# AN INQUIRY INTO THE FACTORS AFFECTING THE SHAPE OF BARTLETT PEAR FRUITS, WITH SPECIAL REFERENCE TO XENIA, METAXENIA AND POLLINATION

by

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## INTRODUCTION

The growth of an individual fruit during development progresses according to a genetic pattern so that at maturity its shape is generally closely similar to that of all other fruits within the same variety. This constancy in shape provides a characteristic which is used by horticulturists in the taxonomic description and identification of varieties, and contributes toward uniformity in the handling and marketing of fruits. Under the influence of certain external factors, however, the genetic pattern may become altered resulting in the development of an abnormal shape, uncharacteristic for the variety. Similar varieties grown in different geographical areas often differ considerably in shape, and even within the same area considerable variations may occur. The Bartlett pear, for example, has a characteristic shape described as oblong-obtuse pyriform, but this variety grown in the Willamette Valley and in certain other areas (86) sometimes assumes an entirely different form during growth. From the commercial standpoint, this abnormality is undesirable since it detracts from the value of the

product, especially when used for canning. Yield also is reduced, because the fruits generally fail to develop to the optimum stage of maturity for commercial use.

Previous investigations (85,86,96) have shown that the abnormal shape of Bartlett pears is associated with failure of the fruit to form seeds, resulting in parthenocarpic development. This suggests that the seedless condition is due to lack of effective pollination and that xenia and metaxenia may be factors affecting the shape of the fruits. Accordingly, the variation in the shape of the Bartlett pear as grown in the Willamette Valley has been approached from the standpoint of pollination and the effects of pollen along the following lines:

(1) The viability, germination and rate of tube growth of different pollens, (2) the influence of growth-regulating chemicals on fruit development and shape, (3) the relationship between xenia and metaxenia following self- and cross-pollination, especially in relation to embryogeny and fruit development, (4) the correlation between the nature and time of development of specific fruit tissues with the variations in fruit shape.

## MATERIALS AND METHODS

Methods of Pollination. The pollination experiments were conducted during the years 1938, 1939, and 1940 at a commercial orchard located near Corvallis, Oregon. Five male parents - Fall Butter, Winter Nelis, Comice, Anjou, and Bartlett - were used for the pollination of the Bartlett pear flowers.

The pollen required for the experiments were collected by forcing the flowers on fruit spurs which had been brought into the laboratory during the pre-pink stage. The pollen was dried and stored at room temperature in vials for future use. All of the pollination and artificial germination experiments were made within 10 days after the pollen had been gathered.

The procedure used in the pollination experiments consisted of emasculation followed by hand pollination with a camel's hair brush. The pollinated clusters were then bagged with Manila paper bags and tagged with the proper labels. For the study of parthenocarpy, the blossoms were emasculated only and then bagged. In the case of self-pollination, two different methods were employed: (1) emasculation followed by hand pollination, and (2) bagging of the flower clusters without emasculation.

Growth-promoting chemicals including indole-3-n-

butyric acid, indole-3-n-acetic acid, indole-3-n-propionic acid, and asparagine were prepared in aqueous solutions of 0.01 to 0.25 per cent. These were then sprayed on the flowers by means of a hand atomizer either preceding or following hand pollination.

Histological Methods. For the purpose of morphological studies relating to xenia and metaxenia, specimens were collected at intervals both before and after pollination. These samples were killed and fixed in three different fixatives: alcohol-formalin solution, Tukey's (88) killing and fixing solution, and Nawaschin's fluid as given by Chamberlin (15). Nawaschin's fluid was used mainly for the ovules while the other two solutions gave satisfactory results with the flowers and fruits. To facilitate removal of air from the tissues, the vials containing the materials in the fixing solutions were placed in a vacuum desicator. This treatment greatly improved the infiltration of paraffin into the tissues.

For the dehydration of the materials, the butyl alcohol schedule given by Rawlins (72) was followed without modification. The usual paraffin infiltration method was employed with the exception that the samples were left in the paraffin for a much longer period of time than specified.

The sections for the morphological studies were

cut either with a rotary or sliding microtome to a thickness of 15 to 18 microns. With the larger and coarser materials the latter gave much better results.

Heidenhain's iron alum-haematoxylin stain was used exclusively according to the complete schedule given by Rawlins (72).

In connection with the histological studies on the development of fruits, the number of cells were counted at different levels (Fig. 1, Plate VII). For this purpose a cross hair tube placed inside the eye piece gave satisfactory results. This tube was prepared by attaching a human hair across the middle of a round cardboard tube fitted inside the eye piece of the microscope. The counts on the number of cells were made along the line of the image of the hair reflected on the section. This method was found to be much simpler than the one adapted by Kim (41) for a similar purpose.

Pollen Germination Methods. The media employed for the artificial germination tests of pollen consisted of the following: distilled water; 10 and 12 per cent solutions of sucrose, glucose, and fructose; 1.5 per cent agar solution either with or without the addition of sugar; various solutions of growth-promoting chemicals added to the sugar solutions; styler and

ovarian extracts of different varieties of pears; and pieces of gynoecium of pear mixed with different media.

All of the germination tests were made either on glass slides or on Van Tieghem cells placed in a moist chamber lined with wet filter paper. The chambers were kept at room temperature during observation and measurement of the rate of germination and pollen tube growth.

## LITERATURE REVIEW

Xenia and Metaxenia. The terms xenia and metaxenia have been used in various ways. Focke(32) used the term xenia in a general way to designate the deviations from the normal color or shape of a fruit through the influence of a foreign pollen. Swingle (81), however, limited this term to define the influence of foreign pollen on the embryo and endosperm, while metaxenia was proposed to designate the changes brought about on the tissues of the fruit other then the embryo and endosperm. Nebel (63) agrees with Swingle in the interpretation and usage of these terms.

The presence of xenia and metaxenia in fruits has been reported by a number of investigators. The most important characteristics found to be influenced

by pollen have been the number of seeds formed and the shape, weight and keeping quality of the fruit. Color, acidity, and certain other physical and chemical characteristics have been affected to a lesser extent. Nebel (63, 64), Nebel and Trump (66), Nebel and Kertesz (67) reported the presence of xenia in apples as expressed in the length and number of the seeds. Reineke (74), Waite (96), Tydeman (93), and Cummings et al (21) observed that in pears self-pollination resulted in less seed formation than cross-pollination. Waite also reported the influence of pollen on the characteristics of seeds in pears. The influence of pollen (xenia) expressed in the formation of seeds has been reported in persimmon (6), gooseberry (17), apple (19, 50, 93, 97), plum (19), and cherry (20). Nebel (64, 65), Nebel and Trump (66), Nebel and Kertesz (67), claimed the presence of metaxenia in the apple affects weight, keeping quality, acidity, shape, and color of the fruits. Reineke (74), Bach (8, 9), Zederbauer (102), Waite (96), and Cummings et al (21), reported the variation in the shape of the apple and pear through the influence of pollen. The effect of metaxenia on the weight, size, and shape of the fruits of apple (3, 19, 50, 97), persimmon (6), gooseberry (17), plum (19,20), cherry (19, 20), melons (92), and tomatoes (59) has been reported

by many investigators.

Self-unfruitfulness and inter-fruitfulness are common among horticultural plants. This phenomenon is brought about through the influence of pollen on the female parent, and can be considered as one of the most important aspects in the study of metaxenia. Munson (59) believes that in some important plant species there is an immediate apparent effect of foreign pollen on the female organism, the most outstanding example being the pea, the kidney bean, and the Indian corn. Roh (76) stated that the presence of xenia and metaxenia in tree fruits should be considered a normal condition.

The presence of xenia and metaxenia among the horticultural plants has been denied by some investigators. Gowen (35) and Wicks (98) working on the apple did not find any change in size, color, shape, and quality of fruits due to the influence of the pollen parents. The former, however, stated that Baldwin and Ben Davis were exceptions in this respect. Tufts and Hansen (86, 87) claimed that according to the results of their investigations there seems to be no significant indication of xenia and metaxenia in pears. Shaw (79, 80) reported that the greater elongation of apple fruits is closely related with the cool temperature for 2 to 3 weeks following the blooming time. Fletcher (31) be-

lieves that while the variation in size of the Bartlett and Kieffer pear fruits is influenced by the kind of pollen used for pollination, the variation in shape is due more to the specific environmental conditions under which the fruits are grown.

Pollination and Sterility. The pollination and sterility problems of horticultural plants have received attention by many investigators.

Some of the more important causes for self-or inter-sterility are: genetic factors; slowness of pollen tube growth in styles; defectiveness of pollen, ovule and embryo-sac; secretion of inhibiting substances by the pistils; and certain environmental conditions such as temperature and amount of rainfall. Cummings et al (21) and Osterwalder (69) after an extensive study on the sterility of pears concluded that the self-sterility is due to the slowness of pollen tube growth and not to the defectiveness of pollen. The slow growth of pollen tube in the pistil has been reported as the main cause of self-sterility in various other plants, including Nicotina (25, 26), apple (35, 75), Secale (40), black currant (49), clover and alfalfa (58), plum (20,77), cherry (20), and other plants.

Yasuda (100) and Crane (20) believe that the incompatibility is due to the inhibition of pollen tube growth in the style. Dorsey (24) thinks that the steri-

lity or fertility is probably caused by the quantity and quality of hormone secretions by the female gametophyte during the period of pollen tube growth in the style and also by the genetic factors of the plant. Defective ovules and embryo-sacs and low viability of pollen appear to be correlated with the failure of seed formation in grapes (68, 70), pears (78), and strawberry (94). Maturity and age of pollen, vigor of fruit spurs, age and health of individual tree and other factors may influence pollination of the apple, according to Auchter (7).

The Bartlett pear appears to be better pollinized by certain varieties than others. Feltcher (31) reported that Anjou, Lawrence, Duchess, and Kieffer are satisfactory pollinizers under Virginia conditions. In California, Tufts (84) found no case of inter-sterility among pear varieties provided that the blooming dates of the two varieties over-lap each other. He recommends Angouleme, Anjou, Clairgeau, Comice, Dana Hovey, Easter Howell, and Winter Nelis as satisfactory pollinizers for Bartlett. Bartlett pears grown under valley conditions, however, were found to be more self-fruitful than those grown in the foothills sections. In Western Oregon, Kraus (44) advised planting Clairgeau, Anjou, Howell, and Kieffer with Bartlett to assure a satisfactory fruit set. Marshall et al (55) stated

that in Michigan only Flemish Beauty can be considered as self-fruitful and that Bosc, Conference, Flemish Beauty and Howell are satisfactory pollinizers for Bartlett. In Germany Schanderl (78) made pollination studies with 198 varieties of pears. According to him no pear variety is self-fruitful enough to produce sufficient amount of fruits for commercial purposes with the exception of Bergamotte Esperen. He mentioned that Buerré Napoleon produced only seedless fruits even after cross-pollination. According to Nagai (61) and Asami (4,5) a majority of the Japanese pears are self-sterile.

Pollen Germination and Pollen Tube Growth. Van Tieghem (95) appears to have been the first investigator to observe pollen germination. Since that time much attention has been paid to the study of pollen germination and tube growth both under artificial and natural conditions.

The slowness of pollen tube growth has been found to be of common occurrence in the case of self-or intersterility. Osterwalder (69) observed that pollen tube growth in selfed pear blossoms ranges from 2 to 4 mm. in a style of 10 mm. in length. Cummings et al (21) working on pollination of the Bartlett pear, found that for the first 18 hours after pollination the growth of pollen tube in both self- and cross-pollinated blossoms

was about the same. However, in the former the tube growth was much retarded at the end of 24 hours and ceased entirely after 12 days. Similar results have been reported with the apple by Eckerson (28) and Knight (42).

Pollen of different plants has been found to vary greatly in germinating ability. Tufts (84) reported 32 per cent germination for Anjou, 19 to 76 per cent for Bartlett, 43 to 74 per cent for Comice, and 36 to 45 per cent for Winter Nelis in 12 per cent sucrose solution. Tufts and Philp (85) stated that pear pollen on the average does not give as high germination as some of the other fruits, although a sufficient number of pollen germinate to assure pollination when the pollen is applied artificially. According to Cummings et al (21), 0.4 M neutral solutions of sucrose and glucose at a temperature of 80° F gave the best results in artificial germination of pear pollen. They also state that in general Bartlett pollen grew better in glucose than in sucrose. Apparently, however, a few varieties of pears produce pollen which fail to germinate under artificial conditions (73). Other investigators have found also that the germination and rate of tube growth vary greatly among different plants according to the kind and concentration of sugar used in the

media (26, 34, 94, 56).

Various substances have been found to stimulate or retard the rate of pollen tube growth. Eckerson (28) and Knight (42) found asparagine to have a stimulative effect on the tube growth of apple pollen. No effects from extracts of stigmata were observed. Osterwalder (69) likewise reported that the addition of stigmatic extracts to the germination media had no beneficial effect. Cooper (16), however, found that the addition of the extracts of pistil and ovary in the germination media retarded germination and tube growth of apple pollen, while Beaumont and Knight (10) obtained increased germination and accelerated tube growth of apple pollen by the addition of stylar extracts and pieces of stigmata from inter-compatible varieties in the media. Similar favorable effects have been observed with snapdragon (43) and petunia pollen (100).

The factors affecting viability have an important bearing on the germination of pollen. Becker (11) found that older plum pollen to be less viable than younger pollen. Pollen remains viable over a longer period when stored under dry conditions at low temperatures than at high temperature and humidity (1, 34, 43). Apple pollen germinated well after 3 months and pear pollen after 10 weeks when stored in a dry condi-

tion (1). Sandsten (77), however, found that the pollen of apple and plum under dry conditions and at temperatures ranging from 7 to 26° C survived for 6 months or longer. Crandell (18) noticed no material difference in the effectiveness of 1 to 11 days old apple pollen.

The food supply and enzymes present in various kinds of pollen have been studied by many investigators. Green (36) isolated invertase and diastase from pollen grains, but was unable to isolate cytase. He concluded that the reserve foods of the pollen grains are starch, dextrin, cane sugar, maltose, and glucose. The style contains the same substances with the exception of dextrin. Sandsten (77) found that diastase and invertase are present in pollen of most plants and that the styles and stigmata of certain plants contain these enzymes. Miyoshi (57) and Knowlton (43) reported the presence of chemotropism in the pollen tube. The former stated that pollen tubes tend to grow from a weak solution to a stronger one.

The phenomenon of bending and septation of pollen tubes under both natural and artificial conditions has been observed. Pollen tubes of peer (69), apple (42), and plum (24) form septa in artificial media. Latimer (48) reported callose formation on apple pollen tubes.

Roberts (75) and Yasuda (100) reported that following self-pollination the pollen tubes of apple and petunia became knotted, but remained straight after cross-pollination.

Parthenocarpy and Growth-Promoting Chemicals. Holly (33), Strawberry (33), tomatoes (37, 38), crook-necked summer squash (37), cucumber (99), water melon and pepper (99) can be induced to form parthenocarpic fruits by applying growth-promoting chemicals to the pistils. The reagents found to be effective were indoleacetic, indolepropionic, indolebutyric, napthaleneacetic, and phenylacetic acids. Apples and grapes, however, failed to form parthenocarpic fruits after treatment with these substances. Yasuda (101) claimed that the ovaries of egg-plant injected with petunia pollen extract and cucumber ovaries injected with its own pollen extract resulted in parthenocarpic growth.

Morphology and Development of Fruit and Embryo. While the literature relating to the embryogeny and development of certain fruits of the family Rosaceae is extensive (2,13,14,29,41,53,60,69,71,81,82,83,90,91), only a limited amount of information is available on the morphology of the pear fruits. Osterwalder (69) has investigated the embryogeny of the Bartlett pear. MacDaniels (53) found that the gross morphology of the

Kieffer pear fruit to be basically the same as that of the apple, with minor differences. Murneek (60) reported on the differential development of various tissues of the Bartlett pear fruit during the maturation phases of the growth period.

## PRESENTATION OF DATA

### POLLINATION EXPERIMENTS

Table I shows the results of Bartlett pear pollination experiments conducted during the years 1938, 1939, and 1940.

TABLE I - POLLINATION OF THE BARTLETT, 1938-1940
at Corvallis, Oregon
(Data Taken After June Drop)

| Pollination | No. Blossoms Used | | | No. Fruits Set | | | Percentage Set | | |
|---|---|---|---|---|---|---|---|---|---|
| | 1938 | 1939 | 1940 | 1938 | 1939 | 1940 | 1938 | 1939 | 1940 |
| Bartlett X Self Sacked only | 740 | - | - | 1 | - | - | 0 | - | - |
| Pollinated X Fall Butter | 770 | 731 | 1342 | 15 | 52 | 49 | 2 | 7 | 4 |
| X Anjou | 644 | 760 | 889 | 112 | 83 | 99 | 17 | 11 | 11 |
| X Winter Nelis | 160 | 511 | 559 | 5 | 77 | 61 | 3 | 15 | 11 |
| X Bosc | 504 | 612 | 1217 | 57 | 99 | 117 | 11 | 16 | 10 |
| X Comice | 142 | - | 795 | 0 | - | 52 | 0 | - | 7 |
| X Open | 104 | 520 | - | 50 | 65 | - | 48 | 14 | - |
| X None (Emasculated and Sacked | 1348 | 1778 | 1794 | 51 | 58 | 23 | 4 | 3 | 1 |
| | 105 | 466 | 1166 | 0 | 17 | 38 | 0 | 4 | 3 |

According to the data, the varieties Fall Butter, Winter Nelis and Comice were cross-fruitful and Bosc cross-unfruitful with Bartlett during all of the three seasons. Self-pollination resulted in a low fruit set. There was, however, an appreciable difference in the number fruit set between the self-pollinated flowers and those which were emasculated and received no pollen. These results definitely show that both aitionomic or stimulative and autonomic or vegetative parthenocarpic developments may occur in Bartlett pear fruits.

The application of growth-promoting chemicals to the pistils at the time of anthesis has shown to induce parthenocarpic development in various fruits (33, 37, 38, 99). To determine if similar effects can be obtained with Bartlett pear, application of aqueous solutions of these reagents in various concentrations were made on the pistils at the time of pollination. The experimental results are summarized in table II.

TABLE II - EFFECT OF GROWTH-PROMOTING SUBSTANCES ON THE FRUIT SET OF THE BARTLETT, 1938, 1939 at Corvallis, Oregon (Data Taken After June Drop)

| Pollination | Chemicals | No. Blossoms Used 1938 | No. Blossoms Used 1939 | No. Fruits Set 1938 | No. Fruits Set 1939 | Percentage Set 1938 | Percentage Set 1939 |
|---|---|---|---|---|---|---|---|
| Bartlett | | | | | | | |
| X | None ---------- | 105 | 466 | 0 | 17 | 0 | 4 |
| X | None 0.04% Asparagine | --- | 191 | --- | 14 | --- | 2 |
| X | None 0.25% Indoleacetic Acid | 220 | --- | 0 | --- | 0 | --- |
| X | None 0.04% Indoleacetic Acid | --- | 269 | --- | 9 | --- | 3 |
| X | None 0.04% Indolebutyric Acid | --- | 313 | --- | 9 | --- | 3 |
| X | None 0.04% Indolepropionic Acid | --- | 189 | --- | 3 | --- | 2 |
| X | None 0.01% Indoleacetic Acid | --- | 85 | --- | 5 | --- | 6 |
| X | None 0.01% Indolebutyric Acid | --- | 185 | --- | 2 | --- | 1 |
| X | None 0.01% Indolepropionic Acid | --- | 71 | --- | 4 | --- | 6 |
| X | Self ---------- | 770 | 731 | 15 | 52 | 2 | 7 |
| X | Self 0.04% Asparagine | 66 | 145 | 2 | 12 | 3 | 8 |
| X | Self 0.25% Indoleacetic Acid | 48 | --- | 1 | --- | 2 | --- |
| X | Self 0.04% Indoleacetic Acid | --- | 418 | --- | 30 | --- | 7 |
| X | Self 0.04% Indolebutyric Acid | --- | 82 | --- | 3 | --- | 4 |
| X | Self 0.04% Indolepropionic Acid | --- | 140 | --- | 3 | --- | 2 |
| X | Self 0.01% Indolebutyric Acid | --- | 120 | --- | 7 | --- | 6 |

None of the growth-promoting chemicals (Table II) had any significant stimulative effect on the number of fruits set. Although asparagine was observed to accelerate fruit growth immediately following its application, the slight increases in final number of fruits set is not significant.

In the spring of 1938 and 1939 pollination experiments were conducted using Anjou variety as female parent in order to study the influence of different pollen, particularly that of Bartlett pollen on the fruit set of this variety.

TABLE III - POLLINATION OF THE ANJOU, 1938, 1939
at Corvallis, Oregon
(Data Taken After June Drop)

| Crosses | 1938 | | | 1939 | | |
|---|---|---|---|---|---|---|
| | No. of Blossoms Used | No. of Fruits Set | Per-cent Set | No. of Blossoms Used | No. of Fruits | Percent Set |
| Anjou | | | | | | |
| X Self | 314 | 0 | 0 | 571 | 3 | 0.5 |
| X Bartlett | 45 | 62 | 13.1 | 563 | 31 | 5.5 |
| X Bosc | 126 | 11 | 8.7 | --- | --- | --- |
| X Winter Nelis | 127 | 6 | 4.6 | --- | --- | --- |
| X Fall Butter | -- | --- | --- | 257 | 6 | 2.3 |
| X Open | 1693 | 9 | 0.5 | 713 | 34 | 4.8 |
| X None | 356 | 0 | 0 | 86 | 0 | 0 |

Table III shows that Anjou is self-unfruitful and that Bartlett is the most effective pollinizer for the Anjou pear followed by Bosc and Winter Nelis. Fall Butter is not as good a pollinizer for Anjou as for Bartlett. Although the results presented here are not conclusive, the fact that Bartlett pollen is capable of affecting fertilization is clearly evident.

## ARTIFICIAL POLLEN GERMINATION AND TUBE GROWTH

Defective Pollen. The physical defectiveness and physiological inability of pollen to germinate would be contributing factors toward self-and inter-sterility. Accordingly, microscopic examinations were made in order to determine the percentage of defective pollen of Bartlett, Anjou, Fall Butter, Comice, and Winter Nelis pears in 1938 and 1940. The pollen of these varieties were placed in water on glass slide and counts were made on the number of defective pollen.

TABLE IV - PERCENTAGE OF DEFECTIVE POLLEN OF DIFFERENT PEAR VARIETIES, 1938, 1940

| Pollen Variety | No. Pollen Examined 1938 | 1940 | No. Defective Pollen 1938 | 1940 | Percentage Defective Pollen 1938 | 1940 |
|---|---|---|---|---|---|---|
| Bartlett | 539 | 293 | 24 | 43 | 5 | 15 |
| Anjou | 543 | --- | 25 | --- | 5 | --- |
| Fall Butter | 578 | 181 | 65 | 49 | 13 | 25 |
| Comice | 523 | --- | 12 | --- | 2 | --- |
| Winter Nelis | 580 | 241 | 32 | 14 | 6 | 6 |

The percentage of defective pollen of the 5 peer varieties ranged from 2 to 25 (Table IV ). The percentage of defective pollen was higher in Bartlett and Fall Butter varieties in 1940 than in 1938. There seems to be a close relationship between the variation in size of pollen and the percentage of defectiveness (Fig. 1, 2, 3, Plate II). The pollen of Fall Butter, for example, which shows the widest variation in size has the highest percentage of defectiveness, while Comice pollen which is uniform in size has the lowest number of defective pollen.

Effect of Media on Pollen Germination and Tube Growth. Germiability of pollen has an important bearing on the effectiveness of the pollen as a pollinizer.

Consequently, artificial germination of pollen and the growth of the pollen tube were tested in various media (Table V).

TABLE V - EFFECT OF DIFFERENT MEDIA ON THE GERMINATION OF BARTLETT AND ANJOU PEAR POLLEN, 1938
(At Room Temperature)

| Media (All Media in Water) | Growth Period in Hours | Bartlett | | | Anjou | | |
|---|---|---|---|---|---|---|---|
| | | No. Pollen | No. Germ. | Percent Germ. | No. Pollen | No. Germ. | Percent Germ. |
| Distilled water | 3½-5 | 47 | 17 | 36 | 95 | 20 | 21 |
| Sucrose 10% | 5- 6 | 70 | 17 | 24 | 41 | 18 | 44 |
| Sucrose 10% - Asparagine 0.25% | 5- 6 | 49 | 13 | 27 | 48 | 22 | 46 |
| Sucrose 10% - Indoleacetic Acid 0.25% | 5- 6 | 50 | 0 | 0 | 60 | 0 | 0 |
| Glucose 10% | 4- 5 | 136 | 37 | 27 | 50 | 20 | 40 |
| Glucose 10% - Asparagine 0.25% | 4- 5 | 160 | 61 | 38 | 88 | 26 | 28 |
| Glucose 10% - Indoleacetic Acid 0.25% | 4- 5 | 75 | 0 | 0 | 50 | 0 | 0 |
| Asparagine 0.25% | 4- 5 | 148 | 25 | 17 | 114 | 10 | 9 |
| Indoleacetic Acid 0.25% | 4- 5 | 80 | 0 | 0 | 60 | 0 | 0 |
| Fructose 10% | 5 | 64 | 8 | 13 | 57 | 3 | 5 |
| Fructose 10% - Asparagine 0.25% | 5 | 80 | 10 | 13 | Most Pollen Bursted | | |
| Fructose 10% - Indoleacetic Acid 0.25% | 5 | 70 | 0 | 0 | 50 | 0 | 0 |

An examination of Tables V and VI shows that there is much variation in the ability of pollen to germinate in different kinds of media. The percentage germination and rate of pollen tube growth were higher in sucrose and glucose than in fructose. Asparagine had no influence on germination but it definitely caused an increase in tube growth. Indoleacetic acid used at a concentration of 0.25 per cent alone or in a combination with sugar showed an inhibitive effect on pollen germination. Lower concentrations of indolebutyric acid had neither an inhibitive nor a stimulative effect on the rate of germination and tube growth of pollen of different pear varieties (Table VI).

TABLE VI - EFFECT OF 0.001 PER CENT INDOLEBUTYRIC ACID ON THE RATE OF GERMINATION AND TUBE GROWTH OF PEAR POLLEN, 1939
(At Room Temperature)

| Media (All in Water) | Growth Period in Hours | Pollen | No. Pollen | No. Germ. | Percentage Germ. | Max. Tube Length (μ) | Min. Tube Length (μ) | Ave. Tube (μ) |
|---|---|---|---|---|---|---|---|---|
| Sucrose 10% | 19 | Bartlett | 117 | 52 | 44 | 324 | 15 | 41 |
| " | 19 | Anjou | 117 | 24 | 21 | 216 | 18 | 49 |
| " | 19 | Fall Butter | Most Pollen Bursted | | | | | |
| " | 19 | Winter Nelis | 103 | 7 | 7 | 20 | 5 | 10 |
| " | 19 | Comice | 104 | 15 | 14 | 160 | 15 | 34 |
| Sucrose 10% -IBA* 0.001% | 19 | Bartlett | 86 | 13 | 15 | 29 | 7 | 14 |
| " | 19 | Anjou | 111 | 42 | 38 | 216 | 20 | 48 |
| " | 19 | Fall Butter | 136 | 17 | 13 | 328 | 18 | 38 |
| " | 19 | Winter Nelis | 111 | 7 | 6 | 20 | 6 | 10 |
| " | 19 | Comice | 107 | 13 | 12 | 220 | 10 | 37 |

IBA* -Indolebutyric Acid

In distilled water medium, pollen of Bartlett, Anjou, Winter Nelis, and Comice showed no difference in the percentage of germination or rate of tube growth after 2 and 10 hour periods. In Winter Nelis, however, both the number of pollen germinated and the length of

the pollen tubes were considerably greater at the end of 10 hours (Table VII). These results indicate that the pollen of most pear varieties are low in food reserves and require an additional nutrition in order to make a growth of 10 mm. which is the length of an average pear pistil.

TABLE VII - THE RATE OF POLLEN GERMINATION AND TUBE GROWTH IN WATER MEDIUM, 1939
(At Room Temperature)

| Media | Growth Period in Hours | Pollen | No. Pollen | No. Germ. | Percentage Germ. | Max. Tube Length (μ) | Min. Tube Length (μ) | Ave. Tube Length (μ) |
|---|---|---|---|---|---|---|---|---|
| Water | 2 | Bartlett | 208 | 44 | 21 | 54 | 6 | 15 |
| " | " | Anjou | 249 | 36 | 15 | 26 | 5 | 14 |
| " | " | Winter Nelis | 215 | 18 | 8 | 10 | 3 | 6 |
| " | " | Fall Butter | 227 | 38 | 17 | 18 | 4 | 9 |
| " | " | Comice | 200 | 26 | 13 | 44 | 5 | 7 |
| " | " | Bartlett | 223 | 44 | 20 | 63 | 5 | 15 |
| " | " | Anjou | 246 | 42 | 17 | 55 | 5 | 15 |
| " | " | Winter Nelis | 225 | 37 | 16 | 11 | 4 | 7 |
| " | " | Fall Butter | 221 | 40 | 18 | 270 | 5 | 23 |
| " | " | Comice | 221 | 23 | 10 | 38 | 5 | 17 |

Effect of Gynoecia on the Rate of Pollen Germination and Tube Growth. Germination tests were made using media containing pieces or extracts of styles and ovaries of Bartlett and Winter Nelis pear varieties.

TABLE VIII- EFFECT OF PIECES OR EXTRACTS OF BARTLETT AND WINTER NELIS GYNOECIA ON THE RATE OF GERMINATION AND TUBE GROWTH OF PEAR POLLEN, 1939-1940
At room temperature

| Media (in Water) | Growth Period in Hours | Pollen | No. Pollen | No. Germ. | Percentage Germ. | Max. Tube Length (μ) | Min. Tube Length (μ) | Ave. Tube Length (μ) |
|---|---|---|---|---|---|---|---|---|
| 10% Sucrose | 2 | Bartlett | 88 | 21 | 24 | 30 | 9 | 15 |
| " | 2½ | Anjou | 117 | 8 | 7 | 32 | 5 | 18 |
| " | 2½ | Fall Butter | 100 | 16 | 16 | 84 | 20 | 40 |
| " | 3 | Winter Nelis | 101 | 4 | 4 | 15 | 5 | 9 |
| " | 3½ | Comice | 102 | 7 | 7 | 140 | 7 | 10 |
| 10% Sucrose-Bartlett or Gynoecia pieces | 2 | Bartlett | 85 | 30 | 35 | 59 | 15 | 39 |
| | 2½ | Anjou | 100 | 64 | 64 | 238 | 40 | 77 |
| | 2½ | Fall Butter | 143 | 40 | 28 | 324 | 40 | 123 |
| " | 3 | Winter Nelis | 115 | 18 | 16 | 110 | 42 | 76 |
| " | 3 | Comice | 81 | 18 | 22 | 290 | 55 | 149 |
| Winter Nelis Stylar Extract | 4 | Winter Nelis | Very slight germination; much pollen bursted. | | | | | |
| | 4 | Bartlett | Slightly more germination than Winter Nelis pollen | | | | | |
| | 4 | Fall Butter | " | " | " | " | | |
| Bartlett Stylar Extract | 4 | Winter Nelis | Very slight germination | | | | | |
| | 4 | Bartlett | " | " | " | | | |
| " | 4 | Fall Butter | No germination | | | | | |

The results show (Table VIII) that both germination and rate of tube growth were greatly stimulated in media containing pieces of styles and ovaries. The growth of Anjou, Fall Butter, Winter Nelis and Comice pollen was stimulated to a much greater extent than that of Bartlett pollen. Aqueous extracts of these materials, however, almost entirely inhibited pollen germination (Fig. 5, Plate III). Similar results have been reported by Cooper (16), Knowlton (43), and Yasuda (100).

A third series of pollen germination experiments using agar media in combination with sugar and styler pieces were conducted in 1940. The experimental results are summarized in Table IX.

TABLE IX - THE RESULTS OF PEAR POLLEN GERMINATION IN AGAR, AGAR-SUGAR, AGAR-SUGAR-STYLE MEDIA, 1940
(At Room Temperature)

| Media | Growth Period in Hours | Pollen | No. Pollen | Percentage Germ. | Max. Tube Length (u) | Min. Tube Length (u) | Ave. Tube Length (u) |
|---|---|---|---|---|---|---|---|
| 1. 5% Agar | 4 | Bartlett | Most pollen bursted | | | | |
| " | 4 | Fall Butter | " | " | " | | |
| " | 4 | Winter Nelis | " | " | " | | |
| 1. 5% Agar- 12% Sucrose | 3 | Bartlett | 100 | 5 | 108 | 43 | 84 |
| " | 3 | Fall Butter | 100 | 28 | 276 | 55 | 131 |
| " | 3 | Winter Nelis | 100 | 52 | 230 | 55 | 108 |
| 1. 5% Agar- 12% Glucose | 3½ | Bartlett | 100 | 1 | 43 | 15 | 30 |
| " | 3½ | Fall Butter | 100 | 20 | 85 | 42 | 59 |
| " | 3½ | Winter Nelis | 100 | 26 | 115 | 43 | 74 |
| 1. 5% Agar-12% Sucrose - Pieces Bartlett Style | 4½ | Bartlett | 100 | 93 | 864 | 85 | 538 |
| | 4½ | Fall Butter | 100 | 95 | 1026 | 160 | 374 |
| " | 4½ | Winter Nelis | 100 | 98 | 1000 | 160 | 414 |

The results show (Table IX) that the media containing agar only resulted in bursting of the pollen (Fig. 3, Plate III). Agar media containing sucrose gave a higher percentage of germination and a greater rate of

tube growth than the glucose-agar media. (Fig. 5, Plate II and Fig. 1, Plate III).

As in the sugar-only media, the addition of stylar pieces to the agar-sugar media had a striking effect on both the germination and tube growth (Fig. 2, Plate III). The extremely high percentage of pollen germination and the accelerated tube growth in the media containing stylar pieces suggest the presence of a certain physiological affinity between the pollen and the style. This condition has been observed in all of the experiments (Table VIII, IX).

It is interesting to note that the pollen of Winter Nelis, which showed the least germination and tube growth in the media containing no agar, had the highest rate of germination and tube growth in the agar media. This fact suggests that under ideal conditions the pollen of Winter Nelis will germinate and grow as much or even better than the pollen of other pear varieties. (Fig. 5, Plate II and Table IX).

The formation of septa on pollen tube has been reported by many investigators (24, 42, 69, 75, 100). It has been observed during the present work that pollen tubes under unfavorable conditions tend to form septa (Fig. 1, Plate III). More septation occurred on pollen tubes in the media containing glucose than in those containing sucrose (Fig. 1, 2, Plate III). According to the

results of the present experiments on the artificial germination of pollen, the former sugar is much inferior to the latter as a germination medium for pear pollen. Cummings et al (21), however, obtained better germination of pear pollen in glucose than in sucrose media.

The data obtained during the course of the pollination and pollen germination experiments appear to warrant the following conclusions. In the Willamette Valley the varieties Fall Butter and Winter Nelis are cross-fruitful with Bartlett, while Anjou appears to be partially cross-fruitful. The choice between Fall Butter and Winter Nelis as pollinizers would depend upon whether the blooming period in any particular area coincides or over-laps with that of Bartlett. The use of Anjou as pollinizer for the Bartlett variety appears questionable until pollination tests have been carried out over a longer period of time.

The failure for obtaining satisfactory fruit set of the Bartlett pear following self-pollination is not due to any inherent or physical defectiveness of the pollen. This is indicated by the ability of Bartlett pollen to effect fertilization of the Anjou pear and the satisfactory viability and germinating ability of the pollen in artificial media. Self-unfruitfulness in the case of the Bartlett pear appears to be due mainly, if not entirely, to the slow growth of the pollen tube

through the style. The evidence obtained strongly indicates that the stylar tissues of pear varieties can exert either an inhibiting or stimulating effect upon the growth of the pollen tubes. This phenomenon may account at least in part for the observed self-or intercompatibility among fruit varieties.

## ONTOGENY OF BARTLETT PEAR FRUIT IN RELATION TO XENIA AND METAXENIA

The pattern for the shape and size of a mature fruit is formed during the early stages of growth. Activities of cell division, increase in cell size, and enlargement of intercellular spaces are the contributing factors to this pattern. In order to determine the relation of xenia and metaxenia to these growth and development processes, morphological studies were made on the Bartlett pear fruits developing after both self-and cross-pollination.

Megagametophyte. The megaspore mother cell of the Bartlett pear is distinguishable about 3 weeks before anthesis (Fig. 1, Plate IV). About 3 to 4 days before full bloom the typical 8-nucleate embryo-sac, containing 4 nuclei at the chalazal end and the other 4 near the micropylar region, is formed. Shortly before full bloom, each of the 4 nuclei at the chalazal end

divides again resulting in the formation of 8 nuclei. Those located at the micropylar zone remain undivided. One of the former group of nuclei migrates toward the center of the embryo-sac followed by the other polar nucleus from the micropylar end. These two polar nuclei remain separate but in close proximity until full bloom, at which time the fusion between them takes place. This fusion nucleus later becomes the primary endosperm nucleus. Thus, the embryo-sac of the Bartlett pear flower contains 1 egg nucleus, 2 synergids, 1 fusion nucleus and 7 antipodals at the time of full bloom (Fig. 2, Plate IV). The writer has no knowledge of any reference to the number of antipodals in the pear being 7 instead of 3. Osterwalder (67) gave the number of antipodals in the "Gute Louise" variety as 3. The number of antipodals, even in the same species, appears to be variable. A further study on the varietal differences among the pears in this respect would be of scientific interest.

Differential Development of the Megagametophyte, Embryo, and Endosperm Following Self-and Cross-Pollination. Extensive microscopic examinations were made on the development of the megagametophyte, embryo, and endosperm of selfed and crossed Bartlett pear fruits collected at different intervals after pollination.

In the self-pollinated blossoms all of the specimens examined showed degeneration of the megagametophyte (Fig. 1, 2, Plate V). There appears to be no regularity as to the order with which the degeneration of the different components took place. In some cases the antipodals persisted as long as 9 days after pollinationk although in most cases they lost their identity immediately following pollination. The 2 synergids degenerated earlier then either the egg or the endosperm nucleus. In some specimens the disintegration of the synergids took place 12 days after pollination, while in others they persisted much longer. The egg nucleus in general survives for a longer period of time than the synergids. The endosperm nucleus appeared to outlast all the other members of a degenerating megagametophyte.

In the cross-pollinated blossoms there appeared to be no development of the embryo for about one week following pollination. Subsequently, however, markedly increased activities occurred. As a result, 12 days after pollination the proembryo reached the quadrant stage while the endosperm became 18-nucleate (Fig. 3, 4, Plate IV). About 15 days after cross-pollination, they reached the octant and 24-nucleate stages, respectively Fig. 5, Plate IV). These observations indicate that the division of the endosperm nucleus precedes that of the zygote, as has been reported for other fruits (13, 14, 69, 88).

Osterwalder (69) reported that in the pear embryo-sac one of the two endosperm nuclei migrates toward the micropylar end, while the other moves to the chalazal end. The former gives rise to the subsequent cellular endosperm. A similar condition seems to exist in the materials examined during the present study.

The free endosperm nuclei in the embryo-sac of a crossed Bartlett pear fruit become invested in bands of food substances; and at the same time, they are in close contact with the chalazal region through which the inflow of the food materials could possibly take place (Fig. 3, Plate V). The endosperm nuclei are also characterized by their association with a large number of nucleoli (Fig. 3, Plate V).

The later growth of the embryo and the endosperm is relatively slow. Thus, 25 days after pollination, the embryo consisted of 22 cells (including the suspensor) and the number of endosperm nuclei had reached 44. Figure 3 in Plate V shows an embryo-sac of the Bartlett pear 30 days after cross-pollination.

The formation of the endosperm cell wall starts about 40 days after pollination, beginning from the micropylar end and extending gradually toward the chalazal region (Fig. 4, Plate V). The endosperm cells surrounding the embryo are smaller, closer to each other and stain more heavily than those located near the chalazal

end. Tukey's (88) observations on the sweet cherry agree with these data. He stated that the nuclei of the chalazal region are longer and far apart, never becoming multicellular, while those of the micropylar region are smaller, closer together and subsequently become cellular. Similar conditions have been reported by other investigators (69, 71).

The embryo of cross-pollinated Bartlett pear fruit reaches maturity 70 to 75 days after fertilization under Willamette Valley conditions.

According to the data obtained in this study, the presence of xenia following cross-pollination is clearly indicated in the Bartlett pear. The influence of different pollen brings about a marked difference in the development of the embryo and the endosperm from the early stages of embryogeny (about one week following pollination). The megagametophyte of the selfed Bartlett flowers degenerated in all of the specimens studied, while the majority of flowers which were cross-pollinated with Fall Butter contained actively developing embryos and endosperms.

## Development of the Bartlett Pear Fruit in Relation to Metaxenia

### Gross Observations and Measurements

Gross observations and measurements were made of

the Bartlett pear fruits at various intervals following self-and cross-pollination. Variations both in shape and size were discernible approximately 20 days after pollination (Fig. 1, Plate VI). The cross-pollinated fruits, particularly those resulting from the crosses with Winter Nelis and Anjou varieties, showed much more extensive growth at the carpellary region than those which were selfed or which received no pollen. As the growth season progressed the degree of variation in shape and size gradually increased. The characteristics of the variation are: (1) that the cross-pollinated fruits make much more rapid growth near the carpels than the selfed fruits, (2) that the latter inversely make more rapid growth in the region of pedicel than the former, and (3) that the selfed fruits and those which received no pollen in general are smaller than the cross-pollinated fruits (Fig. 1-6, Plate VI and Table X).

The magnitude of the variations in shape and size of fruits resulting from self-and cross-pollination are shown in Table X.

TABLE X. MEASUREMENTS AND SEED CONTENTS OF BARTLETT PEAR FRUITS RESULTED FROM DIFFERENT POLLEN 3 MONTHS AFTER POLLINATION, 1940

| Crosses Bartlett | Number of Fruits Used | Ave. Max. diam. Calyx end in mm. | Ave. Diam. of Fruit at position 15 mm. from stem end in mm. | Quotient, stem end diam./ Calyx end diam. | Ave. length of fruit in mm. | Ave. wt. of fruit in gms. | Ave. number seeds per fruit |
|---|---|---|---|---|---|---|---|
| X Self | 45 | 57.0 | 39.8 | 69.8% | 78.5 | 128.7 | 0 |
| X None | 35 | 59.6 | 39.9 | 66.9 | 81.4 | 132.7 | 0 |
| X Open | 22 | 55.4 | 36.6 | 66.0 | 79.6 | 110.6 | 0 |
| X Anjou | 26 | 74.2 | 39.8 | 53.6 | 84.9 | 165.9 | 5 |
| X Winter Nelis | 30 | 63.1 | 38.7 | 61.1 | 82.1 | 153.2 | 5 |
| X Bosc | 33 | 64.6 | 39.0 | 60.3 | 111.0 | 161.1 | 5 |
| X Fall Butter | 36 | 59.2 | 36.3 | 60.1 | 77.6 | 134.1 | 5 |

According to these data (Table X) the quotients, diameter of stem end/diameter of calyx end, are higher in the self-pollinated than in the cross-pollinated fruits. In the former the quotients range from 66 to 69.8 in comparison with a range of 53.6 to 61.1 for the latter. These results verify the observations made that the selfed fruits and those which received no pollen made a greater growth in the region of the pedicel than cross-

pollinated fruits. Furthermore, the latter group shows a higher average weight of fruits than the former.

All of the cross-pollinated fruits contained an average of 5 seeds, while none were present in the selfed or open pollinated fruits.

The above results clearly indicate that the formation of seed and the development of fruit are closely related. The relationship may possibly be one of nutritional or of hormone influence. Reineke (74) found with Bartlett pears that in fruits containing seeds the most extensive tissue development took place in the immediate vicinity of the carpels at the expense apparently of tissue development both at the stem and calyx ends, giving rise to a short smooth-necked pear with its greatest transverse diameter in the seed region of the fruit. In fruits containing no seeds, however, extensive development occurred in the region between the base of the carpels and the apex; consequently an entirely differently shaped fruit resulted.

### Number and Size of Cells at Different Levels of Selfed and Crossed Bartlett Pear Fruits

Median longitudinal sections of selfed and crossed Bartlett pear fruits, collected at intervals from 6 to 40 days after pollination, were used for this study.

The Number of Cells - The number of cells were

counted in the regions extending from the base of the carpels to the apex of the pedicel. For convenience in counting and comparing cell numbers, this region was arbitrarily divided into different levels perpendicular to the longitudinal axis of the fruit, starting with level 1 at the base of carpels and extending toward the apex at distances 1 or 2 millimeters (Fig. 1, Plate VII).

Figures 1 to 7 in Plate VIII show the manner in which the gradual variations in shape of selfed and crossed Bartlett fruits take place. No variation in the comparative number of cells in any different levels occurred during the period from 6 to 7 days following pollination (Fig. 1, Plate VIII). Approximately 10 days after pollination, however, the comparative number of cells at the levels below the carpellary base of the selfed fruit was greater than at the corresponding positions of the crossed fruits, and the proportional differences increased as the season progressed. Thus, 40 days after pollination, the selfed fruit showed much greater increase in cell numbers at the pedicel end than the crossed fruit (Levels 7 and 8, Fig. 7, Plate VIII). The increase in total cell numbers at level 1 of the crossed fruit was from 110 to 600 (545 per cent) in contrast to the increase from 110 to 500 (454 per cent) in the selfed fruit during the period between anthesis and 40 days after pollination (Fig. 2, Plate VII). During the same period, the increas-

es in the total number of cortical cells were from 30 to 400 (1,333 per cent) and 30 to 370 (1,233 per cent) in the crossed and selfed fruits, respectively (Fig. 3, Plate VII). The percentage of increase in cortical cell number, therefore, is much greater than that in the total cell number. There was a very slight difference in the comparative ratio of increases in cell numbers in the pith and the carpellary tissues of selfed and crossed fruits (Fig. 4, 5, Plate VII). There was no difference between the increase in the number of hypodermal cell layers in these two fruits.

The pattern of fruit shape obtained by cell counts at different levels corresponds very closely to the actual shape of the fruit as shown in Fig. 1-6, Plate VI. It is clear, therefore, that the differential increase in cell number at different positions, particularly in the carpellary and pedicel regions during the early stages of fruit growth, is closely correlated with the variation in shape between the self-and cross-pollinated fruits.

It can be recalled that the selfed and crossed Bartlett pear fruits first showed differences in embryo developments about 10 days after pollination. Thus, the initial time of variation in cell number at various levels of the Bartlett fruits following self-and cross-pollination coincides with the initiation of embryo development. The expressions of xenia and metaxenia (with

respect to cell number) are first perceiveable at about the same time.

The data obtained show that the largest increase in cell number in the Bartlett pear fruit takes place between the period of 30 to 40 days after pollination. This observation is of special interest because the general belief at the present time is that in most of the pome and stone fruits cell division ceases about 3 weeks to 30 days after full bloom (2, 52, 71, 88, 91). Kraus and Ralston (47) working on the anatomy of the apple reported that after full bloom the maturity of the structures outside of the seed itself consists mainly in the enlargement of cells already formed. Many mitotic figures have been observed, in the materials collected 40 days after pollination, especially in the cortical tissue. In California, Kim (41) reported the presence of cell divisions in the Bartlett pear fruit collected 48 days after full bloom.

The Size of Cells - Increase in cell size is one of the major changes which occurs in fruits during growth. In order to determine if differences in rates of cell enlargement between cross-and self-pollinated fruits are correlated with the observed differences in shape, a large number of measurements of cell sizes in both types of pears were made during the early growth period. An

average size of 10 representative cells in 10 different areas in the same tissues and levels as described for cell numbers was taken as the final cell size.

In Fig. 1-4, Plate IX are shown the comparative cell sizes in the region extending from the base of the carpels to the apex. The values for cell size at each level are expressed as percentages, with level 1 taken as 100. During the first 15 days following pollination, the comparative cell size was found to be greater in the pedicel region of the selfed fruits than that of the crossed fruit (Fig. 1-2, Plate IX). Twenty days after pollination, however, the comparative cell size in this region was greater for the crossed fruit (Fig. 3, Plate IX), while in the specimens collected 30 days after pollination no appreciable differences were observed (Fig. 4, Plate IX).

These results indicate that the comparative rate of cell enlargement in the carpellary and pedicel regions is not correlated with the differences in shape between the self-and cross-pollinated fruits, as was the case with cell numbers.

The increase in actual cell size in the cortical, pith, carpellary, hypodermal, and epidermal tissues of selfed and crossed fruits are shown in Fig. 5-9, Plate IX and Table X. According to these date, growth as ex-

pressed by increase in cell enlargement begins immediately or shortly after pollination without the short period of inactivity as was the case with cell division previously noted (Fig. 2-5, Plate VII).

There was a much larger increase in the actual size of cortical and pith cells in the crossed than in the selfed fruit during the early stages of growth (Fig. 5-6, Plate IX). Thus, the average increases in the cortical cell sizes of the cross-and self-pollinated fruits were 6- and 4- fold, respectively during the first 40 days following pollination. During the same period the increases in size of the pith cells were 4.5- and 3-fold for the cross-and self-pollinated fruits, respectively. No significant differences in cell sizes in the carpellary, hypodermal, and epidermal tissues were found. Between 30 to 40 days after pollination, however, there was a marked increase in the size of the carpellary cells in both types of fruits. This was due mainly to longitudinal elongation of the cells (Table XI). There was a slight increase in hypodermal cell size, but no significant increase occurred in the epidermal cells (Fig. 8-9, Plate IX).

Table XI - AVERAGE CELL SIZES IN DIFFERENT TISSUES OF SELFED AND CROSSED BARTLETT PEAR FRUITS AT INTERVALS OF GROWTH PERIOD

| Tissues | Full Bloom (Microns) | 20 Days after Pollination | | 40 Days after Pollination | |
|---|---|---|---|---|---|
| | | Selfed (μ) | Crossed (μ) | Selfed (μ) | Crossed (μ) |
| Epidermis | 14x12* | 19x15 | 20x17 | 16x18 | 17x18 |
| Hypodermis | 16x18 | 18x22 | 21x24 | 18x23 | 22x25 |
| Cortex | 26x27 | 32x33 | 39x40 | 40x42 | 47x45 |
| Pith | 27x29 | 24x33 | 36x42 | 34x43 | 39x50 |
| Carpel | 16x18 | 18x22 | 18x31 | 21x68 | 23x61 |

*Radial x Longitudinal

Judging from the data presented, it is evident that in the Bartlett pear, metaxenia (in respect to cell division and enlargement in cell size) plays an important part in the variation of fruit shape. Microscopic studies show that the influence of metaxenia is expressed in the ontogeny of the fruit as early as 10 days after pollination. Both increase in cell number and enlargement in cell size, the two major factors that contribute to the growth of a fruit, are more rapid in the carpellary region of crossed than in the selfed Bartlett pear fruit (Fig. 2-7, Plate VII and Fig. 5-6, Plate IX). A reverse condition seems to exist in the region between the base of the carpels and the apex in respect to the increase in

cell numbers. These differences largely account for the variation in shape between the two types of fruits. It should be pointed out, furthermore, that the cortex and the pith appear to be the most important tissues that contribute to this variation.

## DISCUSSION

Xenia and metaxenia have been used by Swingle (81) and others (63, 87) to designate the gross effect of pollen upon matured seeds and fruits. On the basis of the data obtained in the present investigation these terms can be considered to have a more precise meaning in relation to seed and fruit development. In the Bartlett pear the influence of different pollen on the embryo and the fruit tissues is discernible within 10 days following pollination. Marked differences occur in the rate at which cell division and enlargement take place in various tissues of the fruit, according to lack of pollination or the kind of pollen received. As a result, at an early stage of development a definite growth pattern is formed which determines the shape of the mature fruit and accounts for the variations as observed by previous investigators and during the present study. Consequently, it is appropriate to consider any effect of pollen on the megagametophyte or on the fruit, micro-or macroscopic in nature,

as xenia and metaxenia, respectively.

The data obtained during the present investigation show a close correlation between the variation in development of the Bartlett pear fruit and the presence or absence of seed in the fruit. In the fruit resulting from cross-pollination, the formation of the quadrant proembryo starts about 10 days after pollination, while disintegration of the megagametophyte takes place in the selfed fruits. Differences in the growth patterns between these two types of fruits coincide very closely to these observed differences in megagametophyte or embryo development. In fruits containing developing embryos, there is a more extensive growth in the immediate vicinity of the carpels, as shown in the number and size of the cells.

The differential growth of the tissues of self-and cross-pollinated fruits may possibly be accounted for by difference in nutritional supply or by specific hormones diffusing from the developing embryos. Staining reactions indicated that the developing embryos were able to obtain more rapid intake of food substances through the chalazal tissue than were the megagametophytes which disintegrated following failure of fertilization. A detailed chemical study would be of interest in this respect. It is possible also that specific hormones are synthesized by the developing embryo, and by diffusion into the sur-

rounding tissues influence their growth. This possibility has been suggested in the case of the peach fruit. If this is shown to be true by future experimentation, then the influence of xenia and metaxenia can be defined in specific physiological terms.

## SUMMARY

1. The variations in the development and shape of the Bartlett pear fruit grown in the Willamette Valley have been studied in relation to the effects of pollen and pollination on the embryogeny and the ontogeny of the fruit.

2. Under Willamette Valley conditions the Bartlett pear was found to be partially self-fruitful and the fruits developed parthenocarpically following self-pollination. The results of pollination experiments conducted during a period of 3 years show that varieties Fall Butter, Anjou, and Winter Nelis are the most satisfactory pollinizers for the Bartlett pear. All fruits developing after cross-pollination with these varieties contained seeds, while those resulted from self-pollination contained no seeds. Various growth-promoting chemicals were ineffective for inducing parthenocarpic development of the Bartlett pear fruit. Asparagine applied to the blossoms at the time of pollination stimulated growth

during the first 2 weeks of fruit development but was without effect thereafter.

3. Neither defectiveness of pollen nor lack of germinating ability was found to be the cause of self- or inter-sterility. Failure of fertilization appeared to be due to the inability of the pollen tubes to reach the ovary following pollination. The growth of pollen tubes was found to be stimulated by the presence of pieces of pear gynoecia in the germination media. This effect was especially apparent upon the pollen of a cross-compatible variety. Aqueous extracts of stylar and ovarian tissues had an inhibiting effect on pollen germination.

4. Xenia and metaxenia were observed shortly after pollination of the flower blossoms. Rapid degeneration of the megagametophyte took place after self-pollination, but active growth of the embryo was initiated shortly after cross-pollination. The development or non-development of the embryo appeared to be correlated with the rate of cell division and cell enlargement in specific tissues of the fruit. Following the first cell division of the zygote, there was a marked increase in the number and size of cells in the immediate vicinity of the carpels. In the fruits containing degenerating megagametophytes, however, more rapid increase in cell

numbers in the tissues occurred in the region between the base of the carpels and the pedicel. This differential growth persisted throughout development and accounts for the variation in shape at maturity between the self- and cross-pollinated Bartlett pear fruits.

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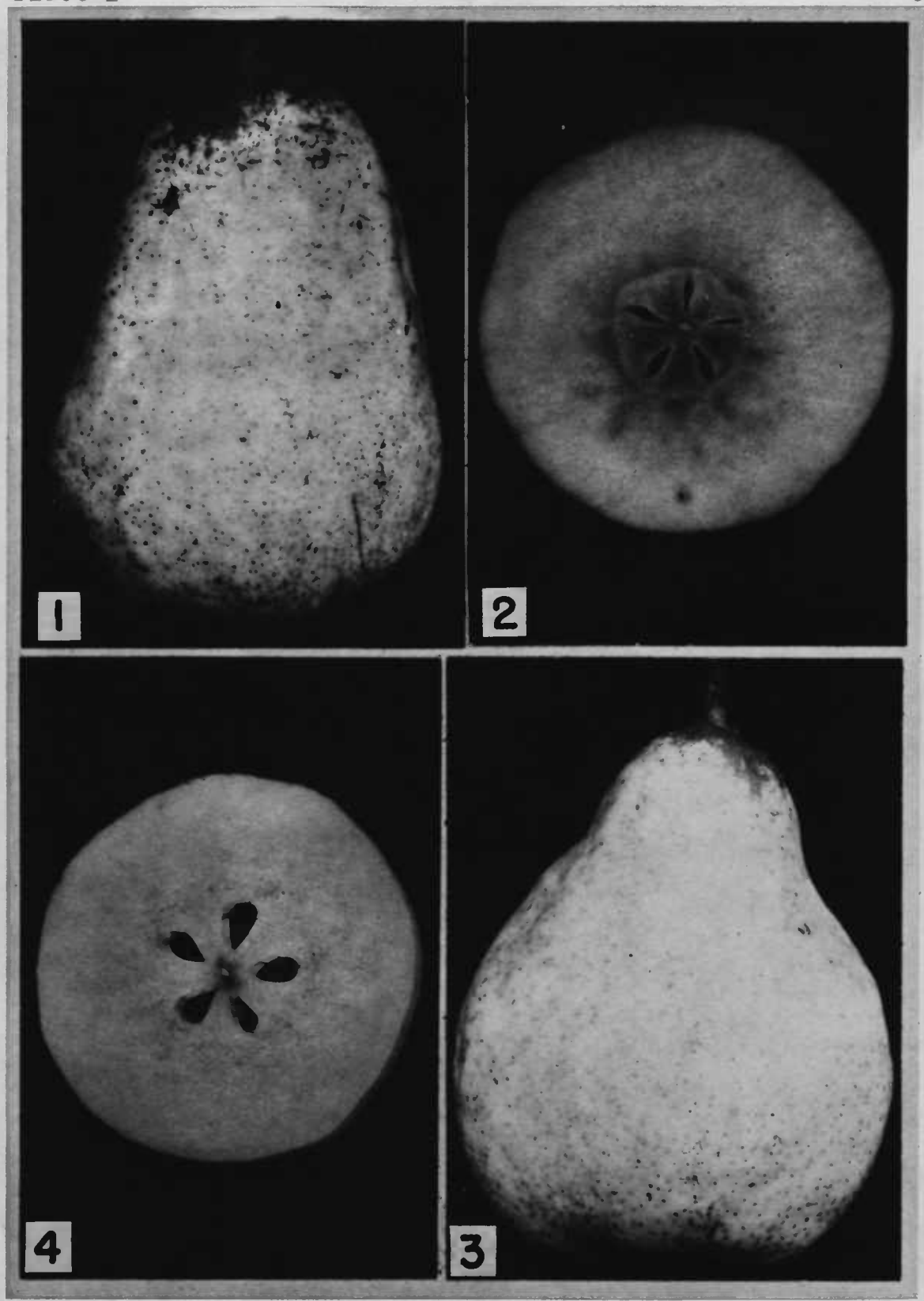
# PLATE I

Fig. 1. Selfed Bartlett pear fruit showing the enlarged stem end.

Fig. 2. Cross-section of Fig. 1 through the carpels showing the absence of mature seeds.

Fig. 3. Bartlett pear fruit crossed with Fall Butter variety showing the typical Bartlett pear shape.

Fig. 4. Cross-section of Fig. 3 through the carpels showing the presence of mature seeds.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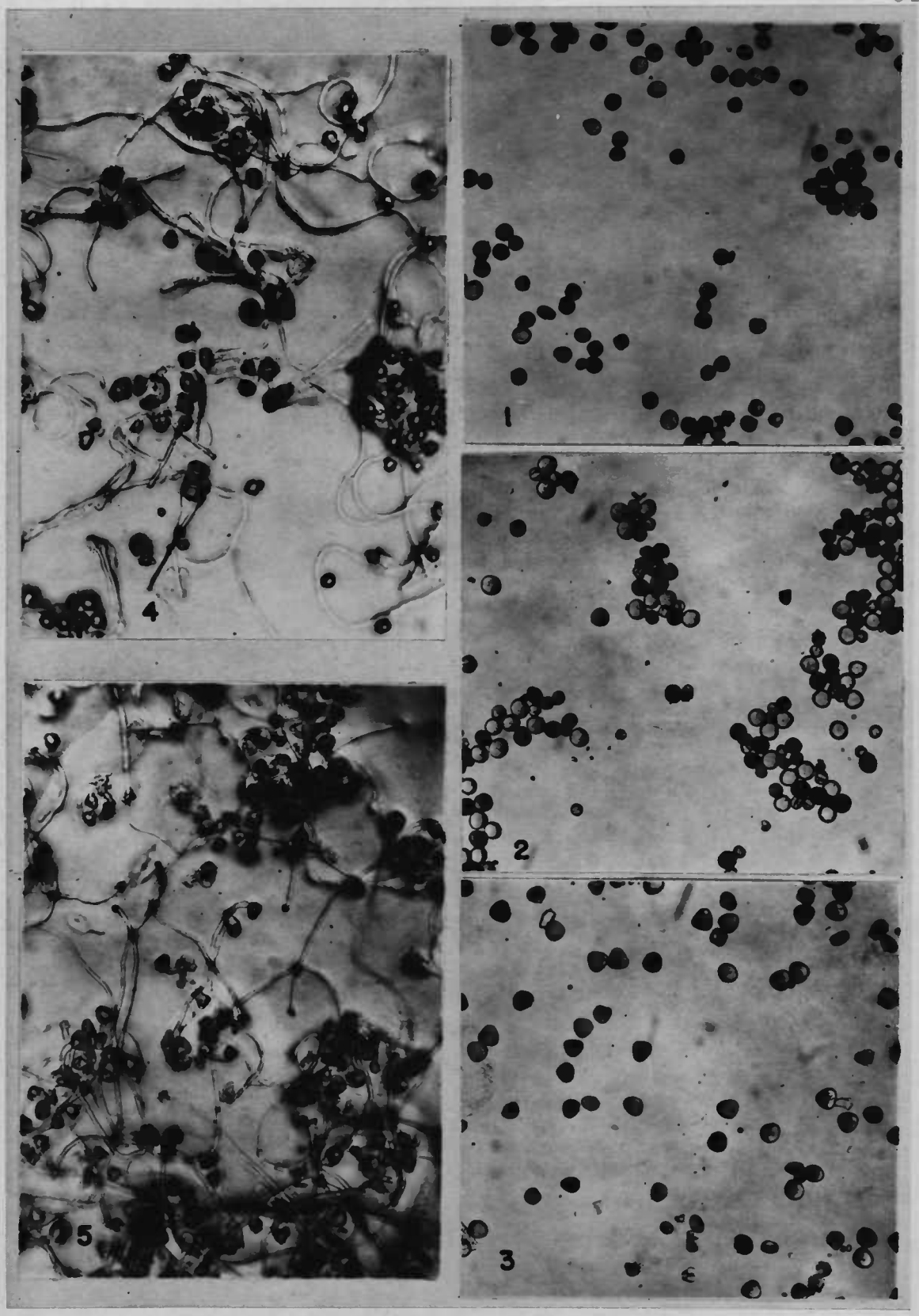
# PLATE II

Fig. 1-3 Photomicrographs of pollen of Bartlett, Fall Butter, and Winter Nelis pear varieties, respectively. Note the comparative size, shape, and the approximate percentage of defective pollen in the different pollen. Photographs were taken of the pollen mounted in water, and a slight swelling has taken place.

Fig. 4 Photomicrograph of germinating pollen of Bartlett pear variety in 12% sucrose - 1.5% agar medium, 5 hours after growth period at room temperature.

Fig. 5 Photomicrograph of germinating pollen of Winter Nelis pear variety in 12% sucrose - 1.5% agar medium 5 hours after growth period at room temperature.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## PLATE III

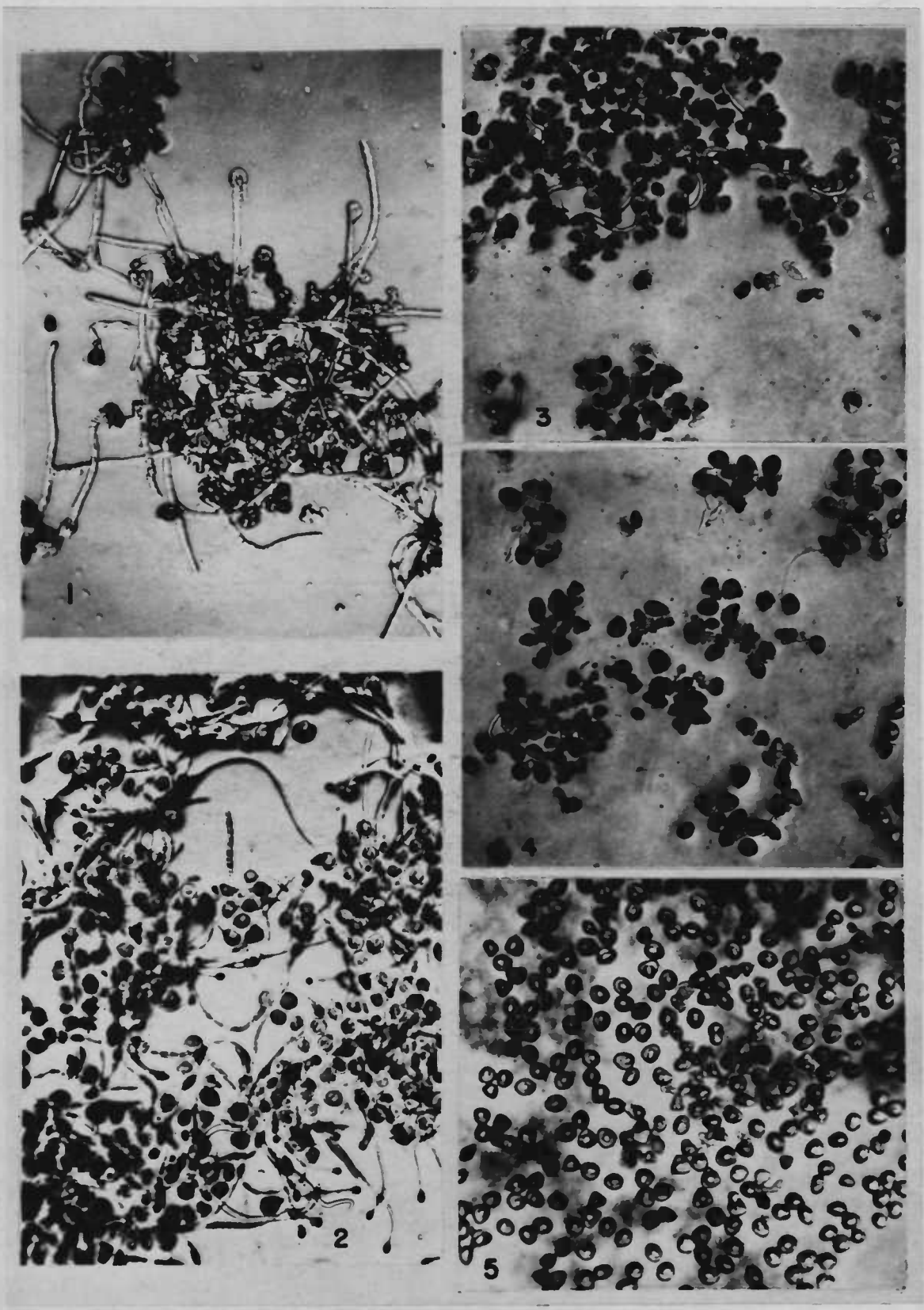
Fig. 1 Photomicrograph of germinating pollen of Winter Nelis pear variety in 12% glucose - 1.5% agar medium 5 hours after growth period at room temperature. Note the formation of septa on the pollen tubes.

Fig. 2 Photomicrograph of germinating pollen of Bartlett pear variety in a medium containing 12% sucrose, 1.5% agar, and pieces of styles of the same variety 2½ hours after growth period.

Fig. 3 Photomicrograph of germinating pollen of Bartlett pear variety in 1.5% agar medium after 5½ hours of growth. Note the poor germination.

Fig. 4 Photomicrograph of Winter Nelis pollen in a medium containing 12% sucrose, 1.5% agar, and 0.002% indole-n-3-butyric acid 5½ hours after growth

Fig. 5 Photomicrograph of Winter Nelis pollen in a medium containing 12% sucrose, 1.5% agar, and Bartlett styler extract 5 hours after growth period. No germination occurred.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## PLATE IV

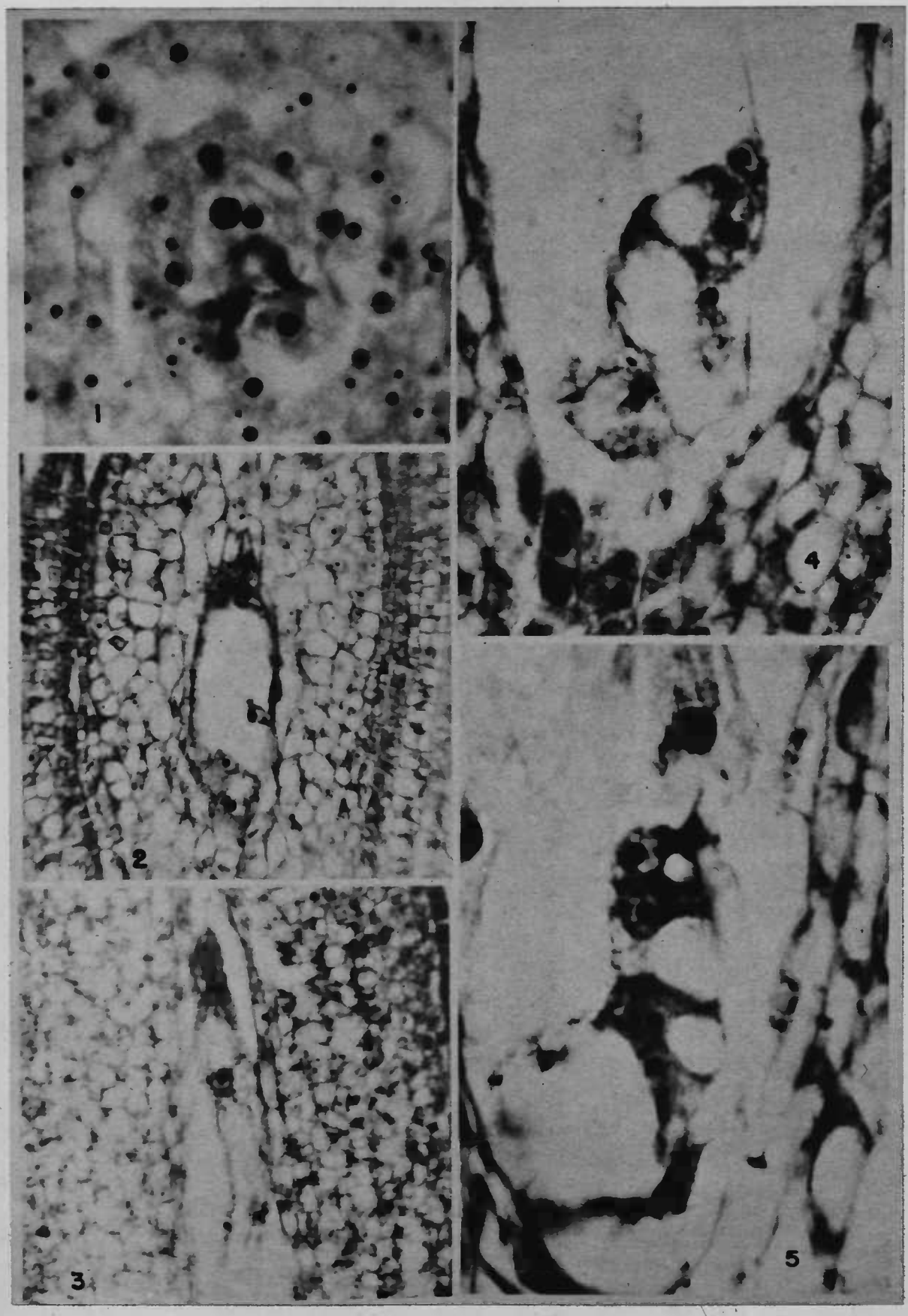
Fig. 1 Photomicrograph of Bartlett pear fruit bud 3 weeks before anthesis showing the initial stage of megaspore mother cell formation.

Fig. 2 Photomicrograph of embryo-sac of Bartlett pear at full bloom showing its inclusions, 7 antipodals, endosperm nucleus, egg nucleus, and one of the two synergids.

Fig. 3 Photomicrograph of embryo-sac of Bartlett flower 12 days after cross-pollination with Fall Butter variety showing free endosperm nuclei which are embedded in food substances in close proximity to the chalazal region.

Fig. 4 Photomicrograph of proembryo of Bartlett pear 12 days after cross-pollination with Fall Butter pollen

Fig. 5 Same as Fig. 4. 15 days after cross-pollination.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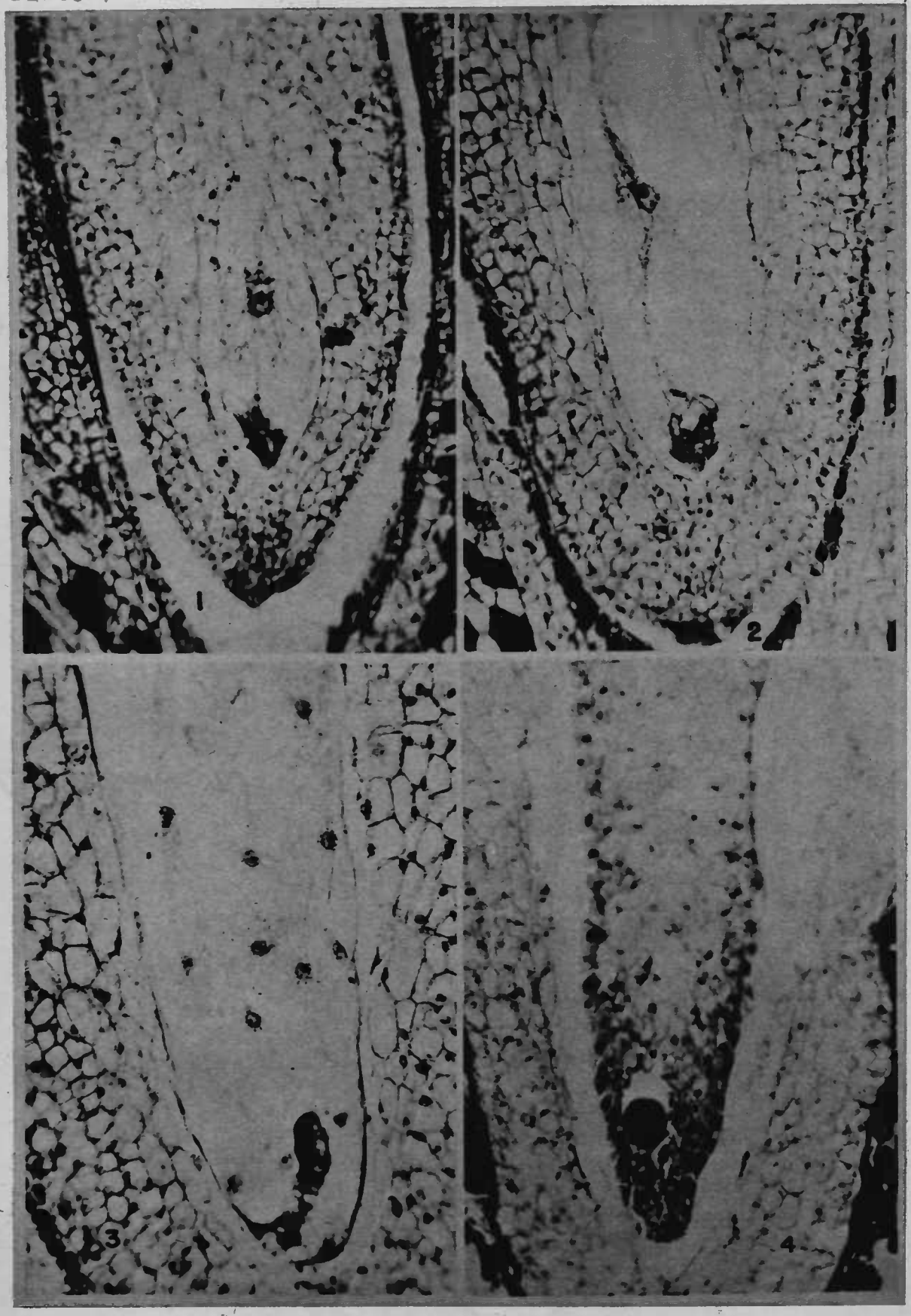
## PLATE V

Fig. 1-2 Photomicrographs of embryo-sacs of selfed Bartlett fruits showing degeneration 12 and 27 days after pollination, respectively.

Fig. 3 Photomicrograph of embryo-sac of Bartlett pear 30 days after cross-pollination showing embryo and free endosperm nuclei.

Fig. 4 Photomicrograph of embryo-sac of Bartlett pear 47 days after cross-pollination showing endosperm cell wall formation.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## PLATE VI

Fig. 1 Bartlett pear fruits 20 days after pollination with pollen of different pear varieties showing the initial stage of variation in shape.
FB = Fall Butter
WN = Winter Nelis

Fig. 2 Same as Fig. 1 1 month after pollination

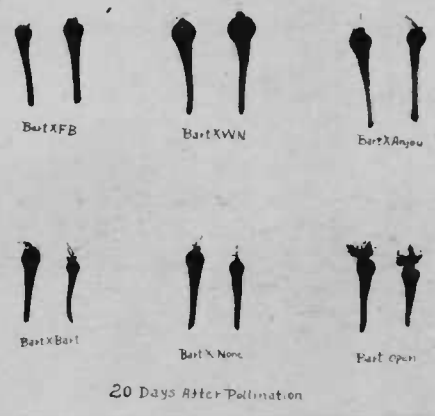
Fig. 3 " " " " 37 days " "

Fig. 4 " " " " 50 " " "

Fig. 5 " " " " 2 months " "

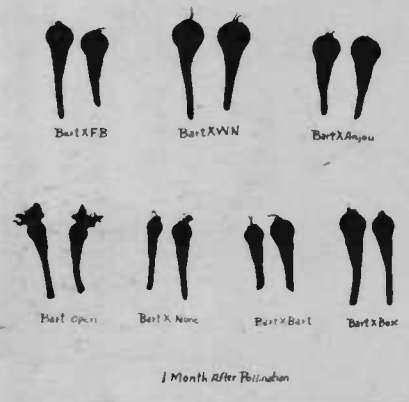
Fig. 6 " " " " 3 " " "

Plate VI



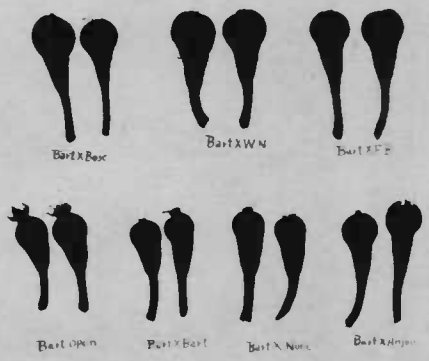

20 Days After Pollination

FIG. 1



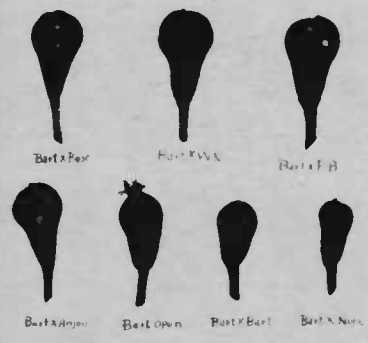

1 Month After Pollination

FIG. 2



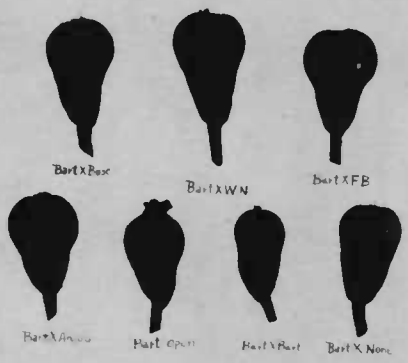

37 Days After Pollination

FIG. 3



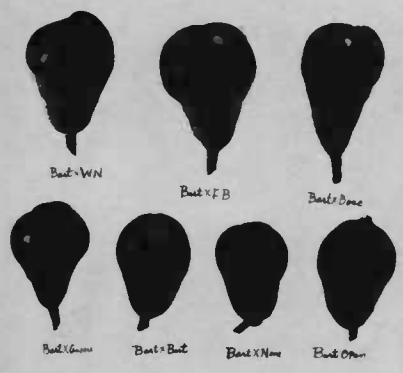

53 Days After Pollination

FIG. 4




2 Months After Pollination

FIG. 5




3 Months After Pollination

FIG. 6

## PLATE VII

Fig. 1 Median longisection of Bartlett pear fruit showing different levels and tissues. c - cortex, car - carpel, pb - pedal bundle, p - pith, dcb - dorsal carpellary bundle, vcb - ventral carpellary bundle, ov - ovule, sb - sepal bundle, rvt - residual vascular tissue. The levels are perpendicular to the longitudinal axis of the fruit.

Fig. 2 Increase in total number of cells through level 1 at intervals 10, 20, 30, and 40 days after self-and cross-pollination of the Bartlett pear flower.

Fig. 3 Same as Fig. 2 for total number of cortical cells (Total number includes the cells on both sides of the symmetry).

Fig. 4 Same as Fig. 3 for the total number of pith cells.

Fig. 5 Same as Fig. 3 for total number of carpellary cells.

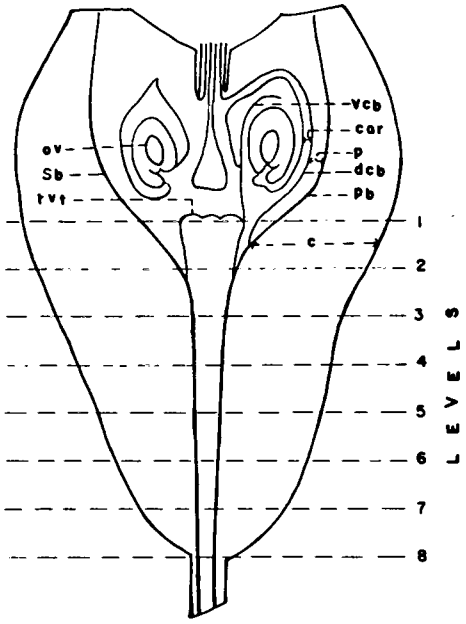



FIG. 1

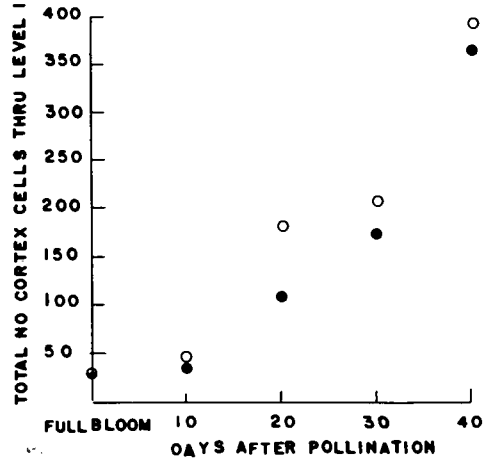



FIG. 3

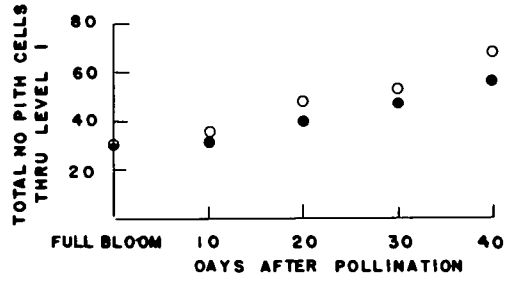



FIG. 4

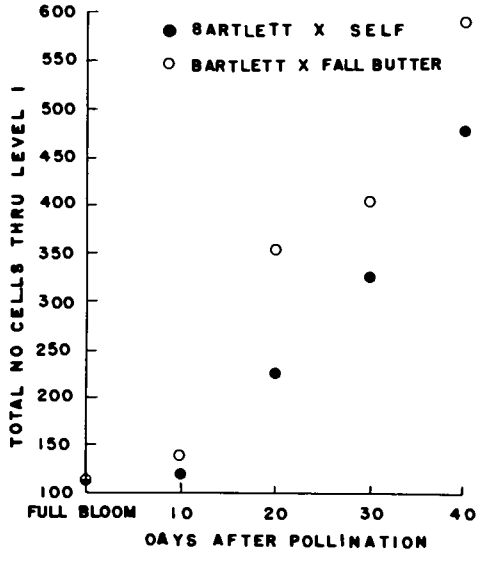



FIG. 2

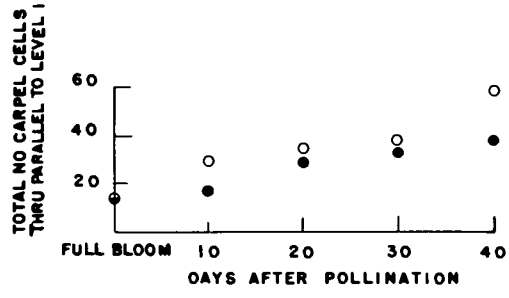



FIG. 5

## PLATE VIII

Fig. 1 The percentage of total cell numbers at different levels on the basis of 100 at Level 1 (carpellary base). Bartlett x Self, 6 days after pollination. Bartlett x Fall Butter, 7 days after pollination.

Fig. 2 Same as Fig. 1 10 days after pollination

Fig. 3 " " " 12 " " "

Fig. 4 " " " 15 " " "

Fig. 5 " " " 20 " " "

Fig. 6 " " " 30 " " "

Fig. 7 " " " 40 " " "

PERCENTAGE OF CELL NUMBERS AT DIFFERENT LEVELS ON THE BASIS OF 100 AT LEVEL 1 ( CARPELLARY BASE)

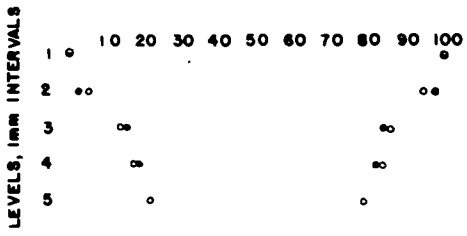



FIG. 1

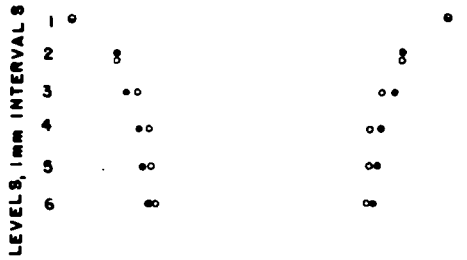



FIG. 2

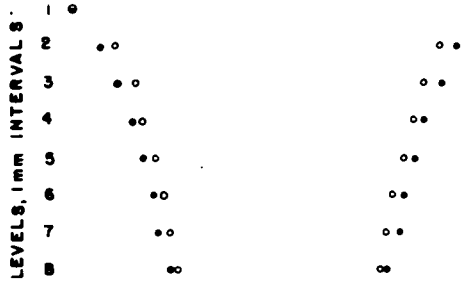



FIG. 3

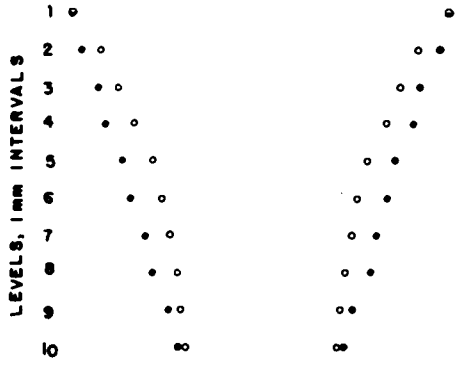



FIG. 4

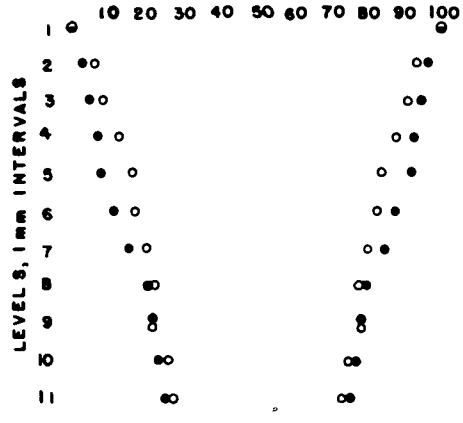



FIG. 5

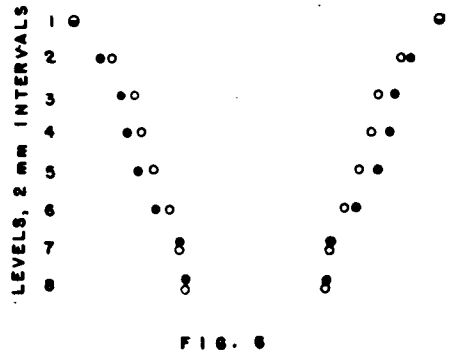



FIG. 6

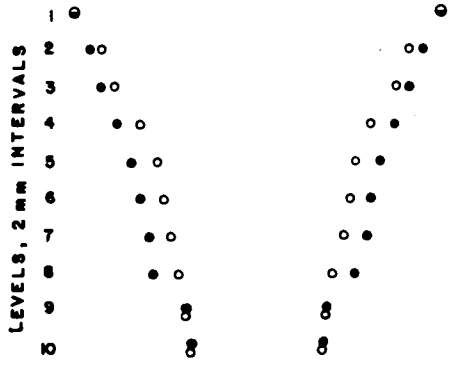



FIG. 7

● BARTLETT X SELF

○ BARTLETT X FALL BUTTER

## PLATE IX

Fig. 1 Percentage of average radial cortical cell size at different levels on the basis of average radial cortical cell size (100) at Level 1. 10 days after self-and cross-pollination of the Bartlett pear flowers.

Fig. 2 Same as Fig. 1 15 days after pollination.

Fig. 3 " " " " 20 " " "

Fig. 4 " " " " 30 " " "

Fig. 5 Average increase in cell size (square microns in cortex at different intervals from anthesis to 40 days after self-and cross-pollination of the Bartlett pear flowers.

Fig. 6 Same as Fig. 5. Increase in pith cell size.

Fig. 7 " " " " " " carpellary cell size.

Fig. 8 " " " " " " hypodermal cell size.

Fig. 9 " " " " " " epidermal cell size.

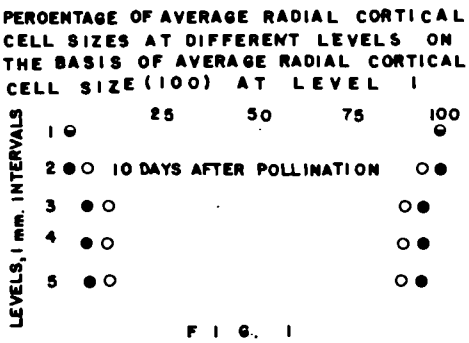



FIG. 1

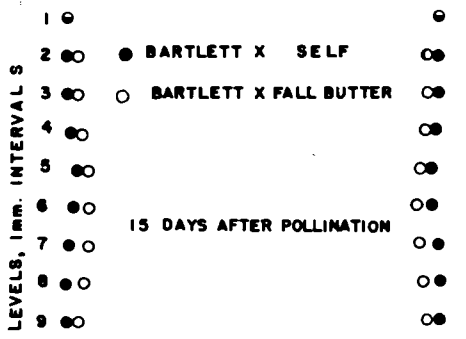



FIG. 2

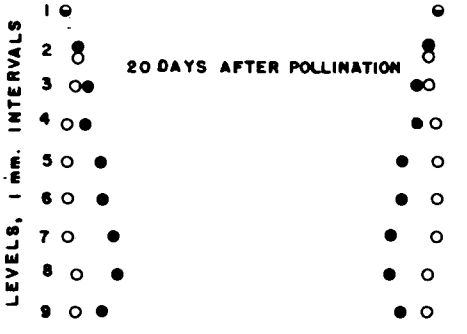



FIG. 3

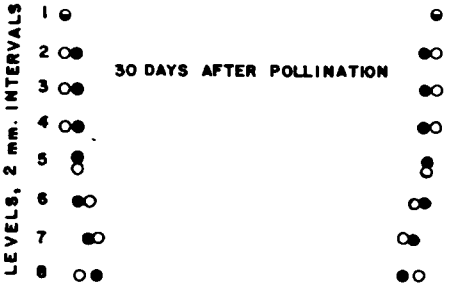



FIG. 4

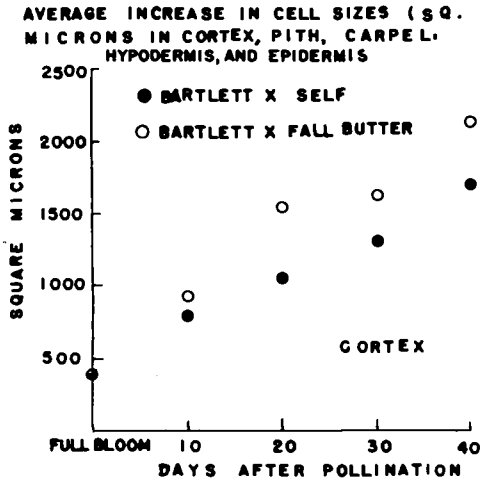



FIG. 5

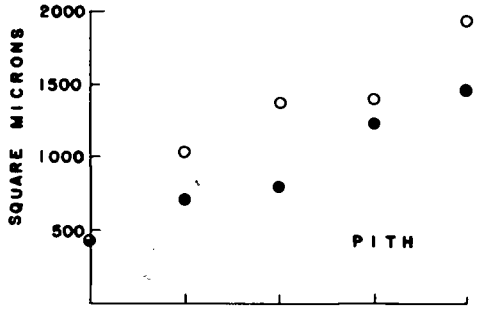



FIG. 6

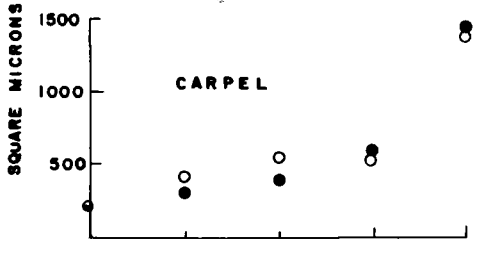



FIG. 7

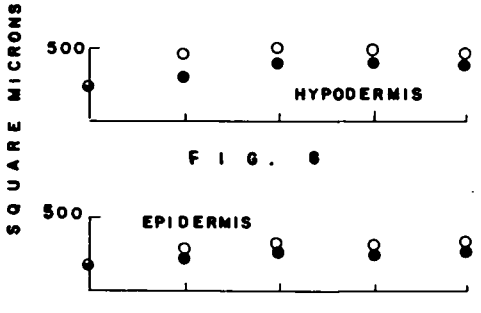



FIG. 8

FIG. 9