

CHROMOSOME BEHAVIOR IN BLACKBERRY-RASPBERRY HYBRIDS ¹

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INTRODUCTION

The genus *Rubus* in the United States is characterized by inter-specific compatibility, frequent lack of complete fertility, and a high degree of heterozygosity. This is shown by the taxonomic work of Brainerd and Peitersen (2)³ on the New England blackberries, by the genetic studies on the same material by Peitersen (10), and by several investigations of Darrow and Longley (4) and of Longley (5, 6). This is further emphasized by the dewberry × raspberry cross made by Ness (9) in 1912. Both first and second generations

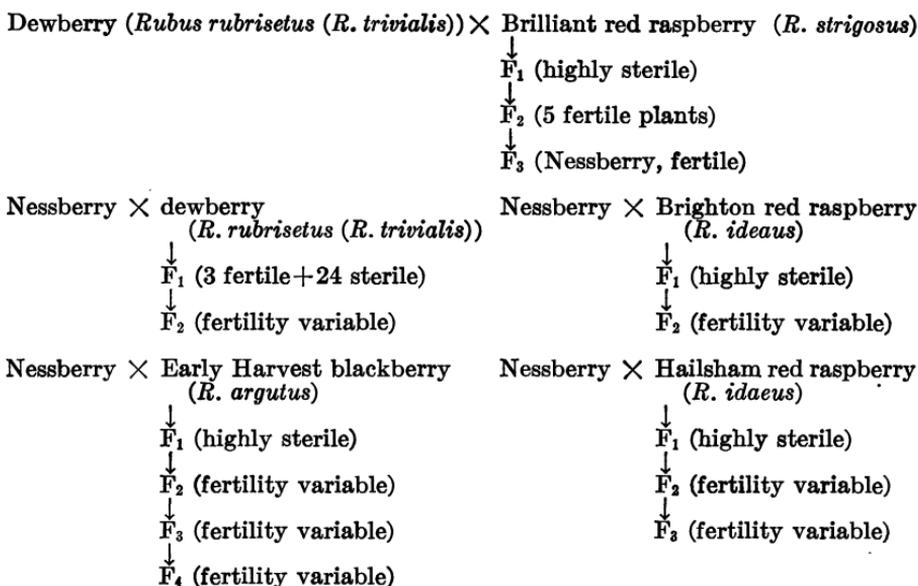


FIGURE 1.—Diagrammatic representation of the origin and later crosses of the Nessberry with blackberry, dewberry, and raspberry.

of this cross (*Rubus trivialis* Michx. = *R. rubrisetus* Rydb. × Brilliant red raspberry, *R. strigosus* Michx.) were quite sterile with the exception of five F₂ (open-pollinated) plants, which were almost completely fertile, giving a third generation of 859 plants. Selections from these were given the name Nessberry. Ness then crossed this fertile hybrid to the dewberry parent, to two raspberries, and a blackberry and grew later generations. The last generation of each cross with the Nessberry, outlined in figure 1, has been available for cytological study.

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² The writer acknowledges the assistance of Fraser Cowart, Dr. U. R. Gore, and Hennie Levy in the preparation of cytological material at different times.

³ Reference is made by number (italic) to Literature Cited, p. 396.

The work here reported was undertaken to obtain further knowledge of chromosome behavior in the genus *Rubus*.

Since all of the crosses were made by the late Helge Ness, with whom the writer had no opportunity to discuss the material, portions of his notebook entries will be given in certain instances. An account of much of this work has been published by Ness (8, 9). In referring to his publications it must be remembered that he named the pollen parent first. For example, his paragraph heading (La \times (Brilliant \times La) F_3) F_1 thus becomes the first generation of the back-cross Nessberry \times *Rubus rubrisetus* (*R. trivialis*) (9).

THE WILD DEWBERRY

Ness (9) considered *Rubus trivialis*, the dewberry found locally, and *R. rubrisetus*, secured for his work from Louisiana, as distinct species, based upon differences in shoot growth. It is doubtful, in view of the amount of variation in this respect observed in dewberries of this locality, if there is sufficient genetic difference between the two to justify this distinction. Root tips of the former have 14 chromosomes at metaphase (fig. 2, A). There are seven pairs at diakinesis, frequently joined by a single terminal chiasma. The movement toward the poles at the anaphase of the first division sometimes tends to be a little uneven (fig. 2, B), otherwise the division appears normal.

THE NESSBERRY

Longley and Darrow (7) illustrate the heterotypic division of the Nessberry with three figures. Diakinesis and metaphase exhibit 14 pairs of chromosomes; 1 pair appears to be lagging at telophase. They say: "It was exceptional to find irregularities during meiosis, but the history of this hybrid shows that it has been selected through several generations and now behaves like a stable species." A slightly greater degree of irregularity than the foregoing account would indicate has been observed in plants grown in Texas. Lagging has been noted during the heterotypic division, and in addition the chromosomes seem to have some difficulty in forming a normal metaphase plate. This interferes with an even movement toward the poles during the anaphase of the first division (fig. 2, C).

NESSBERRY \times RUBUS RUBRISETUS F_2

The first generation of the cross Nessberry \times *Rubus rubrisetus* is discussed by Ness (9, pp. 22-23). The cross was described before it was known that the Nessberry has twice the chromosome number of its parents. This first generation consisted of 27 plants—

intermediate of the parents, except three individuals which show only the Nessberry in all parts and bear a heavy crop of perfect fruits; all the others are more or less sterile, with canes showing traces of both parents. * * * The leaves have the form and size of the Nessberry but their texture and surface are characteristic of the blackberries. The flowering is abundant, but each resulting fruit consists of a few scattered drupelets.

The simplest explanation of these results would seem to be that 3 tetraploid plants of the maternal type and 24 triploid true hybrids had been obtained. None of this generation has been available for study.

A second generation was grown on two occasions. Seed was sown on October 15, 1924, from F_1 plants of the Nessberry type. Five of

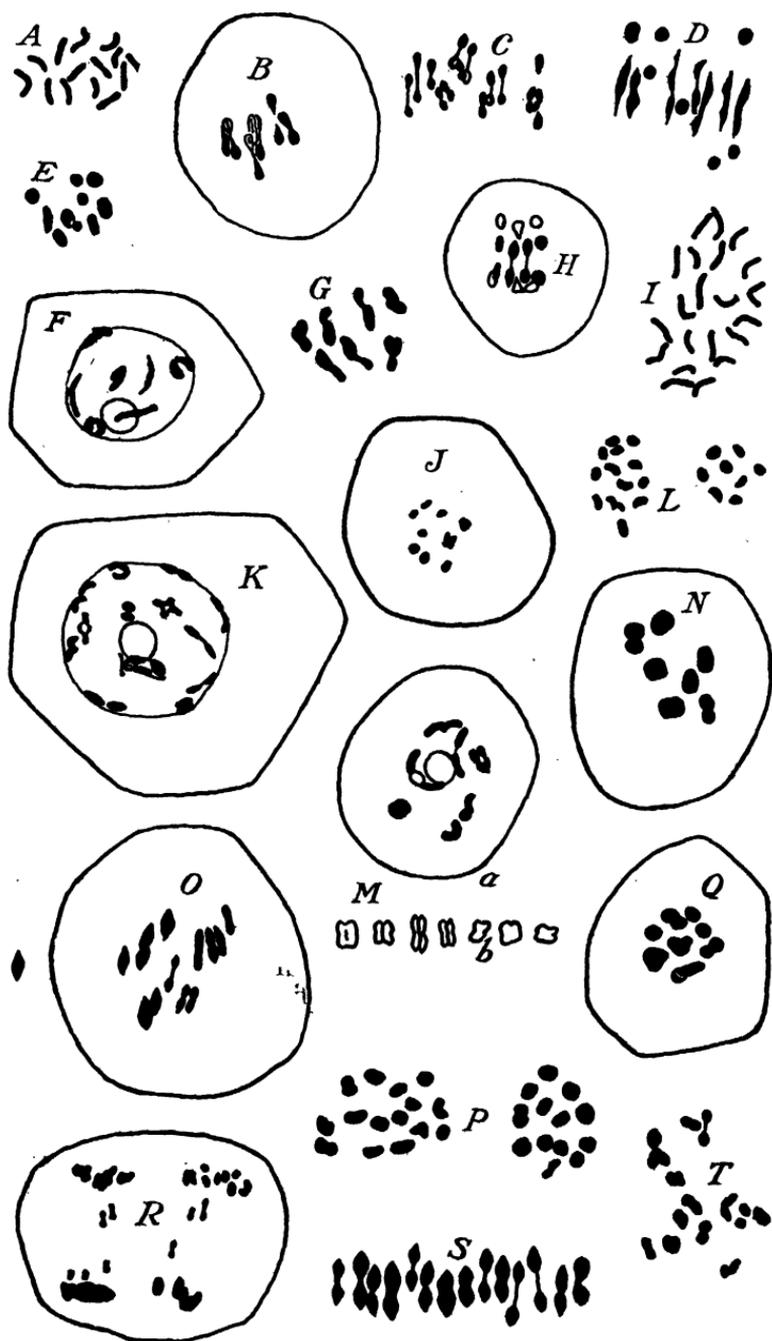


FIGURE 2.—A, *Rubus trivialis*, root tip. B, *R. trivialis*, first anaphase; C, Nessberry, first anaphase. D-J, Nessberry × *R. trivialis* F₂; D, 3n, first anaphase; E, 3n, first metaphase; F, 2n, diakinesis; G, 3n, first metaphase; H, 2n, first anaphase; I, 3n, root tip; J, 3n, first metaphase. K-R, Nessberry × Hallsdam (*R. idaeus*) F₂, 4n; K, diakinesis; L, second metaphase; M, a, diakinesis; M, b, first metaphase; N, first metaphase; O, first anaphase; P, second metaphase; Q, first metaphase; R, second anaphase. S-T, Nessberry × Early Harvest (*R. argutus*) F₁, 4n; S, first anaphase; T, first metaphase-anaphase. × 2,540. Buds and root tips were fixed in Allen's modification of Bouin's solution and paraffin sections made, which were stained in crystal violet. In the buds only pollen mother cells were examined. All drawings were made with the aid of the camera lucida, using a 1.5-mm apochromatic oil-immersion objective and a 12.5 × compensating ocular.

the seventy-one plants are mentioned in the notes. In four of these the Nessberry parent was considered to be dominant; the fifth had "strong growth, many flowers but infertile, similar in all parts to the F_1 ", presumably the intermediate type. The second planting was made October 12, 1927, "Seeds uniformly large." The following February it was noted that the germination was poor, 64 plants being potted. Sixty-eight plants were set in the field during May 1928. Forty-two of these have been available for observation.

The plants may be classified roughly into four groups: (1) A single plant in which the characters of the Nessberry parent are dominant; (2) a variable intermediate group of 10 plants; (3) those almost indistinguishable in appearance of canes from the dewberry parent, 28 plants; and (4) 3 plants similar to those just preceding except that they are more vigorous and show Nessberry characters in the canes. The plants will be discussed in this order.

(1) No. 27 resembles the Nessberry parent very strikingly in type of growth, i. e., the leaflets are large and broad, usually in threes; the canes are strongly branched, with fewer prickles and less pigmentation than the wild dewberry. In addition, the ripe fruit, which is reduced in size because of sterility, crumbles upon picking instead of breaking below the receptacle as in *Rubus trivialis*. Twenty-one chromosomes were observed in root-tip preparations (fig. 2, *I*). There is evidently normal pairing between 14 chromosomes while 7 remain unpaired. This can be seen in the heterotypic anaphase illustrated in figure 2, *D*. Assortment of the unpaired chromosomes is probably at random. Counts of a rather limited number of metaphase plates of the homotypic division indicate that 9 and 12 is the most common distribution, followed by 8 and 13 and then 10 and 11. In figure 2, *L*, the distribution has been 8 to one pole and 13 to the other; one of the chromosomes has split and the halves are about to disjoin.

The 10 plants of the intermediate group (2) differ widely in vigor. Six are highly sterile, the other four having reduced fertility. No. 1, sterile but vigorous, has the tetraploid chromosome number, with complete pairing. Three or four tetrasomes can be observed at diakinesis. Two chromosomes frequently lag at anaphase of the first division. No. 8, sterile and weak, has the diploid chromosome number, which is readily seen at diakinesis (fig. 2, *F*). While the seven pairs seem to behave quite normally, evidence of a loose association between the two components of one of the disomes was noted. No. 12 is fairly fertile; the 14 pairs frequently exhibit a multiple association with from 1 to 6, rarely 7, tetrasomes at diakinesis. The distribution is usually 14 and 14, but 13 and 15 chromosomes are sometimes observed at the homotypic metaphase. Judging from premetaphase and first anaphase stages, plant no. 29 has the tetraploid chromosome number. Chromosomes of certain of the hybrid plants are hard to differentiate clearly, and since no. 29 is one of these, the precise chromosome relationships are hard to determine. There are at least 12 pairs in this case, with a variable amount of multiple association during diakinesis and first metaphase, resulting in 7 or 8 groups of chromosomes in some instances. No. 29 appears to be less fertile than no. 27. The other six plants of this group were not examined cytologically. A summary of chromosome counts for this and other crosses is given in table 1.

An examination has been made of the pollen mother cells from six plants which bear a close resemblance to the dewberry parent (group 3). A count was made of the chromosomes in the root tips of an

additional plant. In each case the diploid number was found. These plants give evidence of their hybrid origin by their vigor, by the immense size of the fruits in many cases, by a peculiar flavor of the fruit of certain of the plants, and in some instances by a reduced fertility. The pairing is complete, although somewhat looser than in *trivialis*. There is a reluctance of one or two chromosome pairs to disjoin promptly (fig. 2, *H*); otherwise the divisions are quite regular. There was a large amount of apparently good pollen—68 and 78 percent for two plants examined in iodine-potassium iodide solution.

TABLE 1.—*Summary of chromosome counts obtained*

Cross	Group no.	Type	Plants				
			2n	3n	4n	Not examined	Total
			Number	Number	Number	Number	Number
Nessberry × <i>R. rubrisetus</i> (dewberry) F ₂ .	1	♀ P dominant.....		1			1
	2	Intermediate.....	1		3	6	10
	3	♂ P dominant.....	7			21	28
	4	♂ P predominates, vigorous.....		3			3
		Total.....		8	4	3	27
Nessberry × Brighton (raspberry) F ₂ .	1	Dewberry type.....				2	2
	2	Nessberry type.....			2	4	6
		Total.....			2	6	8
Nessberry × Hailsham (raspberry) F ₂ .	1	Entirely fertile.....			27	46	73
	2	Fertility reduced.....			28	29	57
	3	Sterile.....			7	16	23
		Total.....			62	91	153
Nessberry × Early Harvest (blackberry) F ₄ .	1	Entirely fertile.....			18	62	80
	2	Reduced fertility.....			29	38	67
	3	Sterile.....			5	27	32
		Total.....			52	127	179

The last group (4) consists of three plants differing from those immediately preceding by their greater vigor, reduced pigmentation and number of prickles, and increased branching of the canes. All three have the triploid chromosome number. Classification of chromosome groups of an early first metaphase of no. 45b on a basis of size suggests three monosomes, three disomes, and four trisomes (fig. 2, *E*). A spindle view of first anaphase, not illustrated, lends support to this interpretation.

The chromosome number of no. 45c was determined from root-tip material only. Both somatic and meiotic chromosomes of no. 55 were examined. There is a strong tendency for the formation of trisomes in the latter plant, as can be seen during the early first metaphase of figure 2, *G*. There are not usually so many trisomes. In figure 2, *J*, also a first metaphase, there is only one obvious trisome, at the upper right.

NESSBERRY × BRIGHTON F₂

Nessberry × Brighton represents a backcross to a raspberry species, *R. idaeus*, L., similar to the original parent. The first generation was discussed by Ness (9, p. 23). It was noted that—

All of the plants set a profusion of flowers, but not a single flower produced perfect fruit. Each fruit consisted, as in other cases of partial sterility, of only

a few drupelets. By gathering nearly every drupelet, an ample amount of seed for a second generation was secured (9, p. 25).

There were 230 plants, all no doubt with the triploid chromosome number.

Seeds for the second generation were sown in boxes on October 12, 1927; "germination very poor." Eleven plants were potted the following March, and 12 plants were set in the field on May 15, 1928. Eight of these have been available for study. In spite of the use in the breeding work of large numbers of insect-proof cages large enough to cover a plant, it seems highly probable that this family resulted from open pollination, as two of the plants are quite similar to the wild dewberry except in fertility. Three plants of the Nessberry type are almost completely sterile and three plants are quite fertile. Two of the latter have the tetraploid chromosome number. Fourteen pairs can be seen at diakinesis and in both cases there is evidence of a multiple association to give anywhere from one to six loose tetrasomes. Lagging occurs at both heterotypic and homotypic anaphases. One of these had 34 percent apparently good pollen.

NESSBERRY \times HAILSHAM F₃

Nessberry \times Hailsham is the same type of cross as the one just discussed, the two first-generation families being very similar. Seed for the second generation was saved from a plant "with perfect, large fruit, foliage differing from rest in texture * * * very similar to Nessberry in all characters." The F₂ consisting of 93 plants, was planted in the field in 1925. Notes were taken the following May on 10 plants. Two were of the Hailsham type, but completely sterile; one was like the wild dewberry, but with "imperfect" fruits; the remainder varied, both in appearance and fertility. On May 16, 1927, an additional plant was described as follows: "Low, compact; leaves, shoots typical of Nessberry; very prolific; flower cluster large; berries large, Nessberry in form and color; drupelets adhering; tendency to break under calyx." While no record is available, this unusual praise, together with the appearance of this third generation, makes it seem quite likely that this plant was its parent. Two hundred and seventy F₃ plants were set in the field on May 14 and 15, 1928. One hundred and fifty-three of these have been available for observation.

With the exception of certain plants of weak growth the family in general favors the Nessberry. All plants have been placed in three groups on a fertility basis, as follows: (1) Entirely fertile, 73 plants; (2) fertility reduced, 57; (3) almost or entirely sterile, 23. The classification is based upon the appearance of the fruit. Buds of 60 plants have been examined. As far as could be determined from pollen mother cell material all plants have the tetraploid chromosome number. The somatic chromosome number of one of these was found to be 28.

While the first group seemed to be completely fertile as judged by achene development, in nine representative plants the percentage of good pollen varied from 45 to 67. In addition, no. 72 had only 16 percent of good pollen, while, in contrast to this, no. 7 had only 3 percent of empty grains, the remainder varying greatly in size, none staining as deeply as pollen from other plants.

Three of the twenty-seven plants examined exhibited no multiple association. Most of the plants had one or two tetrasomes at diakinesis. In four cases as many as seven tetrasomes were sometimes found (fig. 2, *N*), and in one plant six tetrasomes and two disomes. Two of the plants having seven tetrasomes were at first mistaken for diploids (Yarnell (11)), but further examination showed that they as well as the others have the tetraploid number of chromosomes. In spite of an evident reluctance to form a normal plate at first metaphase with consequent lagging of chromosomes during the anaphase following, the usual division is 14 chromosomes to each pole. The great variation in size of pollen grains found in no. 7 is probably due to the loss of lagging chromosomes. The low percentage of good pollen in plant no. 72 was not fully explained by a study of meiosis. There was some evidence of a tendency toward incomplete association at diakinesis but this was rare.

The chromosome behavior of the plants with reduced achene development differs from that of the foregoing group only in degree. The percentage of good pollen from six representative plants was found to vary from 36 to 50, somewhat below that of the previous group. As before, two exceptional plants were found—no. 47 with 85 percent of good pollen and no. 162 with no good pollen.

The diakinesis shown in figure 2, *K*, has 14 pairs of chromosomes. This is from a plant (no. 74) having from none to seven tetrasomes. The figure illustrated in figure 2, *O*, represents a first anaphase of this same plant, and illustrates disjunction without the formation of a metaphase plate. One pair covered by others is drawn outside the cell. The diakinesis of figure 2, *M*, *a*, has seven tetrasomes, which are shown in figure 2, *M*, *b*, as they appear at first metaphase. A polar view of the first metaphase of this plant (fig. 2, *Q*) has five tetrasomes and four disomes. Lagging at second anaphase (fig. 2, *R*) occurs in the group.

The last group was originally classified as: (1) Almost sterile, 13 plants; (2) entirely sterile, 3 plants; and (3) weak growth with no flowers, 7 plants. Three plants were found to have the following percentages of good pollen: 3, 21, and 24, respectively. The amount of multiple association varies from none to seven tetrasomes as before. The lack of organization at the normal period for first metaphase is more pronounced, however. This results in nondisjunction more frequently than in the more fertile plants. A 15 and 13 division (fig. 2, *P*) is fairly common.

NESSBERRY × EARLY HARVEST F₁

Nessberry × Early Harvest represents an outcross to a blackberry type. Early Harvest is said to have been propagated from a selected wild plant growing in southern Illinois. It is referred to *Rubus argutus* Link by Card (3) and by Bailey (1). The cross was made in 1919, the small first generation having black fruit rather than the deep red of the Nessberry. In leaves and stem the plants favored the female parent. The flowers were highly sterile. Seeds to produce the second generation were "medium to small, of Early Harvest type." On May 3, 1923, 10 plants were set in the field. On May 19, 1924, there were "seven plants, intermediate except no. 6 and very uniform in characters." One of the intermediate plants was chosen

as parent of the third generation. There was an abundance of both large and small seeds. Sixty-one F_3 plants were set in the field during November 1925. Notes were made on seven of these plants during May 1927. All were fertile and prolific, but they varied somewhat in character of vegetative growth. Seed was saved from two of these for a fourth generation. The seeds were variable in size; germination was good, 336 plants being set in the field in May 1928.

The plants as a whole do not differ greatly in appearance from those of the previous cross, as the Nessberry influence is dominant in both. In each case there is a great deal of variation, particularly in vigor, in size of leaves and flower clusters, and in general habit of growth, including the amount of branching and the degree of procumbency.

A classification of the fertility of the 179 plants available for study was made from the fruit as before. (1) Eighty plants seemed to be entirely fertile; (2) 67 had reduced fertility, and (3) 32 were almost sterile. Pollen was examined from 11 plants of the "fertile" group. They fell into three classes: Six plants with from 70 to 80 percent of good pollen, four plants with from 57 to 59 percent of good pollen, and one plant with 32 percent of good pollen. Ten of thirteen plants examined critically gave evidence of multivalent association, usually having two or three tetrasomes, although two plants had as many as seven tetrasomes part of the time. The other three plants had only disomes at diakinesis and metaphase of the first division. The drawn-out anaphase resulted in an equal distribution of chromosomes in all cases noted. In figure 2, *T*, the chromosomes are separating without the formation of a metaphase plate. There is a single tetrasome at the upper left. This illustrates an extreme degree of irregularity for this group.

Eight of nine plants with "reduced fertility" had from 64 to 82 percent of apparently good pollen. One other plant, no. 23, had only 1.7 percent of good pollen. Buds were fixed from 23 plants of this second group. No. 23 gave evidence of the association of four chromosomes to give two disomes at the metaphase of the second division. From two to four tetrasomes were usually observed during the first division. Anaphase of the first division of this plant was more regular than for most plants of the group (fig. 2, *S*). The chromosomes have been spread in drawing. Considering all 23 plants examined, there were more tetravalent bodies than in the previous group. Only one plant exhibited disomes. The number of tetrasomes commonly found ranged from two to four, with four plants sometimes having as many as six or seven. There was more lagging near the end of the first division in this than in the preceding group. A division of 13 and 15 was observed in six plants; five spores were sometimes formed from one sporocyte.

The six plants classified as "almost sterile" that were examined cytologically differed but little from the foregoing group. The irregularities were of the same type and appeared to be of about the same degree. One plant was found to have 70 percent of apparently good pollen.

DISCUSSION

As pointed out by Ness (9) and later by Longley and Darrow (?), the five fertile plants of the second generation of the cross wild dewberry (*Rubus trivialis*) \times Brilliant red raspberry (*R. strigosus*) behave

as a true species. Since the fertility is due to chromosome doubling in the hybrid F_1 , the Nessberry should be classed as an amphidiploid rather than as a true tetraploid. A second cross made by Ness with the same dewberry by Haymaker, *R. neglectus* Peck (*occidentalis* \times *strigosus*), appears to have doubled its chromosome complement in a first-generation plant in the same way. Plants of this fertile second generation were fertile with the Nessberry (9).

It is of interest to note that there were only five fertile plants among a second generation otherwise highly sterile. Since the first hybrid generation must have had two genomes of seven chromosomes each it appears that the doubling most likely occurred at a time to produce both egg and pollen grains of an F_1 plant with two genomes—probably in a somatic cell during differentiation of a flower bud, possibly giving a sectorial chimera. If it had happened earlier a larger number of fertile second-generation plants would be expected; if later, sterile $3n$ plants would result. Some, indeed, may have had the triploid chromosome number. It is possible, of course, that these five plants were produced from the union of nonreduced gametes. This explanation seems to be less likely than the first because seeds from first-generation plants were sown 2 years in succession without the appearance of a single fertile plant.

The four families under consideration represent backcrosses to the two parental species and an outcross to a distinct species, *Rubus argutus* (fig. 1). The first-generation plants of these later crosses would normally be expected to have the triploid chromosome number. This expectation seems to have been realized in each case with the exception of three plants of the backcross to the dewberry, which were fertile and of the maternal type—possibly due to accidental self-pollination.

In two cases plants of a second generation of backcrosses to the two parental species have been available for study. Twenty-eight of the forty-two plants of the cross involving *Rubus rubrisetus* (*R. trivialis*) have a marked resemblance to this species. All of these plants examined are diploid. The large number of plants of this type suggests that they may have originated by the open pollination of F_2 plants with pollen from the wild dewberry, the egg contributing a haploid chromosome set. All exhibit hybrid characteristics and so must contain chromosomes, or at least portions of chromosomes, derived from the original red raspberry parent. In spite of the wide genetic differences between corresponding chromosomes (being derived from different sections of the genus) they are able to pair in these plants and behave otherwise in a fairly normal manner. The raspberry genes are obviously in the minority since the appearance of the plants is in striking contrast to that of the F_1 of the cross *R. trivialis* \times Brilliant, which also must have been diploid. Ness (9) reports that the raspberry type was very dominant in the F_1 .

The triploids in the backcross under consideration are of two types, one plant being very similar to the Nessberry, and three plants favoring the dewberry but considerably more vigorous. The appearance of these types can be accounted for by supposing that they carry two genomes most or all of whose genes come from the parent they favor. If the latter three plants result from pollen from *Rubus trivialis*, the egg would then have contributed two sets of chromo-

somes, a part of which must have been derived from *R. strigosus*. If association can be taken to represent genetic similarity in this case one would assume that there are two complete genomes and possibly four additional chromosomes that should be referred to *R. trivialis* and three chromosomes deriving largely from *R. strigosus*. In the case of the plant resembling the Nessberry parent one is tempted to assign two genomes to *R. strigosus* and one to *R. trivialis*.

Since the Nessberry regularly has 14 pairs, it is reasonable, considering the wide genetic differences between the parental species, to suppose that pairing is between genomes from the same species, with a resulting lack of opportunity for their modification by crossing over between chromosomes of the two species involved. The first generation of the backcross to the dewberry parent would then have two genomes derived from *Rubus trivialis* and one from *R. strigosus*. Plants with the triploid chromosome number obtained upon selfing a triploid of this constitution would be expected to favor the wild dewberry. The origin of no. 27, favoring the Nessberry is hard to explain. Its appearance, together with the *Drosera* type of pairing observed, strongly suggests that its chromosomal complement does consist of two genomes from *strigosus* and one from *trivialis*.

Plants with the tetraploid chromosome number appear in both second-generation families. This is also probably true in the F_2 of the crosses of Nessberry with the Hailsham raspberry and Early Harvest blackberry, since a portion of plants of these second generations were highly fertile. Selection of plants of the Nessberry type accounts for the appearance, the fertility, and the chromosome number of the later generations studied.

The meiotic chromosome behavior of these later generation 28-chromosome plants differs from that of the Nessberry in two particulars. The association of four chromosomes is characteristic of the heterotypic division and the degree of irregularity is much greater in the former group of plants. The first may result from the accumulation of more than two homologous chromosomes upon the formation of $4n$ plants from $3n$ individuals. The second is the natural result of the introduction of chromosomes from a distinct species together with the changed balance just noted.

These conditions account for the variability found in the third and fourth generations under study in regard to general plant vigor and morphological characters. Since these depend upon the particular genetic combination obtaining in each plant and since the chromosomal irregularity is probably dependent upon a more general effect of the chromosome complement, a close correlation between the degree of vigor and chromosome regularity is not to be expected. This seems, in some instances at least, to be true also of fertility and chromosome behavior.

All of the crosses were made by Ness with the object of securing a berry combining the high quality of the red raspberries with the ability of the wild dewberry to withstand conditions of heat and drought, and, of course, the work was done without a knowledge of chromosome behavior in the hybrids. The possibility of chromosome doubling in a hybrid that is highly sterile because of wide genetic differences between the parents is recognized as a means of extending the activities of the plant breeder. The ultimate effect is to complicate the breed-

ing behavior of the material through the use of parents with different chromosome numbers, through the apparent loss of important recessive characters where pairing is only between chromosomes of corresponding genomes in the new amphidiploid, and through the fact that a larger number of chromosomes prevents simple segregation and recombination of characters observed in the original parents. The third and fourth generations of the Nessberry outcrosses discussed above are particularly good examples of the last point. Even in the fourth generation few plants exhibit a really stable chromosomal balance. Practically all characters show some influence of both parents. Where such chromosome doubling has occurred, the breeder may expect a high degree of variability both as to degree of fertility and general somatic characters in using the material in outcrosses to secure more desirable combinations.

SUMMARY

A cytological study has been made of crosses involving the amphidiploid hybrid of a dewberry \times red raspberry cross (the Nessberry) with the diploid dewberry parent and with two diploid raspberries and a blackberry.

Plants with the diploid, triploid, and tetraploid chromosome number were found in the second generation of the dewberry backcross. A single diploid was of intermediate type; 28 diploids strongly favored the dewberry type and may represent outcrosses of the F_1 to the wild species. The triploids were of two types; one plant favoring the Nessberry and three plants nearer to the wild dewberry but more vigorous. Seven disomes plus seven single chromosomes were found during the first division of the first triploid; from three to four trisomes (occasionally more) can be distinguished in the second type.

Plants of the third generation of the Nessberry \times Hailsham red raspberry cross and plants of the F_4 of the Nessberry \times Early Harvest blackberry cross all had the tetraploid chromosome number. This is probably due largely to selection of plants favoring the Nessberry in the second and third generations. Meiosis of these plants is distinguished from that of the Nessberry by the frequent occurrence of multivalent association to give from one to as many as seven tetrasomes, and by considerably greater chromosomal irregularity during the reduction division.

It seems likely that such association reflects genetic similarity among the associating chromosomes, since there has been an opportunity for more than two corresponding chromosomes of a genome to become segregated in a single plant.

A wide variation in vigor observed among the plants of these later generations is probably due to genetic differences possible in the recombination of chromosomes from the three species involved.

There was some correlation between chromosome regularity at meiosis and degree of fertility, but the most sterile plants did not exhibit a greater degree of chromosome irregularity than many less sterile.

It is pointed out that a doubling of the chromosomal complement in a sterile hybrid greatly complicates its breeding behavior in subsequent outcrosses.

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