Variability studies of fruit color and other plant characteristics in interspecific crosses of yellow-fruited raspberries

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VARIABILITY STUDIES OF FRUIT COLOR AND OTHER PLANT
CHARACTERISTICS IN INTERSPECIFIC
CROSSES OF YELLOW-FRUITED RASPBERRIES

by

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INTRODUCTION

The various bramble fruits are generally separated into two classes, the raspberries and blackberries. Raspberries have fruit in which the receptacle tissue or torus separates readily from the drupelets, while the blackberries have fruit in which the torus adheres to the drupelets. Both of these types are grown by the home gardener, as well as the commercial grower, in various parts of the country. In the Midwest the raspberry is grown more extensively.

Although the raspberry is grown commonly by many people in this area, at least on a small acreage basis, many difficulties stand in the way of maximum production. Hardiness, viruses and fungus diseases are primary problems with all types of raspberries. The science and art of plant breeding plays an important role in overcoming these problems as well as improving many other plant characteristics. Because of this, it is imperative that more knowledge be obtained pertaining to the inheritance of the multitude of characteristics found in the raspberry.

Crosses between the black raspberry, Rubus occidentalis, and the red raspberries, Rubus idaeus and Rubus strigosus, have offered much promise for raspberry improvement. It has been previously noted that progenies from this type of cross, in general, show a great increase in vigor, greater fruit size, purple fruit color, and higher pulp to seed ratio than either of their parents (18). Yellow-fruited forms are present in both parental types. Very little is known concerning the inheritance of color in crosses between yellow-fruited forms of each
species. Because of the potential importance of progeny from crosses between the two species, it is imperative that breeders understand more about inheritance in crosses of this type. This includes the inheritance of color as well as other plant characteristics.
PURPOSE OF STUDY

A preliminary purpose of this investigation was to assemble the known information on raspberry inheritance. Some inheritance research has been conducted with the European red raspberry, *Rubus idaeus*, and with the common cultivated red raspberry. The latter has been obtained through hybridization of *Rubus idaeus* and its American counterpart, *Rubus strigosus*. Inheritance studies involving the black raspberry and the interspecific hybrids between raspberries of the black and red type have been more limited in scope.

Another purpose of these studies was to evaluate the fruit color of progeny derived from the cross of an amber-fruited *Rubus occidentalis* and an apricot-fruited form of the common cultivated red raspberry. The fruit color observed in this population was to be compared with that found in the parental clones and a population derived from selfing the *Rubus occidentalis* parent. Since interspecific crosses between the common black and red-fruited forms usually result in purple-fruited progeny, it was of particular interest to observe the fruit color resulting when two "yellow-fruited" forms of these species were crossed.

A further purpose was to study sucker production, tip-rooting, autumn-fruited, relative susceptibility to anthracnose, and winter injury in the interspecific hybrids as compared with the parents. General observations on relative vigor were also to be taken.
LITERATURE REVIEW

Introduction

People who work with the red and black raspberries often tend to overlook the many basic similarities between the two types and concentrate upon their differences. Basically, these similarities are used by systematic botanists or horticulturists to group these two types within the genus Rubus or the sub-genus Idaeobatus. Bailey (5) recognized that all raspberries, including Rubus occidentalis, R. idaeus, and R. strigosus, have fruit in which the receptacle tissue separates from the drupelets that comprise the fruit. Varieties or clones differ in how readily this occurs, but it is characteristic of all raspberries.

The species being studied characteristically have biennial canes (3). In standard types the first year of cane development is primarily vegetative, and the canes are referred to as primocanes. Flowers are formed on growth arising from canes in their second year, and these canes are termed floricanes (4). In both Rubus occidentalis and the common cultivated red raspberry there are forms in which flowers and fruit may be produced on canes in both their first and second years. These are the so-called everbearing varieties. This type is more commonly observed in the red rather than the black raspberry. Waldo and Darrow (51) stated that the difference between raspberries of the standard and everbearing types was a difference in their response to photoperiod and temperature. Everbearing or autumn-fruiting types begin to form fruit buds earlier or under longer photoperiods. The standard
types, Latham and Newburgh, do not begin fruit-bud formation as early or until short day lengths are reached. In these types, flowers normally do not appear until the next year.

The two species of red raspberries involved in this investigation differ in several respects. Bailey (5) and Hedrick (27) list the two as distinct species, while, according to Bailey (5), Focke considers the two as botanical varieties of Rubus idaeus. In this study they will be considered distinct species.

Bailey (5) reports that Rubus idaeus has more erect canes, lighter brown cane color, deeper red fruit color, and less hardiness to cold than Rubus strigosus. Yellow-fruited forms occur in each type but are more common in the former.

Many authors (5), (27), (43) have recognized the contrasting characteristics of red and black raspberries. Bailey (5) noted that Rubus idaeus and Rubus strigosus normally increase vegetatively through the production of suckers, while Rubus occidentalis does not form suckers. He also observed that Rubus occidentalis has drooping canes which form roots at the tips when they come in contact with the soil, while the red raspberry species do not have these capabilities. Other characteristics, such as type of spines and foliage, differ in the two types.

Cytology

Crane and Darlington (14) have concluded that the chromosome complements of all species of Rubus are composed of homologous sets of
seven chromosomes. These conclusions are based upon the similarity of form of somatic chromosomes and the occurrence of secondary pairing of chromosomes at meiosis in polyploid forms. Crane (13) believes that raspberry and blackberry chromosomes have become differentiated, not by structural change, but by genic differences controlling such phenomena as chromosome pairing. Darlington (16) expressed the opinion that a certain group of characters such as 'short-lived canes of limited growth, many narrow prickles, pinnate leaves, red fruits, and free plug' in Rubus idaeus behaves like a "supergene" possibly due to an inversion of a segment of chromosome. This conclusion was reached following blackberry-raspberry crosses in which these characters were transferred in a group to all progeny.

The ploidy level in the three basic species of raspberries is diploid or 2n = 14. There are a few exceptions, namely triploids and tetraploids of the Rubus idaeus type. These, however, have not played a major role in raspberry improvement.

Effect of Inbreeding

Inbreeding affects the black raspberry differently than it does the red raspberry or the purple-fruiting hybrids. Jones and Singleton (28) observed no inbreeding depression after three generations of selfing the variety Cumberland. Slate (46) also reports that there is little, if any, inbreeding depression observed when selfing black raspberries.

In contrast, Jones and Singleton (28) observed that a marked
decrease in vigor was obtained upon selfing the red raspberry variety Ranere and purple-fruited variety Columbian. Slate (46) reported similar results with the purple hybrids. The type of segregation obtained upon selfing the purple-fruited F₁ hybrids is of interest. Anthony (2) in 1916 reported that few characteristics in the F₂ generation approached the parent forms. Most characters appeared intermediate. Jones and Singleton (28) and Slate (44) found considerable segregation in the F₂ generation, but fruit color just approached that of the parents.

Inheritance of Various Characteristics

Fruit color

Detailed studies have been carried out in England to determine the inheritance of fruit color in Rubus idaeus. Crane and Lawrence (15) concluded that fruit color in this species was controlled by two factors and was associated with spine color. It was determined that one gene (T) produces anthocyanin in spines and fruits and that a second gene (P) intensifies the color. Thus a T-P- plant has red fruit and red spines; a T-pp plant, red fruit and red-tinged spines; a ttP- plant, apricot fruit and green spines; and a ttpP plant, yellow fruit and green spines. Grubb (24) considers color inheritance in Rubus idaeus to be a little more complex and suggests the presence of two linked color factors other than P. He observed that some green-spined forms have fruit color intermediate between apricot and red. He also noted that red-spined plants can have pale red fruit, and
tinged-spined plants sometimes have dark fruit.

No color inheritance data has been reported concerning *Rubus strigosus*, the American wild red raspberry. Bailey (5) states that similar colored forms exist in this type as in the European red, however, the yellow-fruited types are much less common. Most present day red raspberry varieties have both the American red and European red raspberries in their pedigree. Many varieties such as June, Herbert, and Marlboro appear to carry T in a heterozygous condition as shown by the results of crossing and selfing (1). Anthony (1) obtained 66 red-fruited to 4 yellow-fruited progeny in crosses between the varieties Marlboro and June. This approaches a 15:1 ratio. If Anthony included apricot-fruited individuals within the red-fruited class, the inheritance scheme of Crane and Lawrence (15) could be valid. If, however, he included apricot-fruited individuals with the yellow-fruited group, as is commonly done, it would indicate that the inheritance of fruit color is more complex in the American red raspberry.

No precise system for color inheritance has been proposed for *Rubus occidentalis*. Anthony (1) in 1916 suggested the presence of several pairs of factors controlling color due to the low proportion of yellow-fruited seedlings in crosses between the *R. occidentalis* varieties Cumberland and Palmer and Cumberland and Hilborn. Another worker (59) has observed yellow-fruited seedlings as progeny of crosses between black-fruited parents. All data indicates that yellow-fruit color is associated with recessiveness, but the number of
factor pairs involved is not clear.

Over the years many interspecific crosses have been made between red and black raspberries. The inheritance of color in these crosses and the breeding behavior of the resulting progeny, so far as color is concerned, is quite interesting. Workers including Slate (44), who have attempted to develop good purple varieties, have used black and red-fruit types almost exclusively. Purple-fruit progeny normally resulted. Palmer and Strong (42) reported that purple-fruit raspberries were obtained from crosses of black-fruit Rubus occidentalis with the red raspberry when the black raspberry was used as the female parent. When the reciprocal cross was made, only red-fruit types resulted. This may indicate contamination by pollen from the red raspberry since seed set is known to be quite poor when the red raspberry is used as the female parent (44). Anthony (1), although not suggesting an exact inheritance system for color, reported that a black raspberry which is "pure" for color produces only purple-fruit types when crossed with the red raspberry, even when the red carries the yellow factor. The results obtained by Darrow (20), from crosses between Winfield, a black-fruit Rubus occidentalis, and Golden Queen, a yellow-fruit raspberry of the Rubus idaeus type, support this contention. Darrow found that only purple-fruit raspberries resulted. Anthony (2) crossed Cumberland and June which produced 280 purple: 9 yellow-fruit plants. Cumberland, a black raspberry, and June, a red raspberry, are known to be heterozygous to some degree for color.
There can be much variation in color intensity among the purple-fruited progeny. Jones and Singleton (26) reported that the progeny from black x red raspberry crosses varied from dark red to nearly black. This variation might be expected. Lee and Slate (35) found that some black raspberry varieties possessed over twice the color density of other blacks. The same situation probably exists with the modern red raspberry varieties, since the European red is noted to be dark red in color while *Rubus strigosus* is typically a light, bright red (5).

Two other approaches have been followed in the development of superior types of raspberries, which are of some importance in the study of color inheritance. The first involves the selfing of the purple progeny from a black x red cross. Jones and Singleton (26) reported fruit color ranging from nearly red to true black after one generation of selfing. Slate (44) reported that no progeny from the cross between two purple-fruited interspecific hybrids were either red or black but of various intermediate shades.

A second approach has involved backcrossing of the purple-fruited raspberry to either the black or red type. Davis (22) found that when the variety Royal Purple was crossed to various red raspberry varieties, the progeny had fruit ranging from purple to bright red. Jones and Singleton (26) were also able to produce promising bright red-fruited seedlings through this type of cross. In their crosses of Columbian purple raspberry to an inbred black raspberry, they received 21 black: 63 purple-fruited progeny. The purple class was highly variable and ranged from the parental purple to almost black.
Only one instance of hybridization between yellow-fruited forms of *Rubus occidentalis* and the *R. idaeus-R. strigosus* group has been recorded. Thayer (49) observed that pinkish yellow-fruited progeny resulted from a cross between a wild yellow-fruited form of *Rubus occidentalis* with Golden Queen, an apricot-fruited variety of the red raspberry type. However, a population size of only twenty-four was used.

**Suckering vs. non-suckering**

As mentioned previously, red raspberries commonly increase in number through the production of suckers, while black raspberries do not have this ability but increase by means of tip-rooting. Knight and Keep (31) have determined that three genes influence the ability of *Rubus idaeus* to form suckers. The recessive gene $sk_1$ can cause suckering if homozygous. The two recessive complimentary genes $sk_2$ and $sk_3$, if present in a homozygous condition, can cause suckering in a $SK_1sk_1$ plant. $SK_1SK_1$ plants will not produce suckers regardless of the situation at the $sk_2$ and $sk_3$ loci.

In crosses between black and red raspberries or backcrosses between the purple and either of the parental types, varying results have been obtained. Most of our important present-day purple varieties, such as Sodus and Potomac, are non-suckering in habit. Several purple varieties including Ruddy, however, do produce suckers (7). Many workers have reported contradictory results in black x red raspberry crosses. Anthony (1) reported that no seedlings produced by suckers in crosses between Cumberland and June and Smith No.1 and June. Colby (11),
however, found that the amount of suckering varied among different
crosses. Some produced as high as 25 percent of the plants with the
suckering habit, while one cross, Quillen x Ranere, produced no
seedlings which suckered. The results of backcrosses between purple-
fruited hybrids and the *Rubus idaeus* type have likewise been variable.
Slate (44) obtained some excellent red-fruited progeny from this type
of cross, none of which formed suckers. Davis (22) and Jones and
Singleton (28) reported that suckering and non-suckering types were
produced from this type of cross.

**Tip-rooting vs. non-tip-rooting**

As mentioned in the previous section, the ability to form roots
at the tips of canes is a characteristic of *Rubus occidentalis* and is
not possessed by either *Rubus idaeus* or *Rubus strigosus*. Knight and
Keep (31) have reported that tip-rooting in *Rubus occidentalis* is
controlled by a single dominant gene (Tr).

Hybrids between the black and red type reportedly vary with
regard to their ability to root at the tips of primocanes. The purple
varieties of commercial importance today, including Sodus and Potomac,
root rather easily at the tips. Colby (11), however, reported only
62 percent of the offspring from a cross between Quillen and Ranere
could be propagated by tip-layerage, even though Quillen is considered
homozygous for tip-rooting.

With the backcross system, Slate (44), Davis (22), and Jones and
Singleton (28) reported difficulty in maintaining the tip-rooting
tendency in backcrosses of the purple-fruiting hybrids to the red raspberry parent.

**Autumn-fruiting**

Autumn-fruiting was first recorded by McMahon in 1806 (37). Since then it has been observed frequently, and many attempts have been made to incorporate the characteristic into a plant which also carries the other desirable characteristics of a good variety.

The autumn-fruiting characteristic is found in both the red and black raspberries, although it is more commonly observed in raspberries of the red type. This characteristic has been considered undesirable in *Rubus occidentalis* because its expression precludes the possibility of propagation by tip-layerage, since the tip portion of the cane used in propagation would be occupied with fruit production (31). Because of this, most of the work for the development of superior autumn-fruiting types has dealt with crosses within or between the two species of red raspberries.

Early workers considered autumn-fruiting an expression of the raspberry's polyploid nature, since the early autumn-fruiting varieties were either triploids or tetraploids. Lewis (36) and Moffett (38) recognized that this was not correct. They noted that there were some diploid autumn-fruiting types, Lloyd George and Queen Alexandra, and that not all triploids showed the autumn-fruiting characteristic. Polyploid autumn-fruiting varieties have been used very little in developing superior types since they produce only small amounts of
viable pollen (45).

When breeding for the autumn-fruiting characteristic in the red raspberry, two sources have been used, one from each species of red raspberry. Lloyd George and its derivatives are of the Rubus idaeus type, while Ranere and its derivatives represent Rubus strigosus (17). Although both sources contribute a gene or genes for autumn-fruiting, Oberle, Moore, and Nicholson (41) along with Slate (45) recognize that the Ranere group tends to produce progeny which bear fruit on current season's growth earlier in the season.

Various percentages of autumn-fruiting progeny have been obtained in crosses between red raspberries. Oberle and Moore (40) in Virginia obtained as high as 93 percent autumn-fruiting types in a cross between two autumn-fruiting varieties, Indian Summer and Durham. It must be noted that a rather small population size was used, however. In crosses between autumn-fruiting types in which large populations were grown, the highest percentage of autumn-fruiting types approached 65 percent. Slate and Suit (47) in New York were able to obtain 30 to 35 percent autumn-fruiting progeny in similar crosses. These authors did not attempt to explain why the percentage of autumn-fruiting individuals was not higher. Crosses between an autumn-fruiting variety and a variety not possessing this characteristic have given varying results. Oberle and Moore (40) made a number of these crosses and obtained 4 to 25 percent of the progeny with the autumn-fruiting characteristic.

The actual inheritance scheme for this character has not been
determined. Lewis (36) considers it controlled by a recessive gene. Waldo and Darrow (51) suggest there are probably at least two allelomorphs, spring-fruiting only and spring and fall-fruiting. Keep (29), however, considers that autumn-fruiting is under complex genetic control.

Very little has been reported concerning the transfer of the ability to produce fruit on first year canes from red raspberries to the purple-fruited types. Oberle and Moore (40), with large populations, obtained about 50 percent fall-fruiting types in crosses between standard black raspberry varieties and autumn-fruiting red raspberries. Slate (44) found that only 16.5 percent of the progeny from a cross between Dundee, a black raspberry, and Lloyd George were fall-fruiting.

**Anthracnose resistance**

Anthracnose, a common fungus disease of raspberries, is caused by the organism, *Elsinoe veneta*. Although it attacks the black, red, and purple-fruitied forms, the severity of infection varies among the three types. Most workers, including Burkholder (8) and Colby (12), recognize that, in general, black raspberries are susceptible, while red raspberries tend to be relatively resistant. Varying opinions, however, exist as to the relative resistance or susceptibility of the purple-fruited hybrids.

The previously mentioned generalities have numerous exceptions. Although, in general, the black raspberry is quite susceptible, Lantz
(33) and Colby (12) have reported that certain varieties, such as Quillen, are highly resistant. Colby (10), however, later reported that Quillen showed only partial resistance. From his work he concluded that anthracnose resistance in *Rubus occidentalis* must be controlled by more than a single gene. While the red raspberries are generally relatively resistant, there are again many exceptions. Darrow (19) reported that the variety Viking was particularly susceptible.

Certain authors have contrasting opinions as to the relative resistance or susceptibility of the purple raspberry to anthracnose. Anthony (2) stated that purple raspberries show near immunity to anthracnose. Burkholder (8), however, states that the purple raspberry inherits the susceptibility of its *Rubus occidentalis* parent.

**Winter hardiness**

Winter hardiness of raspberries, cane hardiness in particular, has long been a problem in the successful production of the crop in the Midwest. The relative winter hardiness of the wild species differs to some degree. Darrow (16) reported that the native American red raspberry, *Rubus strigosus*, is the hardest of the three main species. It is found in the wild as far north as some of the Canadian provinces. The other species native to North America, *Rubus occidentalis*, has a similar range as *Rubus strigosus* but extends further south and is less apt to be found near the northermost limits.
The common varieties of red raspberries grown at present vary markedly in the degree of cane hardiness which they possess. The hardiness shown by each variety in turn may vary from year to year and location to location due to differences in the environment. Darrow (18) considers the variety Latham very hardy against cold or winter injury, yet in Iowa much winter injury is often observed with this variety. Brierley and Landon (6) have shown that fluctuating temperatures during the winter may be much more damaging than cold temperatures alone.

The use of *Rubus idaeus* in improving fruit size and quality has resulted in red-fruited varieties which show more winter injury than the native species, *Rubus strigosus*. Even seedlings derived from the wilds of Manitoba, however, do not show complete cane hardiness (23).

The winter hardiness of the common cultivated black raspberry varieties is somewhat less than that of the red raspberries (18). They are normally grown in a more southerly location than the red raspberry.

The purple-fruited hybrids vary in their susceptibility to winter injury. Vaile (50) in Arkansas states that the purple raspberry appeared to have less susceptibility to winter injury than either the black or red raspberry. Darrow (19) reports that the purple variety Potomac is one of the hardiest raspberry varieties in this country.
Sex

It is recognized that there are four sexes in Rubus idaeus, hermaphrodite, female, male, and neuter. Crane and Lawrence (15) report that these sexes are determined by two factors in such a way that an F-M- plant is hermaphroditic; F-mm, female; ffM-, male; and ffmm, neuter.

Resistance to the raspberry aphid

Amphorophora rubi, a species of aphid commonly found on raspberries, has been reported to be the vector of many raspberry virus diseases (9) (48). Since virus diseases can be a serious problem on raspberries, studies concerned with the resistance to the several strains of aphids have been conducted. Knight, Briggs, and Keep (39) (32) have discovered seven genes (A^1 through A^7) which can have some effect on the resistance to the three recognized strains of Amphorophora rubi. Some of these are minor genes. Knight, Briggs, and Keep (30) reported that either the combination A^1A^2 or A^1A^3 would give resistance to the three presently recognized strains.
GENERAL EXPERIMENTAL SET-UP
Materials and Methods

A cross was made between Iowa selection 18-5902, an amber-fruited Rubus occidentalis, and Iowa selection M-127, a yellow-fruited raspberry of the red type. The pedigree of these selections is shown in Figure 1. This cross was made during February of 1962 utilizing plants that were dug and potted the preceding fall and placed in common storage until about January 1. The cross was made using 18-5902 as the female parent. At the same time, seeds were also obtained by selfing Iowa selection 18-5902.

Seeds were collected when the fruit became ripe and were stored until August. They then were planted in a fine soil mix and covered with ground sphagnum moss in a seed flat. The seeds were stratified for three and one-half months at 35° F before they were brought into the greenhouse. In the greenhouse the seeds were germinated at a temperature of 65° F. When the seedlings had two true leaves, they were transplanted into two-inch peat pots.

In the field the potted seedlings were set at a spacing of four feet in the row with rows nine feet apart, in the spring of 1963. This spacing allowed individual study of all seedlings with regard to growth characteristics. The field planting as it looked in July of 1964 is shown in Figure 2. In addition to the populations obtained by selfing

Figure 1. Pedigree of hybrid population (6204) from cross of Iowa selections 18-5902 and M-127.
Figure 2. Field planting during July of 1964
18-5902 and crossing 18-5902 with M-127, some plants of the M-127 parent were available for comparison in an adjacent planting.

General Observations

Seedling vigor in the seed flat was quite uniform, but some variation was observed after transplanting. In the field the growth of the seedlings was also quite variable during the first growing season, and little fruiting wood for the following year was produced on many of the seedlings. Therefore, many observations were made during that season, and fruiting was studied in 1965.
FRUIT COLOR STUDY

Materials and Methods

Fruit was collected during early to mid-July of 1965. An attempt was made to allow all fruit from each clone to reach maximum color before harvesting. This was accomplished by picking only those fruit which would separate from the torus readily. The fruits from each clone were then taken directly into the laboratory for visual observation and were rated on the following color scale:

1. Yellow
2. Apricot
3. Salmon
4. Dark Salmon
5. Red

Immediately after the visual rating of the fruit was finished, the dry berries were placed in plastic bags for quick freezing at -30°C F. At or below -20°C F Guadagni and Nimmo had reported that no significant color change occurred (25).

The method of color measurement utilized was essentially that used by Guadagni and Nimmo (25) in measuring color differences in frozen red raspberries. Twenty-five grams of fruit of each sample were first thawed and then blended with 125 milliliters of MacIlvaine's citrate-phosphate buffer at pH 3.0 for one to two minutes. This was then filtered through Whatman's No. 5 filter paper. Ten milliliters of this filtrate was then diluted to 100 milliliters with the buffer solution. This diluted solution was again filtered. The absorbancy
was then determined utilizing a Spectronic 20 colorimeter at a wavelength of 515 millimicrons. Guadagni and Nimmo (25) had determined that maximum absorption of their color solutions occurred at wavelengths very close to this figure. A color index was calculated by multiplying the photometric density of the diluted filtrate by the total dilution factor. Guadagni and Nimmo (25) had determined that this color index was stable over a wide range of dilutions and pulp to extractant ratios.

Results

Visual observations made on fruit color showed very little variation among the seedlings from selfing 18-5902. Fruit from all of these seedlings were classified as salmon to dark salmon. Figure 3 pictures a fruit cluster from one of these seedlings.

The M-127 parent had fruit which could be classified as apricot when fully ripe. The anthocyanin appeared to develop only in the late stages of fruit ripening.

The fruit color within the hybrid population ranged from red or deep pink to almost pure yellow. Figure 4 shows the color range observed in this population. A high percentage of the seedlings were classified as salmon or dark salmon with respect to fruit color although a smaller percentage was listed in the other three classes. Table 1 gives the percentage of individuals falling within the five color classes.
Figure 3. Fruit cluster from progeny of selfing 18-5902

Figure 4. Range of fruit color in progeny from cross of 18-5902 x M-127
Table 1. Visual classification of fruit color of hybrid individuals from crossing 18-5902 x M-127

<table>
<thead>
<tr>
<th>Color Class</th>
<th>Total Number Observed</th>
<th>Percent of Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Yellow</td>
<td>12</td>
<td>4.2</td>
</tr>
<tr>
<td>Apricot</td>
<td>46</td>
<td>16.1</td>
</tr>
<tr>
<td>Salmon</td>
<td>124</td>
<td>43.4</td>
</tr>
<tr>
<td>Dark Salmon</td>
<td>89</td>
<td>31.1</td>
</tr>
<tr>
<td>Red</td>
<td>15</td>
<td>5.2</td>
</tr>
</tbody>
</table>

The color indices for the hybrid population, calculated from the colorimeter readings, ranged from 2.0 to 18.75. The indices could be grouped into four classes corresponding to yellow, apricot, salmon, and red. Those in the yellow class had a color index ranging from 2.00 to 4.25; the apricot-class, 5.50 to 8.00; the salmon class, 9.75 to 13.25; and the red class, 16.75 to 18.75. Figure 5 shows this distribution of color indices. Table 2 gives the percentage of hybrid individuals within the four classes.

Table 2. Colorimetric classification of fruit color of hybrid individuals from crossing 18-5902 x M-127

<table>
<thead>
<tr>
<th>Color Class</th>
<th>Percent of Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Yellow</td>
<td>3.1</td>
</tr>
<tr>
<td>Apricot</td>
<td>16.8</td>
</tr>
<tr>
<td>Salmon</td>
<td>73.4</td>
</tr>
<tr>
<td>Red</td>
<td>6.7</td>
</tr>
</tbody>
</table>
Figure 5. Distribution of color indices obtained through colorimetric evaluation of fruit color in the hybrid progeny from the cross of 18-902 x M-127.
NUMBER OBSERVED

COLOR INDICES

1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20
The color indices, calculated for the fruit from the selfed population, ranged from 9.50 to 14.00. This range was approximately the same as that for the salmon class in the hybrid population. Fruit from the M-127 parent had a color index of 7.75 which corresponds to the apricot class of the hybrid population.

In general there was agreement between the colorimetric results and those obtained visually, especially if the visual classes for salmon and dark salmon fruit were combined. There was also a small number of samples which were rated more intense in red color with the colorimeter than by visual means. The opposite association was not observed.

Discussion

The general agreement between colorimetric results and visual results was expected. The higher colorimetric rating of a small number of individuals possibly can be attributed to variability in amounts of pubescence. Interspecific hybrids of *Rubus occidentalis* and *Rubus idaeus* characteristically have fruit with more pubescence than the parental types. Fruits with more pubescence tend to appear lighter in color than those with smaller amounts. This may also partially explain why two classes were established for salmon-colored fruit when classifying visually.

It is difficult to set up an exact inheritance scheme for fruit color in interspecific crosses between *Rubus occidentalis* and the species of red raspberries from the information gained in this study.
This is true for a number of reasons. First, in order to propose an exact inheritance system, one would need to draw from past results in addition to the results of this study. Information on fruit color inheritance for each individual species is not plentiful. The study of fruit color in *Rubus occidentalis* is especially vague. Even the scheme proposed by Crane and Lawrence (15) for *Rubus idaeus* has some weak points. Grubb (24) recognized the presence of some intermediate color classes which could not be explained without some modification of the two gene hypothesis of Crane and Lawrence (15). It is felt that the Crane and Lawrence hypothesis does, however, supply the main basis for fruit color inheritance in *Rubus idaeus*.

In attempting to explain fruit color inheritance utilizing apricot and yellow-fruited forms, one also encounters difficulties in explaining past results because of the inadequacy of the literature. In most cases previous authors have failed to distinguish between yellow and apricot-fruited forms of red raspberries and yellow and amber-fruited forms of *Rubus occidentalis*. In most research reports all these forms are referred to as yellow-fruited.

Because of lack of sufficient information, any attempt to explain the fruit colors obtained in this study must be rather general and based on certain assumptions. My first assumption is that the Crane and Lawrence (15) hypothesis has some validity and does serve as the primary mechanism for fruit color inheritance in *Rubus idaeus*. If this is assumed, then fruit color in this species is controlled by a major color gene plus an intensifier gene.
A similar situation could exist in *Rubus occidentalis*. One gene could produce black or yellow fruit depending on the alleles present. An intensifier gene could also be operative. Following this assumption, the parental types used in this study would have the major color genes in a recessive condition and the intensifiers in a heterozygous condition. The presence of some red pigment in the fruit of the parents instead of pure yellow color would be evidence of this. The occurrence of some light red-fruited offspring within the hybrid population could then be due to a cumulative effect of independently acting intensifying genes from the different sources. The presence of salmon and apricot-fruited offspring could be due to the action of one or the other of the intensifiers. Yellow-fruited offspring would be observed when no intensifier was in action.

The above explanation is not presented as a hypothesis but rather as an idea. Much more detailed genetical studies are necessary with the three basic species of raspberries and their interspecific hybrids before a hypothesis can be presented and concretely supported.
STUDY OF GROWTH CHARACTERISTICS

Materials and Methods

Sucker production

Since suckers are generally produced during the spring of each year, observations were first made on all material on July 7, 1964. To further evaluate, additional observations were recorded on July 13 and 14, 1965. During the first summer, plants were evaluated according to the presence or absence of suckers. Because of variations in sucker production, the seedlings were classified according to the number of suckers produced during the following year. Those clones which produced suckers were categorized as suckering sparingly, moderately, or freely. One to three new suckers were required for a seedling to be classified as suckering sparingly; four to seven, suckering moderately, and eight or more, suckering freely.

Tip-rooting

Plants which possess the ability to form roots at the tips of first year canes show this ability during the fall. At this time the terminal portions of the first year canes show elongated internodes with very small leaves. This characteristic is commonly referred to as rat-tailing. In this study if the rat-tail condition was observed, a plant was considered to possess the capability of being propagated by tip-layerage. Observations were taken during September of 1965.
No tip-layerage evaluation was made on those plants that were autumn-fruiting.

Autumn-fruiting

Although neither 18-5902 nor M-127 was known to produce fruit on first year canes, it became obvious that some progeny from crossing the two selections did have this potential. Observations were recorded twice during the summer and fall of 1964. During 1965, observations were made at two week intervals beginning in mid-July and continuing until October 1. All clones which formed flower clusters prior to the last observation were considered to possess a tendency toward fall-fruiting.

Anthracnose susceptibility

On July 7, 1964, and July 13 and 14, 1965, the plants were classified according to their susceptibility to anthracnose. In an attempt to obtain an estimation of the natural susceptibility of each individual, fungicides were not used either year although this is a common practice in commercial fields. The following classes were set up to evaluate the degree of infection:

1. None
2. Slight
3. Moderate
4. Severe
Winter injury

Since cane growth was relatively poor during 1963, no data was recorded on winter injury until after the winter of 1964-1965. The first observations were taken on May 12, 1965. A second set of observations were made on June 20th in order to determine if any delayed bud break or winter injury had occurred. Injury symptoms were denoted as follows:

1. 0 - 20 percent die-back
2. 20 - 40 percent die-back
3. 40 - 60 percent die-back
4. 60 - 80 percent die-back
5. 80 - 100 percent die-back

Plant vigor

Plants were classified for vigor according to average plant height. On July 7, 1964, plants were listed as being low, medium, or high in vigor. On July 13 and 14, 1965, two additional classes were used in classifying the plants. The following classes for vigor were used:

1. Very low
2. Low
3. Medium
4. High
5. Very high
Results

Sucker production

The amber-fruited *Rubus occidentalis* parent, Iowa selection 18-5902, was very typical of its species in that no suckers were ever observed. A population of 449 seedlings from selfing this selection likewise showed no sucker production during 1964 and 1965. During this same period M-127, the other parent, produced suckers moderately.

From the original hybrid population of over 400 plants derived from crossing 18-5902 and M-127, 322 seedlings remained when the first observations were made. At this time there were 207 seedlings of the non-suckering type and 115 seedlings which produced at least one sucker. Figures 6 and 7 show typical suckering and non-suckering plants.

Seventeen seedlings, fourteen of which appeared non-suckering, were killed during the winter of 1964-1965. Thus only 305 seedlings were evaluated for their suckering tendencies during 1965. This evaluation showed 108 non-suckering and 197 suckering progeny. There were approximately equal numbers of seedlings in the three classes for those which did produce suckers. Many hybrid seedlings considered non-suckering in 1964 produced suckers during the spring of 1965. No seedlings that produced suckers in 1964 reverted to the non-suckering habit of growth. The change in sucker production in the hybrid progeny from 1964 to 1965 is shown in Table 3.
Figure 6. Typical sucker-producing plant from the hybrid population

Figure 7. Typical non-suckering plant from the hybrid population
Table 3. Change in sucker production from 1964 to 1965 in hybrid progeny of the cross of 18-5902 x M-127

<table>
<thead>
<tr>
<th>Classes for degree of sucker production (1965)</th>
<th>Number Observed (1965)</th>
<th>Number originally considered non-suckering in 1964</th>
<th>Number originally considered suckering in 1964</th>
</tr>
</thead>
<tbody>
<tr>
<td>Non-suckering</td>
<td>108</td>
<td>108</td>
<td>0</td>
</tr>
<tr>
<td>Suckering sparingly</td>
<td>63</td>
<td>44</td>
<td>19</td>
</tr>
<tr>
<td>Suckering moderately</td>
<td>68</td>
<td>28</td>
<td>40</td>
</tr>
<tr>
<td>Suckering freely</td>
<td>66</td>
<td>13</td>
<td>53</td>
</tr>
</tbody>
</table>

**Tip-rooting**

In observations taken during the fall of 1965 no sign of the characteristic rat-tailing condition was found in the plants of M-127. In addition this characteristic had never been observed on plants of this selection under casual study during the fall of several previous years.

Iowa selection 18-5902 had shown the characteristic growth habit of *Rubus occidentalis* during previous seasons. This included the ability to root at the tips of first year canes. All progeny from selfing 18-5902 showed a very similar type of growth. The rat-tailing condition, characteristic of plants which will propagate by tip-layerage, was observed on all of these seedlings during the fall of 1964.

The hybrid progeny were again quite variable with regard to the characteristic in question. During the fall of 1965, 59.7 percent of
the progeny showed the rat-tailing characteristic while the remainder, or 40.3 percent, did not. Rat-tailing was observed on plants regardless of whether they did or did not produce suckers. Table 4 compares the percentage of tip-rooting and non-tip-rooting plants which produced no suckers, suckered sparingly, moderately, or freely.

Autumn-fruiting

Autumn-fruiting was first discovered in some of the hybrid progeny in mid-July of 1964. Immediately the plants of 18-5902 and M-127 were checked for any signs of fall-fruiting. No signs of this were seen on these parental clones or on the population obtained from selfing 18-5902.

Table 4. Tip-rooting and non-tip-rooting in hybrid individuals from the four classes for sucker production during 1965

<table>
<thead>
<tr>
<th>Class for ability to tip-root</th>
<th>Percent Non-Suckering</th>
<th>Percent Suckering Sparingly</th>
<th>Percent Suckering Moderately</th>
<th>Percent Suckering Freely</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tip-rooting</td>
<td>29.8</td>
<td>24.5</td>
<td>20.5</td>
<td>25.2</td>
</tr>
<tr>
<td>Non-tip-rooting</td>
<td>32.2</td>
<td>19.8</td>
<td>22.5</td>
<td>25.5</td>
</tr>
</tbody>
</table>

On July 18th studies showed that 3.4 percent of the hybrid population had produced flower buds terminally on primocanes. During the rest of the summer more seedlings began to show the autumn-fruiting tendency. The second check during the 1964 season on October 1 showed 10.6 percent of the population with visible flower buds on the terminal portion of
the primocanes. During this time no autumn-fruiting was observed on
the plants of either of the two parental clones. A few plants from
the selfed population appeared to be autumn-fruiting, but on close
inspection these canes were found to have arisen from basal buds on
floricanes rather than from the crown.

During the second season of observations a higher percentage of
individuals with fall-fruiting tendencies appeared in the hybrid
population. By October 1, 19.5 percent of the seedlings had shown
visible flower buds on primocanes. Individuals possessing fall-
fruiting tendencies appeared gradually throughout the latter part of
the summer, as shown in Table 5.

Table 5. Development of autumn-fruiting in hybrid individuals from
the cross of 18-5902 x M-127 during the summer and fall
of 1965

<table>
<thead>
<tr>
<th>Date of observation</th>
<th>Cumulative percentage of autumn-fruiting individuals in the entire population</th>
</tr>
</thead>
<tbody>
<tr>
<td>July 15</td>
<td>4.5</td>
</tr>
<tr>
<td>August 1</td>
<td>6.5</td>
</tr>
<tr>
<td>August 15</td>
<td>8.8</td>
</tr>
<tr>
<td>September 1</td>
<td>11.4</td>
</tr>
<tr>
<td>September 15</td>
<td>15.6</td>
</tr>
<tr>
<td>October 1</td>
<td>19.5</td>
</tr>
</tbody>
</table>

The parental clones, 18-5902 and M-127, showed no autumn-fruiting
tendencies during 1965. The population from selfing 18-5902 was
likewise devoid of autumn-fruiting individuals. These observations are in agreement with those obtained in the preceding year.

**Anthracnose susceptibility**

Iowa selection 18-5902 showed moderate to severe anthracnose infection. The M-127 parent had some plants with no infection during July, 1965, while others suffered slight infection.

The population from selfing 18-5902 was evaluated for anthracnose susceptibility only during July of 1965. All seedlings showed considerable susceptibility to anthracnose. Table 6 lists the rating of seedlings according to the amount of anthracnose infection. The degree of infection during the previous year was considerably less, although most seedlings showed a high degree of susceptibility.

Table 6. Degree of anthracnose infection in July of 1965 on progeny from selfing 18-5902

<table>
<thead>
<tr>
<th>Degree of infection</th>
<th>Percent of total observed seedlings</th>
</tr>
</thead>
<tbody>
<tr>
<td>None</td>
<td>0</td>
</tr>
<tr>
<td>Slight</td>
<td>0</td>
</tr>
<tr>
<td>Moderate</td>
<td>10.4</td>
</tr>
<tr>
<td>Severe</td>
<td>89.6</td>
</tr>
</tbody>
</table>

The hybrid population was evaluated in 1964 and 1965. Figures 8, 9, 10, and 11 show examples of the amount of infection observed
in various seedlings. As in the selfed population, a greater degree of infection was found during 1965 than during the preceding year. The degree of infection was much less, however, than that observed on the selfed population. The plants with moderate or severe infection did not appear weakened like the progeny from selfing.

Table 7 gives the results for the degree of anthracnose infection during 1964 and 1965 on members of the hybrid population.

Table 7. Degree of anthracnose infection on individuals from the cross of 18-5902 x M-127 during 1964 and 1965

<table>
<thead>
<tr>
<th>Degree of infection</th>
<th>Percent of total observed seedlings (1964)</th>
<th>Percent of total observed seedlings (1965)</th>
</tr>
</thead>
<tbody>
<tr>
<td>None</td>
<td>84.2</td>
<td>22.4</td>
</tr>
<tr>
<td>Slight</td>
<td>9.3</td>
<td>44.3</td>
</tr>
<tr>
<td>Moderate</td>
<td>3.1</td>
<td>25.2</td>
</tr>
<tr>
<td>Severe</td>
<td>3.4</td>
<td>8.1</td>
</tr>
</tbody>
</table>

Winter injury

Winter injury on the M-127 parent was rather severe. Some plants showed 100 percent cane die-back following the winter of 1964-1965, which was not considered a severe winter for red raspberries in Iowa. No plants showed less than about 60 percent die-back.

The amount of cane injury on the selfed population coming from the Rubus occidentalis parent was nominal. All seedlings fell within the class of 0 - 20 percent die-back.
Figure 8. Example of no anthracnose infection

Figure 9. Example of slight anthracnose infection
Figure 10. Example of moderate anthracnose infection

Figure 11. Example of severe anthracnose infection
The hybrid population was quite variable with respect to cane hardiness following the winter of 1964-1965. About 50 percent of the seedlings showed 0 - 20 percent cane die-back, while the remainder showed more severe injury. Little delayed injury was apparent. The winter injury observed on the hybrid population is listed in Table 8.

Table 8. Winter injury on progeny from the cross of 18-5902 x M-127 following the winter of 1964-1965

<table>
<thead>
<tr>
<th>Percent cane die-back</th>
<th>Number of individuals observed</th>
</tr>
</thead>
<tbody>
<tr>
<td>0 - 20</td>
<td>157</td>
</tr>
<tr>
<td>20 - 40</td>
<td>23</td>
</tr>
<tr>
<td>40 - 60</td>
<td>34</td>
</tr>
<tr>
<td>60 - 80</td>
<td>32</td>
</tr>
<tr>
<td>80 - 100</td>
<td>75</td>
</tr>
</tbody>
</table>

As stated previously, there was more complete winter-kill among those seedlings that did not produce suckers. This was also true for 100 percent cane die-back without complete kill. The non-suckering type also had a higher percentage of seedlings with 0 - 20 percent die-back than the suckering types. Thus there was a smaller percentage of non-suckering seedlings with partial cane die-back. Table 9 shows the amount of winter injury observed on hybrid individuals of the various classes for sucker production.
Table 9. Amount of winter injury found in hybrid individuals from the various classes for degree of sucker production following the winter of 1964-1965

<table>
<thead>
<tr>
<th>Percent of cane die-back</th>
<th>Percent of non-suckering offspring in each class</th>
<th>Percent of offspring which suckered sparingly in each class</th>
<th>Percent of offspring which suckered moderately in each class</th>
<th>Percent of offspring which suckered freely in each class</th>
</tr>
</thead>
<tbody>
<tr>
<td>0-20</td>
<td>56.1</td>
<td>44.3</td>
<td>41.0</td>
<td>49.2</td>
</tr>
<tr>
<td>20-40</td>
<td>5.1</td>
<td>16.4</td>
<td>13.1</td>
<td>9.5</td>
</tr>
<tr>
<td>40-60</td>
<td>10.2</td>
<td>6.6</td>
<td>14.8</td>
<td>17.5</td>
</tr>
<tr>
<td>60-80</td>
<td>4.1</td>
<td>14.8</td>
<td>18.0</td>
<td>11.1</td>
</tr>
<tr>
<td>80-100</td>
<td>24.5</td>
<td>17.9</td>
<td>13.1</td>
<td>12.7</td>
</tr>
</tbody>
</table>

Plant vigor

The M-127 parent was medium in vigor during the years of observation. The individuals from selfing 18-5902 were likewise rated medium in vigor and showed much uniformity in this respect.

The hybrid population was quite variable in vigor. The average vigor of the hybrids was somewhat higher, however, than that of the parents. Table 10 summarizes the observations on vigor during 1964 and 1965.
Table 10. Plant vigor of progeny from the cross of 18-5902 x M-127 during 1964 and 1965

<table>
<thead>
<tr>
<th>Amount of vigor</th>
<th>Number observed (1964)</th>
<th>Number observed (1965)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Very low</td>
<td></td>
<td>10</td>
</tr>
<tr>
<td>Low</td>
<td>56</td>
<td>38</td>
</tr>
<tr>
<td>Medium</td>
<td>137</td>
<td>130</td>
</tr>
<tr>
<td>High</td>
<td>129</td>
<td>101</td>
</tr>
<tr>
<td>Very high</td>
<td></td>
<td>26</td>
</tr>
</tbody>
</table>

a Progeny were only rated as low, medium, or high in vigor in 1964.
b Seventeen seedlings winter-killed during the winter of 1964-1965.

Discussion

The production of suckers by some of the 18-5902 x M-127 hybrid offspring was not unexpected, but the percentage which did produce suckers was higher than reported by Colby (11) with similar crosses. It should be mentioned that the susceptibility to complete winter-kill of non-suckering plants probably significantly influences the observed percentage of suckering and non-suckering plants.

The increase in percentage of suckering individuals from 1964 to 1965 could have two possible explanations. First, environmental conditions may affect the absence or presence of sucker production. No detailed studies on environment's effect on suckering were found in the literature. Second, plant maturity could also be involved.
Often in other plants certain characteristics, such as runner production in strawberries, are not expressed until the individual reaches maturity.

In accordance with the inheritance scheme of Knight and Keep (31), selection 18-5902 must be homozygous dominant for the SK1 gene; otherwise suckering individuals would have been present in the population from selfing this clone. Following this assumption, 18-5902 must also have some favorable gene forms for sucker production which could have combined with favorable genes from the M-127 parent.

The population of hybrids from the cross of 18-5902 and M-127 showed as much variability with regard to tip-rooting as those previously recorded by other workers. In attempting to explain this variability by the Knight and Keep (31) proposal of control by a single dominant gene, one must assume that selection 18-5902 is homozygous dominant for the gene in control of tip-rooting. This assumption is made since all seedlings derived from selfing 18-5902 were capable of tip-rooting as indicated by their formation of rat-tails. With this assumption, one would expect that the entire hybrid population would propagate by tip-layerage. The failure to obtain such results indicates that tip-rooting is probably controlled by more than one gene.

It was interesting to note that the ability to tip-layer was not restricted to those clones which did not produce suckers but also was found in some which produced suckers sparingly, moderately, and freely. Thus one should be able to produce new varieties which
would propagate quite easily.

The variation in the number of autumn-fruiting, hybrid offspring from 1964 to 1965 is not too surprising. Slate (45), among others, has recognized that environment can strongly influence the expression of this trait. Some of those individuals considered to be fall-fruiting during 1965 may not be dependable in this respect. Certain standard varieties produce a small fall crop in certain years (21).

The strong effect that environment has in influencing the expression of fall-fruiting suggests quantitative inheritance. The fact that selection M-127 is considered to have both Rubus idaeus and Rubus strigosus in its background also complicates the inheritance of autumn-fruiting. As mentioned previously, several workers feel that varieties derived from each of these species carry different genes for controlling autumn-fruiting. Even though M-127 is not autumn-fruiting itself, it is likely that it carries some of the genes for this characteristic. This assumption is made since no autumn-fruiting types were observed in the population obtained from selfing the other parent, 18-5902. A study of a population from selfing M-127 could help verify this assumption.

The degree of anthracnose susceptibility of the parent clones is representative of plants with their background. The degree of susceptibility of the progeny from selfing 18-5902 agrees with the results obtained by Colby (10) from selfing clones which showed a high degree of susceptibility.
An increase in anthracnose infection from one year to the next in raspberry plantings is commonly due to a build up of the organism within the plantings rather than a breakdown in resistance. Certain environmental conditions can also be more favorable to the development and spread of the organism. The organism was distributed throughout the plantings, as severely infected plants were observed in all parts of the field. The resistance shown by some hybrid seedlings was undeniable since adjacent seedlings quite often showed considerable infection. A nearby planting of the standard black raspberry variety Black Hawk showed moderate infection, even though it is reportedly somewhat resistant to anthracnose (34).

The amount of winter injury suffered by the M-127 parent was somewhat higher than is usually observed on Rubus strigosus and more like that found on Rubus idaeus. In certain years, however, even the hardiest types suffer considerable cane injury. The offspring from selfing 18-5902 showed less injury than is common on Rubus occidentalis. It is likely that more injury would have been observed after future winters when the plants had become further weakened due to anthracnose infection.

The extreme variability observed in the hybrids was of interest. Seedlings were produced which showed more, as well as less, hardiness than either of the parents. Since a fairly high percentage of the population showed greater hardiness than the parents, it should be possible to produce a very hardy purple raspberry. The parental types are not particularly noted for their hardiness. If the
hardiest *Rubus occidentalis* and *Rubus strigosus* were used in producing a hybrid, an extremely hardy purple raspberry might result. It is important to stress that winter hardiness is strongly influenced by many environmental conditions during the previous growing season as well as during the winter. From this, one can propose that the inheritance of winter hardiness is controlled by a number of genes.

A high amount of complete winter-kill in non-suckering plants was not surprising. These plants can not produce new growing shoots as freely as those of the suckering type. If the crown portion of the plant is severely injured, the non-suckering plant will most probably be killed; while the suckering plant can survive through the production of more suckers from adventitious buds on the roots which have been protected by their underground location.

The high percentage of individuals in the hybrid population with equal or greater vigor than the parents is consistent with the reports of earlier workers, including Darrow (18). This reality should enable the plant breeder to develop very vigorous new varieties of the purple type.
SUMMARY

A study of the inheritance of fruit color, suckering and tip-rooting tendencies, anthracnose resistance, autumn-fruiting, as well as other more general growth characteristics with raspberry interspecific hybrids was conducted. The parents were Iowa selection M-127, an apricot-fruited form with *Rubus idaeus* and *Rubus strigosus* background, and selection 18-5902, an amber-fruited *Rubus occidentalis*. These parents were under study along with a seedling population derived from selfing 18-5902 and the hybrid population from crossing 18-5902 with M-127.

Fruit color was evaluated on all available material by visual and colorimetric methods. Five classes for visual evaluation were set up, i.e. yellow, apricot, salmon, dark salmon, and red. The colorimetric results delineated only four classes, essentially due to the combining of the salmon and dark salmon classes. Aside from this, there was general agreement between visual and colorimetric evaluations although some fruit samples were rated more intense in color with the colorimeter than by visual means. This seemed due to the presence of larger amounts of pubescence on some fruit which made the fruit appear lighter in color upon visual inspection. A high percentage of the hybrid offspring had fruit which were classified as salmon in color with smaller percentages in each of the other three classes. Selection 18-5902 had fruit which was considered salmon, while M-127 had apricot fruit.
Growth habits of the interspecific hybrids were evaluated and compared with those of related material. Plants were described as non-suckering, suckering sparingly, suckering moderately, and suckering freely. There were 197 suckering to 108 non-suckering. This represented an almost complete reversal of results from the previous year. It was felt that seedling maturity could explain the delayed expression of the suckering characteristic. All individuals from selfing 18-5902 were non-suckering, while M-127 produced suckers moderately.

In evaluating plants for tip-rooting tendencies, any plant which developed the characteristic rat-tail condition was considered to have tip-rooting tendencies. Transfer of the tip-rooting characteristic from the *Rabun occidentalis* parent to the hybrid offspring was incomplete, as only about 60 percent of the hybrids showed the rat-tailing characteristic. There were some individuals which could be propagated either by tip-rooting or suckers and others which could be propagated by neither method. The autumn-fruiting plants were not evaluated for their tip-rooting tendencies.

The ability to form flowers and fruit on primocanes was evaluated at two week intervals beginning in mid-July and ending on October 1. Autumn-fruiting was observed on 19.5 percent of the hybrid individuals. M-127 has never been observed to be fall-fruiting, and the population from selfing 18-5902 was also devoid of any fall-fruiting plants.

The degree of anthracnose infection was rated as none, slight,
moderate, or severe. Plants of M-127 showed no or occasionally slight infection, while almost 90 percent of plants of the selfed population showed severe infection. The interspecific hybrids showed much variability with respect to anthracnose infection. These hybrids, however, did show much more resistance than their Rubus occidentalis parent.

The amount of winter injury was classified according to the percentage of observed cane die-back. Plants of M-127 showed 60 to 100 percent cane die-back. All individuals from selfing 18-5902 suffered 0 - 20 percent cane injury. The hybrid population was quite variable in cane hardiness, with the highest number of seedlings in the 0 to 20 percent die-back class. The next largest number fell in the class for 80 to 100 percent die-back. Non-suckering individuals were more susceptible to complete winter-kill than those clones which produced suckers.

During the first year of study, all material was rated low, medium, or high in plant vigor. The following year two additional classes for plant vigor were added, i.e. very low and very high. Both M-127 and the population from selfing 18-5902 were considered medium in vigor. The hybrid population was variable in this respect. The average vigor of the hybrids was somewhat higher, however, than that of the parents.
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