny were immune.

V. tilifolia and *V. simpsoni* are of value to the breeder as a source of high resistance against *Physopella.*

Vitis shuttleworthii has been virtually free from rust, though it is not so strongly resistant as the two preceding species. Its resistance appears to be conditioned by multiple factors. When this moderately resistant species was crossed with very susceptible varieties of *V. labrusca, V. vinifera* and *V. aestivalis,* all F_1 progeny have been susceptible to varying and intermediate degrees.

Downy Mildew

Downy Mildew (*Plasmopara viticola,* [B. & C.] Berl. & Det.) is perhaps the most complex and at times the most misunderstood of all fungus diseases of *Vitis.* In the humid tropics it may be destructive as in the temperate regions. Resistance to this pathogen presents confusing problems. It is a common occurrence that varieties, thought to be resistant, become susceptible when moved to a different climate or location. A variety may show striking freedom from mildew, even when surrounded by badly infested plants only to be severely attacked at a later date. In such cases, the question obviously is not one of true resistance, but what would seem more likely, that of environmentally induced protection, or perhaps even of genetic protection during some limited growth stage.

It is established[7] that variations in temperature and soil moisture, when correlated with atmospheric humidity, exert a powerful influence in respect to infestations of *Plasmopara.* Such influences obscure the understanding of just what constitutes true or genetic resistance.

No known species of true bunch grape (*Euvitis*) is completely immune to downy mildew. Probably the nearest approach can be found in some types of the *Aestivales* series, as in forms of *V. rufotomentosa.* Studies by the author indicate that various widely different factors exist within the genus that may contribute toward an over-all resistance when combined in a single hybrid plant.

In Table I it will be noted that resistance to *Plasmopara* is expressed in two distinct ways: (a) resistance in newly developed tissue; and (b) resistance in mature tissue. Each is equally important.

When mature plants of *V. shuttleworthii* grew intertwined with those of Feher Szagos and Cabernet Sauvignon (*V. vinifera*) young leaves and flower buds of the first species have been badly attacked while at the same time those of the two *vinifera* varieties in a comparable growth stage showed no sign of infection. Later in the season, when all leaves were mature, the reverse condition existed.

When these kinds, resistant and susceptible in different ways, were crossed, selections were obtained that showed better resistance, as expressed in practical results, than was possessed by either parent or parent species.

The dual-phase resistance to *Plasmopara* might be accounted for in this manner: Some forms of susceptible European grape are free of downy mildew in early growth, probably due to lack of food in the newly formed cells and to closed stomata.[5] Mature foliage of the *V. shuttleworthii*, though rich with food and obviously at times with open stomata, would seem to be resistant as a result of chemical or physical constitution of protoplasm and cell walls.

In these studies, resistance to downy mildew in stage (a) seems to be inherited mostly as a dominant, while in stage (b) it would appear that complex quantitative factors are involved anl inheritance is, at least in part, recessive.

A still different expression of resistance to this disease has been observed in the muscalinia section of the genus. When *V. shuttleworthii* was hybridized with *V. munsoniana*, the factors of resistance in both (a) and (b) stages possessed by the muscadine staminate parent have been completely dominant. Whether this dominance is a simple or multiple factor inheritance could not be determined, since these hybrids have been sterile and no F_2 progeny was obtained. In most other plant characters this complete dominance has not been manifest.

Anthracnose

Resistance to anthracose (*Elsinoe ampelina* [DeBy.] Shear.) is closely conditioned by multiple factors. The majority of our experiments indicate that no more than two or possibly three, major factors condition susceptibility. Results obtained by the author have shown susceptibility usually to be dominant, with resistance transmitted as a recessive, which segregates in the second and later generations. The results of some of these studies are given in Table II.

The majority of wild tropical species show moderate to good resistance to anthracnose, but when they were crossed with the highly susceptible *V. vinifera*, susceptibility of the latter in all cases was transmitted as a dominant to the F_1 progeny. (See Table II).

Leaf Spot

Leaf spot diseases of the *Alternaria* and *Cercospora* group are very destructive to some species when grown in tropical America. The temperate North American species, *labrusca*, *aestivalis*, and *lincecumii*, and most of those native to the dryer southwest regions, have been severely attacked as is the case in some of the humid sections of the southern United States.[4] When these leaf-spot-susceptible species were crossed with *V. tiliaefolia* and *V. shuttleworthii*, or with some forms of *Vitis vinifera*; hybrids with satisfactory resistance were obtained. Since most tropical species have good resistance to this disease, it has not been of major importance in our experiments.

Diseases of Minor Importance

The disease known as black-rot (*Guignardia bidwellii* [Ell.] V. & R.) has not been

TABLE II.—Inheritance of susceptibility to anthracnose in certain crosses.

Homozygous for resistance (unless indicated otherwise)		Susceptible varieties	Progeny: Badly suscep.	Progeny: Mod. suscep.	Progeny: Resistant*
1. No. 9 (*V. rufo.*)	×	Alphonse Lavellee (vin.)	23	0	0
2. *V. tiliaefolia*	×	Alphonse Lavellee (vin.)	14	0	0
3. No. 5 (*V. shut.*)	×	Feher Szagos (vin.)	13	0	0
4. No. 9 (*V. rufo.*)	×	Alexandria, Red Muscat, Sultanina, Feher Szagos, Lignan Blanc, Chasselas Golden, Black Monukka, etc. (vin.)	187	0	0
5. No. 23 (*V. shut.* × *V. rufo.*)	×	No. 105 (cross no. 1)	42	76	37
6. No. 23	×	No. 106 (cross no. 2)	2	5	3
7. No. 106 (suscep.)	×	selfed	5	0	0
8. No. 23	×	Gros Colman (vin.)	12	0	0
9. No. 6 (*V. rufo.* × *V. shut.*)	×	Malaga (vin.)	4	3	0
10. No. 18 (*V. gigas*)	×	Malaga (vin.)	14	5	0
11. No. 18	×	(No. 9 × Lomanto) slightly suscep.	6	0	4
12. No. 23	×	Portland (*V. can.* × Rommel, both resistant)	0	0	27
13. No. 18	×	Extra (resistant)	0	0	7
14. No. 18	×	Cabernet Sauvignon (vin.)	64	0	0

*Even resistant kinds may occasionally show a few lesions on tendrils and petioles, but if of no consequence the variety is considered resistant.

a problem thus far with the tropical species. The relation of this disease to these new sorts will need to be more fully determined, but as yet there is no indication that it will be a limiting factor.

The so-called ripe and bitter rots (*Glomerella cingulata* [Ston.] Sp. & Von. S) and (*Melanconium fuligineum*) [Scrib. & Viala] Cav.) have not seriously attacked the best selections. Our observations suggest that these diseases prefer fruit with a high acid content and a low percentage of sugar. Selections that have produced berries rich in sugar and with the moderately firm fruit texture of *vinifera* have seldom been attacked. It is not anticipated that these rots will become a problem with our better tropical kinds.

Powdery mildew (*Uncinula necator* [Schw.] Burr.) is almost universally prevalent, though in our experience its ravages have been confined to the Old World temperate varieties and it has not been a major hazard to the tropical varieties or species.

Neither Phylloxera nor Nematodes have been a problem during our present investigations. Although both parasites are of common distribution and galls of the former may be found on the foliage of wild vines, the root systems of the tropical types have been unusually healthy. Obviously, a high degree of genetic resistance to these most destructive pests is an inherent characteristic in most of our material.

In the literature of grape breeding it has been commonly stated that characteristics of *V. vinifera,* always are dominant when crossed with western hemisphere types, and for this reason carry with them into the hybrid progeny a host of weaknesses. Our own results indicate that this is only partly true. Although *vinifera* generally has impressed its characters upon the progeny—good as well as bad—just how bad such inheritance proves to be has depended upon the nature of the combination. As an example, when we crossed a form having high susceptibility to downy mildew in either growth stage with another of the same type nearly all progeny were badly attacked. Little of value could be expected by this approach, yet it has been a common error that has prevented best results in the hybridizing of *Vitis vinifera* in North America.

General Inheritance

Most of the data available on the genetics of *Vitis* are based on such a small and specialized part of the genus as to have limited value in general application. As a genus the grape is polygamo-dioecious in flower function and thereby has a rather heterozygous genetic constitution. In the *Euvitis* (bunch grape) section the somatic chromosome number is 38. Since all species freely intercross and since dominance is variously expressed, the difficulty of predicting inheritance in new hybrids is obvious.

In the present work with tropical species, as in other comparable efforts, it has been found that certain parental combinations produce much better progeny than others. To isolate these complementary genotypes from the vast quantity of breeding material is a large undertaking in itself.

Inheritance of flower morphology and function has proved to be of a complex nature and widely varying progeny ratios are obtained according to parentage. When functionally hermaphrodite types were crossed with functionally pistillate forms, results in many cases have given considerably more pistillate than hermaphrodite progeny. In other cases, ratios as high as three hermaphrodite to one pistillate have been obtained in relatively large populations. In rare cases, all of the progeny have been hermaphrodite, which indicates homozygosity for this condition on the part of one parent as has been shown by Oberle.[6] The author has given considerable study to this subject and hopes to publish his findings in the near future.

Transmission of Fruit Character

Fruit size is one of the most important and at times most difficult qualities to obtain. In crosses of North American (*V. labrusca*) and the European species this matter has seldom been given serious consideration, since both parent types produced large fruit. As a result there are little if any data available on berry size inheritance in grapes.

When small fruited species must be used to obtain certain essential vine characters the question of berry size inheritance becomes extremely important. Our experiments have shown that berry size is controlled by several factors and that wide variation in its expression is shown in the F_2 and later generations.

When *Vitis rufotomentosa,* with a maximum berry diameter of 12 mm., was crossed with varieties of *V. vinifera* and *V. labrusca* of 20 mm. diameter, berries of the F_1 hybrids (more than 400) ranged between 13 mm. and 16 mm. maximum diameter. When we crossed several of these 13 mm. F_1 hybrids with similar though unrelated F_1 plants, berries of the resultant double cross progeny ranged between 11 mm. and 21 mm. maximum diameter. Approximately eight percent of a population of 135 fruiting plants of such crosses have produced berries larger than those of either F_1 parent. Less than two percent of the progeny have equalled either of the larger-berried grandparents in respect to fruit size. That would indicate that three or more factors condition berry size in these instances.

Of fruit flavor, considerable dominance often is shown in first generation hybrids. Ordinarily, the European grape transmits superior fruit qualities to hybrids with American species though the percentage of individuals showing this quality has varied in different crosses.

When musky-flavored *V. labrusca* varieties were crossed with the clear flavored *V. gigas* and *V. rufotomentosa,* many of the F_1 progeny possessed the full *labrusca* flavor and most of the plants had it to some extent. When the same *labrusca* varieties were crossed with the mild flavored *V. shuttleworthii,* equal dominance in flavor expression has not been shown; a high percentage of the progeny possessed little or no pronounced flavor of any kind. From this it is believed that certain flavor-inhibiting genes may be carried by *shuttleworthii.*

Berry texture is as important as flavor, and in general, the American species are inferior in this respect. For the more refined qualities of texture we have had to rely upon the disease susceptible *V. vinifera.* In these crosses it has been difficult to separate good texture from undesirable vine weaknesses. Many genes appear to influence texture of pulp and our results suggest that in most cases the tough inner-pulp characters of American varieties are at least partially dominant when crossed with *V. vinifera.* Selection of desirable combinations has been possible in the course of our present work.

With the tropical species adherence of the berry to the pedicel is usually adequate in favorable contrast to most of the temperate-zone American species.

Sugar content of berry depends upon both genetic and environmental factors. The *aestivalis* series of species (*V. gigas, V. smalliana,* and *V. vinifera*), have been the best source of this character. Though the sugar content of *V. shuttleworthii* and *V. tiliaefolia* is comparatively low, some of the complex hybrids between them and the *aestivalis* group have had remarkably sweet fruit, even under wet weather conditions. Sugary raisins have been made from a few of these selections in Costa Rica.

Shape, type, and size of cluster is apparently controlled by only a few genes. The situation is complicated by the influence of various environmental conditions. In many crosses inheritance of cluster type and size is variable, with some dominance of a tendency to form large compound bunches. However in other crosses the small compact type of bunch has been dominant.

Seedlessness is an important asset for a table grape. Seedlessness appears in some first generation progenies, to an extent of about 12 percent when one parent is seedless.[8] In our tropical selections this has not been an easy character to obtain. The few popular European varieties that produce seedless fruit (Sultanina, Black Monukka, etc.) are unusually susceptible to downy mildew, especially through the early growth stage. During these experiments we have grown hundreds of hybrids between the seedless *vinifera* and the tropical species. Nearly all have been badly attacked by disease and few have fruited. From crosses with certain seeded *vinifera* types, healthy F_1 progeny have been ob-

TABLE III.—Ideal specific background for a tropical bunch grape.

Species (select types)	Species proportionment	Fruit quality	Fruit size
V. shuttleworthii	5/16	pulpy, acid	18-20 mm.
V. tilaefolia or, *V. simpsoni*	4/16	poor, acid	8 mm.
V. gigas	3/16	sweet, good	12-14 mm.
V. vinifera	3/16	sweet, good	16-22 mm.
V. labrusca	1/16	pulpy, fair	18-20 mm.

tained which show seed abortion of 70 to 80 percent. It is believed that we may eventually obtain complete seedlessness in an otherwise satisfactory variety.

In general small seeds have been recessive to large seeds, with a complete dominance in F_1. When the large seeded variety Alphonse Lavallee (*V. vinifera*) was crossed with the very small seeded *V. tiliaefolia* all the F_1 had seeds as large, or nearly as large, as the *vinifera* parent. Some of these plants had berries only slightly larger than those of the very small fruited parent. No pronounced correlation existed between size of seed and size of berry.

The ideal tropical vineyard grape, in contrast to the situation in temperate zones, can scarcely be expected to emerge as a selection from a species or even from the progeny of a simple species cross.

So far as there is record this is the first attempt to develop tropical grape varieties through inter-breeding of wild tropical species. Success will not come through "improving" any of these wild species. Through an intricate compounding of several of these with temperate-zone varieties we are developing a "cultivated" race altogether different from those now known to viticulture.

On the basis of the author's experiments, he believes that the goal will be achieved by a combination of at least five—possibly six—species. The results obtained to date allow us to name the most promising parental species, and also to predict about the proportion in which they will be represented in the final selections. (See Table III). The illustrations accompanying this article show the extent to which the goal has now been achieved, and point to complete success in the not very distant future.

Summary

The development of new tropical grape varieties has involved many unusual and complex cultural factors: Warm dormant seasons, continuous epidemics of several unusual vine diseases, extremes of rainfall and drought, relatively short day-lengths, and often strongly acid soils, have imposed many new problems. A survey is given of important wild species and their adaptability. The genetic basis for these responses has been studied with especial reference to the more destructive grape diseases and their inheritance. Inheritance of such characters as fruit size and flavor, cluster and seed type are reported.

The development of tropical viticulture, as seen from our present viewpoint, is discussed. *Vitis shuttleworthii, V. gigas,* and *V. tiliaefolia* in combination with a slight amount of *V. vinifera* appears to offer the greatest promise as foundation material.

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