

GENETICAL STUDIES IN PEARS

I. THE ORIGIN AND BEHAVIOUR OF A NEW GIANT FORM

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(With Plates IX-XI and Seven Text-figures)

IN 1936 Messrs W. Seabrook drew our attention to a new pear which had arisen as a bud-sport on a tree of the variety Fertility at their nurseries near Chelmsford. The original Fertility was raised by Messrs Rivers of Sawbridgeworth about 1875 from a seed of the variety Beurre Goubalt; its male parent is not known. This variety was examined by Moffett (1934) and found to be a diploid, $2n=34$. The new form has been named "Improved Fertility", and, as shown in Pl. IX, figs. 7 and 8, it is a tetraploid, $2n=68$. The principal differences between these two forms are as follows.

MORPHOLOGICAL CHARACTERS

In general all the characters of the tetraploid are larger and more pronounced than those of the diploid, but, as shown in Pl. IX, fig. 2, and Table I, the most conspicuous difference is the increase in weight and size of its fruits. In shape the tetraploid is broader than the diploid. The weights and measurements detailed in Table I were taken from a random sample of six fruits of each form.

TABLE I

	Fertility, $2n=34$			Improved fertility, $2n=68$		
	Weight	Length	Breadth	Weight	Length	Breadth
	g.	mm.	mm.	g.	mm.	mm.
	125	82	56	172	83	67
	129	82	58	229	91	71
	144	80	63	178	74	70
	119	78	59	182	76	71
	127	78	61	214	88	73
	106	79	55	210	90	71
Total	750	479	352	1185	502	423
Mean	125.0	79.8	58.7	197.5	83.6	70.5
		L/B = 1.359			L/B = 1.185	

POLLEN

The pollen of the two types differs appreciably. The tetraploid has a higher proportion of defective pollen grains than the diploid, and, as shown in Pl. IX, figs. 3, 4, differences occur in the size and shape of the

grains. In solution, those of the diploid are in general round-oval in shape, up to 75μ in length, with thin walls, and germination and pollen tube growth in comparatively rapid. In the tetraploid the pollen is triangular, up to 100μ long, with thicker walls; the initial germination is slower than in the diploid, but the eventual pollen tubes are appreciably broader than those of the diploid. A peculiarity of the tetraploid is the frequent development of forked pollen tubes (Pl. IX, fig. 5). Such tubes were never seen in any of the diploid cultures. When dry the pollen grains of both types are oval-long in shape, but those of the tetraploid are the longer.

TABLE II

Pollinations	No. of flowers pollinated	% matured	Average seeds per fruit	No. of seeds sown	% germi- nation
	Fertility $2x$				
Self-pollinated	*1701	0.8	2.0	23	87
× Beurre Clairgeau ($2x$)	134	18.6	5.8	—	—
× Beurre Giffard ($2x$)	127	15.7	8.0	58	98
× Beurre Hardy ($2x$)	118	5.1	8.8	53	94
× Conference ($2x$)	431	5.3	9.4	80	98
× Dr Jules Guyot ($2x$)	135	18.5	5.5	139	96
× Doyenne du Comice ($2x$)	241	13.7	8.5	57	96
× Williams' Bon Chrétien ($2x$)	52	23.1	4.4	53	18
× Beurre d'Amanlis ($3x$)	268	0.7	1.5	3	100
× Beurre Diel ($3x$)	362	14.9	4.0	125	84
× Catillac ($3x$)	127	21.2	3.1	—	—
× Pitmaston Duchess ($3x$)	337	4.4	2.6	17	100
× Fertility ($4x$)	103	20.4	6.23	—	—
Fertility $4x$					
Self-pollinated	8	37.5	5.7	—	—
× Glou Morceau ($2x$)	11	27.3	4.7	—	—

* Fertility $2x$ has been self-pollinated in several different years, and the total results are given above. The highest proportion of fruit which reached maturity in any one year was 3.2%.

PRODUCTIVITY AND FERTILITY

For the past six years we have had under investigation a number of problems which arise from the occurrence of incompatibility and sterility in pears. So far no detailed report on these studies has been published. This is mainly due to a proportion of the pollinations made in the course of the work failing to set or setting very few fruits, and before such results can be established with any degree of confidence repetition and confirmation are necessary. The main results of the work will be published later, but a number of them which directly concern the variety Fertility are detailed in Tables II-IV.

In Table II the results are given of self- and cross-pollinations between

the diploid and tetraploid forms of Fertility, and also of pollinating these varieties with a number of diploid and triploid varieties. The data relating to the tetraploid Fertility are small owing to its recent introduction into the experiments, but they show that whereas the diploid Fertility is only slightly self-fertile, i.e. following self-pollination it only set 0.8 % of fruits with an average of two good seeds per fruit¹, the tetraploid Fertility is highly self-fertile, setting 37.5 % of fruit with an average of 5.7 good seeds per fruit. The diploid Fertility is also highly fertile when pollinated by its tetraploid derivative, setting 20.4 % of fruits with an average of 6.23 good seeds per fruit.

The duplication of the chromosome complement is therefore associated with an increase of self- and cross-fertility, but precisely what this is due to is not at present clear. There are four possibilities which may be considered: (1) the remote possibility of a gene change conferring fertility, (2) segregation of the increased number of genes resulting in a higher proportion of compatible pollen grains, (3) the possibility of apomixis playing a part and (4) the possibility of the mere increase in chromosome number, which results in larger pollen grains and wider tubes, enabling a larger proportion to travel down the style and function in fertilization.

APOMIXIS OR GAMETIC SELECTION IN DIPLOID-TRIPLOID CROSSES

A high degree of sterility is usually expressed when diploids and triploids are intercrossed. Such sterility is sometimes reflected in the lower percentage of fruits which set and reach maturity, but is seen more particularly in the lower proportion of viable seeds obtained. Further it is usual in families raised from such crosses for the majority of the seedlings to have an aneuploid chromosome constitution and to be characterized by weak and feeble growth; see for example an analysis of families of apples derived from diploids crossed by triploids (Crane & Lawrence, 1930; Darlington & Moffett, 1930).

In Table III we have detailed the results obtained from crossing the diploid variety Conference with a number of diploid and triploid varieties, and it will be seen that though variation occurs, in all cases the percentage of fruit which reaches maturity and the average number of seeds per fruit is higher in the diploid crossed diploid than in the diploid crossed triploid combinations. Table IV, which gives the results from crossing a number of diploids by triploids, again shows the sterility characteristic

¹ In *Pyrus* the ovary consists of five carpels with two ovules in each, therefore the maximum number of seeds per fruit would be ten.

of the diploid-triploid crosses. The majority set few fruits and in most cases the proportion of seeds per fruit was low. The results detailed in Table II, however, show two exceptions, namely, when the diploid Fertility was crossed with the triploid varieties Beurre Diel and Catillac; in these cases the proportion of fruit set to flowers was high and well up to the average obtained from diploid-diploid crosses, 14.9 and 21.2% of fruits maturing with an average of 4 and 3.1 seeds per fruit respectively.

TABLE III

	No. of flowers pollinated	% matured	Average seeds per fruit	No. of seeds sown	% germi- nation
Conference 2x					
× Beurre Clairgeau (2x)	274	8.0	5.4	26	88.5
× Beurre Giffard (2x)	90	7.7	6.8	48	93.7
× Beurre Hardy (2x)	284	9.5	5.5	151	93.3
× Dr Jules Guyot (2x)	439	13.2	5.3	50	92.0
× Doyenne du Comice (2x)	65	15.4	5.5	55	92.7
× Fertility (2x)	83	19.3	4.3	59	98.4
× Williams' Bon Chrétien (2x)	302	6.9	5.7	88	85.2
× Beurre d'Amanlis (3x)	183	3.8	2.0	14	78.6
× Beurre Diel (3x)	138	5.1	2.7	19	73.6
× Catillac (3x)	163	0.6	1.0	1	100.0
× Vicar of Winkfield (3x)	109	0.0	0.0	—	—

TABLE IV

2x vars.	Pollinations 3x vars.	No. of flowers polli- nated	% fruit matured	% seeds per fruit	No. of seeds sown	% germi- nation
Beurre Hardy	× Beurre Diel	280	0.0	0	—	—
Dr J. Guyot	× Beurre Diel	148	1.3	4.5	9	66.6
Durondeau	× Beurre Diel	151	0.0	0	—	—
Glou Morceau	× Beurre Diel	375	0.0	0	—	—
Doyenne du Comice	× Beurre d'Amanlis	52	1.9	2.0	2	50.0
Durondeau	× Beurre d'Amanlis	40	2.5	3.0	6	100.0
Marguerite Marillat	× Beurre d'Amanlis	276	0.7	1.5	3	33.3
Beurre Hardy	× Pitmaston Duchess	49	2.0	2.0	2	50.0
Beurre Giffard	× Pitmaston Duchess	34	2.9	2.0	2	100.0
Dr J. Guyot	× Pitmaston Duchess	163	1.2	4.5	9	77.7
Beurre Hardy	× Catillac	93	0.0	0	—	—
Durondeau	× Vicar of Winkfield	97	5.1	1.4	7	85.7
Doyenne du Comice	× St Germain	153	0.0	0	—	—

The diploid Fertility was first crossed with the triploid variety Catillac this year and the resulting seeds have not yet germinated. The cross, Fertility diploid with Beurre Diel triploid, has been made on three separate occasions, the total results being given in Table II. From the first cross a small family was raised in 1935, and in contrast to our experience with families of apples derived from crossing diploids with triploids, the majority of the seedlings made good growth, corresponding to the growth of normal diploid seedlings, and formed vigorous plants;

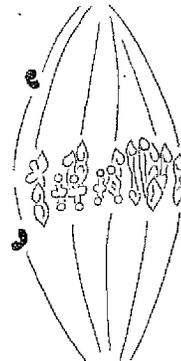
only a small proportion were weak and dwarf. Eleven plants of this 1935 family were cytologically examined by Dr A. C. Faberge, now of the Galton Laboratory. He found that six plants had 34, three plants 34 ± 1 , one plant 39 and one plant 43 ± 1 chromosomes. The nine plants with the diploid or approximately diploid number have made normal growth, whereas the two aneuploid plants with the higher chromosome numbers are weak growing and comparatively dwarf. The high proportion of plants with the diploid or approximately diploid number of chromosomes in this family derived from diploid crossed triploid suggests (1) apomictic origin or (2) high selection of haploid male gametes. Further cytological and genetical investigation will show which of these is operating. For example, the triploid variety Catillac has a pronounced hairy character which is dominant, and the behaviour of this character in a family from Fertility crossed Catillac will show directly whether apomixis, gametic selection or both together occur.

CYTOLOGICAL BEHAVIOUR

Meiosis was studied in the two types of Fertility pear after staining with acetocarmine following pre-fixation in 3/1 absolute alcohol/glacial acetic acid. By placing slight pressure on the cover slip before heating the slide the nuclei could be flattened out somewhat, so that the configurations could be examined more or less in one plane and studied in greater detail. The slides were made permanent by a combination of the methods of Buck (1935) and McClintock (1929) perfected by La Cour. Permanent slides, however, show a certain contraction in the size of the chromosomes as compared with the temporary slides, and this is evident in the drawings and photographs, some of which were made from temporary and others from permanent preparations.

Pairing of chromosomes in the diploid pear was normal at the first metaphase of meiosis, although pollen mother-cells showing two univalents were encountered very rarely (Text-fig. 1). As a rarity a bridge and fragment were seen at anaphase (Pl. X, fig. 2), indicating the presence of an inversion, and since inversions often lead to difficulties in pairing at pachytene it is probable that the occurrence of univalents was due to this cause.

Text-fig. 2 and Pl. XI, figs. 1 and 2, illustrate typical configurations at first metaphase in the diploid.



Text-fig. 1. Metaphase I in Fertility pear 2x, showing two univalents ($\times 2000$).

Chiasma frequency counts were made for thirty-five complete nuclei at this stage; the results are shown in Table V and represented graphically in Text-fig. 3. Nearly 70% of the bivalents contain only one chiasma, while 27.7% have two chiasmata, the average number per bivalent being 1.33.



Text-fig. 2. Typical bivalents from metaphase I in Fertility 2x. ($\times 2000$.)

TABLE V

Xta.	Total/ Percentage	Term. coeff.					Term. coeff.
		0.0	0.33	0.5	0.67	1.0	
0	1 / 0.2	—					—
1	413 / 69.4	} 167 40.4%		} 246 59.6%			0.59
2	141 / 23.7	0	9 6.4%	132 39.6%			0.97
	24 / 4.0	} 24					0.50
3	13 / 2.2	0	13				0.66
4	3 / 0.5	3					0.50

Mean chiasma frequency per bivalent = 1.33

Terminalization coefficient:

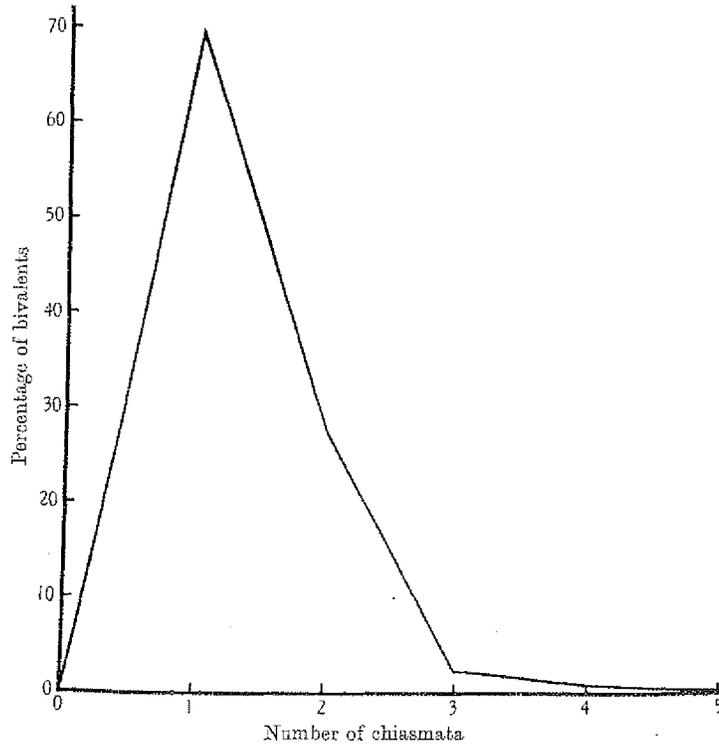
Open bivalents = $\frac{167}{296} = .568$

Closed bivalents = $\frac{132}{296} = .446$

The terminalization coefficient was also determined for the different bivalents. It will be observed from Table V that 59.6% of the bivalents with one chiasma are completely terminalized, while in the ring type of bivalent 93.6% of the bivalents are completely terminalized. Calculated in terms of open and closed¹ bivalents the terminalization coefficient for

¹ A closed bivalent contains one or more chiasmata on each side of the centromere, whereas in an open bivalent chiasmata occur only on one side of the centromere.

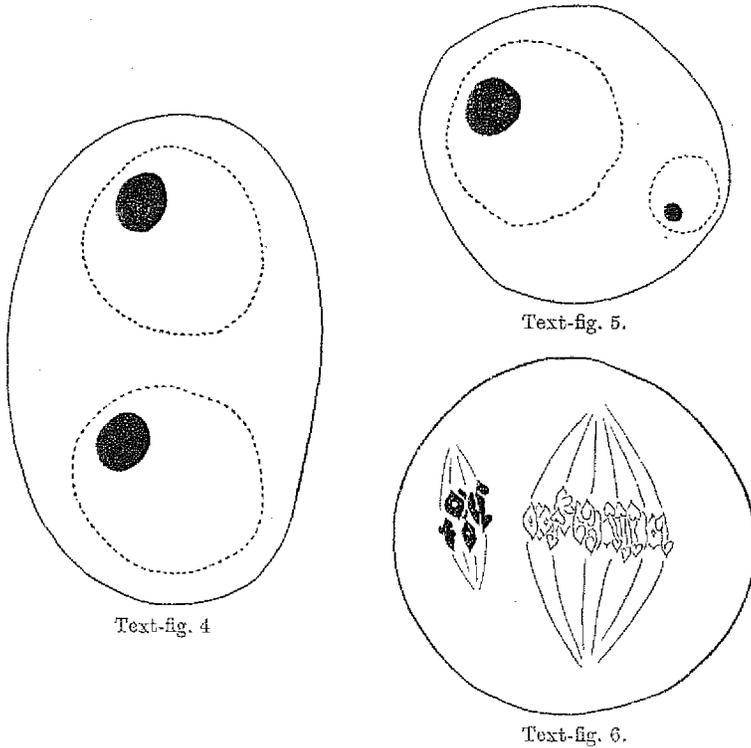
the open bivalents is as low as 0.588, while for the closed bivalents it is as high as 0.906. Evidently, therefore, as pointed out by Darlington & Janaki-Ammal (1932), the repulsion between the centromeres is more effective within a closed bivalent than in an open bivalent in bringing about terminalization of chiasmata.



Text-fig. 3. Graph illustrating chiasma frequency in Fertility 2a.

The existence at metaphase I, however, of a state of tension between the centromeres and the first chiasma in the type of bivalent with two chiasmata in one arm (indicated by the fine thread joining them) indicates that this first chiasma has not undergone serious movement away from the centromere, and that therefore terminalization is responsible for only minor changes in the shape of the bivalents before metaphase I. It seems not unlikely that even in these small chromosomes there is a localization of pachytene pairing near the ends and near the centromeres which is primarily responsible for the chief types of distribution of chiasmata observed at metaphase I. We have in fact in *Pyrus* the *Chrysochraon* type of chiasma distribution (Darlington, 1938).

Although we have stated that meiosis occurs normally in the diploid Fertility pear, certain abnormalities were observed. These, however, are due to somatic instability rather than to any defect in the process of meiosis itself. Pollen mother cells were observed at pachytene which contained either two large, normal-sized, nuclei or one large and one small nucleus (Text-figs. 4, 5). Pl. X, fig. 1, illustrates a pollen mother



Text-figs. 4-6. Fertility 2x. Fig. 4. Giant P.M.C. with two normal sized nuclei at pachytene ($\times 2000$). Fig. 5. P.M.C. containing a small nucleus in addition to a normal nucleus at pachytene ($\times 2000$). Fig. 6. Same as Fig. 5 at metaphase ($\times 2000$).

cell containing in addition to the normal complement of chromosomes, another smaller nucleus. Here the larger nucleus is at the metaphase stage while the smaller one, which contains seven bivalents and one univalent, is at late diakinesis. In Text-fig. 6, on the other hand, both the normal and the small nucleus are at the metaphase stage.

Evidence at later stages of meiosis shows that in both types of syndiploidy, i.e. (1) the occurrence of two normal nuclei in one pollen mother cell and (2) the occurrence of one normal and one small, the nuclei behave independently throughout meiosis. As a result of this independent

behaviour we find in the first type (1) eight haploid pollen grains at the tetrad stage; Pl. X, figs. 3-6, but in the second type (2) four haploid and two to four subhaploid pollen grains. If they did not behave independently a doubling or increase in the number of chromosomes in the pollen grains would occur. The number and the association of the chromosomes in the small nucleus varied. In no case was complete failure of pairing observed, although in some pairing was complete, while in others only a proportion paired. This variation in chromosome pairing results in the formation of two, three or four extra pollen grains in a cell.

The origin of the small nuclei in the pollen mother cells is not at present clear. The pollen mother cells containing two normal nuclei doubtless originated by suppression of wall formation at the pre-meiotic mitosis, while a delay in wall formation may lead to the other type in

TABLE VI

IV	II	No. of nuclei
12	10	1
11	12	2
10	14	1
9	16	3*
8	18	4*
7	20	4*
5	24	2
4	26	2*
3	28	1
		20 nuclei
Total possible multivalents		= 340
Total formed		= 147
Mean frequency of multivalents		= 42.3%

* Contains one nucleus with one trivalent and univalent.

which the small nucleus is involved. Abnormal spindle behaviour, such as failure of co-ordination of one of the spindle poles at the pre-meiotic mitosis, may also have played a part in producing the latter type of pollen mother cell.

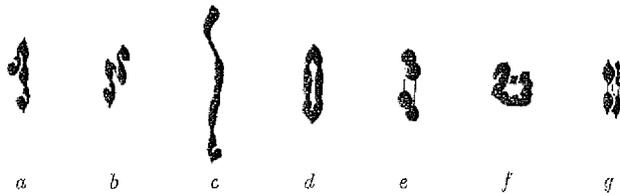
The diploid Fertility pear must therefore be regarded as being unstable somatically, and we can conclude that this somatic instability does not upset the normal process of meiosis in any way. An occasional cell containing the tetraploid number of chromosomes was also seen in the anther wall tissue of this pear and is further evidence of its somatic instability.

Pairing of chromosomes at metaphase of meiosis in the tetraploid pear was exceedingly good, there being very few pollen mother cells showing any univalents. Table VI shows chromosome association at metaphase from an analysis of twenty complete nuclei.

It was not found possible to analyse complete nuclei for chiasma frequency due to the large number of configurations per nucleus, but

Text-fig. 7 illustrates the types of quadrivalents encountered. The type of quadrivalent illustrated in Text-fig. 7 *a, b* and (Pl. XI, fig. 4) was probably the most common, although quite a large proportion of these configurations were of the ring type with 4 chiasmata (cf. Pl. XI, fig. 3).

Reference to Table VI shows that the proportion of quadrivalents per nucleus appears to be exceedingly high when one considers that 70% of the bivalents in the diploid had only one chiasma. The frequency of quadrivalents in the tetraploid manifestly demands a higher frequency than that found in the diploid, but since single samples of material have been taken from both types it is possible that this inconsistency may be due to the effects of different external conditions such as temperature, pruning, spraying or other cultural operations. Meiosis actually occurred in the tetraploid appreciably later than in the diploid. On the other hand, it is possible that some unknown factor may be concerned.



Text-fig. 7. Typical quadrivalents from Fertility pear 4x ($\times 2000$).

All that can be said therefore is that the behaviour of the Improved Fertility is consistent with that of other tetraploids in showing an incomplete and variable number of quadrivalents. In the tetraploid *Primula sinensis*, 90% of the potential multivalents are formed as quadrivalents (Darlington, 1931), while the value for the tetraploid tomato is as low as 31.4% (Upcott, 1935). The auto-tetraploid pear with a value of 42.3% is therefore intermediate between these two extreme types. Also compare (Upcott, 1939) in *Tulipa sylvestris*, in which the value is 33.0%.

SOMATIC VARIATIONS

The number of known bud-sports in cultivated fruits is very considerable, but they are less frequent in pears than in apples and certain other fruits. They have given rise to differences which depart from the type in both small and large respects, and by asexual propagation lead to the establishment of subclones, some of which are superior and others inferior to the original clonal variety.

The longer and more widely an individual is grown as a clone the greater is the opportunity for somatic variations to occur. It is, therefore,

obvious that the conditions under which cultivated fruits are propagated and grown are favourable for the development of vegetative variations. The diploid Fertility pear has been propagated asexually for the past 60 years. It is a commercial variety, and consequently many thousand trees of it are grown; and as we have described, on one of these trees a branch arose, and from it a subclone was established having twice as many chromosomes as the type. Recently, Shamel (1937) has reported that the diploid variety Bartlett has similarly given rise to a large-fruited tetraploid¹ form. Bartlett is synonymous with Williams' Bon Chrétien, and it is probably more widely grown than any other variety of pear in America. In the same publication Shamel figures and describes a bud sport of the pear variety Winter Nelis which has much larger fruits than the type. This somatic variation, however, is presumably the result of a gene change, as it has the same chromosome number, $2n=34$, as the type.

As far as we are aware, the large-fruited forms of Fertility and Bartlett are the only tetraploid varieties of pears in existence, and both are of somatic origin. In families of pears we have raised from intercrossing triploids with diploids, occasional seedlings with the tetraploid number of chromosomes occur, but they are as yet too young to fruit, and until they reach maturity it will not be possible to see if they are of a balanced and productive type.

Used in breeding experiments the new tetraploid varieties should rapidly give rise to further polyploid races of pears. Tetraploids crossed with diploids should give triploid offspring, and the crossing of tetraploids with triploids will probably give rise to new tetraploids as a result of the fusion of diploid gametes in fertilization.

SUMMARY

1. The diploid variety of pear "Fertility", $2n=34$, gave rise by somatic mutation to a new large-fruited form. This new form was found to be tetraploid, $2n=68$.
2. The tetraploid form was found to be more self-fertile than the type.
3. Pollen formation was that expected in a non-hybrid tetraploid.
4. The results obtained from using the diploid form of "Fertility" as female in crosses with triploids indicate that in certain crosses apomixis and/or gametic selection occurs.

¹ The chromosome number is given as $n=34$ or 34 ± 1 .

5. The diploid form is shown to be somatically unstable, though meiosis proceeds normally.

6. The value of tetraploidy in producing new polyploid forms of pears is briefly discussed.

ACKNOWLEDGEMENTS

We are indebted to Mr W. P. Seabrook for presenting us with trees of the tetraploid pear, and to Dr C. D. Darlington for the interest he has taken in the cytological aspects of this study. The details given in Tables I to IV are from unpublished results of investigations on incompatibility and sterility in pears in which Mr D. Lewis, Mr A. G. Brown and Mr D. B. Fanshawe have collaborated.

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EXPLANATION OF PLATES IX—XI

PLATE IX

- Fig. 1. Fruit of Fertility pear, diploid.
 Fig. 2. Fruit of Fertility tetraploid.
 Fig. 3. Pollen of diploid, $\times 70$.
 Fig. 4. Pollen of tetraploid, $\times 70$.
 Fig. 5. Forked pollen tube of tetraploid.
 Fig. 6. Somatic chromosomes of diploid, $\times 2120$, from root tip fixed in medium Flemming, stained gentian violet.
 Figs. 7 and 8. Somatic chromosomes of tetraploid, $\times 2120$, from anther wall tissue, fixed in acetic alcohol, stained aestic carmine.

PLATE X

All figures show behaviour in the diploid form. Figs. 1 and 2 $\times 1400$, remainder all $\times 750$.

- Fig. 1. Pollen mother cell showing an extra small nucleus in addition to the normal nucleus at metaphase I. (Owing to difficulties in reproduction the cell outline, especially in the lower left hand corner, is not well defined.)
 Fig. 2. Telophase I, showing a bridge, fragment and dividing univalent.
 Fig. 3. Telophase II, showing two normal, four nuclear pollen mother cells and one giant eight-nuclear pollen mother cell.
 Fig. 4. Early tetrad stage.
 Fig. 5. "Tetrad stage" with 8 pollen grains, derived from the giant cells in Figs. 3 and 4.
 Fig. 6. Normal tetrad.

PLATE XI

All the figures in Plate XI are reproduced at $\times 2120$.

- Fig. 1. Side view of metaphase I in the diploid.
 Fig. 2. Polar view of metaphase I in the diploid, showing some degree of secondary association.
 Fig. 3. Side view of metaphase I in the tetraploid at three different foci. The nucleus has an unusually large number of ring quadrivalents.
 Fig. 4. Metaphase I in the tetraploid, showing the more usual types of quadrivalents.