

FERTILITY AND VIGOUR OF APPLES IN RELATION TO CHROMOSOME NUMBER.

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CONTENTS.

	PAGE
Introduction	153
Polyploidy in relation to fertility	154
"Triploidy" in apples	154
Vigour in relation to chromosome number	157
Sterility and incompatibility	159
Summary	162
References	162

INTRODUCTION.

EXPERIMENTS relating to sterility and incompatibility in plums, cherries and apples have been carried out at this Institution since 1911. Reports on the results obtained have appeared from time to time, and in the last publication (Crane and Lawrence, 1929) the results of the investigations from 1911 to 1928 were briefly summarised.

As the experiments progressed it became evident that among cultivated apples sterility and incompatibility differed in several respects from the similar phenomena in plums and cherries. The salient differences were: (1) as far as our investigations go, incompatibility occurs in varying degree, but is rarely, if ever, completely expressed in apples, as it is in plums and cherries¹; (2) as a rule the degree of generational sterility is much higher in apples—especially in certain varieties—than in cultivated varieties of plums and cherries; and (3) in certain crosses not only were few seeds formed, but the seedlings which germinated were extremely weak and remained feeble throughout their growth.

¹ About 50 distinct varieties of apples have been used, and out of a total of 243 cross-pollinations, involving over 23,000 flowers, only five entirely failed to give fruits. As comparatively few flowers were used in these five crosses too much importance should not be attached to them and repetition is desirable.

By way of comparison, all the sweet cherries (= varieties of *Prunus avium*) we have used are self-incompatible, and out of 36 varieties 20 form six incompatible groups within which all self- and cross-pollinations fail. In plums, *Prunus domestica*, the behaviour of incompatibility is more complex, but complete self-compatibility and self-incompatibility is common, and several examples of cross-incompatibility have been established. The above cherries are approximately diploid and the plums hexaploid ($2n=48$).

POLYPLOIDY IN RELATION TO FERTILITY.

Until comparatively recently these experiments were carried out without any knowledge of the chromosome complement of the various forms used, but during the past few years cytological investigations have shown that among our cultivated fruits polyploidy is common.

In general odd multiple polyploids are relatively infertile, and apparently the only known exception to this is in the hyacinth, where triploid forms set seed comparatively freely. Where seed and fruit development are closely associated, as in *Prunus* and *Rubus*, triploid and other odd multiple forms are relatively unproductive. When such forms do appear in cultivation, as for example in *Rubus*, their fertility and productivity is lower than that of even numbered and balanced polyploid varieties. In a recent paper (Crane and Darlington, 1927) an apparent exception was described, viz. the Himalaya berry, but this has been re-examined and found to be tetraploid ($2n = 28$). In *Prunus* the only triploids known to occur are ornamental varieties grown for their flowers.

In both *Prunus* and *Rubus* development of the bi- or uni-ovular drupes is very largely dependent on the development of the seed. In *Pyrus*, however, the greater number of seeds per fruit and the much lower proportion of fruit to flower required to give a crop enables the triploid to become fruitful enough to be of economic importance. In apples a single seed is often sufficient for the development of the fruit, and even this seed may be imperfect. This approaches parthenocarpy and renders fruit production still less dependent on the formation of seeds. In some varieties of apples entirely seedless fruits are not uncommon.

"TRIPLOIDY" IN APPLES.

Rybin (1926) first observed triploidy in apples, finding Reinette du Canada, an established variety, to be triploid ($2n = 51$). Kobel (1927) reported 13 of the varieties he examined to be diploids ($n = 17$) and 15 varieties to have intermediate numbers (see Table I). In a previous paper we assumed several of his varieties with intermediate numbers to be triploids, viz. Warner's King, Ribston Pippin, Gravenstein and Baldwin. In a recent paper Nebel (1929) has shown that Ribston Pippin, Gravenstein and Baldwin are triploids. He particularly investigated the Gravenstein group of apples (apparently a group of eight clonal variations) and found them all to be triploid. Bramley's Seedling and its bud-sport, Crimson Bramley, are also triploids. In our publication

(1929) we gave an account of preliminary observations and showed that Blenheim Orange, Bramley's Seedling and Genet Moyle were triploid varieties. If we take Kobel's varieties with intermediate numbers to indicate triploidy, and include the clonal variations of Gravenstein and Bramley's Seedling, a total of 24 varieties has been found to be triploid and about 48 varieties to be diploid. It is therefore evident that among cultivated apples triploidy is common.

Darlington and Moffett (1930), in the paper which this article accompanies, show that the chromosome complement in apples is complex, and have concluded that the forms with $2n = 34$, generally regarded as diploids, are secondary polyploids, being hexasomic in respect of three chromosomes and tetrasomic in four. Thus the varieties we refer to as "triploids" are partly hexasomic and partly nonasomic.

TABLE I.

Variety	Chromosome numbers ($2n$)				% pollen germination		
	Rybin	Kobel	Nebel	Darlington and Moffett	Kobel	Kvaale	Florin
Baldwin	—	48-49	51	51	11.0	12.3	0-30
Belle de Boskoop	—	ca. 46	51	—	13.0	—	0-30
Blenheim Orange	—	—	51	51	—	—	0-30
Bolnapfel	—	46-49	—	—	10.0	—	—
Bramley's Seedling	—	—	—	51	—	20.9	0-30
Crimson Bramley	—	—	—	51	—	—	—
Damson Reimette	—	45-47	—	—	23.0	—	—
Genet Moyle	—	—	—	51	—	—	—
Gravenstein	—	45-46	51	—	7.0	13.0	0-30
Gravenstein (7 clonal varieties)	—	—	51	—	—	—	—
Harbert's Reimette	—	45	—	—	16.0	—	—
Jacques Lebel	—	49-51	—	—	13.0	—	—
Reimette du Canada	51	38-40	51	—	4.0	—	0-30
Ribston Pippin	—	42	51	51	—	21.4	0-30
Roter Eiseraffel	—	47	—	—	—	—	—
Stäffner Rosenapfel	—	48-49	—	—	25.0	—	0-30
Warner's King	—	42	—	—	27.0	14.8	0-30
Winter Zitronenapfel	—	48-49	—	—	21.0	—	0-30
Lane's Prince Albert (1)	—	—	—	34	—	57.6	70
Lane's Prince Albert (2)	—	—	51	—	—	—	—

In Table I are given the chromosome numbers of the varieties under discussion as found by Rybin, Kobel, Nebel, and Darlington and Moffett, and the percentage of pollen germination as found by Kobel (1927), Kvaale (1926) and Florin (1926). At the bottom of the table is the variety, Lane's Prince Albert, which was reported by us (1929) to be a diploid ($2n = 34$), and by Nebel (1929) as a triploid ($2n = 51$). We have no reason to doubt either our material or observations. Nebel, however,

states that our breeding results agree with the conception of Lane's as a triploid, but the argument he advances is insufficient and ignores the fact that it is only in certain crosses with Lane's that relatively poor results are obtained. Presumably he refers to the results presented in Table IX of our paper, viz. Cox's Orange Pippin (a diploid) \times Lane's Prince Albert and its reciprocal, in which only 2.7 and 1.6 seeds per fruit were obtained from 26 and 22 fruits respectively. Among the diploid varieties of apples varying degrees of generational sterility occur, nor can the possibility of zygotic lethals be precluded. We believe, however, that the few seeds obtained in the above and similar examples where diploid \times diploid gave poor results are mainly due to degrees of incompatibility. But the "poor" seed results obtained when a triploid is involved in crosses are mainly the expression of its high degree of generational sterility, and no appreciably better results will be secured by crossing it with any other variety. On the other hand, lack of incompatibility is the expression of genetic differentiation, and as such will vary according to the particular parents used. For example, Lane's \times Cox's gave only 1.6 and Cox's \times Lane's 2.7 good seeds per fruit. Royal Jubilee \times Lane's, however, gave 5.4 good seeds per fruit, a much higher proportion than a diploid-triploid cross has ever given in our experiments. It will be noted in Table II that the vigour of the seedlings from the Lane's-Cox's crosses further confirms the diploid constitution of Lane's, and that the pollen tests of Florin and Kvaale are also in agreement.

Kobel, Kvaale and Florin made extensive pollen-germination tests on apples, and from their work it appears to be possible to discriminate between diploid and triploid varieties by the percentage of pollen germination. Kobel and Kvaale give the actual percentage of pollen which germinated, but Florin divides his results into three classes: (1) "poor," with an average pollen-germination not above 30 per cent.; (2) "medium," 30-70 per cent.; (3) "good," at least 70 per cent.

In Table I we have tabulated their results, and it will be seen that all the triploids used by Florin in his germination tests are in his "poor" class (less than 30 per cent. good) and those examined by Kobel and Kvaale range from 4 to 27 per cent. By comparison the varieties at present known to be diploid, with one exception¹, range from 50 to 97 per cent.

Although there is considerable variation in the proportion of good pollen among the known diploids, the worst diploid has a much higher proportion than the best triploid.

¹ The exception is Allington Pippin, a diploid variety included in Florin's "poor" germinating class.

The variations in generational sterility among diploids may be due to two causes: (i) segregation of dissimilar chromosomes normally pairing; (ii) irregularities resulting from the formation of quadrivalents, *i.e.* from an insufficient differentiation of the usually non-pairing homologues in a polyploid (cf. Darlington and Moffett, Table II). The low fertility of Cox's Orange, a diploid, alleged to be a seedling from Ribston Pippin, a triploid, is probably due to the second of these causes. In this connection it is significant that in certain crosses made with Cox's Orange as one parent the progeny have been distinctly more vigorous and fertile than Cox's Orange.

VIGOUR IN RELATION TO CHROMOSOME NUMBER

In Table II germination results and growth measurements are given (*a*) of families derived from diploid \times diploid varieties, and (*b*) of families where one of the parents is a triploid. The measurements were taken in November 1929, after the 1927 families had completed two seasons' and the 1928 families one season's growth. The seedlings were grown under uniform conditions without pruning or any other interference. The difference between the average height for the diploid \times diploid and the diploid \times triploid families is very large, and the vigour of the former contrasts strikingly with the feeble growth of the diploid-triploid offspring.

A number of the seedlings of the family 6/28 (natural seedlings from

TABLE II.

Fam. No.	Parentage	Flowers pollinated	Fruits matured	Apparently good seed	Good seeds per fruit	No. seeds germinated	No. seedlings surviving	Average height of seedlings in inches
Diploid \times Diploid								
1/27	Lane's Prince Albert \times Cox's Orange Pippin	87	10	27	2.7	26	25	30.2
3/27	Cox's Orange Pippin \times Lane's Prince Albert	110	8	10	1.2	8	7	24.1
9/27	Cox's Orange Pippin \times Peasgood's Nonsuch	89	10	28	2.8	28	18	18.2
Diploid \times Triploid								
2/27	Lane's Prince Albert \times Blenheim Orange	18	3	9	3.0	8	3	3.5
4/27	Cox's Orange Pippin \times Blenheim Orange	160	12	14	1.1	9	4	6.1
5/27	Peasgood's Nonsuch \times Blenheim Orange	42	2	4	2.0	2	2	9.1
Triploid								
7/27	Blenheim Orange selfed	218	5	11	2.2	3	1	7.3
Diploid \times Diploid								
3/28	Northern Spy \times Old English Broadleaf	117	10	84	8.4	82	78	12.0
1/28	Jaune de Metz \times Northern Spy	—	—	—	—	—	22	16.2
Diploid \times Triploid								
4/28	Cox's Orange Pippin \times Blenheim Orange	36	3	5	1.6	2	1	2.0
6/28	Lane's Prince Albert \times Blenheim Orange	109	4	2	0.5	2	1	4.5
Triploid								
7/28	Brandley's Seedling—open pollination	—	60	135	2.0	94	74	3.0

Bramley's Seedling) have been examined and all were found to be aneuploids (see Darlington and Moffett, Table III).

It is significant that all the established varieties of apples examined by Rybin, Nebel and ourselves were diploids or triploids, and that re-examination of five of the varieties reported by Kobel to be aneuploids showed them to be triploids.

Further examination of the other varieties reported by Kobel to be aneuploids is desirable, but on present knowledge it seems probable that aneuploid forms do not occur among cultivated apples, and that it would be exceptional to obtain fertile and vigorous offspring by breeding triploids either *inter se* or with diploids. It may be remarked that triploid varieties are invariably vigorous.

Reference to lack of vigour in seedlings is common in the literature relating to breeding experiments with apples. Wellington (1924) reports that 27 trees of Baldwin selfed were planted in 1909 and that all but one died, and when 11 years old the one that survived was a small and weak tree. Wellington also used the variety Gravenstein in crosses, sometimes as a male and sometimes as a female parent, and from the weakness of many of the offspring he concluded that Gravenstein carried one or more determiners for weak growth. Lantz (1925) found that the progeny from certain crosses were decidedly less vigorous than those of others. He also states that Crandall (1924), from work on 148 forms of *Malus* involving 22,619 pollinations, secured 1486 fruits or 6.5 per cent. A total of 2840 selfed seeds gave 703 seedlings, 219 of which survived. Dickson (1928) also refers to the variability of vigour in apple seedlings.

In our own breeding work, most of the seedlings raised from selfing apples, whether $2n$ or $3n$ varieties, have usually been weak and many have died. Two varieties, however, which as yet have not been cytologically examined, viz. Antonovka and Rev. W. Wilks, have given quite vigorous offspring when selfed. The selfed seedlings from Antonovka are as large and vigorous as any we have raised from crosses. Approximately a quarter of the selfed seedlings from Rev. W. Wilks were albinos and died. The internodes of the growth of Rev. W. Wilks are comparatively short, and its viable seedlings are in general dwarf, but their leaves are large and the trees are by no means weak.

The chromosome complement of most of the varieties used by the above workers is not known, but it is interesting to note that the varieties Baldwin and Gravenstein used by Wellington are triploids, and consequently the extreme feebleness of their offspring is probably due to an unbalanced aneuploid chromosome constitution.

It is evident that cytological examination is an essential preliminary to any critical investigation relating to sterility or breeding work with apples. The present cytological observations of Darlington and Moffett, in conjunction with our genetical observations, however, make it possible for us to say fairly definitely from fertility and progeny whether a particular apple is $2n$, $3n$ or aneuploid.

STERILITY AND INCOMPATIBILITY.

Fruitfulness in cultivated fruits is associated with:

- (1) Generational fertility.
- (2) Compatibility.
- (3) Morphological fertility, *i.e.* no suppression of sex organs.
- (4) Parthenocarpy.
- (5) Number of seeds per ovary¹.
- (6) Variation in the proportion of fruit to flowers required to give an economic yield (this is usually correlated with fruit size).

TABLE III.

	% of fruits necessary for good crop	% of embryos necessary for good crop
<i>Rubus</i>		
1 embryo per ovule	50-100	50-100
Many ovules per fruit		
<i>Prunus</i>		
1 embryo per ovule	19-32	*10-20
2 ovules per fruit		
<i>Pyrus</i>		
1 embryo per ovule	5-10	0-1
10 ovules per fruit		

* The proportion of fruits with double embryos in *Prunus* varies with the maternal variety. This is not incompatible with the view assumed that the development of the embryos is independent because, for example, where only 10 per cent. of the ovules develop, the 19 per cent. of fruits formed will have double embryos in the proportion of 1 : 18, while, with 99 per cent. of the embryos developing, double embryos will be in the proportion 9 : 2 (81 : 18).

In all cases initial embryos are referred to because, as we have previously pointed out (Crane, 1926), although fertilisation is always essential for fruit development in *Prunus*, the fruits may reach maturity following an embryonic breakdown. This is more common in cherries than in plums.

An approximate estimation of the influence of (4), (5) and (6) above on fruit production is tentatively presented in Table III. It will be seen that those apple varieties which are relatively infertile may yet maintain

¹ Many varieties of apples set seed freely; others set few seeds.

their economic value (1) because of the small number of fruits required to give a satisfactory yield (often 5 per cent. is sufficient), and (2) because fertilisation apparently supplies the requisite initial stimulus to fruit development, and a subsequent embryonic breakdown does not necessarily arrest the growth of the fruit. Thus analysis of over 23,000 pollinations involving 243 different crosses (182 $2n \times 2n$; 55 $3n \times 2n$; and

TABLE IV.

Parentage.	Flowers	Fruits matured	Seeds			Good seeds per fruit
			Apparently good	Shrivelled	Empty testas	
(1)						
Cox's Orange Pippin ($2n=34$) selfed	1950	13	10	10	38	0.7
Lane's Prince Albert ($2n=34$) selfed	481	9	7	0	7	0.7
Charles Ross selfed	35	1	1	0	0	1.0
Ellison's Orange selfed	229	4	9	0	2	2.2
Mother selfed	284	2	5	0	1	2.5
(2)						
Cox's Orange Pippin ($2n=34$) \times Ellison's Orange	336	15	6	42	52	0.4
Lane's Prince Albert ($2n=34$) \times McIntosh Red	23	2	1	0	20	0.5
Jaune de Metz ($2n=34$) \times Northern Spy ($2n=34$)	307	11	13	0	1	1.1
Cox's Orange Pippin ($2n=34$) \times McIntosh Red	326	21	38	32	75	1.8
Lane's Prince Albert ($2n=34$) \times Ellison's Orange	32	1	2	1	6	2.0
Charles Ross \times Ellison's Orange	23	3	8	5	14	2.6
Lane's Prince Albert ($2n=34$) \times Mother	20	4	13	0	40	3.2
Lane's Prince Albert ($2n=34$) \times Cox's Orange Pippin ($2n=34$)	70	5	18	2	27	3.6
Margil \times Cox's Orange Pippin ($2n=34$)	50	7	49	6	0	7.0
Northern Spy ($2n=34$) \times Malling Type VII	29	1	7	2	0	7.0
Ellison's Orange \times Cox's Orange Pippin ($2n=34$)	121	1	9	0	0	9.0
(3)						
Blenheim Orange ($2n=51$) selfed	339	8	12	1	12	1.5
Ribston Pippin ($2n=51$) selfed	123	8	20	6	13	2.5
(4)						
Lane's Prince Albert ($2n=34$) \times Blenheim Orange ($2n=51$)	38	2	0	1	11	0.0
Cox's Orange Pippin ($2n=34$) \times Blenheim Orange ($2n=51$)	155	8	0	5	47	0.0
Cox's Orange Pippin ($2n=34$) \times Ribston Pippin ($2n=51$)	124	9	1	10	48	0.1
Lane's Prince Albert ($2n=34$) \times Crimson Bramley ($2n=51$)	57	4	3	7	12	0.7
(5)						
Blenheim Orange ($2n=51$) \times Ellison's Orange	24	2	1	1	10	0.5
Crimson Bramley ($2n=51$) \times Cox's Orange Pippin ($2n=34$)	10	1	1	1	6	1.0
Blenheim Orange ($2n=51$) \times Cox's Orange Pippin ($2n=34$)	107	8	11	17	26	1.3
Blenheim Orange ($2n=51$) \times McIntosh Red	79	7	15	11	15	2.0
Blenheim Orange ($2n=51$) \times Mother	59	1	2	2	2	2.0
(6)						
Ribston Pippin ($2n=51$) \times Blenheim Orange ($2n=51$)	12	1	0	2	2	0.0
Blenheim Orange ($2n=51$) \times Ribston Pippin ($2n=51$)	35	3	3	3	5	1.0
Blenheim Orange ($2n=51$) \times Crimson Bramley ($2n=51$)	72	1	2	0	0	2.0
Crimson Bramley ($2n=51$) \times Blenheim Orange ($2n=51$)	51	1	2	2	4	2.0

5 $3n \times 3n$) shows that triploid-diploid crosses are slightly more fertile than diploid-diploid, giving 6.8 and 6.1 per cent. of fruit to flowers respectively. The seed content of the fruits of these two series of crosses is, however, markedly different, and reveals a higher degree of generational sterility operating in triploid-diploid combinations.

In the past the measure of fertility has often been taken from the proportion of fruit set to flowers pollinated, but it is evident that this is merely an estimation of fruitfulness, and that examination of the seeds provides a better measure of fertility. Indeed, as is shown in Table II, the best criterion of fertility is the vigour of the progeny of the plant.

In Table IV will be found the results we obtained in 1929 from self- and cross-pollinations. Where known, the chromosome numbers follow the names of the varieties, which as far as possible are arranged as follows: (1) diploids selfed, (2) diploids \times diploids, (3) triploids selfed, (4) diploids \times triploids, (5) triploids \times diploids, (6) triploids \times triploids. It is apparent that although a low degree of fertility occurs in certain diploid-diploid crosses, none of the combinations involving triploids has given a result commensurate with the best of the diploid crosses. As we have previously pointed out, although a good deal of generational sterility occurs even among diploids, and the possibility of zygotic lethals cannot be precluded, there is but little doubt that the variation within the diploid crosses is often due to degrees of incompatibility.

Since the triploid varieties of apples have a range of only 4 to 27 per cent. good pollen, whereas the diploids range from 50 to 97 per cent., it is obvious that, if we neglect incompatibility, the diploids would be more effective as pollinisers in the field for other varieties than would the triploids. As is shown above, however, the triploid combinations have in our experiments given even slightly better results in the production of fruits than the diploids. Since incompatibility is due to lack of genetic differentiation, the good results obtained from the triploids are probably due to a greater variety in the gametic output of triploid than of diploid varieties, thereby providing a greater chance of compatible combinations. The high degree of generational sterility of the triploids is expressed by the formation of imperfect seeds and weak offspring, rather than by failure to form fruits.

In the approximately diploid sweet cherry *P. avium* incompatibility is clearly expressed, self-incompatibility is the rule and cross-incompatibility common. In the tetraploid sour cherries, *P. cerasus* and the Dukes, tetraploidy appears to have removed the bar to self-compatibility as degrees of self-compatibility occur. In the hexaploid plums, *P. domestica*, complete self- and cross-compatibility, complete self- and cross-incompatibility and degrees of self- and cross-incompatibility occur. In apples degrees of incompatibility are common even in the so-called diploid varieties; this may be attributed to their secondary polyploid complement, which involves a polysomic condition of the incompatibility

factors. Every chromosome and hence its factors may be represented two or three times in the gametophyte, which provides a basis for greater variation in the number of possible combinations of a given factor.

Admitting that the "diploid" apples are secondary polyploids, it is worthy of note that degrees of compatibility are expressed in the yield of polyploids only, *viz.* the sour cherries, the domestic plums and apples.

SUMMARY.

Odd multiple polyploids are relatively infertile, consequently in fruits such as *Rubus* and *Prunus*, where seed and fruit development are closely associated, triploid and other odd multiple forms are relatively unproductive. Triploid apples however are productive, *e.g.* Bramley's Seedling, a triploid, is probably more widely cultivated in this country than any other apple.

In apples a very low proportion of fruit to flowers is sufficient to give a yield. The apple has ten embryos, and often a single seed is sufficient for the development of a fruit, and even this seed may be imperfect. This approaches parthenocarpy and renders fruit production still less dependent on the formation of seeds. Fruitfulness in apples may therefore be maintained in spite of a high degree of generational sterility.

Triploidy in apples is another example of the occurrence of sterile forms in species where a substitute has been found (either in nature or in cultivation) for normal seed and fruit production. The substitution in apples is more complex than usual for, while sexual reproduction is now replaced by grafting, the necessity for the stimulus of seed growth in the formation of a fruit is largely evaded. Therefore triploids are able to fruit although incapable as a rule of yielding offspring of any value.

The offspring of triploids, whether derived from selfing or crossing with diploids, lack vigour, presumably owing to their aneuploid constitution (*cf.* Darlington and Moffett). Consequently triploid varieties are likely to be of little value in practical breeding as the necessary vigour and fertility would rarely be obtained in the resulting offspring.

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