

THE CAUSAL SEQUENCE OF FRUIT DEVELOPMENT

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(With Three Text-figures)

During the course of our pollination and breeding work with plums some pollinations gave earlier ripening fruits than others and also significant differences in fruit size. The details are as follows.

In 1940 we self-pollinated flowers on a tree of *Prunus divaricata*, var. Myrobalan Red, $2n=16$. At the same time and on the same tree we cross-pollinated flowers with *P. spinosa* $2n=32$, and a number with *P. domestica*, var. Blue Rock, $2n=48$. As the fruits approached maturity there was a striking difference in the fruits derived from the three pollinations. Those pollinated with Blue Rock ripened much earlier than those self-pollinated; the crossed fruits being red and almost ripe, whilst the selfed fruits were still green. Those crossed with *P. spinosa* ripened at an intermediate time; after the fruits pollinated with Blue Rock, but before the self-pollinated fruits. After the fruits had matured it was found that 100% of the self-pollinated fruits, and 94% of the fruits crossed with *P. spinosa* had good seeds, whilst none of the fruits crossed with Blue Rock formed seeds. The details are given in Table 1.

Table 1

Pollinations (1940)	No. of flowers pollinated	No. of fruits matured	% matured	No. of good seeds	No. of empty stones
Myrobalan Red (selfed)	726	83	11.6	83	0
" " × <i>P. spinosa</i>	260	51	19.6	48	3
" " × Blue Rock	174	25	14.3	0	25

In 1941 we made further self-pollinations on Myrobalan Red and also crossed flowers with the pollen of Blue Rock, the pollinations again being made at the same time and on the same tree. The size and other details of the developing fruits were recorded and the results are given in Figs. 1 and 2 and Tables 2 and 3.

From the self-pollinations 105 fruits were obtained and sixty-five fruits from the flowers pollinated with Blue Rock, and there were again considerable differences. As shown in Fig. 1, fifty-four of the crossed fruits and two of the selfed fruits reached maturity during the period 2-16 July, the remainder, 103 selfed and eleven crossed fruits, ripening during the period 20-24 July. There was thus a marked difference in the time of ripening, 83% of the crossed fruits ripening in the first period, whilst 98% of the selfed fruits did not ripen until the second period.

As shown in Fig. 1, fifty-four of the fifty-six fruits which reached maturity in the first period were seedless. The remaining two fruits had seeds but they were not ripe until 16 July, the last day of the period. In the second period 114 fruits matured, 103 from self and eleven from cross-pollinations. The whole of the selfed and eight of the crossed fruits had well-developed seeds. Thus there is a close correlation between embryonic development and seed formation and the time of fruit maturity: 96% of the fruit which

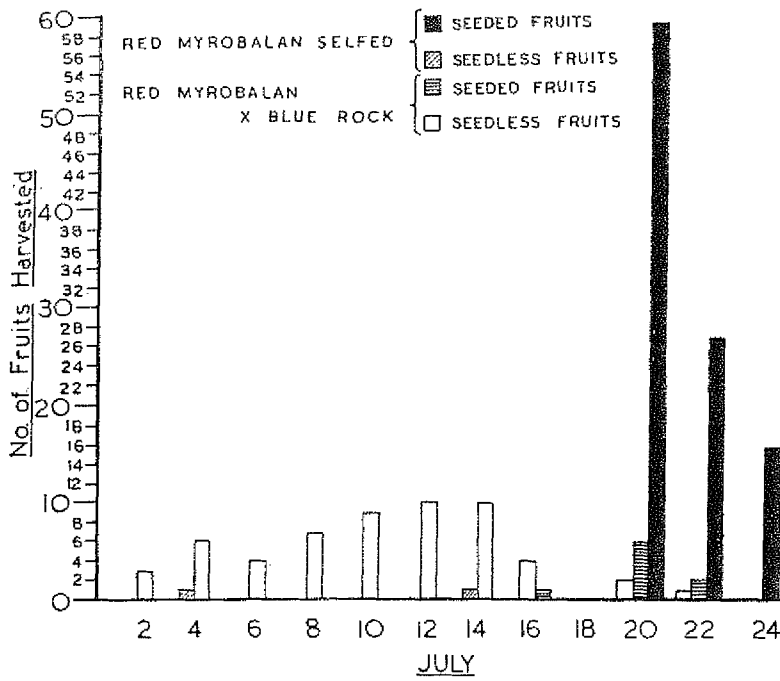


Fig. 1

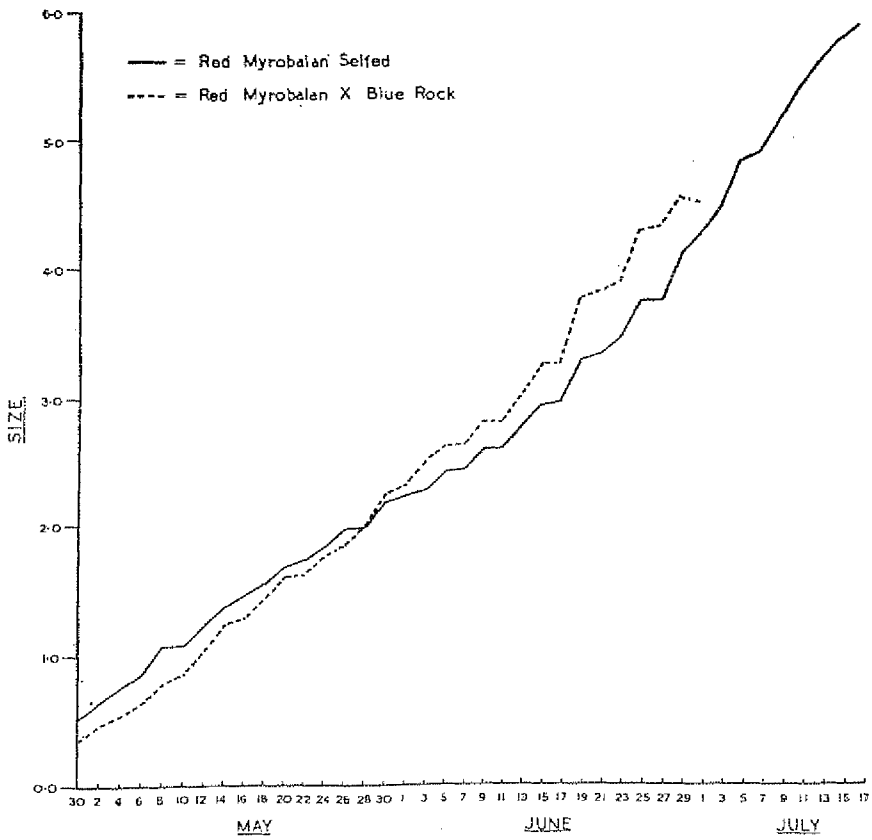


Fig. 2

Table 2

Pollinations (1941)		Flowers pollinated	Fruit matured	% fruit matured	Seeded fruits	Seedless fruits	Mean fruit weight g.	Mean weight seeded fruits g.	Mean weight seedless fruits g.	Mean size seeded fruits	Mean size seedless fruits
Red Myrobalan selfed	680	105	16.4	103	2	13.4 ± 0.206	13.43 ± 0.205	10.0 ± 1.00	5.675 ± 0.074	4.261 ± 0.245	
Red Myrobalan × Blue Rock	538	65	12.1	9	56	10.5 ± 0.302	13.94 ± 0.796	9.82 ± 0.255	5.961 ± 0.362	4.217 ± 0.101	

Table 3.

No. fruits	Mean weight g.	Difference D	Standard error E_D	D/E_D	P	Mean size $\frac{1000}{l \times r^2}$ mm.	Difference D	Standard error E_D	D/E_D	P
105	13.4 ± 0.206	2.0	0.365	7.5338	<0.01	5.648 ± 0.076	1.190	0.146	8.1506	<0.01
65	10.5 ± 0.302					4.468 ± 0.125				
108	13.43 ± 0.205	0.51	0.822	0.6204	0.53	5.675 ± 0.074	0.286	0.389	0.7357	0.46
9	13.94 ± 0.796					5.961 ± 0.382				
2	10.0 ± 1.00	0.18	1.029	0.1488	0.88	4.261 ± 0.245	0.044	0.265	0.0166	0.99
56	9.82 ± 0.255					4.217 ± 0.101				
56	13.94 ± 0.796	4.12	0.885	4.6341	<0.01	5.961 ± 0.382	1.744	0.395	4.4152	<0.01
112	13.48 ± 0.221	3.66	0.321	11.4018	<0.01	5.698 ± 0.076	1.481	0.123	11.2276	<0.01
68	9.82 ± 0.247					4.217 ± 0.097				

ripened in the first period were seedless, whilst 97% of those which ripened in the second period had seeds. Other differences occurred in the fruits which were also correlated with the parthenocarpic, seedless, condition. As shown in Fig. 2 and Table 3 the fruits without seeds were smaller in size and lighter in weight than those with seeds. The growth rates given in Fig. 2 were obtained from measurements, taken in mm. at intervals of 48 hr., of the length and breadth of the developing fruits. For this purpose ten fruits from each pollination were taken at random, but only eight of the self and four of the cross-pollinated fruits reached maturity. As Fig. 2 shows the crossed fruits were smaller than the selfed fruits during the first four or five weeks of development, but the crossed fruits then grew more rapidly and were larger than the selfed fruits up to the time they reached maturity. The selfed fruits continued to grow, and by the time they reached maturity they had exceeded the size of the crossed fruits. The figure denoting fruit size in Fig. 2 are derived from the formula $\frac{\text{length} \times (\text{radius})^2}{1000}$.

As shown in Table 2 the difference in the average weight of the fruits from the two pollinations was 3.9 g. This can be regarded as fully significant in the statistical sense, since the standard error in such differences is 0.365. Further, as shown in Table 3 the difference in weight between fruits with seeds and those without seeds is even greater, the seeded fruits being 3.6 g. or more heavier than the seedless fruits.

In the pollinations we made in 1940, 100% of the Myrobalan self-pollinated fruits and 94% of the fruits resulting from pollinating Myrobalan $2n=16$ with *P. spinosa* $2n=32$ had good seeds whilst none of the fruits of Myrobalan pollinated with Blue Rock $2n=48$ formed seeds. In the 1941 pollinations 98% of the selfed fruits but only 14% of the fruits crossed with Blue Rock formed seeds. From considerable experience with pollination and breeding experiments with plums and other stone fruits, we had concluded (Crane & Lawrence, 1929) that in these fruits fertilization is essential for fruit development, but that a subsequent breakdown in embryonic growth may occur. Such a breakdown may result from several causes, the most probable of which is a discordance of the parental chromosome distributions to the nucleus and endosperm of the zygote, or between the nucleus and endosperm, the consequences of these inharmonious relations being seen in the degree of the development of the embryo and in extreme cases in the absence of seeds. Now when the diploid Myrobalan is pollinated with the tetraploid *P. spinosa*, the endosperm will be tetraploid, but when pollinated with the hexaploid Blue Rock, the endosperm will be pentaploid, and it is probable that these differences in balance between the chromosome complements of the potential embryos and endosperm may account for the differences in embryonic development and seed formation, the tetraploid endosperm being more effective than pentaploid endosperm in these cases.

In the 1940 pollinations no measurements were made of the size and weight of the fruits. The order of ripening was as follows:

Order of ripening	Cross	Embryo	Endosperm
1	$2x \times 6x$	$4x$	$5x$
2	$2x \times 4x$	$3x$	$4x$
3	$2x \times 2x$	$2x$	$3x$

Thus the seedless fruits, potentially with tetraploid embryos and pentaploid endosperms, ripened first. The seeded fruits with triploid embryos and tetraploid endosperm were the second, and the seeded fruits with diploid embryos and triploid endosperm were the last to ripen.

It may be recalled that the conditions and developmental effects which we have described are commonly referred to as *xenia*, a term first used by Foche in 1881 to denote any deviation from a normal form or colour in any part of a plant due to the action of foreign pollen. From the examples Foche described, it appears possible to place them into one or the other of the following three classes: (1) where the developing zygote is affected, (2) where the endosperm is affected, and (3) where the effect is on the maternal tissue. Two of these effects are now readily explicable. They were the result of the action of paternal genes in heredity. Thus (1) in the garden pea yellow cotyledons are dominant to green, and if a green variety is pollinated with a yellow variety the cotyledons of the developing zygote will be yellow. (2) Navashin's discovery in 1898 that the pollen nuclei of the endosperm fuse with the second male nucleus provides an explanation of endosperm differences of which a number of well-known cases occur in maize. Since these effects, in classes 1 and 2, are now well understood and readily explained on a simple genetic basis there is no reason why they should continue to be referred to as *xenia*. In class (3) where, as in our cases with plums, the maternal tissue is affected, we have not such a precise or simple explanation of the cause of the effect, but many examples as described in Table 4 have been reported upon in recent times.

In our example of developmental differences in plums, small size and early ripening of the fruit appears directly attributable to the lack of embryonic development. In dates, Nixon (1928-36) found that most pollinations which gave smaller seeds also gave earlier ripening fruits. This appears to be true throughout the pollinations made with the species *Phoenix dactylifera*, but in some interspecific pollinations, especially where the pollen of *P. canariensis* was applied to *P. dactylifera*, small seeds gave late ripening fruits. In all cases, both in varietal and interspecific pollinations, small seeds and small fruits go together. In melons, Rosa (1926) found that fruits with a larger number of seeds were heavier than those with a smaller number. In chestnuts, McKay & Crane (1939) found that some pollinations gave larger nuts than others, in cotton, Harrison (1931), and in oaks, Schreiner & Duffield (1942), found some pollinations gave heavier seeds than others.

Swingle (1926) introduced the term *metaxenia* to describe differences in the time of maturity in dates, and it is becoming the fashion to describe any effect, associated with foreign pollen, on the maternal tissue under this name. Since, however, Foche's original description of *xenia* covered effects on any part of the plant, whether embryonic or maternal, and especially since classes (1) and (2) are now well understood, it is a pity that the effect on the maternal tissue has been unnecessarily described as *metaxenia*.

In addition to the publications cited in Table 4, many papers have been published dealing with closely related phenomena. In Gustafson's experiments (1936-40), where in many species of plants he obtained parthenocarpic fruits by the use of growth-promoting chemicals and pollen extracts, the induced parthenocarpic fruits were invariably smaller than the normally developed seeded fruits. In plums, cherries and peaches Tukey (1936) has shown that an asymmetrical shape of the fruit is due to one of the two ovules in the carpel failing to develop, the one which does develop into a seed being attached to the larger and better developed side of the fruit. In numerous papers dealing with pollination experiments in apples and pears, cases have been reported, where lack of, or few seeds, affect the size and shape of the fruit.

Parthenocarpy may be induced in certain varieties of pears by cold temperature. Thus in our pollination experiments the variety Fertility has never set seedless fruit when

Female	Pollinated by	Effect on fruit-	Effect on seed	Author
<i>Crotalaria crenata</i> var.	<i>C. crenata</i> var.	---	Size	McKay & Crane (1939)
<i>C. crenata</i> var.	<i>C. mollissima</i> var.	---	Size	McKay & Crane (1939)
<i>C. mollissima</i> var.	<i>C. mollissima</i> var.	---	Size	McKay & Crane (1939)
<i>C. mollissima</i> var.	<i>C. crenata</i> var.	---	Size	McKay & Crane (1939)
<i>C. sativa</i> var.	<i>C. mollissima</i> var.	---	Size	McKay & Crane (1939)
<i>Citronerops humilis</i>	<i>Phoenix dactylifera</i>		Increase in number	Jannleart, vide Rosa (1936)
<i>Cucumis melo</i> var.	<i>C. melo</i> var.		Development	Rosa (1926)
<i>Diospyros kaki</i> var.	<i>D. kaki</i> var.			Hume (1913)
<i>D. kaki</i> var.	<i>D. kaki</i> var.			Noguclii (1934)
<i>Gossypium barbadense</i> var.	<i>G. hirsutum</i> var.		Size, lint length, fuzziness	Harrison (1931)
<i>G. barbadense</i> var.	<i>G. barbadense</i> var.		Lint length, fuzziness	Harrison (1931)
<i>G. hirsutum</i> var.	<i>G. hirsutum</i> var.		Size, lint length	Harrison (1931)
<i>Morus alba</i> var.	<i>M. alba</i> var.		Lint length	Harrison (1931)
<i>Phoenix dactylifera</i> var.	<i>P. dactylifera</i> var.			Erme & Schablovskaja (1933)
<i>P. dactylifera</i> var.	<i>P. canariensis</i>	Size, time of maturity	Size, development	Svingle (1926, 1928)
<i>P. dactylifera</i> var.	<i>R. reticulata</i>	Size, time of maturity	Size, shape, development	Nixon (1928, 1935, 1936)
<i>P. dactylifera</i> var.	<i>P. rupsicola</i>	Size, time of maturity	Size, shape, development	Nixon (1928, 1935, 1936)
<i>P. dactylifera</i> var.	<i>P. roboronensis</i>	Size, time of maturity	Size, development	Nixon (1928, 1935, 1936)
<i>P. dactylifera</i> var.	<i>P. sylvestris</i>	Size, time of maturity	Size, development	Nixon (1928, 1935, 1936)
<i>P. rupsicola</i> x <i>P. reticulata</i>	<i>P. dactylifera</i> var.	Size, time of maturity	Size, development	Nixon (1928, 1935, 1936)
<i>P. rupsicola</i> x <i>P. reticulata</i>	<i>P. rupsicola</i>	Size, time of maturity	Size, development	Nixon (1928, 1935, 1936)
<i>P. dactylifera</i> var.	<i>P. dactylifera</i> var.	Size, time of maturity	Size, development	Nixon (1928, 1935, 1936)
<i>P. dactylifera</i> var.	<i>P. reticulata</i>	Size, time of maturity	Size, development	Nixon (1928, 1935, 1936)
<i>Pistacia vera</i>	<i>P. algeriensis</i>	Length, splitting	Development	Crawford (1936)
<i>P. vera</i>	<i>P. chinensis</i>	Length, splitting	Development	Crawford (1936)
<i>Prunus tinarioides</i> var.	<i>P. domestica</i> var.	Size, time of maturity	Development	Peebles & Hope (1937)
<i>P. tinarioides</i> var.	<i>P. domestica</i>	Size, time of maturity	Development	Peebles & Hope (1937)
<i>Pyrus communis</i> var.	<i>P. spinosa</i>	Time of maturity	Development	Crane & Brown (1942)
<i>P. malus</i> var.	<i>P. communis</i> var.	Misshapen	Development	Crane & Brown (1942)
<i>P. malus</i> var.	<i>P. malus</i> var.	Shape, colour	Development	Crane & Brown (1942)
<i>P. malus</i> var.	<i>P. malus</i> var.	Size, colour	Development	Crane & Brown (1942)
<i>P. malus</i> var.	<i>P. malus</i> var.	Size, shape	Development	Crane & Brown (1942)
<i>P. malus</i> var.	<i>P. malus</i> var.	Shape	Development	Crane & Brown (1942)
<i>P. malus</i> var.	<i>P. malus</i> var.	Shape, shape	Development	Crane & Brown (1942)
<i>P. malus</i> var.	<i>P. malus</i> var.	Shape, colour	Development	Crane & Brown (1942)
<i>P. malus</i> var.	<i>P. malus</i> var.	Size, shape, colour, keeping quality, specific gravity, chemical composition	Development	Crane & Brown (1942)
<i>P. malus</i> var.	<i>P. malus</i> var.	Chemical composition, acidity, keeping quality	Development	Crane & Brown (1942)
<i>P. malus</i> var.	<i>P. malus</i> var.	Size, shape, colour	Development	Crane & Brown (1942)
<i>P. malus</i> var.	<i>P. malus</i> var.	Chemical composition, acidity, keeping quality	Development	Crane & Brown (1942)
<i>P. malus</i> var.	<i>P. malus</i> var.	Size, acidity	Development	Crane & Brown (1942)
<i>P. malus</i> var.	<i>P. malus</i> var.	Size	Development	Crane & Brown (1942)
<i>P. malus</i> var.	<i>P. malus</i> var.	Size	Development	Crane & Brown (1942)
<i>P. malus</i> var.	<i>P. malus</i> var.	Size, time of maturity	Development	Crane & Brown (1942)
<i>Quercus alba</i>	<i>Q. robur</i>	Size, colour	Development	Crane & Brown (1942)
<i>Solanum citralifolium</i>	<i>S. desieri</i>	Size, colour	Development	Crane & Brown (1942)
<i>S. citralifolium</i>	<i>S. aggregatum</i>	Size, colour	Development	Crane & Brown (1942)
			Length	Nebel (1930, 1932, 1936)
				Nebel & Trump (1932)
			Length	Nebel & Kertesz (1934)
			Length	Nebel & Kertesz (1934)
			Size	Krambholz (1932)
				EBBhard (1934)
			Size	Schreiner & Duffield (1942)
			Development	Yasuda & Kitamaru (1930)
			Development	Yasuda & Kitamaru (1930)

grown in a greenhouse where the temperature is always above freezing-point, but it has freely set seedless fruits out of doors following frost damage to the styles (Crane & Lewis, 1942). Lewis (1942) has also obtained seedless fruits of the variety Conference after artificial-cold treatment, the flowers being kept in a temperature of -9° C. for 17 hrs.

The pollen of the variety Beurre Bedford also induces the formation of parthenocarpic fruits. This variety, although a diploid, produces pollen ranging from haploid to tetraploid, and when applied to other varieties the abnormal pollen grains frequently stimulate fruit formation without seeds.

Heterosis is frequently discussed in connexion with xenia and the two phenomena often overlap. For example, Nebel & Kertesz (1934) state: 'Xenia of seed length have been shown to occur. Whether the term heterosis is preferable in this case is a matter of definition or interpretation.' As we have seen xenia sometimes has negative and some-

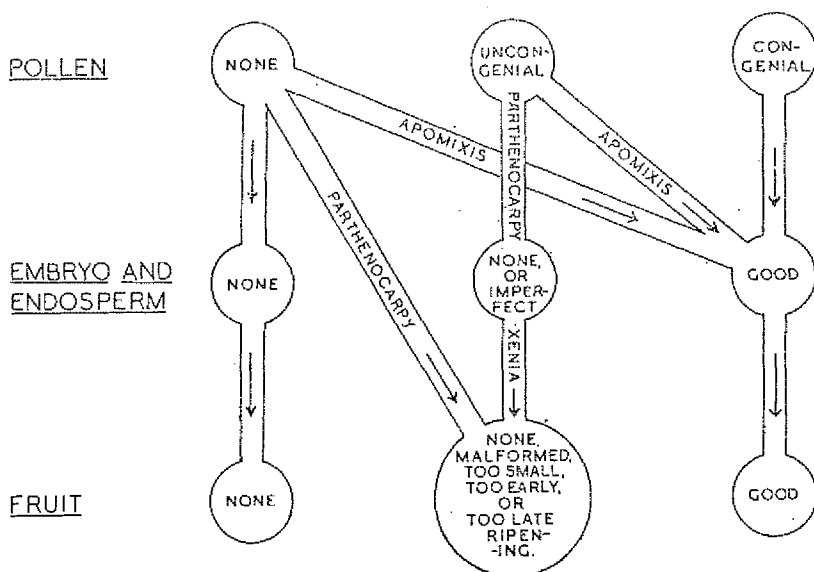


Fig. 3

times positive effects. Thus the decrease in size of fruits as occurs in dates and plums can be regarded as negative and the increase length of lint in cotton as a positive effect. This is similar to the phenomenon of heterosis, where in the next generation the seeds from some pollinations give positive results such as an increase in growth rate, yield, etc., whilst in plants raised from other pollinations no increase or even a decrease occurs. In the case of xenia the effect is on the maternal tissue of the potential female parent and in heterosis in the resulting zygote or its offspring. Parthenocarpy and heterosis, indeed all conditions between none and many, bad and good, small and large seeds; may affect the maternal tissue, and such conditions are determined by the absence of or kind of pollen that takes part, or potentially takes part, in fertilization as is diagrammatically shown in Fig. 3. In this figure apomixis is used in a broad sense and includes pseudogamy.

All cases of so-called xenia in which the maternal tissue is affected are doubtless due to differences in the constitution and development of the embryo. That is to say, embryonic differences are transferred to and expressed in the maternal tissues. In most cases no seeds, few seeds or small seeds result in smaller fruits, and often in earlier ripening. In

the exceptional cases where late ripening and small seeds go together, it is probably due to a slower rate of embryonic development occurring in the later than in the earlier ripening cases.

SUMMARY

In plums different pollinations can result in differences in the time of maturity and in the size of the fruit. The pollen influences the development of the fruit inasmuch as defective embryos promote earlier ripening and smaller fruits. Further, the wider the difference between the two parents, the more defective the embryos. The developmental differences in the fruit are an expression of different degrees of seed growth.

In some varieties of pears frost injury to the styles induces parthenocarpy, i.e. the complete absence of embryo development.

Difference in the fruit due to the action of the pollen (formerly known as xenia) fall into three classes: (1) where the developing zygote is affected, (2) where the endosperm is affected, (3) where the effect is on the maternal tissues. In classes (1) and (2) the effects or differences are due to the action of paternal genes in heredity, and since they are readily explicable on a simple genetic basis there is no reason why they should continue to be referred to as xenia. In class (3) they are due to differences in the constitution and development of the embryo, endosperm and seed which affect the development of the maternal tissue. At one extreme the fruits are seedless (parthenocarpy), and at the other they have seeds larger than normal.

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