# STERILITY AND INCOMPATIBILITY IN DIPLOID AND POLYPLOID FRUITS.

By M. B. CRANE and W. J. C. LAWRENCE.
(*The John Innes Horticultural Institution.*)

## Introduction.

Experiments in heredity and sterility of a number of cultivated fruits have been in progress at this Institution since 1911, and reports on various aspects of the investigations have been published from time to time (1918–29). The experiments have been continued on trees grown in pots, under the methods of control described in earlier papers.

The investigations are naturally prolonged by the length of time which elapses from one generation to another, and limited by the space occupied by a family of even moderate size. We have ventured, therefore, at this stage to analyse genetically such of our results as relate to the behaviour of incompatibility.

## Material.

The following are fruits used in these investigations and their chromosome numbers. The actual varieties and seedlings studied are subsequently referred to in detail.

| | | Chromosome No. | | |
|---|---|---|---|---|
| *Prunus avium* | (Sweet cherry) | 16* | $2n$ | Diploid |
| *P. cerasus* | (Sour cherry) | 32 | $2n$ | Tetraploid |
| *P. cerasus × avium* | (Seedlings) | 24 | $2n$ | Triploid |
| *P. cerasus × avium* | (Duke cherries) | 32 | $2n$ | Tetraploid |
| *P. domestica* | (European plum) | 48 | $2n$ | Hexaploid |
| *Pyrus malus* | (Apple) | 34 | $2n$ | Partly tetraploid and partly hexaploid |
| *Pyrus malus* | (Apple) | 51 | $2n$ | Partly hexaploid and partly nonaploid |

* Among the cultivated sweet cherries extra chromosomes beyond the diploid number have been observed (Darlington, 1928, 1930).

## Incompatibility.

### *Cherries.*

In Table I are given the varieties of the sweet cherry—*P. avium*—used in the experiments and the compatible and incompatible combinations so far elucidated: + = compatible; − = incompatible combinations.

With the possible exception of Black Tartarian "D," a tree first used this year, there is no question of any of the varieties mentioned in Table I not being distinct, but the identity of some remains obscure. Different individuals are frequently met with under the same name, and to find one variety under two or more names is also common. It will be noted that four individuals bear the name of Black Tartarian and are de-

TABLE I.

Males.

| Females. | Bedford Prolific. | Black Eagle. | Tartarian 'A'. | " 'B'. | Early Rivers | Knight's E. Black. | Roundell. | Schrecken. | Frogmore. | Belle Agathe. | Waterloo. | Cluster. | Black Heart 'B'. | Napoleon. | Emp. Francis. | Kentish Big. | Ludwig's Big. | Late Black. | Turkey Heart. | Governor Wood. | Elton. | Hedelfingen. | Mezel. | Ursula Rivers. | Noir de Schmidt. | Peggy Rivers. | Jaboulay. | Tartarian 'D'. | Belle d'Orleans. | Black Heart 'A'. | Tartarian 'E'. | Bohemian Blk 'D'. | Early Purple. | Florence. | G. d'annonay. | Noble. | Noir de Guben. | White Heart. |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Bedford Prolific. | - | - | - | - | - | - | - | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + |  | + | + | + |  | + |  | + | + | + | + |  | + | + | + |
| Black Eagle. | - | - | - | - | - | - | - | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + |  | + | + | + |  |  |  | + | + |  | + |  |  |
| Tartarian 'A'. | - | - | - | - | - | - | - | + | + | + | + | + |  | + | + |  |  | + | + | + |  |  |  |  |  |  |  |  | + |  | + |  |  |  |  | + |  |  |
| " 'B'. | - | - | - | - | - | - | - | + | + | + | + |  |  | + | + |  |  |  | + |  | + |  |  |  | + |  | + |  |  |  | + |  |  |  | + |  |  |  |
| Early Rivers | - | - | - | - | - | - | - | + | + | + | + | + | + | + | + | + |  | + | + | + |  | + | + |  | + |  | + |  | + |  |  |  | + | + |  | + |  |  |
| Knight's E. Black. | - | - | - | - | - | - | - | + | + | + | + |  |  | + | + | + |  |  | + | + |  |  |  |  | + |  | + |  | + |  | + | + |  |  |  |  |  |  |
| Roundell. | - | - | - | - | - | - | - |  |  | + | + |  |  | + | + |  |  |  | + |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| Schrecken. | + | + | + | + | + | + | + | - | - | - | - | - | - | + | + | + | + |  | + | + | + | + | + |  | + | + | + |  | + | + | + |  | + | + | + | + | + |  |
| Frogmore. | + | + | + | + | + | + | + | - | - | - | - | - | - | + | + | + |  |  | + | + | + | + | + | + | + |  | + |  | + | + | + |  | + | + |  | + |  |  |
| Belle Agathe. | + | + | + | + | + | + | + | - | - | - | - | - | - | + | + | + | + |  | + | + | + | + | + |  | + |  | + |  | + |  | + |  | + |  |  | + | + |  |
| Waterloo. | + | + | + | + | + | + | + | - | - | - | - | - |  | + | + | + |  |  | + |  |  | + |  |  | + |  |  | + |  |  |  |  |  |  |  |  |  |  |
| Cluster | + |  |  |  | + |  |  | - | - |  | - | - |  | + |  | + |  |  | + |  |  |  |  |  | + |  |  |  |  |  |  |  | + |  |  |  |  |  |
| Black Heart 'B'. |  | + |  |  |  |  |  |  |  |  |  |  | - | + |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| Napoleon. | + | + | + | + | + | + | + | + | + | + | + | + | + | - | - | + | + | + | + | + | + | + | + |  | + | + | + |  | + |  |  | + | + | + | + | + | + |  |
| Emp. Francis. | + | + | + | + | + | + | + | + | + | + | + | + | + | - | - | + | + | + | + | + | + | + | + | + | + | + | + |  | + |  | + |  | + | + |  | + | + |  |
| Kentish Big |  | + |  |  | + |  |  | + | + | + | + |  | + | + |  | - | - |  | + |  |  |  |  |  | + | + | + |  |  |  |  |  |  | + | + |  | + |  |
| Ludwig's Big. | + |  |  |  |  | + |  |  |  |  | + | + |  | + | + | - | - |  |  |  | + |  | + |  | + |  | + |  | + |  |  |  | + |  |  | + |  |  |
| Late Black. | + |  |  | + |  |  | + | + | + |  | + | + |  | + | + | + |  | - | - | + |  |  |  |  | + |  |  |  | + |  |  |  | + | + |  |  | + |  |
| Turkey Heart. | + | + |  |  | + | + | + | + | + | + | + |  |  | + | + | + | + | - | - | + | + | + | + | + | + | + | + |  | + |  |  |  | + | + |  | + |  |  |
| Governor Wood. | + | + | + | + | + | + | + | + | + | + | + | + |  | + | + | + |  |  | + | - | - | + | + | + | + | + |  |  | + |  | + | + | + | + |  | + | + |  |
| Elton. | + |  | + |  | + |  |  | + | + |  |  |  |  | + | + | + |  |  | + | - | - | + |  |  |  | + | + |  | + | + |  |  | + | + | + | + |  |  |
| Hedelfingen. |  | + |  |  | + |  |  |  | + | + |  |  |  | + |  |  |  |  |  | + | + | - | - | - |  |  |  |  |  |  |  | + |  | + |  | + |  |  |
| Mezel | + | + |  |  |  |  |  | + |  | + |  | + | + | + | + | + | + |  | + | + | + | - | - |  | + | + |  | + | + |  |  | + |  | + |  |  |  |  |
| Ursula Rivers. |  |  |  |  | + |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  | - |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| Noir de Schmidt. | + | + |  |  | + |  | + | + | + |  | + | + | + | + | + | + | + | + | + | + | + | + | + |  | - | - | + |  |  |  |  |  | + | + |  | + |  |  |
| Peggy Rivers. |  |  |  |  | + |  |  | + |  |  |  |  |  | + |  |  |  |  |  |  |  |  |  |  |  | - |  |  |  |  |  |  | + |  |  |  |  |  |
| Jaboulay. | + |  |  | + | + | + | + | + | + |  | + |  | + | + | + | + |  | + | + | + |  | + |  |  | + | + | - | - | + |  |  | + | + | + |  | + | + |  |
| Tartarian 'D'. |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  | - |  |  |  |  |  |  |  |  |  |  |
| Belle d'orleans. | + |  | + |  | + |  |  | + | + | + |  | + |  | + |  | + |  |  | + | + | + |  | + |  | + |  | + |  | - |  |  | + |  | + |  | + | + |  |
| Black Heart 'A'. |  |  |  |  | + |  |  |  | + | + |  |  |  |  |  |  |  |  |  |  | + |  |  |  |  |  |  |  |  | - |  |  |  |  |  |  |  |  |
| Tartarian 'E'. | + |  | + | + | + |  |  |  |  | + |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  | - |  |  |  |  |  |  |  |
| Bohemian Blk. 'D'. |  |  |  |  | + |  |  |  |  |  |  |  |  |  | + |  |  | + |  |  |  | + |  |  |  |  |  |  |  |  |  | - |  |  |  |  |  |  |
| Early Purple. |  |  |  |  | + |  | + |  |  |  |  |  |  | + |  | + |  |  |  | + |  |  |  |  |  |  |  |  |  |  |  |  | - |  |  | + |  |  |
| Florence. | + |  |  |  |  |  | + | + |  | + |  |  |  | + | + | + | + |  | + | + |  | + | + |  | + | + | + |  |  |  |  |  |  | - |  | + |  |  |
| G. d'annonay. |  |  |  |  | + |  |  |  | + |  |  |  |  |  | + |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  | - |  |  |  |
| Noble. | + |  | + |  | + |  |  | + | + | + |  | + | + | + | + | + |  |  | + | + | + |  | + |  | + |  | + |  |  |  |  |  |  | + |  | - |  |  |
| Noir de Guben. |  |  |  |  | + |  | + | + | + | + |  |  |  |  |  |  |  |  |  |  |  |  |  |  | + |  |  |  | + |  | + | + | + |  |  |  | - |  |
| White Heart. |  |  |  |  | + |  |  |  | + |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  | - |

signated "A," "B," "D" and "E," and two Black Heart, "A" and "B"; they are all distinct. Our Hedelfingen is not the true variety.

It will be seen that all the varieties have proved to be self-incompatible and that 29 of the 38 varieties investigated fall into nine intra-sterile inter-fertile groups. Groups 8 and 9 were only found this year and the pollinations require repetition, but from general experience we have little doubt of their validity.

The gross totals of (*a*) self-pollinations, (*b*) cross-incompatible pollinations and (*c*) cross-compatible pollinations made between the varieties in Table I, and the results obtained are summarised in Table II.

TABLE II.

| | No. of flowers pollinated | No. of fruits set | Percentage set |
|---|---|---|---|
| Self-pollinations ... ... | 33,500 | 35 | 0·1 |
| Cross-incompatible pollinations | 26,826 | 35 | 0·13 |
| Cross-compatible pollinations | 72,573 | 18,777 | 24·4 |

In this and all subsequent summaries "number of fruits set" means the number which reached maturity.

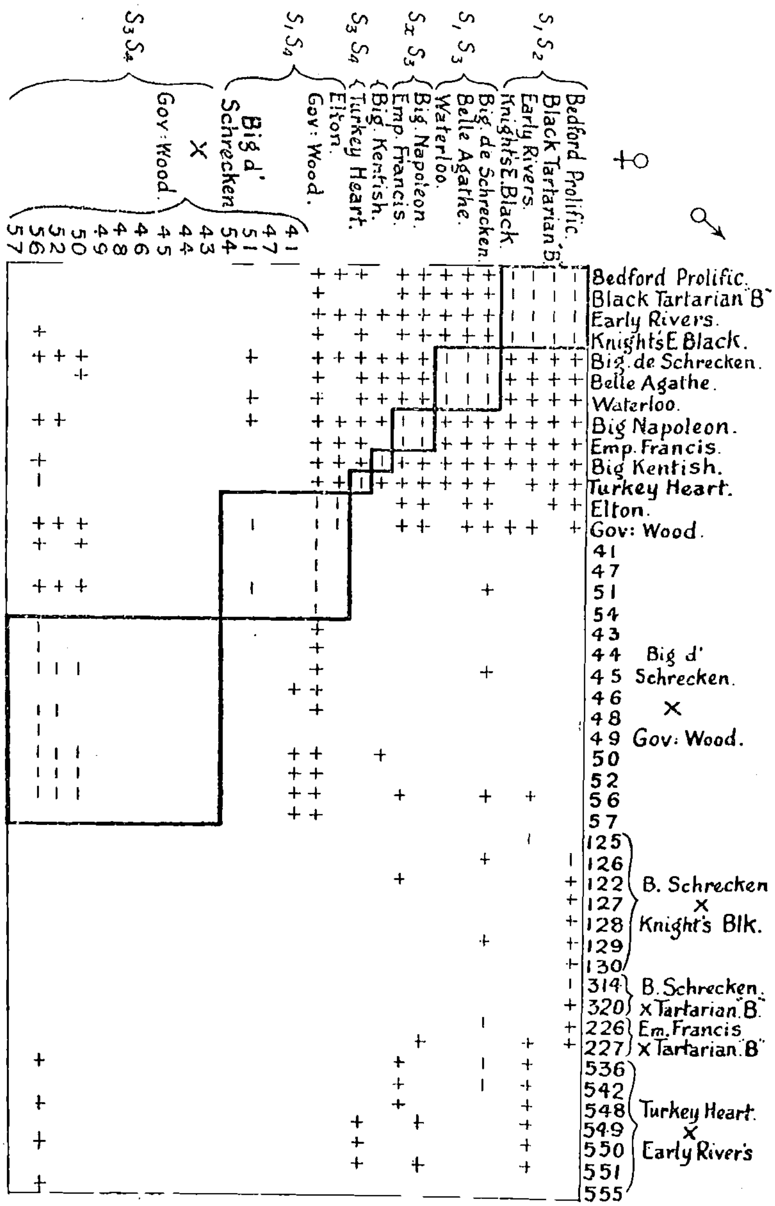
It is shown in Table II that a few fruits have been obtained both from selfing and from cross-incompatible pollinations. Possibly they are the result of accident but, on the other hand, occasional fruits have set under very stringent conditions, which suggests that as a rarity a pollen tube travels the full length of the style and effects fertilisation. It is hoped that when seedlings raised from these occasional fruits reach maturity the behaviour of pollinations between them and their parents may afford evidence as to their origin.

In Table III are the results obtained from pollinations between a number of seedlings, and between them and their parents.

Details of the pollinations in which *seedlings* have been used in Table III are as follows: compatible pollinations, 4808 flowers: 1091 fruits = 22·7 per cent. set; incompatible pollinations, 972 flowers: 1 fruit set.

Analysis of Tables I and III shows that so far as our investigations have progressed, the behaviour of incompatibility in the sweet cherry is comparatively simple. Self-incompatibility is the rule, cross-incompatibility common and always reciprocally expressed. Among cultivated varieties nine intra-sterile, inter-fertile groups have been recognised, and the preliminary investigations with seedlings have also given results which are orderly and amenable to the genetic interpretation of incompatibility as advanced by East and Mangelsdorf (1925, 1926) in *Nicotiana*, by Lehmann (1926) in *Veronica*, and to some extent by Sirks (1926 *a*, *b*) in *Verbascum*. By taking advantage of the end-season (pseudo) fertility which occurs in *Nicotiana*, East obtained individuals which were compatible in one way of a cross but incompatible in the reciprocal, *i.e.* by selfing $S_1S_2$ he obtained $S_1S_2$, $S_1S_1$, and $S_2S_2$ individuals. The homozygous forms used as males fail on their mother, but the reciprocal combinations are effective. Sirks, working with *Verbascum*, obtained many examples

TABLE III.


♀
♂
$S_1 S_2$
$S_1 S_3$
$S_x S_3$
$S_3 S_4$
$S_1 S_4$
$S_3 S_4$
Bedford Prolific.
Black Tartarian B.
Early Rivers.
Knight's E. Black.
Big. de Schrecken.
Belle Agathe.
Waterloo.
Big. Napoleon.
Emp. Francis.
Big. Kentish.
Turkey Heart.
Elton.
Gov: Wood.
Big d' Schrecken × Gov: Wood.
41 47 51 54 43 44 45 46 48 49 50 52 56 57
125 126 122 127 128 129 130
B. Schrecken × Knight's Blk.
314 320
B. Schrecken × Tartarian B.
226 227
Em. Francis × Tartarian B.
536 542 548 549 550 551 555
Turkey Heart × Early Rivers

of one-way incompatibility, especially during the early stages of his investigations, and East (1929) suggests that this may be due to pseudo-fertility. We feel, however, that the frequency of the reciprocal differences and other complications encountered by Sirks are significant, and may possibly be the result of a polysomic condition of the factors determining incompatibility in *Verbascum*. Consequently we have ventured to refer to his results in more detail when discussing the behaviour of incompatibility in the polyploid fruits.

In the sweet cherry we have begun a factorial analysis of incompatibility by determining the behaviour of pollinations among the progeny of intergroup crosses.

Reference to Table III shows that Big. de Schrecken × Governor Wood gives two (intra-sterile, inter-fertile) groups, one of which fails with its male parent, Governor Wood. Two groups will appear in $F_1$ when the parents have a factor in common and, following East's terminology, we have provisionally assigned the factors $S_1S_3$ to Big. de Schrecken and $S_1S_4$ to Governor Wood.

A similar result was obtained from the crosses Big. de Schrecken × Knight's Early Black and Big. de Schrecken × Black Tartarian "B" (both male parents coming from Group I), which indicates that either $S_1$ or $S_3$ is common to the three parents and their respective groups. Pending further work we have assigned the factors $S_1S_2$ to Group I.

Three other failures with seedlings are of interest in that they disclose the identity of a factor in Groups III and IV. Seedling 226 (Emperor Francis III[1] × Black Tartarian "B" II) fails as male on Big. de Schrecken II. Since Black Tartarian "B" is $S_1S_2$ it follows that Emperor Francis contributed the $S_3$ factor.

Seedlings 536 and 542 (Turkey Heart V × Early Rivers I) failed on Big. de Schrecken II. Early Rivers I is $S_1S_2$ and Big. de Schrecken II $S_1S_3$; therefore Turkey Heart V must have contributed an $S_3$ factor. This is supported by the failure of Turkey Heart on Seedling 56, and it seems probable that Group V can, in its relations to the other groups, be designated $S_3S_4$. It is of course evident that the factors assigned to the groups are provisional, but each new factor disclosed aids in the final elucidation of the incompatible groups. Of the 38 varieties tested, at least 13 different combinations and a minimum of 6 incompatibility factors are necessary to interpret the results so far obtained.

In the sour cherries (*P. cerasus*) and the Duke cherries complete and varying degrees of self-compatibility occur. Our results with these—the

[1]The roman numerals refer to the incompatible groups to which the varieties belong.

tetraploid cherries—have already been published in detail (Crane and Lawrence, 1929).

*Plums.*

We have investigated 52 varieties of plums (Crane and Lawrence, 1929), *P. domestica*, and from the results obtained they can be primarily classified as follows.

| | | |
|---|---|---|
| (1) | Self-compatible. | (20 varieties) |
| (2) | Self-incompatible | (23 ,, ) |
| (3) | Partially self-compatible | (29 ,, ) |

Cross-incompatibility has only occurred among the varieties within Classes (2) and (3). The pollen of self-compatible varieties is always effective on self-incompatible kinds. In the sweet cherry reciprocal pollinations have always given similar results, but in *P. domestica* incompatibility occurring in one way of a cross and compatibility in the other is common.

The partial compatibles constitute a definite class setting about 3 per cent. of fruit with their own pollen and the same proportion in the partial compatible crosses. In compatible crosses they set a full crop.

In Table IV are shown the cross-incompatible combinations we have found in plums:

+ = compatible, ∓ = partially compatible and − = incompatible.

Compared with the sweet cherry not only are the results much more complex, but fewer groups occur, and those found include self-incompatible, self-compatible, partially self- and cross-compatible, cross-compatible, cross-incompatible, and reciprocal differences involving both partial and complete incompatibility.

A summary of the results from pollinations made in plums is given in Table V.

Analysis of Table IV shows that many of the varieties and seedlings must be similar in constitution with respect to incompatibility factors. For example, the results from pollinating seedlings 1024, 1029 and 1027 with Jefferson, their male parent, indicate that these individuals differ by a factor or two at the most. The established varieties, *e.g.* (1) Blue Rock and Early Rivers, and (2) Cambridge Gage, President and Late Orange are further examples of this.

Seedling 969 is noteworthy, since it is a self-incompatible seedling from a self-compatible mother, Denniston's Superb, a result which suggests that Denniston's carries at least three factors for incompatibility.

The degrees of fertility and the complexity of results in *P. domestica* are undoubtedly due to its hexaploid constitution and manner of chromosome pairing (Darlington 1930). In a diploid each gamete carries but one incompatibility factor, and no plant produces more than two types of

TABLE IV.

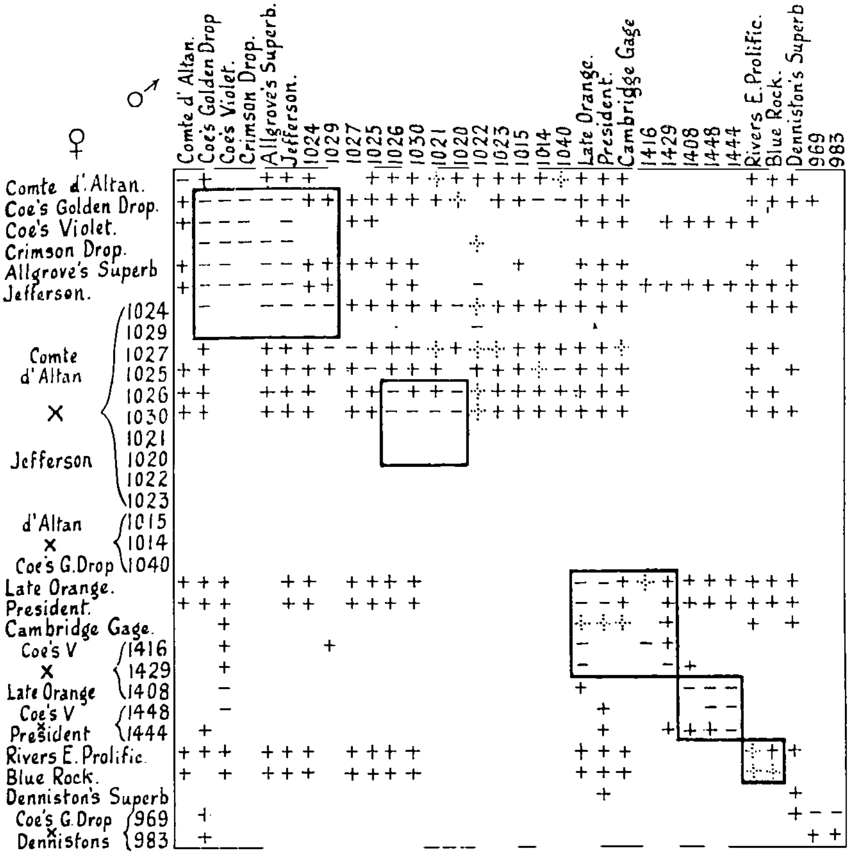



TABLE V.

| | No. of flowers pollinated | No. of fruits set | Percentage set |
|---|---|---|---|
| Self-incompatibles—selfed | 24,638 | 21 | 0·08 |
| Cross-incompatibles—crossed | 9,032 | 26 | 0·28 |
| Partial compatibles—selfed | 38,950 | 989 | 2·6 |
| Partial compatibles—crossed | 2,614 | 71 | 2·7 |
| Compatibles—selfed | 29,806 | 6,819 | 22·8 |
| Compatibles—crossed | 48,256 | 13,552 | 28·0 |

gametes. In a hexaploid, however, each gamete may carry three incompatibility factors, and the number of gametic types will be greatly increased. Hence a greater variability in the behaviour of incompatibility is to be expected in polyploid plants, and the chances of individuals of similar constitution meeting to form incompatible groups is correspondingly lessened.

The more complex the polyploidy the less frequently will complete incompatibility occur, and an examination of our results shows that incompatibility is not so common in the hexaploid plums as in the diploid cherries, and even less frequent in the more complexly polyploid apples.

We have remarked on the frequent occurrence of one-way incompatibility in the plum. This probably occurs between plants which are of a similar constitution, except that one carries another factor. Thus in a hypothetical hexaploid cross, $S_1S_1S_1S_2S_2S_2 \times S_1S_1S_2S_2S_3S_3$, those gametes of the male which carry $S_3$ might be expected to function, whereas in the reciprocal cross the gametes of the male carrying no factors different from the female might be expected to fail.

Similarly in a cross between tetraploids, as for example $S_1S_1S_2S_2 \times S_1S_1S_2S_3$, it is conceivable that the plant carrying $S_3$ might be effective as male, whereas the reciprocal combination would fail.

It seems clear, therefore, that one-way incompatibility is a phenomenon directly attributable to the multiplicity of factors in a polyploid. It has not been observed in known diploids except under the circumstances in *Nicotiana* we have previously detailed, and we suspect that its frequent occurrence in *Verbascum phoeniceum* and other plants *e.g. Cardamine pratensis* (Correns, 1912), is an indication that they are polyploid species[1]. In the Scrophulariacea eight is a common basic chromosome number, and Håkansson (1925) has shown that *V. phoeniceum* has 32 chromosomes, which suggests that it is a tetraploid.

We have mentioned that self-compatible varieties have always proved compatible as males and females with all other classes. Theoretically, however, it is to be expected that self-incompatible individuals will be found which will fail as males on self-compatibles.

For example, it is probable that, in addition to fertility factors, Denniston's Superb carries three incompatibility factors, and an individual whose constitution included no factors other than those three

[1] A difference in reciprocal pollinations in the sweet cherry has been reported by Gardner, *Bull.* No. 116, Oregon Agric. Exper. Sta., 1913. Gardner, however, points out that definite conclusions should not be drawn from a single season's work, and since this is the only example of one-way incompatibility reported in the sweet cherry we feel that repetition is desirable.

would fail on the self-compatible Denniston's. East and Yarnell (1929) have shown in *Nicotiana* that there is a self-fertility factor, $S_f$, allelomorphic to the incompatibility factors $S_1S_2$, etc. Possibly this is also true of the plum, since self-compatible varieties have segregated self-incompatibles in their progeny.

In this account of plums and cherries we have dealt with incompatibility only, but among the varieties referred to varying proportions of defective pollen and ovules occur. We have, however, previously shown that the degree of generational sterility in these varieties is not sufficiently high to prevent a satisfactory yield in compatible combinations.

*Apples.*

Cytologically, cultivated apples are of two kinds, the so-called "diploids" and "triploids" with 34 and 51 chromosomes respectively. Darlington and Moffett (1930) have shown that the "diploids" are secondary polyploids, being hexasomic in respect of three chromosomes and tetrasomic in four. Thus the varieties referred to as "triploids" are partly hexasomic and partly nonasomic.

We have investigated forty varieties of cultivated apples, and among them varying degrees of self-incompatibility occur, but only two have entirely failed upon selfing and three upon crossing. Since comparatively few flowers were used in these five pollinations, too much importance cannot be attached to them.

Among the triploid apples a high degree of generational sterility prevails, and the proportion of good pollen varies from 4 to 27 per cent.; whereas that of known diploids ranges from 50 to 97 per cent.

In apples we have made a total of 290 different self- and cross-pollinations involving 40,000 flowers. An analysis of the cross-pollinations shows that triploid-diploid combinations are as productive as diploid-diploid. 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 and reciprocal combinations. The offspring of the triploid-diploid crosses are also extremely weak, due to aneuploidy, and contrast sharply with the vigorous diploid-diploid progeny.

Since incompatibility is due to lack of genetic differentiation it is concluded that the good results obtained from the triploids are due to a greater variety in the gametic output of triploid than of diploid varieties, thereby providing a greater chance of compatible combinations. The rarity or absence of complete incompatibility and the common occurrence of partial compatibility in apples is doubtless associated with the complexity of their chromosome constitution.

Fuller details of our investigations with apples have appeared in a recent paper (Crane and Lawrence, 1930).


### Summary.

Sterility in fruits is of three kinds: (1) generational sterility; (2) morphological sterility; and (3) incompatibility. In the sweet cherry, *P. avium* (diploid), the behaviour of incompatibility is comparatively simple. Self-incompatibility is the rule, cross-incompatibility common and always reciprocally expressed. Among established varieties we have so far been able to recognise nine intra-sterile, inter-fertile groups.

A factorial analysis of preliminary investigations with seedlings shows that incompatibility in the sweet cherry is an orderly phenomenon and amenable to the genetic interpretation advanced by East and Mangelsdorf in *Nicotiana*, Lehmann in *Veronica* and, to some extent, to Sirks' interpretation in *Verbascum*. In the sour cherry (*P. cerasus*) and the Dukes (tetraploids) different degrees of compatibility occur.

In the plums, *P. domestica* (hexaploid), incompatibility is complex. Self- and cross-compatibility, self- and cross-incompatibility, degrees of self- and cross-incompatibility and differences in reciprocal matings, both complete and in partial degree, occur.

Cytologically, apples are of two kinds, (1) the secondarily balanced hexasomic tetraploids, and (2) the nonasomic hexaploids—the so-called "diploid" and "triploid" varieties respectively. The "triploids" are characterised by a high degree of generational sterility, but it is expressed in the formation of imperfect seeds and weak offspring rather than by failure to form fruits. In apples compatibility is common in partial degree, but rarely completely expressed.

The expression of incompatibility is more complex and variable in polyploids than in diploids. It is concluded that this is attributable to the polysomic condition of the factors which determine incompatibility in polyploids, and consequent interactions favourable to a greater variation in pollen-tube growth.

The more complex the polyploidy the less frequently will incompatibility occur, since the chances of individuals of similar constitution meeting to form incompatible groups are considerably reduced.

One way incompatibility is a phenomenon directly attributable to the multiplicity of factors in a polyploid, and we have suggested that

the frequency with which Sirks (1926 *a*) and others encountered such differences in reciprocal matings would indicate that the plants they investigated are polyploids.

## REFERENCES.

CORRENS, C. (1912). "Selbststerilität und Individualstoffe." *Festschr. d. med.-naturwiss. Ges. z. 84 Versamml. deutsch. Naturforscher u. Ärzte* 1912. Münster-i.-W.

CRANE, M. B. and LAWRENCE, W. J. C. (1929). "Genetical and cytological aspects of incompatibility and sterility in cultivated fruits." *Journ. Pom. and Hort. Sci.* VII, No. 4, pp. 276–301.

—— —— (1930). "Fertility and vigour of apples in relation to chromosome number." *Journ. Gen.* XXII, 153–63.

DARLINGTON, C. D. (1928). "Studies in *Prunus*, I and II." *Ibid.* XIX, 213–56.

—— (1930). "Studies in *Prunus*, III." *Ibid.* XXII, 65–93.

DARLINGTON, C. D. and MOFFETT, A. A. (1930). "Primary and secondary chromosome balance in *Pyrus*." *Ibid.* XXII, 129–52.

EAST, E. M. (1929). "Self-Sterility." *Biblio. Genetica*, V, 331–368.

EAST, E. M. and MANGELSDORF, A. J. (1925). "A new interpretation of the hereditary behaviour of self-sterile plants." *Proc. Nat. Acad.* XI, 166–71.

—— —— (1926). "The genetics and physiology of self-sterility in *Nicotiana*." *Memoirs of the Hort. Soc. of New York.* III. *Int. Conf. on Flower and Fruit sterility*, pp. 321–3.

EAST, E. M. and YARNELL, S. H. (1929). "Studies on self-sterility." *Genetics*, XIV, 455.

HÅKANSSON, A. (1925). "Zur Zytologie von *Celsia* und *Verbascum*." *Lunds Univ. Årssk.* XXI, No. 10, p. 1.

LEHMANN, E. (1926). "The heredity of self-sterility in *Veronica Syriaca*." *Memoirs of the Hort. Soc. of New York.* III. *Int. Conf. on Flower and Fruit sterility*, pp. 313–20.

SIRKS, M. J. (1926 *a*). "The genotypical problems of self- and cross-incompatibility." *Memoirs of the Hort. Soc. of New York.* III. *Int. Conf. on Flower and Fruit sterility*, pp. 325–43.

—— (1926 *b*). "Further data on the self- and cross-incompatibility of *Verbascum phoeniceum*." *Genetica*, VIII, 345–67.