OVULE AND SEED STUDIES IN RELATION TO FRUIT GROWTH IN CARICA PAPAYA L. CL. HONEY GOLD

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by

ABEL LUIZ PEREIRA
B.Sc. (Agric.)

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- DECLARATION -

I hereby certify that this thesis is basically my own work and that it is not being submitted concurrently for any other degree.

SIGNED .....

A. L. PEREIRA

- A C K N O W L E D G E M E N T S -

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- ADDENDUM TO PLATES -

Magnifications of cleared material understated.

Should read 1,2 x greater.

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- ABBREVIATIONS -

∇ ..... - see p. (xvi).

A ..... - Fruit subregion: top quarter along carpellary margins, adjacent to stigma or apical end of fruit. See Figures 2 and 3; Plate 2a.

a ..... - Fruit subregion: top quarter along placental edges, adjacent to stigma or apical end of fruit. See Figures 2 and 3; Plate 2a.

a ..... - Ovule/seed type: unfertilized ovule; undeveloped as a seed; equivalent to "U" ovule/seed type. See Plate 2b.

Aa ..... - Fruit subregion: top quarter, inclusive of "A" and two adjacent "a" subregions, adjacent to stigma or apical end of fruit. See Figures 2 and 3; Plate 2a.

alg .... - Aleurone grain.

B ..... - Fruit subregion: second quarter, along carpellary margins, between "A" and "C". See Figures 2 and 3; Plate 2a.

b ..... - Fruit subregion: second quarter along placental edges, between "a" and "c". See Figures 2 and 3; Plate 2a.

b ..... - Seed type: small; flattened or twisted; white or brown; slightly developed: component of "S" seed type. See Plate 2b.

Bb ..... - Fruit subregion: second quarter, inclusive of "B" and two adjacent "b" subregions, between "Aa" and "Cc". See Figures 2 and 3; Plate 2a.

C ..... - Fruit subregion: third quarter, along carpellary margins, between "B" and "D". See Figures 2 and 3; Plate 2a.

c ..... - Fruit subregion: third quarter, along placental edges, between "b" and "d". See Figures 2 and 3; Plate 2a.

Cax .... - Calcium oxylate crystal.

cbc .... - Cardboard cup.

Cc ..... - Fruit subregion: third quarter, inclusive of "C" and two adjacent "c" subregions, between "Bb" and "Dd". See Figures 2 and 3; Plate 2a.

cc ..... - Cellular contents.

cDL .... - Seed type c: larger, darker, partially developed; component of "P" seed type. See Plate 2b.

cen .... - Cellular endosperm.

cen s .. - Cellular endosperm sheath.

ch ..... - Chalaza.

cl ems . - Collapsed embryo sac.

cl nuc . - Collapsed nucellar tissue.

cm ..... - Carpellary margin(s). See Figures 1b to 3; Plate 2a.

crt .... - Crystalloid.

cs ..... - "Apparently" deepest layer of sarcotesta; contiguous layer with endotesta in furrow between endotestal ridges.

ctl .... - Cotyledon.

cWL .... - Seed type c: larger, white, partially developed; component of "P" seed type. See Plate 2b.

cWs .... - Seed type c: small, rounded, white; slightly developed; component of "S" seed type. See Plate 2b.

cyt .... - Cytoplasm.

D ..... - Fruit subregion: bottom quarter along carpellary margins, adjacent to basal or fruit stalk end. See Figures 2 and 3; Plate 2a.

d ..... - Fruit subregion: bottom quarter along placental edges, adjacent to basal or fruit stalk end. See Figures 2 and 3; Plate 2a.

dB ..... - Seed type d: larger, black, fully developed; component of "F" seed type. See Plate 2b.

db ..... - Dorsal bundle.

Dd ..... - Fruit subregion: bottom quarter, inclusive of "D" and two adjacent "d" subregions, adjacent to basal or fruit stalk end. See Figures 2 and 3; Plate 2a.

den .... - Degenerated endosperm.

dG ..... - Seed type d: large, grey, fully developed; component of "F" seed type. See Plate 2b.

ds ..... - "Dense staining" tissue, according to the literature.

dvc .... - Divided cell.

e(L) ... - Large-celled endotestal tissue, forming ridges of seed coat.

em ..... - Embryo.

ems .... - Embryo sac.

emsp ... - Embryo suspensor.

epc .... - Epicotyl.

e(s) ... - Small-celled endotestal tissue; forming inner band of endotesta, underlying ridges of seed coat.

F ..... - Seed type: fully developed seeds; inclusive of "dG" and "dB" seed types. See Plate 2b.

fa ..... - Fruit apex.

fb ..... - Fruit base.

fn ..... - Funiculus.

fnc 4 .. - Finger-like nucellus - region 4.

fne .... - Free nuclear endosperm.

gl em .. - Globular embryo.

hp ..... - Hat-pin, used to demarcate intra-fruit subregions.

hyp 1 .. - Hypostase - region 1.

ie 1 ... - Inner epidermis of outer integument or testa.

ie 2 ... - Inner epidermis of inner integument or testa.

ii ..... - Inner integument or testa.

in ..... - Inter-epidermal tissue of inner integument or testa.

lp ..... - 1/5th longitudinal portion of fruit. See Plates 1 and 2, or Figures 1b and 3.

mp ..... - Micropyle.

mr ..... - Midrib of a lobe of palmate papaya leaf.

msc .... - Mesocarp of fruit.

muc .... - Mucilaginous deposit.

nc ..... - Nucleus.

nuc .... - Nucellus.

nuc d .. - Nucellus "disc" region.

nuc s .. - Nucellar sheath.

oe 1 ... - Outer epidermis of outer integument or testa.

oe 2 ... - Outer epidermis of inner integument or testa.

oi ..... - Outer integument or testa.

ovf .... - Ovule (or seed) - free region in internal furrows or grooves of papaya flower or fruit.

P ..... - Seed type: partially developed seeds; inclusive of "cDL" and "cWL" seed types. See Plate 2b.

pc ..... - Pitted cell wall.

pe ..... - Placental edges of ovule or seed bearing inner surfaces of papaya fruits. See Figures 1b to 3; Plate 2a.

pem .... - Pro-embryo.

pem s .. - Pro-embryo sheath.

pf ..... - Pistillate flower.

pg ..... - Phytin globoid.

pnc .... - Polar nucleus (of megagametophyte).

ptb .... - Pollen tube or pollen tube tip.

ptl .... - Leaf petiole.

pvst ... - Provascular strand.

R^2 ..... - Multiple coefficient of determination.

r_{ij} .... - Simple or total correlation coefficient between i and j variables.

$r_{ij, m(n)}$ - Partial correlation coefficient between i and j variables given m (or/and n): that is, the correlation between i and j after first allowing for the degree of association of m (or/and n) with both i and j .

S ..... - Seed type: slightly developed seeds; inclusive of "cWs" and "b" seed types. See Plate 2b.

sc ..... - Sarcotesta

st ..... - Stamen of male flower, after removing petals.

sub .... - Sub-epidermal layer(s) of sarcotesta.

sy ..... - Synergid.

tiw .... - Thickened inner wall.

tn ..... - Tannin deposit.

tnc .... - Tannin deposited into centre of cell.

tnw .... - Tannin deposited along walls.

U ..... - Ovule/seed type: unfertilized ovule; undeveloped as a seed; equivalent to "a" ovule/seed type. See Plate 2b.

vb ..... - Ventral bundle.

vl ..... - Vacuole.

vsb .... - Vascular bundle.

yml .... - Youngest measured leaf in canopy.

∇ ..... - This symbol along the top margin of a figure indicates approximate transition points from one designated phase of general seed development to another. Phases of seed development are specified by a certain cluster of qualitative and/or quantitative seed tissue events or changes. In this thesis, these clusters and phases are related as such for the first time in the GENERAL DISCUSSION AND CONCLUSIONS and SUMMARY sections. The symbol in the figures is meant to aid the discussions in those sections.

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INTRODUCTION

The papaw or papaya (Carica papaya L.) is indigenous to tropical America where it is one of the most important and popular of fruits. It is also an important plantation crop in other tropical areas of the world. Apart from its mild and pleasant flavour, its popularity is also due to its early-bearing habit and, in the tropics, its production of fruit all year round (Chandler, 1958). The plant has also spread into the frost-free subtropical areas of the world. In the latter areas, however, there is a strong seasonal trend in production. Winter conditions can adversely affect flower production and fruit set (Kuhne & Allan, 1970).

In South Africa, papaya is the most important "subtropical" fruit after citrus, pineapple and bananas (Allan, 1977). As a commercial crop, it is grown mainly in the warmer subtropical areas of the Transvaal lowveld, where peak production occurs during the spring months. A rather limited extent of commerci production also occurs in the frost-free coastal areas of Natal and the Eastern Cape.

Pietermaritzburg (latitude 29° 40' S., longitude 30° 25' E., altitude 770 metres) falls within the latter areas. The normal period of fruit setting at Ukulinga Research Station, Pietermaritzburg, is from late December (early summer to May (late autumn) (Allan, 1967 a). Fruits setting in summer (between Decembe and February) mature nine to ten months later in spring, (during the peak supply period from the hotter areas) and early summer (i.e. September to December). But the fruits that set in autumn (March to May) at Pietermaritzburg have to gro through less favourable conditions of winter during the important early (cell division) stage of development. These fruits mature and ripen ten to eleven months later, from mid-summer to mid-autumn (January to April). The latter happens to be the period when supplies are at their lowest, and prices at their highest. The potential exists, therefore, for increasing the amount of the frui available in this scarce and expensive period (or conversely, of obtaining highe returns during the relative scarcity). One prevailing problem, however, is that fruit size is much reduced.

According to Kuhne and Allan (1970), the most important factor affecting eventual fruit size is the temperature during the first few months of growth, provided they have been well pollinated. This extends from a pre-anthesis perio to an initial phase of fruit growth corresponding to the period when the log of the volume is linear. The growth pattern of papaya fruit is sigmoid, and this initial phase correspondingly extends up to the time the inflexion point in the

sigmoid growth curve occurs. The warmer the temperature during these two periods the faster the rate of growth. Conversely, if these periods occur during cold winter conditions (monthly mean less than 19°C - usually at 14° to 16°C), both the rate of and the number of cell divisions in the fruit are adversely affected. The cell enlargement phase that follows the initial cell division phase can proceed at temperatures between 11° and 19°C, but the relative loss in potential laid down during the cell division phase cannot be made up. This is so even when the cell enlargement phase occurs in warmer, optimal conditions (above about 20°C).

Some potential exists for altering the micro-climate by using tunnels to ensure more favourable temperatures (Allan, 1976 a). However, cold night tempera tures were not much improved upon and this method may only be of value in sub-tropical areas with warmer winter nights than those of Pietermaritzburg.

There are other within-plant factors affecting final fruit size:-

(a) There are genetic differences. Larger-fruited clones or lines produce somewhat larger fruits in the scarce period than smaller-fruited ones (Kuhne & Allan, 1970). The latter authors also demonstrated genetic differences in the length of the developmental period. One valuable potential in this difference is that in the cooler subtropical areas, clones with longer developmental periods can be set earlier, so as to profit in size from growing in the earlier warm conditions, yet only ripening in the scarce period.

(b) Kuhne and Allan (1970) also believed that leaf surface area (and thus presumably available assimilates) during the maximum fruit growth period may influence ultimate fruit size.

(c) Competition with other fruits on the plant (Allan, 1967 b). This competition affects both size and the time required for the fruit to reach maturity. Firstly, the larger the crop load, the smaller the fruit. On the other hand, if the earlier summer-set fruits are removed to ensure a greater fruit set in autumn, and thus a greater supply during the scarce period, the autumn-set fruits mature up to two months sooner (thus defeating the purpose of producing an out-of-season crop).

(d) Adequate pollination (by insects or by hand) is necessary to ensure ovule fertilization, and correlations between fruit mass and seed mass (or seed number) are reported to range between 0,74 and 0,88 (Allan, 1969).

With regard to the latter, regression co-efficients for fruit mass on seed number or on seed mass are reported to have been significantly higher for fruits maturing in spring and autumn than for those maturing in summer (peak harvest) (Allan, 1969). The latter author also found that the correlation was better between mass of seeds and fruit mass than between seed number and fruit mass whe relatively large seeds were present in the fruit. Underdeveloped seeds apparent also stimulated fruit growth.

On examination, some "unfertilized ovules" showed no further development after anthesis (Allan, 1969). Many underdeveloped seeds that were found in the last fruits of the crop which ripened in autumn showed partial development of th integuments, while in some there was also endosperm development without concurre embryo growth. Allan (1969) suggested that hormones which influence fruit growt may be produced in the integuments, nucellus and endosperm, and that the seeds affect fruit growth not only in the early stages of development but throughout the whole period of development of the fruit. A detailed investigation of the anatomical development and hormone production of the different tissues of papaya seeds and fruit flesh throughout fruit development, and the effect of these hormones in attracting metabolites to the fruits from other regions of the plant was suggested as a useful area for further research.

The work in the thesis that follows was aimed at meeting some of the above needs. Although anatomical studies on the development of the seeds of Carica papaya L. exist, none of these provide the sort of quantitative information which would be useful in relating seed development to that of the fruit, and bot in relation to possible seasonal variables. The same holds true for underdevelo ed seeds. And are there critical times or developmental phases at which abortio occurs?

It is also not clearly established why fewer seeds are formed in the fruits that set in autumn (i.e. in the fruits that go on to mature in the scarce period the following late summer and autumn). Is it because fewer ovules are formed during flower-fruit formation, or because fewer ovules are fertilized? Why do seeds abort, or remain underdeveloped in the fruits which set in autumn? If mor ovules were fertilized - (how many are?) - and if more of these developed furthe would the fruits be larger? Why has hand-pollination not improved the size of fruits that ripen in the out-of-season autumn period (Allan, 1958)? To what ext can the small-fruit problem of out-of-season papaya production in cooler sub-tropical regions be alleviated by understanding and modifying seed/fruit inter-actions?

Some of these questions were in mind when the author began his investigatio most, however, sprang to mind as the project developed. No attempt has been ma

to investigate the hormonal or other physiological relationships between seeds and fruit during their course of concomitant growth and development. What follows could hopefully lay the foundations more firmly for such studies.

The author has used seeds and fruits from a recently named clone, Honey Gold, a vegetatively reproduced selection from a seedling of the variety Hortus Gold (Allan, 1976 b). The female plants from which this material was taken were growing at the Ukulinga Research Station near Pietermaritzburg. Continuous testing of this clone has shown it to produce fruits of excellent quality, especially in late summer. It also has a fairly slow rate of fruit development (Allan, 1976 b). Also, "the fruits that ripen in late spring and early summer at Pietermaritzburg have a mass of about 1 kg while the last fruit to ripen in early autumn may be as small as mangoes". Hence the desirability of using this material for a study on the small-fruit problem in autumn out-of-season production. And there was also the need to check this clone's seed development against that of previously reported anatomical studies.

These previous anatomical studies are reviewed in Chapter 1, followed by comparative studies on normal seed development from fruits set in late summer and late autumn. (These normally or fully developing seeds will be referred to as "F" seeds.) These studies included cell measurements of all the major seed tissues during development.

Chapter 2 compares the anatomical development of various kinds of aborted or underdeveloped seeds. This is followed by a detailed study on the intra-fruit distribution pattern of abortion. Various hypotheses were used to predic likely seed abortion patterns within the fruit, and these were tested against the data collected.

In Chapter 3 the correlation and regression between seed mass and fruit-flesh mass when other factors such as leaf area, prevailing temperatures and number (only) of competing fruit were allowed for is examined. Multiple regression analysis was used for this. The simple correlation between seed mass and fruit-flesh mass for specific intra-fruit sub-regions was also examined. And the growth pattern of fruits set in autumn was analyzed from anthesis until maturity in relation to amounts of seed and seed abortion. A survey of pollen tube growth in different seasons was also carried out. Finally, the overall conclusions and implications of all of these studies are summarized. A glossary of abbreviations and some symbols used in this thesis is provided for quick reference.

CHAPTER 1

NORMAL DEVELOPMENT OF OVULES AND SEEDS

1.1 LITERATURE REVIEW

There have been quite a number of morphological and cytological studies on the ovules and seeds of Carica papaya L. (Caricaceae), some of them going back to the turn of this century (Foster, 1943). Singh (1950, 1961) has published more recent work, and Davis (1966) describes the embryology of Caricaceae.

With regard to the related terms, ovule and seed, the embryo and endosperm are products of fertilizations following the penetration of a pollen tube into the embryo sac of the ovule. The various structural details of the ovule are more or less preserved during the transformation of the ovule into the seed (Esau, 1960). Other accounts and distinctions are possible, but the above will be the basis for distinguishing the terms ovule and seed. More specifically, it is intended that with the event of fertilization, what was erstwhile an ovule will then be referred to as a seed, and all further developments, seed development. Finally, for the purposes of this chapter, the emphasis will be on normal development. Abortion phenomena will be dealt with in the chapters which follow. For purposes of orientation, Figure 1a provides a schematic representation of the spatial relationships of various ovule/seed tissues to be referred to.

1.1.1 Ovule development

1.1.1.1 Nucellus and integuments. According to Foster (1943) the nucellus first appears as a slight enlargement at the end of a long stalk. This is followed by the initiation of the two integuments. At about the same time the archesporial cell becomes distinguishable. The integuments continue to develop further, and the whole ovule begins to curve towards its final anatropous position.

In Davis' (1966) account the archesporial cell cuts off a primary parietal cell, which in turn forms at least eight parietal layers, thus imbedding the megaspore mother cell further in. Above this, a nucellar cap four cells in thickness originates from periclinal divisions of the apical nucellar epidermal cells.

In Foster's (1943) study, the vascular tissue consisted of a single provascular strand in the funiculus and outer integument. This differentiated into spiral xylem elements and sieve tubes by the time of pollination. At this time both the outer and inner integuments consisted of about five layers each.

After pollination, but before fertilization, Foster (1943) reported a slight increase in width of the outer integument through cell divisions. She also

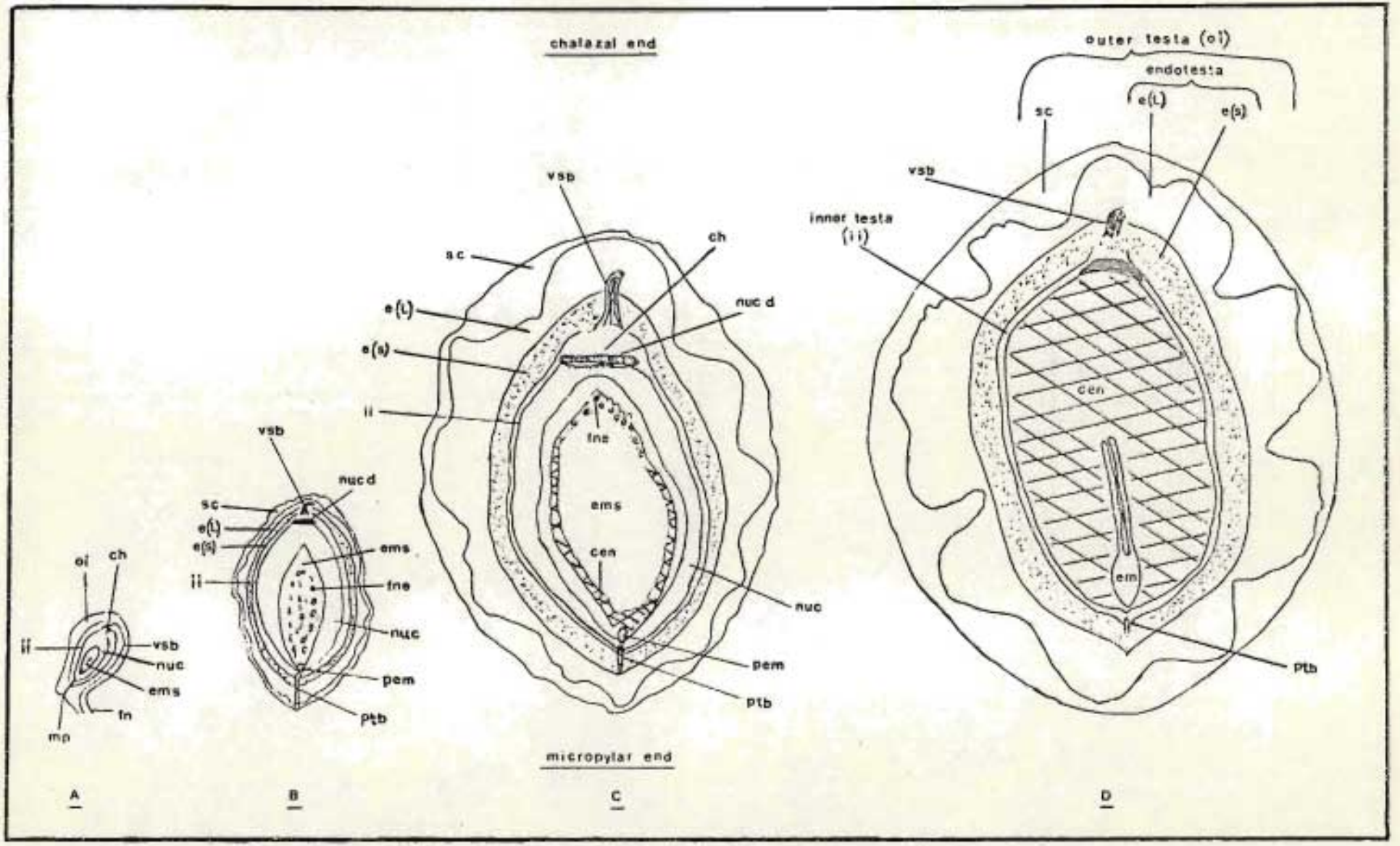

FIGURE 1A Spatial relationships of various ovule and seed tissues.

A: ovule at anthesis; B: seed, few weeks after fertilization; C: at transition from free-

reported that the first signs of tannin deposition in the inner epidermis of the inner integument occurred in this period. At fertilization, she found that well differentiated vascular tissue had reached the chalaza.

1.1.1.2 Megagametophyte. By means of two meiotic divisions "... the megaspore mother cell produces an axial row of four megaspores, the chalazal one of which develops into a normal (Polygonum type) seven-celled, eight-nucleate megagametophyte; the other three megaspores disintegrate ...." (Foster, 1943). In Davis' (1966) review he reported that occasionally the micropylar megaspore is functional.

The mature megagametophyte (described above) is minute compared with the massive integuments and nucellus (Foster, 1943). The synergids are reported to broad apically, and it is characteristic for them to have their nuclei at their micropylar ends and conspicuous vacuoles at their free ends. A filiform apparat develops late in their differentiation. The antipodal cells disintegrate almost immediately they are formed (Foster, 1943). Davis (1966) states that the polar nuclei become closely associated near the egg. Various stages of megagametophyt development - i.e. from two-nucleate to the mature seven-celled, eight-nucleate forms - are found in a single pistil (Foster, 1943).

1.1.1.3 Pollen tube penetration. Traub and O'Rork (1939) have reported th pollen tubes reach the ovules at the apical end of the pistil within two days, and those at the proximal end within five days. Under the greenhouse conditions (unspecified) in Foster's (1943) study, pollen tubes entered the ovules about te days after pollination. Fertilization occurred about 14 days after pollination, i.e. about four days after entering the ovules. The pollen tube is characterist ally broad where it enters the nucellus (Foster, 1943; Singh, 1960) and it is said to crush the cells that come in its path in the nucellus (Singh, 1960). It is found to be persistent, at least up to 60 days, and Foster (1943) suggested a haustorial, nutritive function for it.

1.1.2 Seed development

1.1.2.1 Nucellus. Both Foster (1943) and Singh (1960) reported a speciali zation of the nucellus at the chalazal end. Foster found this to start between 30 and 35 days after pollination in her study. It appears that between these authors they described four sub-regions in this specialized region.

Firstly, the most basal six to seven layers contain thin walls, granular or dense cytoplasmic contents (Foster, 1943; Singh, 1960) and stain red with

safrannin (Singh, 1960). The latter author referred to these layers as an hypostase.

According to a summary review by Maheshwari (1950), in those plants in which it occurs, the hypostase arises "just at the level of the two integuments and directly below the embryo sac". It consists of a "well-defined but irregularily outlined group of nucellar cells ...." The cells may develop lignified or suberized walls, and they usually have poor cytoplasmic contents. The hypostase was once thought to regulate the water economy of the embryo sac, because of its position just above the termination of the vascular supply. This is no longer thought to be necessarily so (Bhatnagar & Johri, 1972). According to the latter authors, the cells may or may not contain dense cytoplasm, and the cell walls may also be thin-walled. In some Leguminosae the cells of the hypostase ("barrier tissue") become thick-walled and probably contain tannin (Dnyansagar, 1954).

Secondly, above the hypostase, and developing into a disc of four or six layers and which can be dissected out (with ease, as a whole, presumably) is a sub-region of thick-walled cells (Singh, 1960). This sub-region is not described or drawn in Foster's (1943) account.

Thirdly, above the latter, or else actually a continuation of the last mentioned sub-region (but without the wall thickening), are a few layers of cells which take a dense stain with haematoxylin (Foster, 1943). Finally, there is a fourth sub-region of "finger-like" cells pointed towards the embryo sac (Foster, 1943). It appears that at least the two most basal sub-regions (hypostase and disc of thick-walled cells) persist into the mature seed (Singh, 1960).

With regard to the remaining major mass of nucellar tissue, this increases in size both as a result of cell division (Foster, 1943) and cell enlargement (Foster, 1943; Singh, 1960) in the period immediately following fertilization. The enlarging nucellar cells lose their contents and become vacuolated (Singh, 1960). The nucellar epidermal cells at the micropylar end undergo some cutinization of their outer and radial walls (Singh, 1960).

During seed development, particularly during endosperm development, most of the nucellus is consumed. Only a few layers remain in the micropylar and hypostase regions (Singh, 1960). From Foster's (1943) account it appears that consumption occurred before the transition of the free nuclear endosperm to its cellular state. All that remains is a peripheral layer of enlarged cells and the specialized region at the chalaza.

1.1.2.2 Endosperm. In contrast to the slow development of the pro-embryo during the early stages of seed development, endosperm development is more activ At first the endosperm formation is free nuclear (Foster, 1943; Singh, 1960). The nuclei and cytoplasm remain along the periphery of the embryo sac, being mor concentrated at the micropylar and chalazal ends (Singh, 1960).

In the course of further development, nucleated cytoplasm may intrude sligh into the central vacuole in the form of bulges (Singh, 1960). This tendency is apparently more noticeable in plants collected from higher altitudes or cold countries (Singh, 1961). After numerous nuclei have been formed, wall formation occurs and is centripetal. The cells undergo further periclinal divisions, addi considerably to the bulk of this tissue (Singh, 1960). Foster (1943) found that the cellularization process began after about 80 days, at the micropylar end, an proceeded towards the chalaza. At first the cytoplasm became less dense, with many minute vacuoles, followed by the laying down of cell walls.

At maturity the endosperm occupies the major portion of the seed's interior and is completely cellular. There are abundant food reserves (Singh, 1960). According to Foster (1943) the reserves are aleurone grains and oil, but not starch. Singh's (1960) drawings show the same features.

1.1.2.3 Embryo. Following fertilization the zygote is said to persist up to about eight days before dividing, and thereafter the divisions are irregular (Foster, 1943). Singh (1960) has confirmed the irregularity of divisions. Johansen (1950) has pointed out that there is a resemblance to the Trifolium variation of the Onagrad type. At the time the nucellus in the region of the chalaza began to undergo specialization (30 to 35 days after pollination) in Foster's (1943) study, pro-embryos had only been seen to be four- to eight-celle The pro-embryo is characteristically ensheathed, and not in contact with the fre nuclear endosperm, at this stage.

In the later stages of free nuclear endosperm development, the embryo reach a many-celled (and presumably bulbous) stage of development (Foster, 1943). During the transition from free nuclear to cellular endosperm (80 days after pollination), Foster (1943) found the embryo to have assumed the shape, but not the size, of mature embryos. At this stage of development, with the cotyledons already differentiated, Singh (1960) found a suspensor group of cells at the end of the radicle, and this persisted into the mature embryo. The latter possesses two thin and leafy cotyledons, and its vascular supply consists of procambial strands only (Singh, 1960).

1.1.2.4 Testal tissues derived from the outer integument. At the time of fertilization, the sub-epidermal cells form a continuous meristematic tissue, and by periclinal divisions continue to add to the thickness of the erstwhile outer integument (Singh, 1960). But then at places destined to form ridges, these cells divide more actively than in the positions destined to be the furrows of the surface of the seed coat. At the same time, the cells of the outer epidermis elongate radially, and also divide periclinally in the furrow positions (Singh, 1960).

Foster (1943) reported that by 30 to 35 days after pollination, a well-differentiated vascular bundle, amphicribral in type, extends along the inner region of the erstwhile outer integument into the former inner integument at the chalazal end. Here it branches out into an umbrella-like structure. Singh (196 reported that he found the vascular supply confined to the chalaza only, and not entering the erstwhile inner integument.

At seed maturity, six cell types or tissues can be identified in the outer testal tissues. These can be divided into two major parts: the sarcotesta and the endotesta. The sarcotesta, which in the mature seed appears smooth, succule and translucent, forms the outermost covering of the fresh seed (Singh, 1960). Singh also reports that it is whitish. The endotesta forms a firm, compact tiss beneath the soft and gelatinous sarcotesta; and in dried seed is the outermost covering (the sarcotesta having dried up and disintegrated). The endotesta appe black, rough, and shows the ridges and furrows (mentioned above) lying parallel to the seed's long axis (Singh, 1960).

Anatomically the sarcotesta consists of the outer epidermis of the seed together with one to three epidermally derived layers in the furrows that are formed by the endotestal ridges. All the cells are large, with the outer epider mal cells being smaller opposite the ridges and larger in the position of the furrows (Singh, 1960). Their outer wall is covered by a cuticle. Finally, in what appears to be implicit in Foster's (1943) account, although contended by Singh (1960), the large cells at the bottom of the furrows are also epidermally derived and form part of the sarcotesta.

The endotesta is made up of four types of cells. The innermost layer, the inner epidermis, increases in size, and a calcium oxalate crystal is deposited in each cell (Foster, 1943). During further development, the walls of the inner epidermis thicken, and the crystals are retained. Adjacent to the inner epiderm are a number of layers of relatively small compact cells. They will be referred to as e(s) in these studies. Their walls eventually thicken and develop numerou pits (Foster, 1943).

In the position of the ridges, and above the e(s) region, are relatively larger cells, to be referred to as e(L). These enlarge considerably during development; and when their walls also thicken, the process starts from the corners of the cell walls (Singh, 1960) and gradually extends to other parts. In the position of the furrows, a layer of elongated cells, interpreted by Singh (1960) to be a contiguous layer of the endotesta, also becomes thick-walled. Finally, all the cells of the chalaza persist in the mature seed and the outer layers have the same sequence of developments as the outer testal tissues (Singh 1960).

1.1.2.5 Testal tissues derived from the inner integument. After fertilization, all the cells except for those in the inner epidermal layer, start elongating transversely (Foster, 1943). Tannin is deposited in the inner epidermal cells. Besides the inner and outer epidermal layers, no more than about four inter-epidermal layers are laid down.

With the exception of the inner epidermis, the other layers appear as a compact layer between the erstwhile outer integument and the nucellus (Foster, 1943). According to the latter author the inner epidermal cells enlarge considerably during development and contain much tannin. In Singh's (1960) account he confirmed the presence of tannin but reported that these cells hardly increased in size.

The outer epidermal cells undergo considerable increase in size and become sclerified (Singh, 1960). The thickening increases further, and in the mature seed they have been described as stone cells (Foster, 1943; Singh, 1960), and, in contrast, as longitudinally elongated fibres with thick walls (Winton & Winton 1935). According to Singh (1960) the outer epidermis of the inner testal tissue forms the main mechanical layer of the mature seed coat.

Of the remaining layers, both Foster (1943) and Singh (1960) consider that they become only slightly enlarged and tangentially elongated, and have only relatively thin walls. These cells lose their contents. They persist in the mature seed together with the inner and outer epidermises. Winton and Winton (1935) considered these layers between the epidermises to be transversely elongated fibres.

1.2 MATERIALS AND METHODS

1.2.1 General placental distribution of ovules

Before describing the selection of material, it would be useful to note the distribution of ovules in the pistil. In Carica papaya L. the pistil is five-carpellate and unilocular, and the placentation is parietal. As seen in transverse section (Fig. 1b), the outer wall of the pistil is ribbed in the radial planes through the dorsal bundles. The inner wall, on the other hand, is ridged where two adjacent carpel margins are fused, i.e. through the radial plane passing through the fused ventral bundles. Ovules are borne on the inner ridges. In between any two adjacent ridges, i.e. in the furrows opposite the dorsal bundles, the inner surface is free of ovules.

For purposes of these studies, each one of the five placental regions (Figs. 1b and 2) was considered as a unit. The upper half of the ovule bearing ridge, i.e. closest to the carpellary margins, was designated as the c.m. region. The lower regions, on either side of the ridge and adjacent to the ovule-free furrows, the p.e. (placentary edge) region (Fig. 2).

Figure 3 and Plate 1a depict one of the placental units in longitudinal view. The placental region was further subdivided into quarters (Fig. 3 and Plate 2a) between the stigma and proximal ends of the placenta. Thus for any one of the five placental regions, ovules were characterized as coming from one of eight sub-regions; designated A, B, C or D if along the carpellary margin ridge (c.m.) or a, b, c or d if along the placentary edge next to the furrows (p.e.), with A/a closest to the stigma end, and D/d to the proximal (stem) end.

1.2.2 Selection of material for ovule and early seed development

1.2.2.1 Autumn fruit-set. For this study, about 50 flowers of the clone Honey Gold were labelled when at the anthesis stage on May 9, 1971. Each newly opened flower was hand-pollinated with pollen from two to three full balloon-stage male flowers picked the same day.

On the same day, four flowers were sampled for anatomic studies, and subsequently samples were taken at fortnightly intervals. At each sampling period, the flowers or young developing fruits were cut up into the eight sub-regions described in the previous section, and fixed in Randolph's fluid (Brooks, Bradley & Anderson, 1950). They were then preserved in 50% ethanol in separate bottles.

From each sampling period, about 40 ovules or seeds per placental sub-region were randomly chosen for subsequent dehydration, infiltration, embedding,

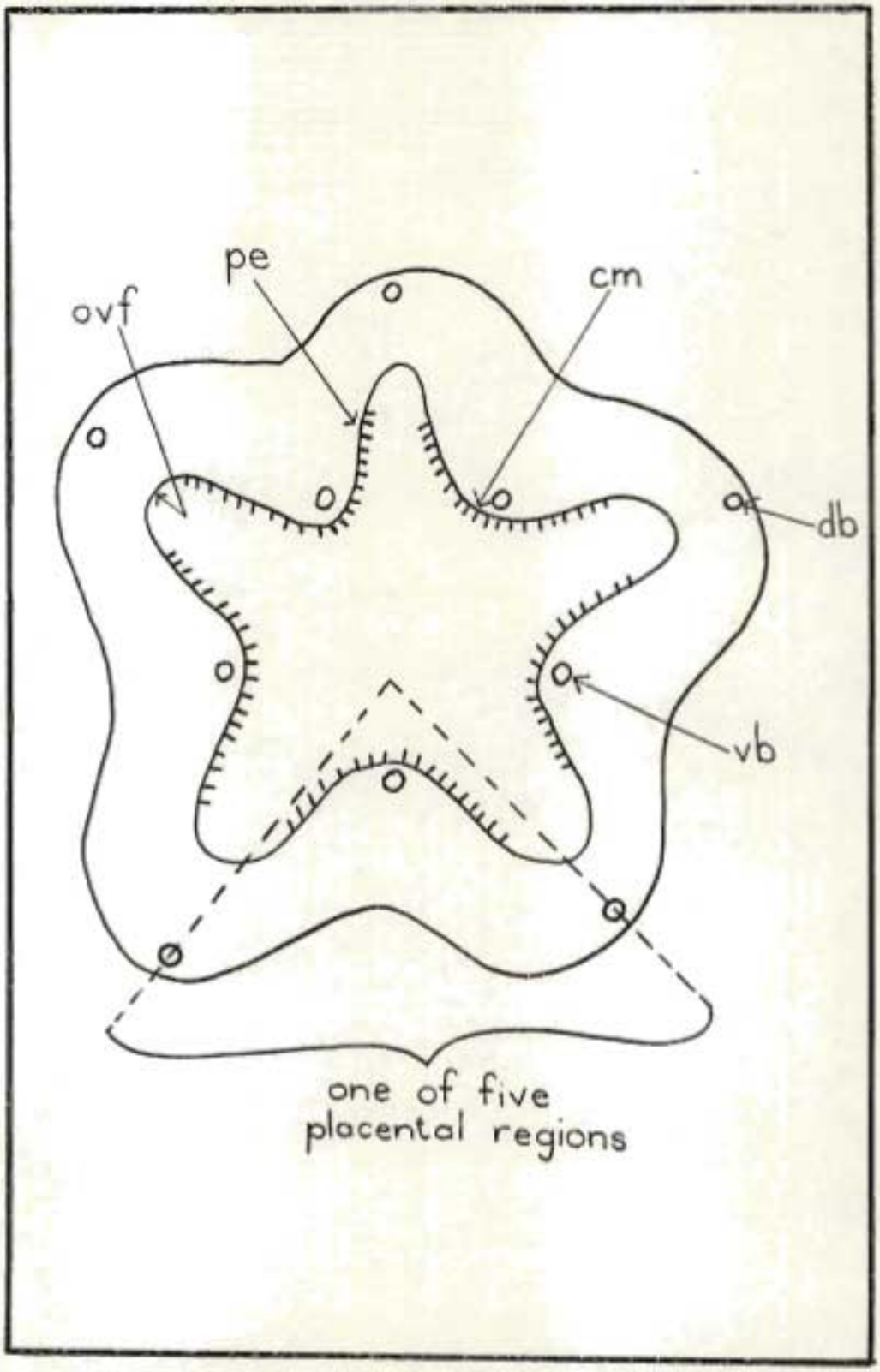

FIGURE 1b Transverse plane of 5-carpellate, unilocular pistil of Carica papaya L., parietal placentation. (For cm, pe, db, vb and ovf, see ABBREVIATIONS.)

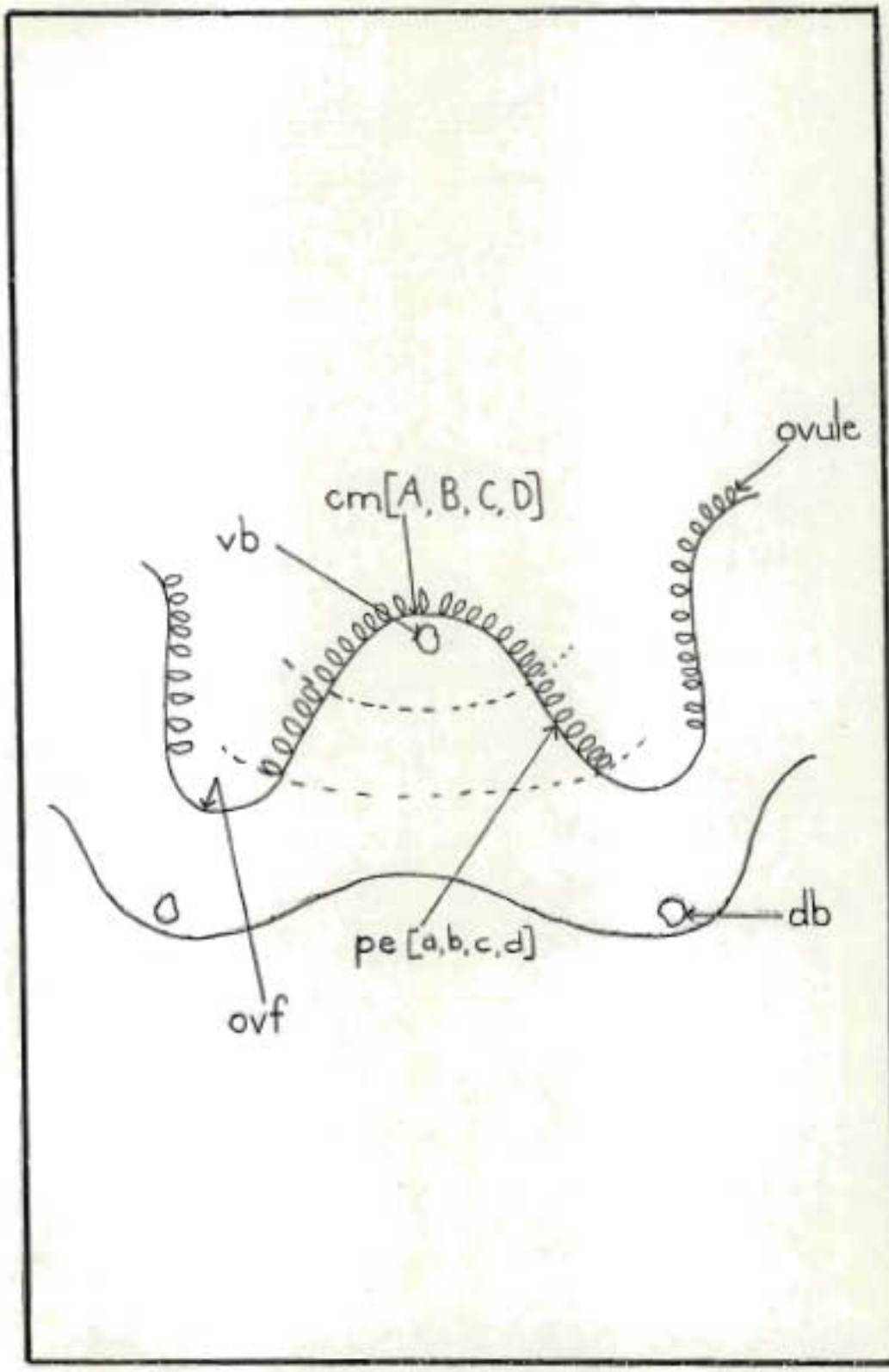

FIGURE 2 One of five placental regions in transverse section. (For cm, pe, A, B, C, D, a, b, c, d, ovf, db and vb, see ABBREVIATIONS.)

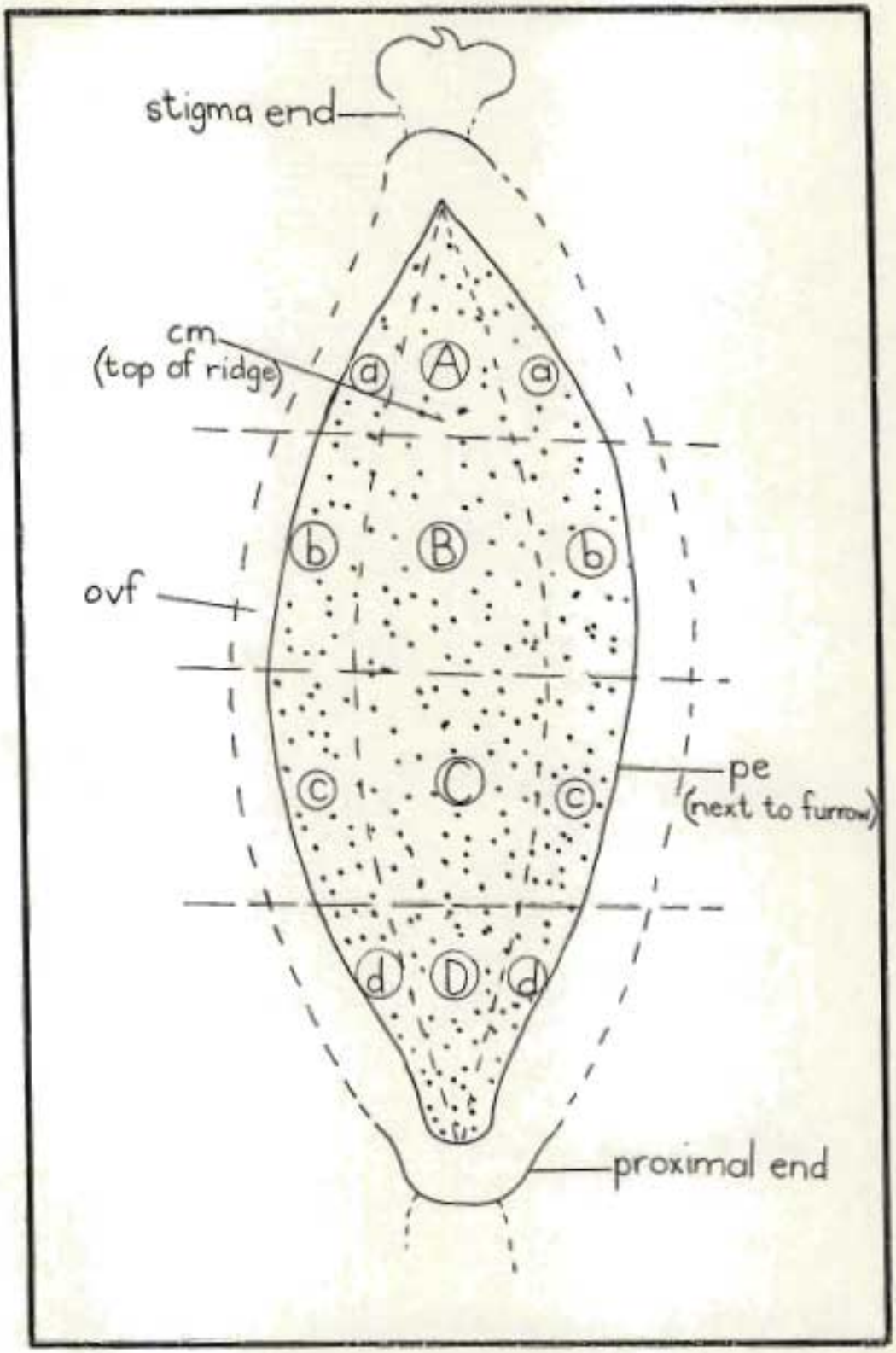

FIGURE 3 One of five placental regions along the longitudinal axis. (For ovf, cm, pe, A, B, C, D, and a, b, c, d, see ABBREVIATIONS.)

sectioning and staining. Another 50 to 60 ovules or seeds per placental sub-region per sampling period were also randomly chosen, and treated according to a clearing procedure to be described. The fairly large number of ovules selected from this autumn-set was in order to carry out a careful examination not only of ovule and early seed development, but to look for signs of early ovule or seed abortion, i.e. within the first eight weeks.

1.2.2.2 Summer fruit-set. In the period 5th to 9th February, 1970, about 190 female flowers of the same clone Honey Gold were labelled and hand-pollinated at anthesis as described for the autumn-set above. This summer-set was used mainly for the study of normal seed development ("F" type seeds) to be described. But as a limited comparison for the above mentioned autumn-set, ovul and/or seeds were selected at anthesis and again two weeks later, cleared and examined as for the autumn-set. Less emphasis was placed on this summer-set for ovule and early seed development because seed abortion is a less frequent phenom enon in fruits set in summer (see Chapter 2).

1.2.3 Selection of material for normal seed development

1.2.3.1 Summer fruit-set. This study was based on the same set mentioned in section 1.2.2.2. Samples of four randomly chosen fruit were taken at varying intervals. At first the samples were taken at weekly and then fortnightly intervals, but as the losses due to abscission increased, the sampling intervals were extended to three, four and eventually six weeks.

From each fruit, seeds that appeared to be of average size and of normal development in the B/b sub-regions were selected. These were fixed and preserve according to either Randolph or Carnoy procedures (Brooks et al., 1950). These were called "F" for "fully-developing" or "fully-developed". See Chapter 2, (2.2.1) for abortive types.

1.2.3.2 Autumn fruit-sets. In addition to the fruits of the autumn-set of 1971 mentioned in section 1.2.2.1, material was also available from a batch o fruit set between the last week of April and the first week of May, 1970. Three fruits were picked per sample, and the samples were taken every week for the first three months, and every third week thereafter. Seeds were selected and preserved as described for the summer fruit-set above. In addition, material wa available from fruit set over the month of April, 1969.

1.2.3.3 Material for whole seed and fruit growth. Apart from the need for ovules and seeds for anatomic studies served by the above-mentioned materials, whole (i.e. non-dissected) seeds and fruits were also needed for measurements of growth. The 1969 autumn fruit-set and the summer and autumn fruit-sets (1970) served these purposes. Measurements were carried out at the time other ovules and/or seeds were sampled for preservation and anatomic studies.

1.2.4 Microtechnique

1.2.4.1 Embedding and microtome sectioning. The dehydration method of Zirkle (Gray, 1954) was followed, and the material was embedded in tissuemat (melting point ± 61°C). At the absolute ethanol : tertiary butanol change, cryst of erythrosin dye were added to render identification easier whilst sectioning. At this last-mentioned stage, and at the final 'pure' tertiary butanol and also final wax changes, the procedures were carried out under vacuum.

Sectioning was carried out on a Cambridge rotary rocking microtome set at 12 microns. The resulting ribbons were laid out on paper. As it was intended to detect the presence or absence of pollen tubes, endosperm and embryo, the selecti of sections of ribbon were carried out as follows. Selected wax sections were cu out at intervals from the ribbons, placed on a slide, and melted onto the slide over a methylated spirits flame. The melted sections were then quickly observed under the microscope before the wax re-crystallized and solidified. By this meth it was possible to converge onto those regions of the ovules or seeds which were most likely to contain pollen tube, endosperm and/or embryo tissue.

Although this stage of the procedure was time-consuming, it was deemed more efficient and economical in terms of time and materials in the staining procedure An alternative would have been to make very many slides to ensure coverage of the tissues concerned. But for the later, normal seed development, this elaborate method of examining melted wax sections was not followed.

Finally, free-hand and cylinder hand microtome sectionings were also carried out on preserved but non-embedded seeds.

1.2.4.2 Staining of microtomed sections. Some of the material was stained according to the Carazzi haematoxylin method (Gray, 1954), but most of it was stained with either Heidenhains aqueous iron-alum haematoxylin method (Johansen, 1940), or with a modified ethanolic variant of this method. In the latter, the ethanolic content of any one stage was never below 50%. This method was found more reliable than the aqueous method on such delicate tissues as embryos and fre nuclear endosperm. The latter often floated off the slides during the change to

Johansen's (1940) fast green counter-stain was also incorporated and the process finished off in absolute ethanol (and not in xylene). The cover slips were mounted in euparal.

1.2.4.3 Clearing procedure. A clearing technique developed by Herr (1971) for the study of megagametophyte and ovule development in angiosperms was extend here for the ovule and early seed development studies. The clearing fluid used by Herr consisted of lactic acid (85%), chloral hydrate, phenol, clove oil and xylene - (LCPCX) - in the proportions 2 : 2 : 2 : 2 : 1 , by mass.

In order to get the constituents to dissolve and remain in a stable homo-genized suspension, it was found necessary to add the constituents in that order viz. L, C, P, C, X. Based on the densities of these respective constituents, th above formulation was approximated as follows:-

Lactic acid ..... 50 ml ;
chloral hydrate .. 60 g ;
phenol crystals .. 60 g (previously kept in a dark-coloured bottle);
clove oil ..... 55 ml ; and
xylene ..... 35 ml .

The resultant fluid was kept in a cupboard, away from light when not being used. (The fluid turned a rather dark colour when left exposed to light.)

With this procedure, ovules and young seeds were removed from their preser-vative and transferred directly into a vial with LCPCX fluid. After 12 to 24 hours they were ready for examination. The ovules and young seeds were also preservable in this fluid for at least two weeks (maybe more) without undesirabl effects.

By means of a large (wide-tipped) pipette, several whole ovules/young seeds were transferred with some of the fluid into a cavity (depression) slide. The cavity was then filled with the fluid and a cover slip carefully placed so as no to trap any air bubbles.

1.2.4.4 Use of microscope with cleared whole ovules and seeds. In Herr's (1971) work, the material studied was no more than about ten cell layers (approx mately 150μ) up to the focal plane of interest. He was thus able to use an oil immersion objective and also phase contrast optics. The Carica papaya L. ovules and seeds were considerably thicker, and their focal planes of interest beyond t working distance of the oil immersion objective.

However, using an objective of 40 x (Olympus microscope) with a working distance of 500 to 600μ , the outlines of nuclei within the embryo sac were theoretically resolvable (Barer, 1959). But resolution without contrast is of little use. Also, the use of phase contrast microscopy with an objective of 40 x did not prove satisfactory with these ovules/seeds, slides or fluid.

Instead, after adjusting the microscope according to the principles of Kohlër illumination, the substage iris diaphragm was closed down further, and the fine focus re-adjusted according to the recommendations of Barer (1959). In addition, use was made of a grey filter.

Although a bit of a strain on the eyes, this technique proved satisfactory in rendering the pollen tube, endosperm, egg and synergid nuclei visible, in addition to the cell walls of the nucellus and integuments. Plate 6c shows Carica papaya L. ovules at the mature megagametophyte stage as seen in conventionally microtome sectioned, stained etc. procedures, and in Plate 3a for comparison, as seen in unstained, cleared whole ovules with this technique.

Details of, and within, individual cells comprising the erstwhile egg and synergids after fertilization proved more difficult to resolve. Endospermic development however, remained detectable. Plates 7a, 6a and 3b contrast the two techniques for free nuclear endosperm.

Nevertheless, the sheath outlining the developing pro-embryo usually contrasted enough with the surrounding tissue mass of erstwhile synergids, pollen tube tip and adjacent free nuclear endosperm (Plates 3c, 7b).

1.2.4.5 Staining of cleared material. At the time of Herr's (1971) work, no suitable staining procedures had yet been devised in conjunction with the LCPCX fluid. In the present studies attempts were made to stain the material after it had been cleared in the fluid. Haematoxylin, aniline blue, safrannin O, toluedine blue, bismark brown, crystal violet and fast green FCF - all of these, singly and in combinations, were tried according to the schedules mentioned by Morley (1949) for cleared material.

It was found that ethanolic staining schedules were successful in imparting the desired stains, but unfortunately the tissues tended to shrink (a phenomenon also noticed with conventionally microtome sectioned and stained material).

Acetone as a stain solvent also caused tissue shrinkage. Dissolving the stains in the clearing fluid itself did not result in discernably better contrast and in addition the stain itself cleared away in the LCPCX fluid overnight.

Following up the success Fisher (1970) had by first staining his material, dehydrating with methyl cellosolve (which also reduces shrinkage), and then clearing with clove oil, various staining schedules were modified and tried.

Basically these were modifications of the following:-

(a) tannic acid-ferric chloride-safrannin O (Sass, 1958);

(b) Heidenhain's aqueous iron-alum (ferric chloride) haematoxylin (Johansen, 1940); and

(c) the previous with Johansen's fast green FCF incorporated as a counterstain.

A general feature of all these schedules is that it is required that the ethanolically preserved whole ovules and seeds be gradually hydrated, followed by the application of aqueous stains. After differentiation of the staining (judged on external appearance of the ovules/seeds), the material was dehydrated in methyl cellosolve and then cleared in LCPCX fluid.

Of the schedules tried, the following appeared to be the best:-

Placental piece with ovules/seeds attached fixed in

Crafs (viz. Randolph's fluids, Brooks et al., 1950);
|
50% ethanol (preservative, until ready to proceed further);
|
30% ethanol ..... 45 minutes;
|
distilled water ..... 45 minutes;
|
3% aqueous ferric chloride ..... 4 hours;
|
two changes: distilled water ..... 5 minutes each;
|
0,5% aqueous haematoxylin ..... 24 hours;
|
two changes in distilled water ..... 5 minutes each;
|
3% aqueous ferric chloride - until blue/black;
|
outer appearance of ovules/seeds take on greyer appearance: 10 - 15 minutes;
|
several changes in distilled water until no more (yellow) ferric chloride diffuses out of the material;
|
methyl cellosolve ..... 8 - 12 hours;
|
LCPCX ..... 8 - 12 hours;
|
transfer individual ovules/seeds to cavity slides for examination in the fluid as previously described for cleared, unstained material.

Although the stained ovules/seeds were certainly distinguishable from unstained ones, the differences were not photographically important enough to warrant the trouble of the staining procedure. It was therefore discontinued in the routine examinations of these studies.

1.2.4.6 Measurement of tissues, cells, whole seeds and fruits. Measurement were carried out on the nucellus and the embryo sacs of cleared whole ovules/see as seen in the median longitudinal focal plane. A graticule divided into 100 divisions was used in the eyepiece. Noting an adjustive magnification on the body tube, and magnifications of the objectives used, eyepieces and substage condenser, it was possible to calibrate the graticule measurements against a specially graduated slide. Cross-sectional areas of these tissues (above) were estimated from an approximating formula, viz. that of an ellipse.

With regard to the estimation of the cross-sectional areas of individual cells of the various tissue types, the formulae used were those for the rectangl and the ellipse. The number of measurements taken per cell type per sampling period varied. It depended partially on the number of 'whole' cells seen in a microtome section for a given tissue: for the integumentary or testal tissues, about 10 cells per seed for each of the epidermises, and from 50 to 150 for the other tissues. About 100 cellular endosperm cells were measured per seed, whils the number of cells for nucellus and embryo depended on the size of these tissue With regard to the number of seeds, since approximately average sized seeds had been selected for preservation, only three to six were used per sampling period for measuring the cell types.

Most of the seeds were sectioned along the longitudinal plane, and the meas ments were taken from sections lying approximately along the median l/s. The idea of taking cell measurements only occurred after the sectioning had been don Examination of those transverse sections that had been made reveal that the transverse dimension of cells not represented in the longisections is quite ofte a major dimension, particularly in some of the testal tissues.

Thus the results only apply to the median longitudinal plane, and cell volumes may not necessarily be well correlated with the longitudinal cross-sectional areas computed. Nevertheless, within the plane examined, comparisons can be made between developmental periods and between various cell types. Anoth aim was to compare the growth or size of cells of individual tissues found in normally developing seeds and that found in abortive ones.

With regard to whole seeds and fruit growth, measurements of length, breadt and fresh mass (before removal of seeds) were determined for all sampled fruits.

The author had previously found that the formula for the volume of a sphere, viz. in the form $\frac{\pi}{6} B^3$, where B is the mean fruit diameter, is a satisfactory approximation for the volume of fruits of the clone 'Honey Gold' (Pereira, 1968).

With regard to the 1969 autumn-set, 48 fruits were set aside for fruit growt i.e. these were not sampled from for the anatomical studies. Of these 48, only 18 survived to fruit ripening, the others abscissing. Measurements taken fortnightly provided a continuous record on this sub-set.

Measurements of whole seed growth in the 1969 autumn-set were taken as follo from the 15th week's sample onwards, 50 (normally developing) seeds were removed from each of the B - C (carpellary margin) and b - c (placentary edge) regions, respectively. The mean seed (fresh) mass for each of these regions, and their combined mean, were determined. In addition, length and diameter measurements were taken on a further five (normally developing) seeds from each of the above sub-regions. This sample size of five was calculated to give a sample estimate o the mean with a margin of error of 10%. The calculation, based on standard error data, is from Cochran (1964). The measurements were made by means of either a microscope fitted with the calibrated graticule or else a screw-micrometer. Finally, the same sampling and measuring procedures were carried out on the ovule and seeds of the 1970 summer- and autumn-sets.

Volumes of seeds of a wide range in size were determined by paraffin displacement (the seeds floating in water, but sinking in paraffin). Of the various approximating forms tried, it was found that the formula of the volume of a prola spheroid gave a good fit. The latter geometric form is obtained by rotating an ellipse about its major axis, and the formula for the volume is $\frac{4}{3} \pi ab^2$, where a and b are the major and minor axes respectively (Hale, 1965). As applied to these seeds, the major and minor axes were the length and diameter respectively.

In fitting the curves to the various data from the seed and fruit anatomic and growth studies, the method of "freehand smoothing" for curvilinear relations as explained by Ezekiel and Fox (1959) was used. The method entails grouping set of data into appropriate groups to obtain group averages; then drawing in a smoo free-hand curve which passes near all the group averages and approximately throug the middle of the original data. The process is repeated afresh several times, and an average curve selected from these. In addition, the curves should be subject to certain logical limitations as regards shape, sign of slope, presence or absence of inflexion points, etc. Previous fruit growth studies on papaya (Kuhne & Allan, 1970) suggested a simple sigmoid curve for the fruits, and famili arity and inspection of the data suggested the same for the whole seed growth curves as well. The curves for the individual cell types were often more comple

and it was assumed that growth curves were never negative, and that the responses were 'smooth'. The latter, of course, was probably unlikely for any individual seed. Nevertheless, the smooth curves are meant to suggest the population mean response type. Otherwise, the form of the curves were judged from the data available. Only a few tissues proved problematic.

1.3 RESULTS AND DISCUSSIONS

1.3.1 Ovule and early seed development: Autumn

1.3.1.1 Nucellus and integuments before fertilization. Ovules were at different stages of megagametophytic development at the time of anthesis, as also found by Foster (1943). In those in which the megagametophyte had reached the mature form (Plate 8a), the inner and outer integuments both consisted of about five layers each, as also found by Foster (1943).

All the ovules had differentiated a vascular bundle in the funiculus and in parts of the inner portion of the outer integument. Table 1 shows the percentage of ovules which had already differentiated the vascular bundle into the chalaza.

TABLE 1 Percentage of ovules/seeds with vascular bundle differentiated at chalazal region, for fruit set in autumn, 1971. Sample size equal to 50 for each fruit sub-region for each sampling period

Fruit sub-region	SAMPLING PERIOD		
	At anthesis	Week 2	Week 4
A	66	100	100
a	16	72	92
B	90	100	100
b	0	44	88
C	82	86	100
c	2	22	100
D	68	68	100
d	18	Not examined	98

Referring now only to the ovules at anthesis, it is evident that those along the c.m. ridge (sub-regions A, B, C, D) were more advanced in this respect than those along the p.e. edge along the furrows (sub-regions a, b, c, d). The author has also made observations on unopened flower buds at various stages of development, and it is evident that the first ovules to be initiated are in the c.m. ridge region. This helps to explain why vascular bundle development is more advanced along the c.m. ridge. These ovules are also closer to the underlying ventral bundle (Figs. 1 and 2) from which all the ovules receive their vascular connections.

Figure 4 shows the cross-sectional area of nucellar tissue as seen in the longitudinal focal plane. At the time of anthesis, the ovules of A, B, C and D along the c.m. ridge region had more nucellar tissue than those nearer the furrows (p.e.; a, b, c, d).

1.3.1.2 Megagametophyte. It has been said that ovules were at various stages of megagametophyte development at anthesis. Plate 5a shows an ovule whose megagametophyte was at the four-nucleate stage. At the focal plane photographed one of the two nuclei at the micropylar end is in focus, and the other two can be seen in the centre of the megagametophyte. In Plate 5b, at a slightly different focal plane, the other micropylar nucleus is in focus, whereas the three other nuclei are slightly out of focus. Plate 5c is a photomicrograph of what was an eight-nucleate megagametophyte. Three of the four micropylar nuclei are in focus, the innermost one being the micropylar polar nucleus. At the chalazal end, only the other polar nucleus is in focus; the three antipodals are out of focus and were very faint.

Plates 6c and 3a show megagametophytes at the mature stage. As can be seen, the synergid vacuoles in focus are quite prominent. The filiform apparatus (not shown here) was not detected in cleared material.

In over thirteen hundred ovules examined - with the exception of four ovules, pollen tubes were not seen to be penetrating into nucellus tissue of ovules lacking mature megagametophytes. In the four exceptions, the pollen tubes penetrated into what appeared to have been embryo sacs devoid of contents, as seen in second and fourth week samples. There were a few other ovules in which pollen tubes had entered the micropyle, but not the nucellus, of ovules with immature megagametophytes.

There were also the occasional "oddities". A few ovules showed more than one pollen tube. Plate 5d shows an ovule that was focused at a plane to show that one pollen tube had entered into the nucellus, whilst a second had doubled

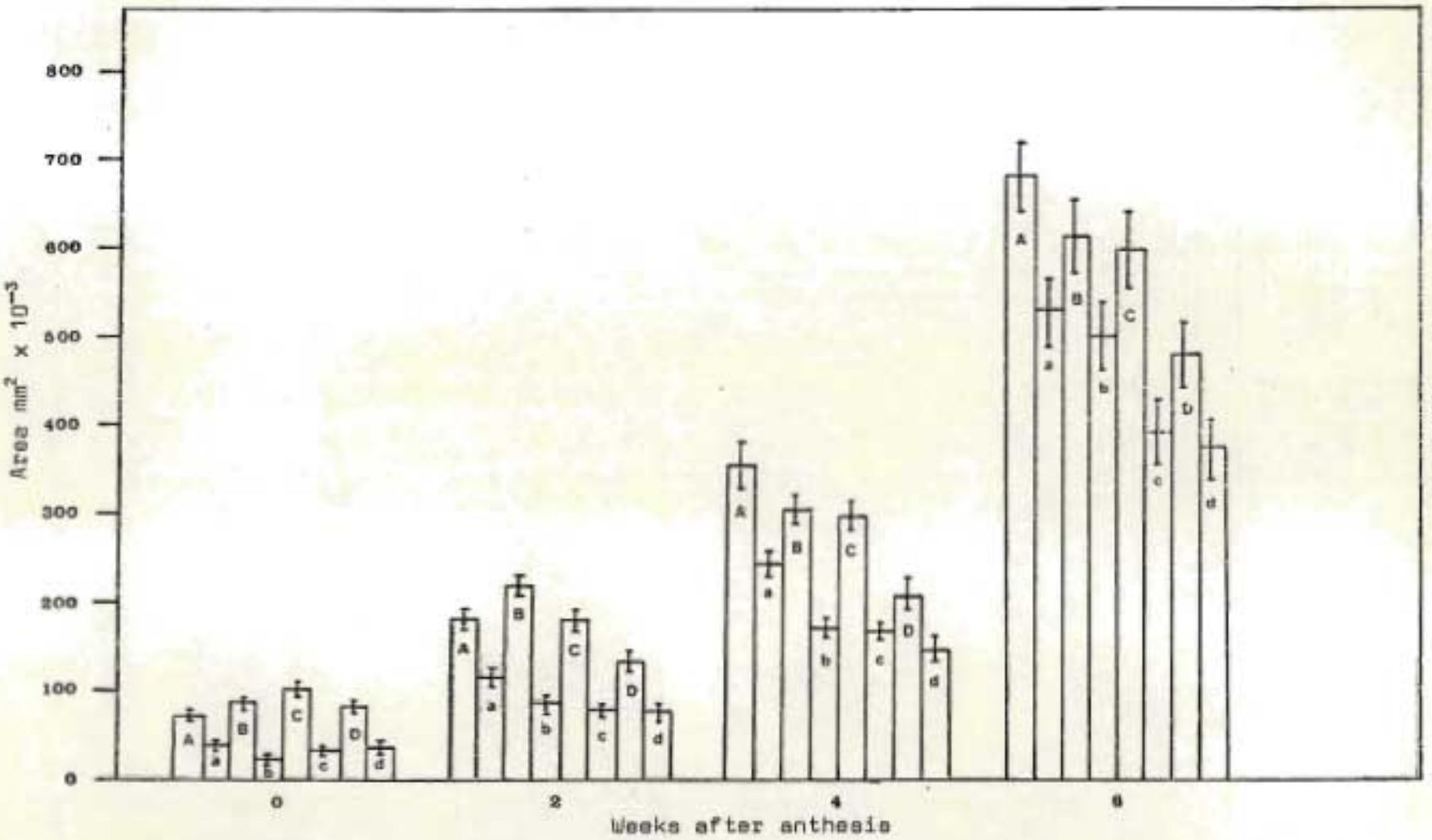

FIGURE 4 Mean cross-sectional area of nucellus tissue along the median longitudinal plane of ovules/seeds from intra-fruit sub-regions during early growth, autumn set, 1971. 'I' indicates 95% confidence

back in the micropylar region of the inner integument. No ovules, however, were seen with more than one pollen tube in the embryo sac.

An interesting feature of the four exceptions mentioned earlier was that the pollen tube appeared to have penetrated a good deal further into the embryo sac than usual. In spite of the caution made by Maheshwari (1950) against the view that the synergids necessarily control the entrance of the pollen tube, this could well be the case in Carica papaya L. Bhatnagar and Johri (1972) have reviewed more recent work which supports the role of the synergids, although they also echo Maheshwari's caution.

Figure 5 depicts the proportion of ovules in the various placental sub-regions which had mature megagametophytes. It is evident that the ovules near the c.m. ridges (A, B, C, D) were more advanced in this respect in comparison to ovules nearer the furrows (a, b, c, d) at anthesis. This is also borne out by the X^2 analyses of Appendix Table 2.1 which shows that whereas no significant differences existed within A, B, C, D or a, b, c, d respectively, differences were certainly present when both these were taken together.

Figure 5 further shows that by the second week after anthesis, the differ between the ridge and furrow ovules had been narrowed considerably.

It may seem surprising that the sub-regions along the c.m. ridge had a lower proportion of mature megagametophytes at the second week after anthesis. If one recalls that although the sample size of ovules per placental sub-regio was relatively high, that of the flowers/fruits was small. The discrepancy then was probably within the limits of natural variability between the flowers/ fruits.

Table 2 shows the percentage of ovules in the various placental sub-regio which had not yet developed an embryo sac (and therefore no megagametophyte, e.g. Plate 4a). In comparing the sample at anthesis with that at the second week, it is again evident that there was a generally lower level of developmen in the second week's sample. Notwithstanding the above, the following can be seen. At the anthesis sample, the ovules nearer the furrows (a, b, c, d) appe ed to be less advanced (i.e. fewer ovules with embryo sacs) than those nearer the c.m. ridge (A, B, C, D). In the subsequent samples, these differences between "ridge" and "furrow" ovules became less clear-cut. A possible reason that after anthesis the differentiation of new ovules probably ceased, and tho that were already present tended to go on to develop an embryo sac (and mega- gametophyte).

It was difficult to know definitively what proportion of ovules eventuall developed mature megagametophytes. This is because after the second week, the

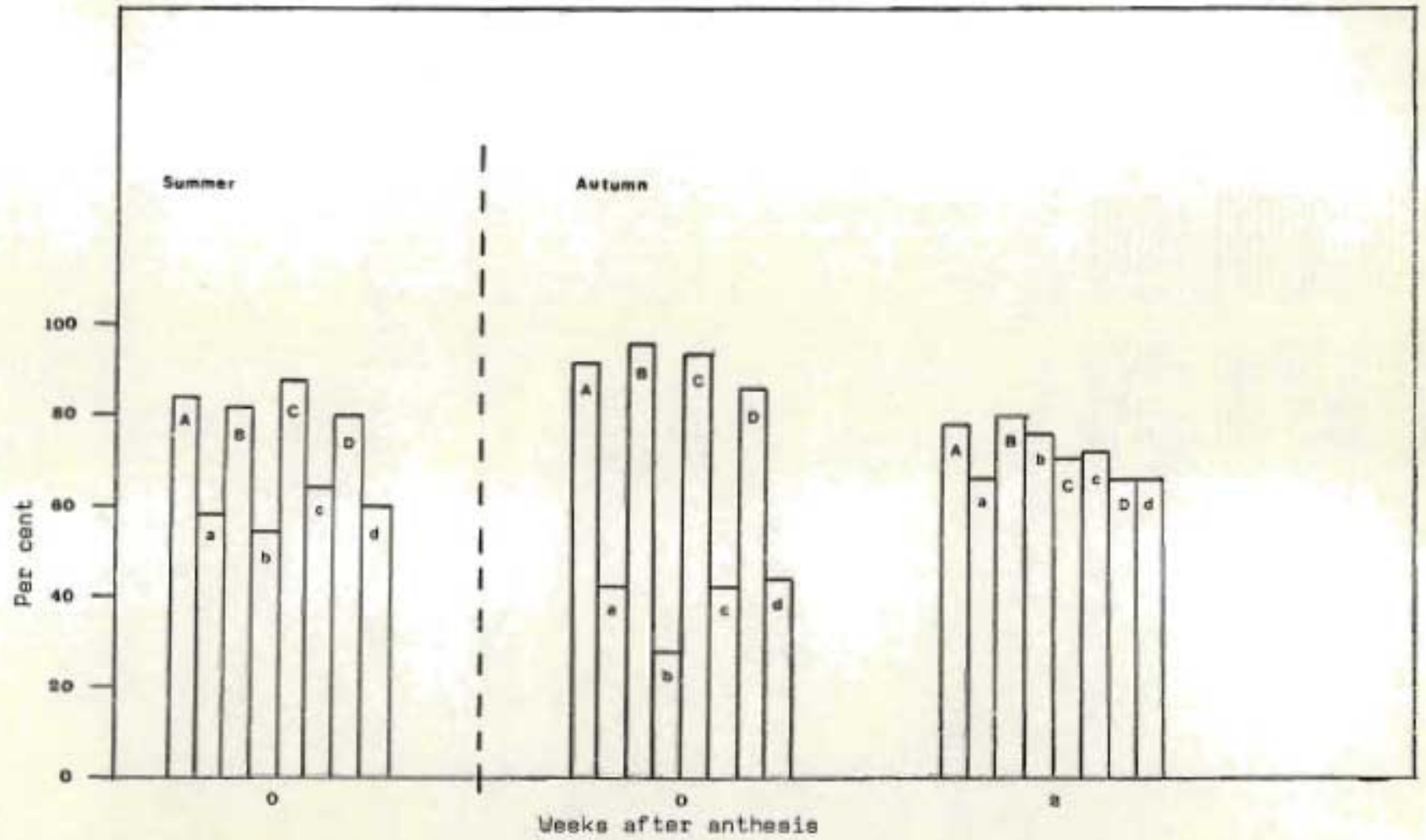

FIGURE 5 Percentage of ovules from intra-fruit sub-regions with mature megagametophytes at anthesis

TABLE 2 Percentage of ovules/seeds without embryonic sacs for fruit set in autumn, 1971. Sample size equal to 50 for each fruit sub-region for each sampling period

Fruit sub-region	SAMPLING PERIOD			
	At anthesis	Week 2	Week 4	Week 6
A	4	18	2	4
a	6	14	0	6
B	2	14	2	2
b	8	6	2	2
C	2	12	4	2
c	2	12	6	1
D	0	10	4	2
d	8	6	2	2

presence of pollen tubes in ovules resulted in, or else was associated with, collapsed synergids and other changes in the embryo sac. This obscured the status of the megagametophytes. One possible way to find the answer would be to examine megagametophyte development in protected, unpollinated flowers/fruit One would have to ensure that these fruits did not abscise too soon.

1.3.1.3 Placental distribution of pollen tube penetration. Figure 6 illu trates the pattern of pollen tube penetration into ovules. If one looks at the histogram at the second week after anthesis, it appears that the ovules closer to the stigma end have a greater likelihood of receiving the earlier penetratio There also appears to be an obvious difference between ovules closer to the c.m ridges at A, B as opposed to those adjacent ovules closer to the furrows a, b, even although they were virtually equidistant from the stigma. It may be re-called that pollen tubes only appeared to penetrate an embryo sac if the mega-gametophyte was mature, and that the general pattern of distribution of megage-metophyte maturity (Fig. 5) probably carried over into the following week or so Pollen tubes were more likely to have entered first the ovules with mature mega gametophytes closest to the stigma end, and then those ovules with mature mega-gametophytes in the next closest sub-regions.

Table 3 is a X^2 analysis of the pattern of pollen tube penetration. Consi ing the period between anthesis and the second week, all the regions except for the basal quarter (D/d) and (c) furrow received pollen tube penetrations at a (statistically) significant level. The largest penetrations were along the c.m

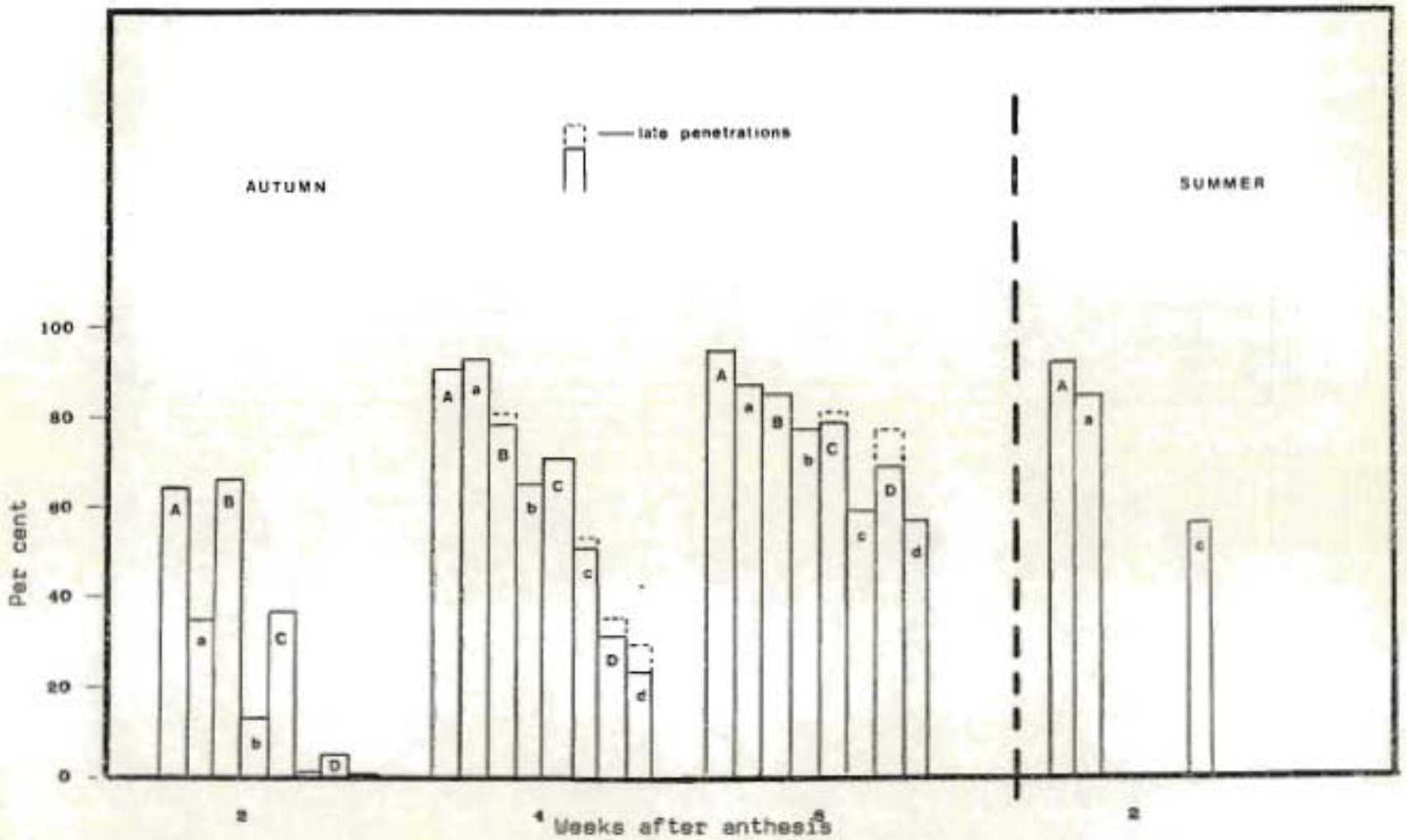

FIGURE 6 Percentage of embryo sacs in the intra-fruit sub-regions penetrated by a pollen tube during early growth (autumn, 1971); and by the second week in three selected sub-regions (summer, 1970). See ABBREVIATIONS for A to d .

TABLE 3 X^2 differences (df = 1) for the proportion of ovules penetrated by pollen tubes between successive sampling periods for a given fruit sub-region

FRUIT SUB-REGION	BETWEEN ANTHESIS AND WEEK 2		BETWEEN WEEK 2 AND WEEK 4		BETWEEN WEEK 4 AND WEEK 6	
Set in Autumn, 1971	X^2	Significance level	X^2	Significance level	X^2	Significance level
A	45,314	***	8,680	**	0,177	NS
a	19,580	***	34,462	***	0,488	NS
B	48,529	***	1,920	NS	0,074	NS
b	5,530	*	26,042	***	1,240	NS
C	21,053	***	10,343	**	0,493	NS
c	No penetration	-	32,484	***	0,365	NS
D	1,375	NS	9,357	**	12,965	***
d	No penetration	-	11,458	***	10,583	**
Set in Summer, 1970			Probability significance levels			
			NS $p > 0,05$			
A	84,946	***	* $p \leq 0,05$			
a	71,971	***	** $p \leq 0,01$			
c	38,077	***	*** $p \leq 0,001$			

ridge (B, A, C) and the first quarter furrow (a) next to the stigma end. Betw the second and fourth weeks, all the sub-regions with the exception of the second quarter along the ridge (B) received additional pollen tube penetration at significant levels. The largest increases were for the three upper furrow regions (a, c, and b). Between the fourth and sixth weeks, only the lower qua (D/d) received significant additional penetrations.

This analysis suggests further confirmation of the idea that pollen tubes tend towards the nearest available ovules with mature megagametophytes; at an rate towards sub-regions with such megagametophytes. Such regions may have be producing more chemotropic substance(s).

For the histograms covering the fourth and sixth weeks after anthesis in Figure 6, certain additions have been drawn in. These are represented as brok

lines, and the sub-regions concerned are B, c, D, d for the fourth week, and C, D in the sixth week's sample. The additional ovules represented here had been penetrated by pollen tubes, but no changes had been effected in the megagametophytes. Either the pollen tubes had just arrived, or else possibly by that time those pollen tubes no longer contained potent male gametes.

1.3.1.4 Nucellus of early seed development. Following fertilization, cell divisions were occurring in the nucellus. At first the divisions occurred throughout the tissue, whilst later (about the eighth week) they appeared to be confined to the periphery. Cell enlargement proceeded throughout this period. The cells at the periphery tended to be smaller, partially because more divisio were occurring there.

Plate 3d shows a young developing seed in which 'tannin' was just beginnin to be deposited in the chalazal region, and Plate 4b shows one at a stage prior to this. Plate 4c shows one in which several layers had already been deposited giving rise to the disc seen in cleared whole seeds. This disc occurs just abo the hypostase identified by Singh (1960) and shown in Plate 7c, d. He did not mention tannin deposition, nor did Foster (1943). But in Singh's further accou and drawings he shows a region of cells four to six layers abutting upon the hypostase (embryo sac side) which look like the tannin disc region seen here. said they became "thick-walled". (The contents of the cells of this 'disc' loo like that of the inner epidermis of the inner integument, called 'tannin' by Foster, 1943.)

Table 4 shows the proportion of ovules/seeds in the various placental sub-regions in which the tanninized disc had become evident. It appears that the process began between the second and fourth week after anthesis. Again, the process was more pronounced in ovules/seeds nearer the c.m. ridge.

Figure 4 shows the mean cross-sectional areas of nucellar tissue as seen i the median longitudinal focal plane. Ninety-five per cent confidence intervals have been drawn in and these were estimated as twice the standard errors of the means (Ezekiel & Fox, 1959). The differences between ovules along the c.m. ridges and p.e. furrows at anthesis have already been pointed out. In the week that followed, the relative size of the expanding tissue seems to have been a function of its relative size at anthesis on the one hand, and on the other of the ovule's/seed's position relative to the temporal pattern of pollen tube penetration. In other words, the earlier a placental sub-region received pollen tube penetrations, the larger was the average size of the nucellus.

Finally, Figure 7 shows the cross-sectional areas of the embryo sacs alone

TABLE 4 Percentage of ovules/seeds with tanninized disc of cells adjacent to the hypostase region for fruit set in autumn, 1971. Sample size equal to 50 for each fruit sub-region for each sampling period

FRUIT SUB-REGION	SAMPLING PERIOD			
	At anthesis	Week 2	Week 4	Week 6
A	0	0	100	96
a	0	0	96	90
B	0	2	100	88
b	0	0	78	82
C	0	0	96	98
c	0	0	72	84
D	0	0	76	94
d	0	0	48	72

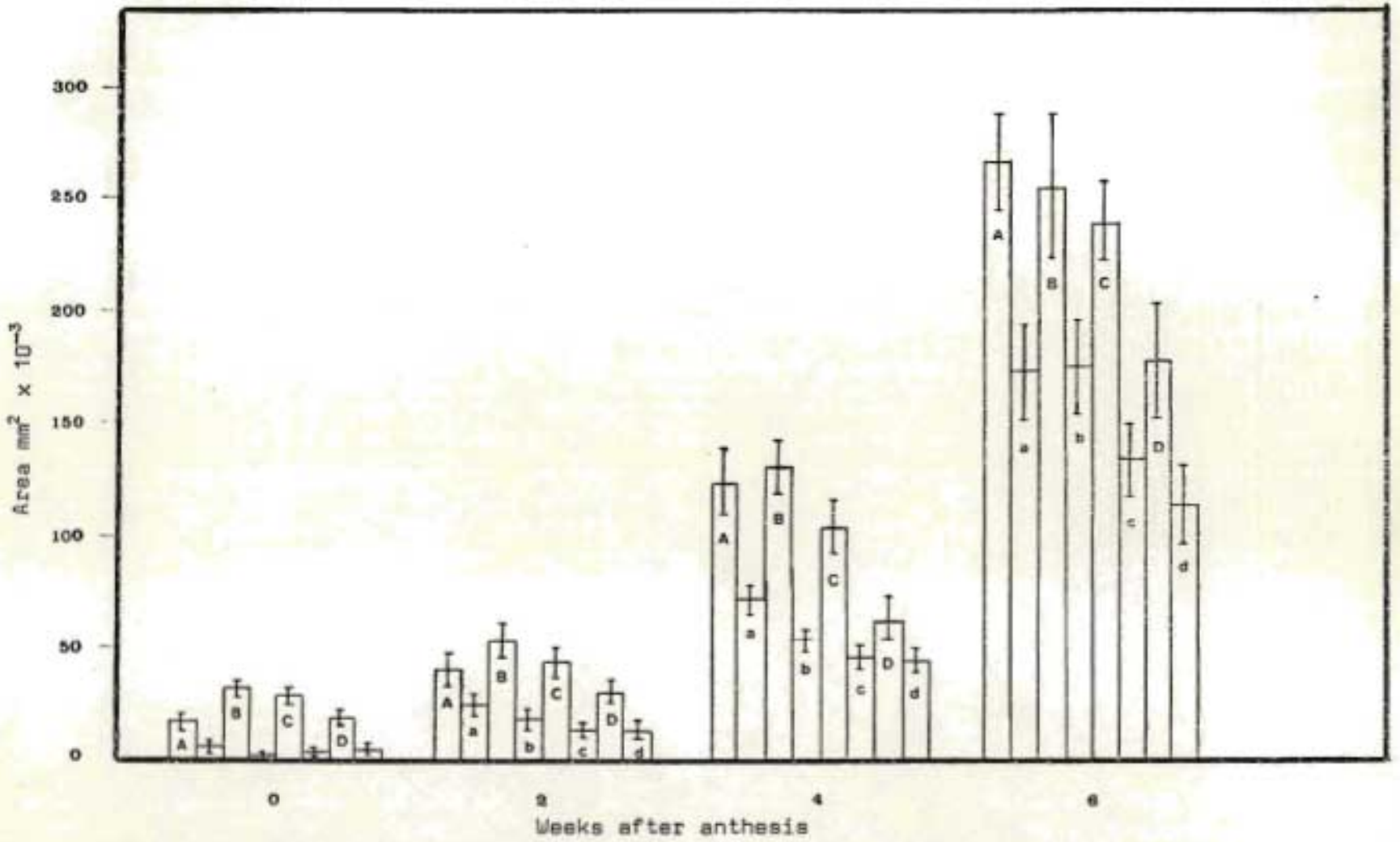

FIGURE 7 Mean cross-sectional area of embryo sacs along the median longitudinal plane of ovulee/seeds from intra-fruit sub-regions during early growth, autumn, 1971. 'I' indicates 95% confidence limits of estimated mean. Sample size 50 per sub-region. See ABBREVIATIONS for A to d .

generally the same as that of the nucellus. Of interest also is that embryo sac growth was quite slow until about the fourth week.

1.3.1.5 Endosperm. Endosperm growth was relatively rapid (unlike the embr and easy to follow with the LCPCX clearing method. Development was only free nuclear during the early seed development (six to eight weeks) looked at with th method, and the endosperm appeared in strands as shown in Plates 7a and 6a. The nuclei tended to be more concentrated at the micropylar and chalazal ends than in the mid-region, as was also found by Foster (1943) and Singh (1960).

From Appendix 2, Table 2.2, it is evident that differences existed between intra-fruit sub-regions in respect of the proportion of ovules/seeds with normal developing endosperm. Four weeks after anthesis there was a gradient down both the carpellary margin and the placental ovules/seeds. Along both major sub-regions, this proportion was greater the closer the sub-region was to the stigma end. This no doubt was due to the earlier and greater concentration of pollen tube penetrations at the top of the fruit as compared with the bottom of the fr

When carpellary margin and placental edge sub-regions are compared together for within the top half or bottom half of the fruit respectively, significant differences only existed within the bottom half. This indicates a greater fall off in the proportion of seeds showing development in the lower half. This will be examined further in Chapter 2.

Figure 8 depicts the percentage of just those ovules which had been penetrated by pollen tubes (and presumably fertilized) which showed normally develop ing endosperm. (Non-normally developing endosperm usually appeared "flimsy", or else markedly different in some other way from that of the appearance of normall developing endosperm.) In terms of this judgement, the percentage of fertilized seeds showing normally developing endosperm at the fourth week ranged from just below 80% to just below 100% for the various sub-regions. However, at the sixth week, sub-region 'd' had a markedly lower percentage (about 50) than the rest of the fruit (over 80%). This lowered percentage will be discussed further in Chapter 2 on seed abortion.

For the present purposes it is interesting to note that whilst intra-fruit differences existed in the proportion of the total ovules/seeds showing endosper development (Appendix 2, Table 2.2), little difference existed between sub-regions when only fertilized seeds are considered (the exception being sub-regi 'd' at the sixth week).

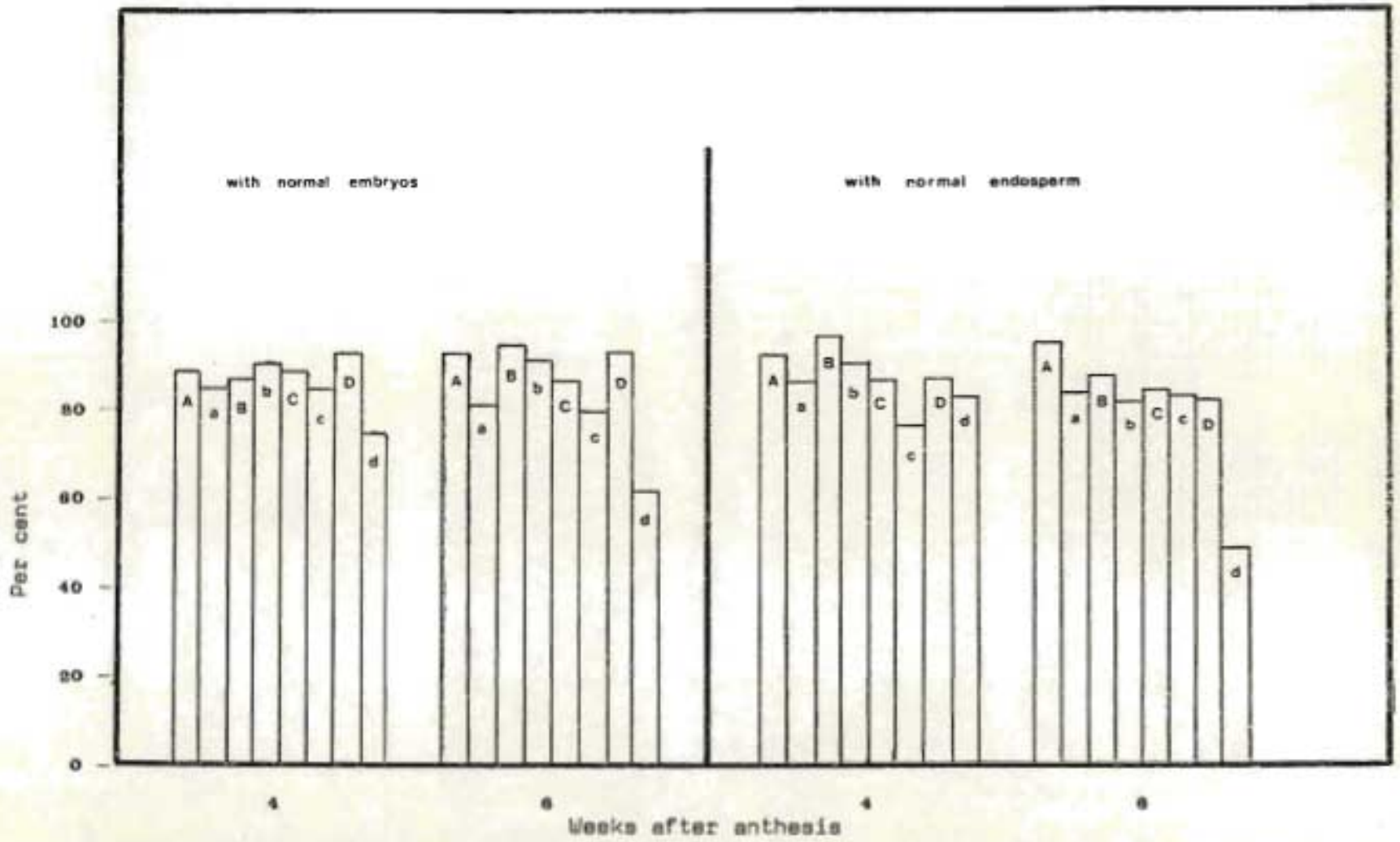

FIGURE 8 Percentage of fertilized seeds per intra-fruit sub-region having normally developing embryos and endosperm, autumn 1971. See ABBREVIATIONS for A to d .

1.3.1.6 Pro-embryo. Embryo development was very slow - never getting beyond the globular pro-embryo stage. Because the individual cells were relatively small, and because of the close proximity of the pollen tube tip and surrounding free nuclear endosperm, it was usually difficult to distinguish features of the pro-embryo when using the clearing method. Neither did the author have much success with the conventional technique, i.e. with microtome sectioning, etc. Apart from losing pro-embryos during the pre-staining procedur staining itself provided further difficulties.

Plates 7b and 6d are of the same seed (eight weeks after anthesis) with a two-celled pro-embryo. It was ensheathed (as also found by Foster, 1943) and there was quite a bit of mucilagenous-like material around it. The free nuclear endosperm nearby, as well as the pollen tube tip are heavily stained. This heavy staining is apparently a common difficulty put down to the release of certain substances in the interaction between pollen tube and synergids (Maheshwari, 1950). One consequence of the above difficulties is that the autho was not able to check this material for irregular early embryo cell divisions (cf. Foster, 1943; Singh, 1960).

Plates 3c and 6b show young pro-embryos at six weeks after anthesis as seen through the clearing fluid. These Plates - 3c, 7b, 6b and d - reveal how close the free nuclear endosperm strands lay to the pro-embryo. Foster (1943) claimed that there is no contact. Whatever contact there might be is very slight, as by pressing lightly on the coverslip, the endosperm strands gave way. But ultra-structural analyses would have to be used to really know what the relationship is during the early stages.

Turning again to Figure 8, 80 to 95% of all fertilized seeds showed apparen normally developing embryos at the fourth and sixth weeks, bar one exception. That exception was again at sub-region 'd', (as for endosperm), which had about 75% and 60% at the fourth and sixth weeks respectively.

1.3.1.7 Tissues derived from the outer integument. By the eighth week af anthesis, i.e. at the end of this study, the tissues derived from the outer integument had differentiated into five or six cell types. Plate 8b, c shows part of these as seen in longisection. The tissue between the outer and inner epidermises had increased by cell division and enlargement and was differentiat into two tissues destined to become part of the endotesta of the mature seed coat, viz. the e(s) and e(L) tissues. Cell divisions near the top of the latte tissue, e(L), can be seen in Plate 8c.

In many regions of the developing seed coat, the e(s) and e(L) formed a continuous double "layer", except in the furrows. Several large cells filled the latter. The outermost is the continuation of the outer epidermis, recogniz able by its thickened outer wall. The layer immediately below it as shown in Plate 8b, c was derived from the outer epidermis by periclinal divisions. Thes large-celled derivatives, together with the outer epidermis, were destined to become the sarcotesta of the mature seed.

The interpretation of the innermost layer of large cells in the furrow, i. immediately above e(s), as seen in Plate 8b, c, has been controversial (litera- ture review). Kratzer (1918) and, apparently, Foster (1943), regarded it as epidermal in origin. Singh (1960) contended that it is part of the outermost layer of the e(s)/e(L) tissue. The present author is inclined to concur with Singh's (1960) view. Examination of Plate 8b, c (and of other material) shows that the layer of large cells in question is continuous with that of the outer- most layer of the e(s)/e(L) tissue. (This point will be further discussed unde the later seed development section.) The point at issue here has been whether the seed structures of Caricaceae and Cucurbitaceae are similar. If this botto layer is derived from the epidermis, then apparently they are similar (Singh, 1953), otherwise not (Singh, 1960, who also advanced additional reasons).

The final tissue of the endotesta to be referred to is the inner epidermis These cells had begun to expand, both radially and tangentially, by the eighth week after anthesis.

1.3.1.8 Tissues derived from the inner integument. By the end of the eighth week, these tissues contributed about eight layers: an inner and outer epidermis plus about six layers in between. The outer epidermis had elongated tangentially to a considerable extent. The underlying five or six layers had also expanded tangentially, but to a much more limited extent. The inner epi- dermis had enlarged somewhat, and tannin deposition was often seen at the micr pylar end of the layer.

1.3.1.9 Growth of mature ovules not penetrated by pollen tubes. Measure- ments were also carried out on mature ovules not penetrated by pollen tubes to see what their comparative pattern of growth was after anthesis. Figure 9 depicts nucellar growth for three classes of ovules or seeds:-

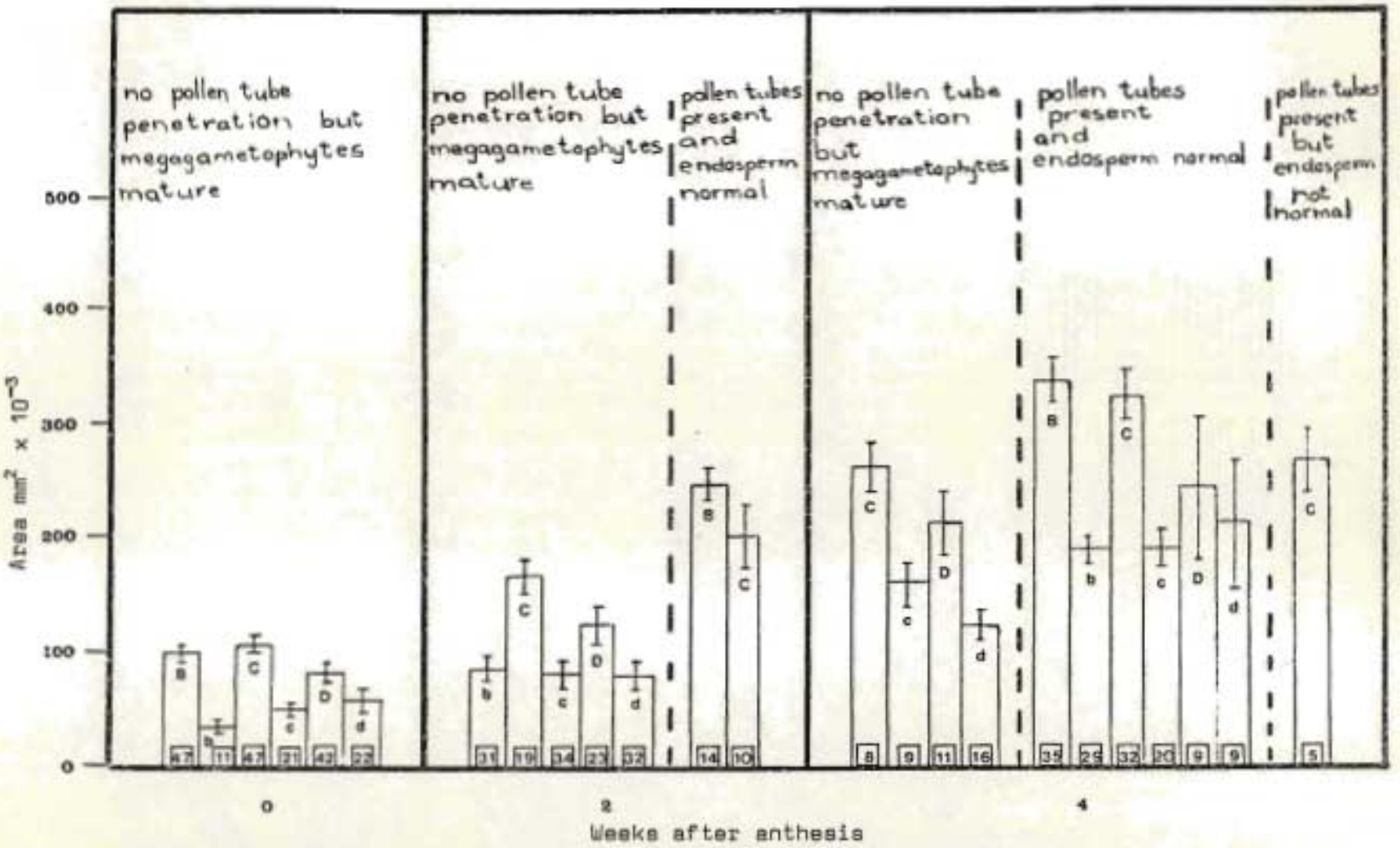

FIGURE 9 Mean cross-sectional area of nucellus tissue for certain developmental states, from selected intra-fruit sub-regions during early growth, autumn 1971. 'I' indicates 95% confidence limits of estimated mean. Sample sizes in boxes. See ABBREVIATIONS for A to d .

(i) ovules with mature megagametophytes which had not yet been penetrated by a pollen tube;

(ii) young seed which appeared to have normally developing free nuclear endosperm; and

(iii) for the C (c.m. ridge) sub-region at the fourth week, young seeds whose endosperm appeared to be disintegrating.

It is evident that all the mean values increased over the four weeks, i.e. irrespective of the class of ovule/seed or of placental sub-region. All had produced more nucellus. With the exception of the developing seeds in the D/d sub-regions at the fourth week, there were also evident differences between ovules/seeds along the ridges (c.m.) versus those next to the furrows (p.e.). In the D/d sub-regions at the fourth week, the larger standard errors with correspondingly larger confidence intervals preclude one from saying whether th observed means were different from their neighbouring sub-regions.

For any given sampling period, the young seeds were larger than their unpenetrated (but mature) ovule counterparts in the same placental sub-region. The exception was in the D sub-region of the fourth week. Apart from its large confidence intervals, a further reason for the lack of definite difference migh have been that fertilization occurred relatively late in this region (as previously discussed) and the difference had not become established.

With regard to the ovules/seeds in sub-region C at the fourth week, it is interesting to note the following. Those seeds that had been penetrated by pollen tubes but whose endosperm was not developing "normally" had no more nucellus than their mature but unpenetrated ovule counterparts. Both these latter two classes had less nucellus than those seeds which appeared to have normally developing endosperm.

Examining Figure 9 with regard to mature but unpenetrated ovules only, it appears that such ovules that were in sub-regions of earlier and more wide-spre endospermic development were themselves producing more nucellus. Taking sub-regions c, D and d as an illustration, the mature but unpenetrated ovules of D had more nucellus than those of c and d over the first two weeks. But with the subsequent penetration of pollen tubes and the greater concentration of develop ing seeds in sub-regions above D/d, the gap between the confidence intervals of the c and D sub-regions had narrowed by the fourth week. By that time too, the unpenetrated ovules in c had also more nucellus than their counterparts in d.

Figure 10 shows cross-sectional areas of the embryo sac of the same ovules seeds depicted in Figure 9 and discussed above. The general patterns are the

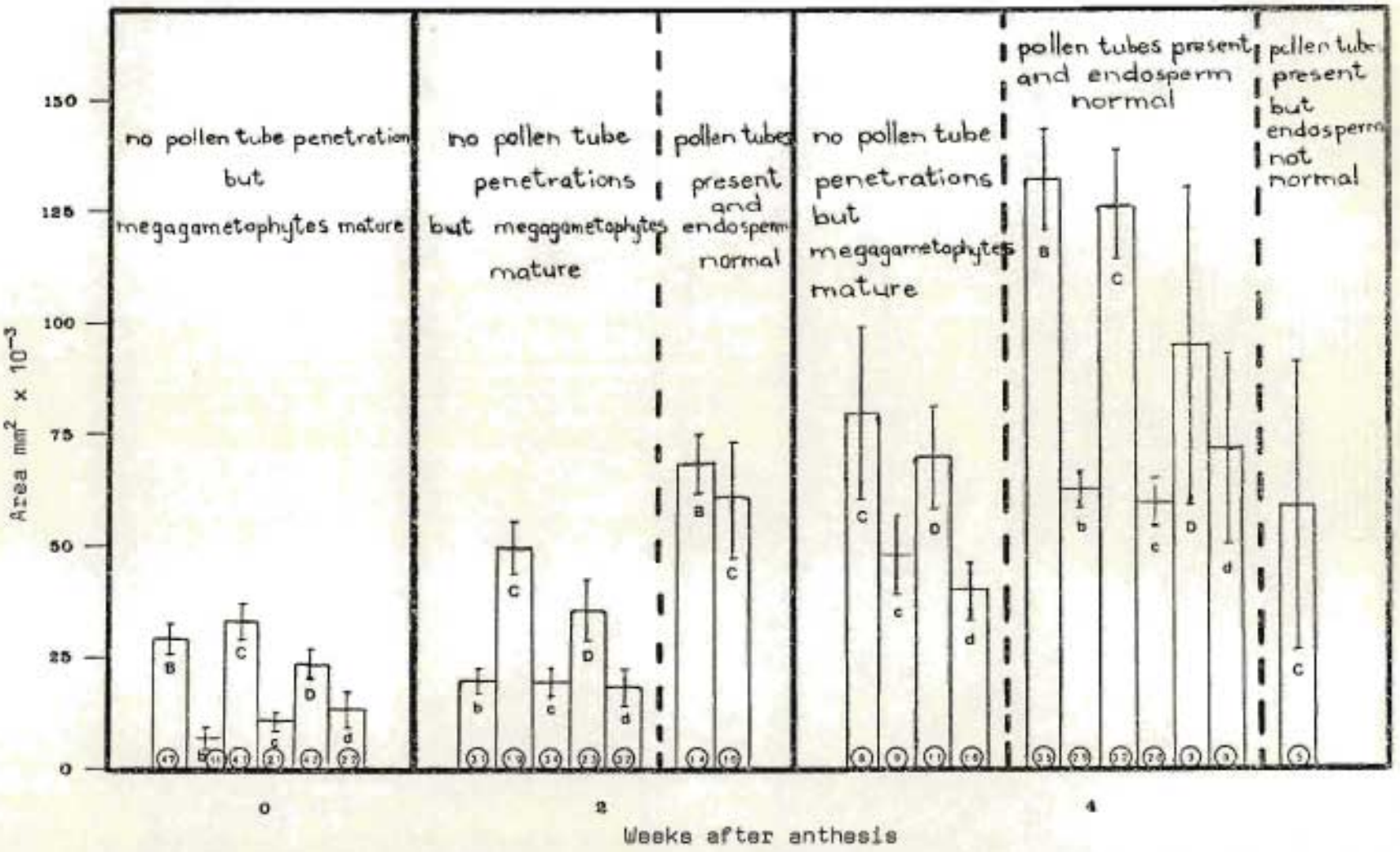

FIGURE 10 Mean cross-sectional area of embryo sacs for certain developmental states, from selected intra-fruit sub-regions during early growth, autumn 1971. 'I' indicates 95% confidence limits of estimated mean. Sample sizes encircled. See ABBREVIATIONS for A to d .

the same, but the confidence intervals are somewhat larger. Thus the mature but unpenetrated ovules of (c) did not clearly have larger embryo sacs than their counterparts in the (d) sub-region at the fourth week.

1.3.2 Ovule and early seed development: Summer

As previously mentioned in the methods and materials section, the ovule and early seed development from fruit set in summer was not examined in detail. Nevertheless the main difference between the summer- and autumn-set ovules/seeds was that the rate of development of various features was often more rapid in the former. A few examples follow.

The first is in regard to vascular bundle differentiation at the chalaza (Table 5). In comparing autumn and summer sets at anthesis, it is clear that

TABLE 5 Percentage of ovules/seeds with vascular bundle differentiated at chalazal region, for fruit set in summer, 1970. Sample size equal to 50 for each fruit sub-region indicated, for each sampling period

FRUIT SUB-REGION	SAMPLING PERIOD	
	At anthesis	Week 2
A	20	100
a	6	100
B	64	-
b	2	-
C	86	-
c	4	100
D	84	-
d	0	-

a similar pattern existed in both, viz. the ovules along the c.m. ridge were more advanced. Comparison between the two sets (Tables 1 and 5) suggests that the autumn set as a whole were slightly ahead of the summer set, except that quite a number of ovules (not shown here) in all sub-regions of the latter had very nearly differentiated the vascular bundle at the chalaza. The limited comparison at the second week after anthesis in summer shows that all the ovules/seeds in even the third-quarter furrow region (c) had already differentiated the vascular bundle at the chalaza. This was not the case in the

furrow sub-regions of the autumn set. With regard to the proportion of ovules without megagametophytes or embryo sacs (Tables 2 and 6), little difference existed between the two sets.

TABLE 6 Percentage of ovules/seeds without embryonic sacs for fruit set in summer, 1970. Sample size equal to 50 for each fruit sub-region indicated, for each sampling period

FRUIT SUB-REGION	SAMPLING PERIOD	
	At anthesis	Week 2
A	8	4
a	8	2
B	8	-
b	6	-
C	6	-
c	6	4
D	2	-
d	12	-

Figure 5 (proportion of ovules with mature megagametophytes) shows that at anthesis the summer pattern was much the same as that of the autumn set. The exception was that the summer ovules nearer the furrow (a, b, c, d) were more advanced than their autumn counterparts. The X^2 analyses of Appendix 2, Table 2.3, are in the same direction as that for the autumn set (Appendix 2, Table 2.1), although less pronounced.

With regard to the pattern of pollen tube penetrations (Fig. 6) the scores for the A, a and c sub-regions at the second week were noticeably higher in the summer than in the autumn sets. At that sampling period, the proportions in both the ridge and furrow sub-regions of the top-end quarter (A/a) were much more alike in summer than was the case in autumn. In the latter case, similari was only observed at the sample taken two weeks later. It is likely of course, that in the summer set, the ridge sub-region (A) received more of the earlier pollen tube penetrations than the furrow sub-region (a) before the sample was taken at the end of the second week. The reason for saying this is that initially there was a greater proportion of mature megagametophytes in the ridge sub region (cf. Fig. 5 and previous discussion).

As far as the anatomical development of the summer ovules/seeds were concerned, the pattern was essentially the same as that for the autumn ones. The main difference was that the developments reached after eight weeks in the autumn set had already been reached after three or four weeks in the summer set. (Comparing Tables 4 and 7 at the second week, this difference was not yet marked. There also appeared to be more layers in the e(L)/e(s) tissue in the young summer-set seeds.

TABLE 7 Percentage of ovules/seeds with tanninized disc of cells adjacent to the hypostase region for fruit set in summer, 1970. Sample size equal to 50 for each fruit sub-region indicated, for each sampling period

FRUIT SUB-REGION	SAMPLING PERIOD	
	At anthesis	Week 2
A	0	8
a	0	0
B	0	-
b	0	-
C	0	-
c	0	0
D	0	-
d	0	-

Finally, a relationship tested in some of the young summer seeds (but not in the autumn ones) was the degree of association between the number of free nuclear endosperm nuclei in a seed and that seed's size. The correlation coefficient (r) between these two parameters of seeds from selected placental sub regions at the second week ranged between +0,62 and +0,84, all significant beyond the 1% level (Appendix 1, Table 1.1). This would seem to imply that the developments in the embryo sac (largely endospermic at that stage) and the over all early seed development, were interrelated.

1.3.3 Normal seed development: Summer

1.3.3.1 Nucellus. Right from the early phases, even whilst the endosperm was still free nuclear, the inner surface of the nucellar tissue adjacent to th endosperm was characterized by a mucilaginous-like sheath depicted in Plates 7a

and 4d. This sheath appears to be a breakdown by-product of the nucellus as it is utilized by the endosperm (Strasburger, 1965). Until the time that the endosperm had surrounded the developing embryo, i.e. after the onset of cellularization, the embryo itself was in contact with the nucellar tissue. Here, too, a breakdown sheath was also seen to develop at the embryo/nucellus interface.

With regard to cell size, Figure 11 relates changes in the mean cross-sectional area of individual nucellar cells. This mean size increased at a rapid rate, (although diminishing after the fourth week) until a maximum mean size was reached at about the 17th week. After this, the mean size dropped. The explanation for this is not that the cells began to shrink but that the larger cells were digested by the adjacent, expanding endosperm and embryo tissues. More specifically, this drop in mean nucellar cell size was correlate with the period of rapid embryo growth rate and the filling up of the central vacuole with cellular endosperm.

An examination of the tissues also revealed that cell divisions were occur ring in samples taken up to the 13th week (but then no longer from the 16th wee onwards). Cell divisions were more frequent in the peripheral layers. This probably explains the observation that cell sizes were generally smaller in the peripheral layers. The cessation of cell divisions coincided approximately wit the period of maximal rate of embryo growth.

An interesting feature of the peripheral nucellus was that it was usually still nucleated and contained cytoplasm even at the time of fruit ripening. Th was not the case with the nucellus in the "specialized" region at the chalazal end. These latter nucellar cells lost their contents after the 33rd week sampl during the final seed maturation phase. On the other hand, many of the larger nucellar cells interior to the peripheral layers were seen to be without conten by about the time of endosperm cellularization. This appeared to be the case even when their walls had not broken down. However, the explanation for the latter might be that the depth of the microtome sections (12μ) was smaller than the depth of these cells, resulting in some cells appearing to be "empty", yet intact.

The four sub-regions of the nucellus at the chalazal end (as discussed in the literature review) were found in the material examined. Plate 8d (and 7c) shows their relative positions. After the endosperm became cellular, the two inner regions, i.e. the finger-like cells (originally nearest to the endosperm) and the adjacent dense-staining region were apparently digested by the endosper leaving only the "disc" and hypostase regions. This sequence of events was als reported by Singh (1960).

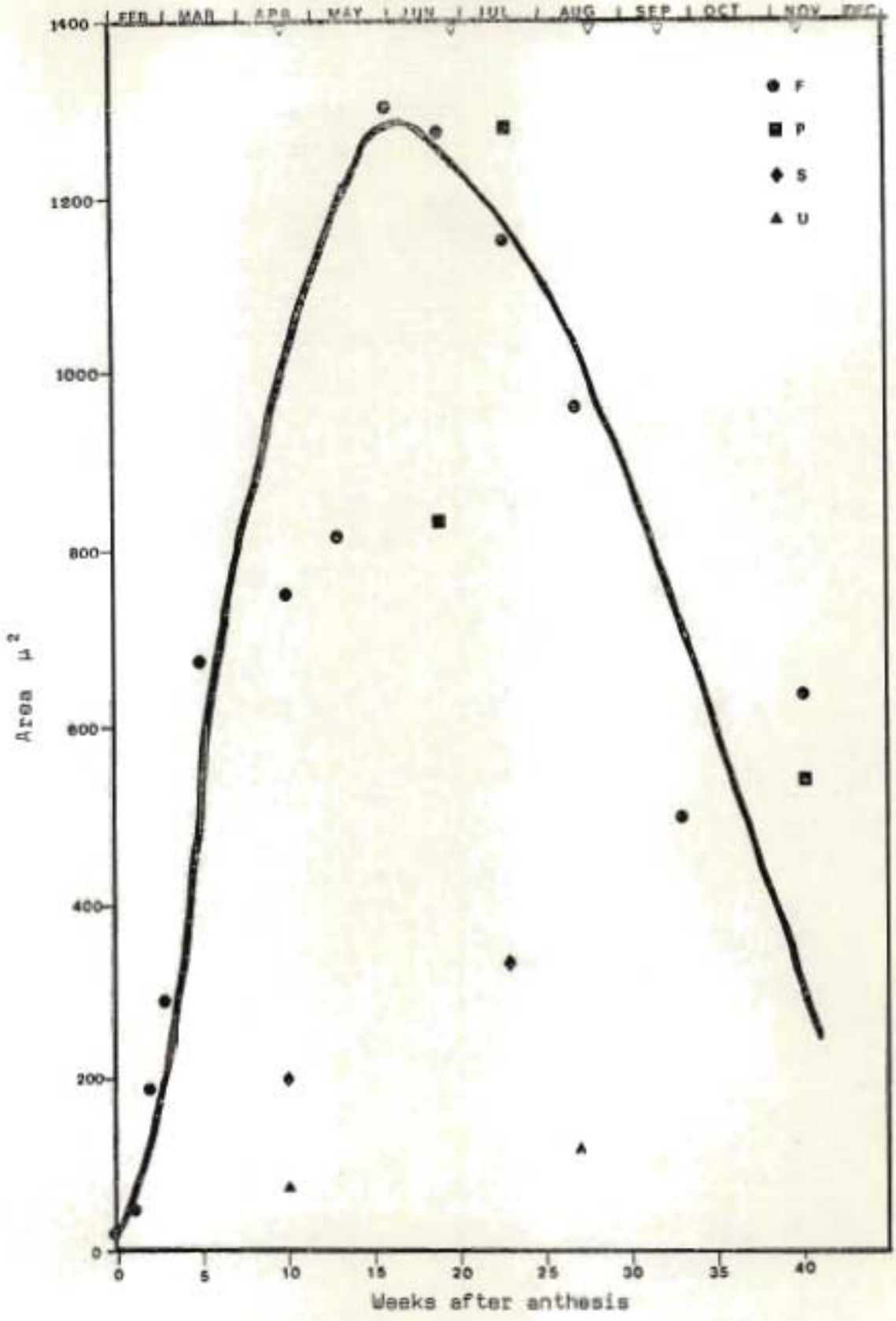

FIGURE 11 Cross-sectional area of nucellar cells of seeds in fruit set in summer, 1970.

▽ indicate phases of general seed development.

See ABBREVIATIONS for F, P, S and U .

Up to the 20th week, the thickening of the walls of the "disc" region (Plate 9a) appears to have been of the same type as depicted in Singh's (1960) drawings. However, in some seeds sampled after this period, a tannin deposition into the centre of the cells (rather than along the walls) was also seen (Plate 9b). These cases resembled the central deposition of tannin into the inner epidermis of the inner testal tissues (erstwhile inner integument). In the latter tissue type, this kind of deposition was already occurring before the 13th week. Of further interest, the thickening of the disc region nucellar cell walls mentioned above also appears to have been due to a deposition of tannin. The explanation for these two different ways of tannin deposition is not clear to the author.

After the 33rd week, the cells of the hypostase region adjacent to the "disc" region also started to thicken their walls (Plate 9c), and this occurred whilst the cells of this tissue were still nucleated. Interestingly, the cytoplasm in the cells of the hypostase could already be seen to be lined up against the walls (Plate 9d) as early as the seventh week. Thickening of the walls of the few remaining cells of the "dense-staining" sub-region interior to the disc was also seen. This also occurred in the period prior to final seed maturation.

1.3.3.2 Endosperm. Both free-hand and microtome sectioning of seeds up to the seventh week revealed only free nuclear endosperm. In the 10th week sample however, cellularization of the endosperm had begun in some seeds. This transitional phase was found in seeds sampled up to the 13th week. Foster's (1943) seeds, developed in a greenhouse (conditions not stated), reached this endosperm transition phase at about 11 - 12 weeks after pollination. Cellularization in the present author's material was seen to proceed from the micropylar region and progress towards the chalazal end, as shown in Plate 10a, b. This was also the sequence reported by Foster (1943). In addition, however, some seeds did show that cellularization had begun at the chalazal end first.

In general the free nuclear endosperm was seen to be spread out along the periphery of the embryo sac, close to disintegrating nucellar tissue. The central region was presumably a large vacuole, judging from the way the free nuclear endosperm strands moved when pressure was applied to LCPCX-cleared seeds. The development of nucleated cytoplasmic nodules as reported by Singh (1961) was not seen in this material.

During the transition phase cell walls were formed around the existing nuclei. At that stage the central vacuole still accounted for a large proportion of the embryo sac volume. There then followed a period during which nuclear

divisions were associated with cytokinesis. The cell divisions appeared most noticeable on the outer surface of the endosperm, next to the nucellus and especially at the micropylar and chalazal ends, as shown in Plates 10c, d and 12a respectively. Cellular endosperm formation thus progressed inwards from the periphery towards the central vacuole. However, cell divisions were also seen to be occurring in some cells further within the endosperm mass, as can be seen in Plate 12b.

By the 19th week some seeds had virtually filled up the central region wit cellular endosperm. In others, this was the case by the 23rd week. After the central vacuole had been filled, further cell divisions were still seen to be occurring, particularly in the chalazal and micropylar regions. However, the extent of this further cell division was not much. Table 8, although based on only a small number of seeds, also suggests that cell divisions tailed off afte the 23rd week (there being little difference in the cell number counted after that period).

Maturation of seeds is accompanied by dehydration which in turn is apparen in such signs as the formation of many smaller vacuoles and the deposition of cytoplasmic constituents (Guilliermond, 1941). In these (summer fruit-set) see "maturation" as depicted in Plate 11a was seen to start occurring in some of th seeds of the 23rd and 27th week samples. Prior to this phase of development, the cells of the endosperm appeared comparatively well filled, only slightly vacuolated and the nuclei were quite prominent (as seen in Plate 11b). From th 33rd week onwards the dehydration process had begun in all the seeds examined. Plates 13a, b, c show that the nuclei were no longer distinguishable amongst th mass of deposited cytoplasm. In those seeds which appeared to have developed normally, the storage form seems to have been aleurone grains, and its structur was amorphous, without crystalloids or globoids. According to Foster (1943), mature seeds contained aleurone grains and oil, but no starch. This appears (anatomically) to have been the case here too, although it would need to be con firmed by histo-chemical methods.

Mention has already been made of the apparent nutritive relationship at th endosperm/nucellus interface and that this was already noticeable during the early phases of free nuclear endosperm development. In contrast to that, a mucilagenous sheath only developed at the endosperm/embryo interface during the dehydration (maturation) phase. Plates 11c (16th week) and 11b (27th week) sho seeds which had not started any noticeable dehydration of the endosperm, whereas Plates 11a (23rd week) and 13b (42nd week) show dehydrating seeds. Only the latter two cases show the breakdown sheath, and it appears that it was the endo sperm that had been breaking down. This association was also often seen in the

TABLE 6 Cell counts in stained sections of embryo and endosperm of normal seeds from fruit set in summer, 1970

Weeks after anthesis	EMBRYO	ENDOSPERM	OTHER REMARKS
	Mean number of cells along the protoderm from the base of hypocotyl to apex of one cotyledon	Mean number of cells along the median diameter perpendicular to the median l/s	
13	21	-	Central vacuole being filled by endosperm cells: expansion and division proceeding.
16	53	-	
19	92	54	Central vacuole nearly filled.
23	136	64	Central vacuole nearly filled.
27	106	63	Division of endosperm cells in micropylar and chalazal regions still occurring.
33	108	66	Dehydration of cells has begun; nuclei still discernible in some cells.
39	95	70	Cells appear dehydrated.
44	115	79	Dehydrated; nuclei of some cells of embryo still visible amongst dehydrated cell constituents.

centre of the embryo sac along rather disorganized cellular endosperm tissue next to the tips of the cotyledons. As will be seen from the discussion of the seed coat tissues that is to follow, the passage of nutrients from the rest of the plant or fruit through the testa (via the chalaza and/or micropyle) would appear to have been blocked off during the seed maturation phase. The embryo may thus come to depend more heavily on the endosperm at about the maturation phase.

Figure 12 depicts the mean cross-sectional area of individual cellular end sperm cells. The growth of these cells appears to have followed a simple sigmo form. As noted previously, cellularization set in at about the 10th week. As estimated from these free-hand curves, the maximal rate of cell expansion was reached at about the 26th week. A diminishing rate appears to have set in afte the 33rd week, i.e. at approximately the time the maturation process had been seen in some cells of all seeds examined.

1.3.3.3 Embryo. During the period of the transition of endosperm from th free nuclear to the cellular state (10th to 13th week), the embryo was seen to be of the globular shape (Plate 11d). By the 16th week, the heart-shape had become evident, as shown in Plate 12c. The latter also shows a persistent poll tube tip. From the 19th week's sample onwards, embryos had reached the final shape, i.e. the dicotyledonous or torpedo shape, as shown in Plate 12d, althoug not their final size (Figs. 13 and 14). By contrast, the embryos in Foster's (1943) study had reached the final torpedo shape (but not the final size) by th 11th - 12th week, at the time the endosperm was undergoing transition to the cellular state.

The apparent dehydration and maturation of embryo cells appears to have been closely associated with that of the cellular endosperm cells already described. Plates 11b and 13a, b, c referred to during the discussion on cellu endosperm, show the visible signs of this association. However, some embryo cells in some of the seeds examined did still have nuclei which could be distinguished, even during the final maturation phase.

In the discussion of the endosperm, reference has been made to the possibl nutritive relationship between the endosperm and the embryo during the later stages. Prior to these stages, the embryo might have been utilizing the nucell or else have been nourished through the developing testal tissues. Foster (19 has previously suggested that a persistent pollen tube tip might have an haustorial function linking the embryo to the developing testal tissues. Plat 13d shows a mature seed (44th week) with a persistent pollen tube tip. Howeve

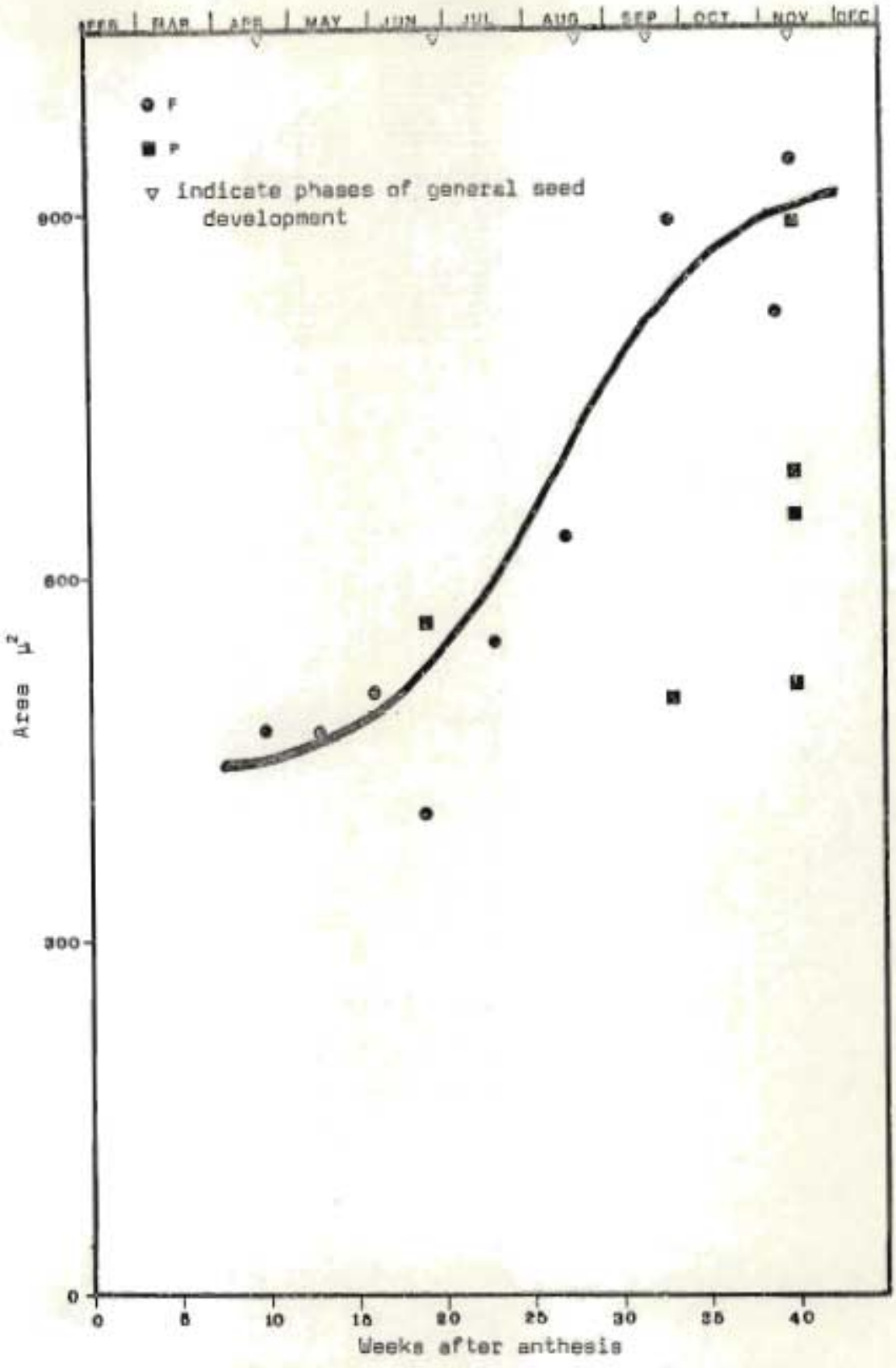

FIGURE 12 Cross-sectional area of cellular endosperm cells of seeds in fruit set in summer, 1970.

See ABBREVIATIONS for F and P .

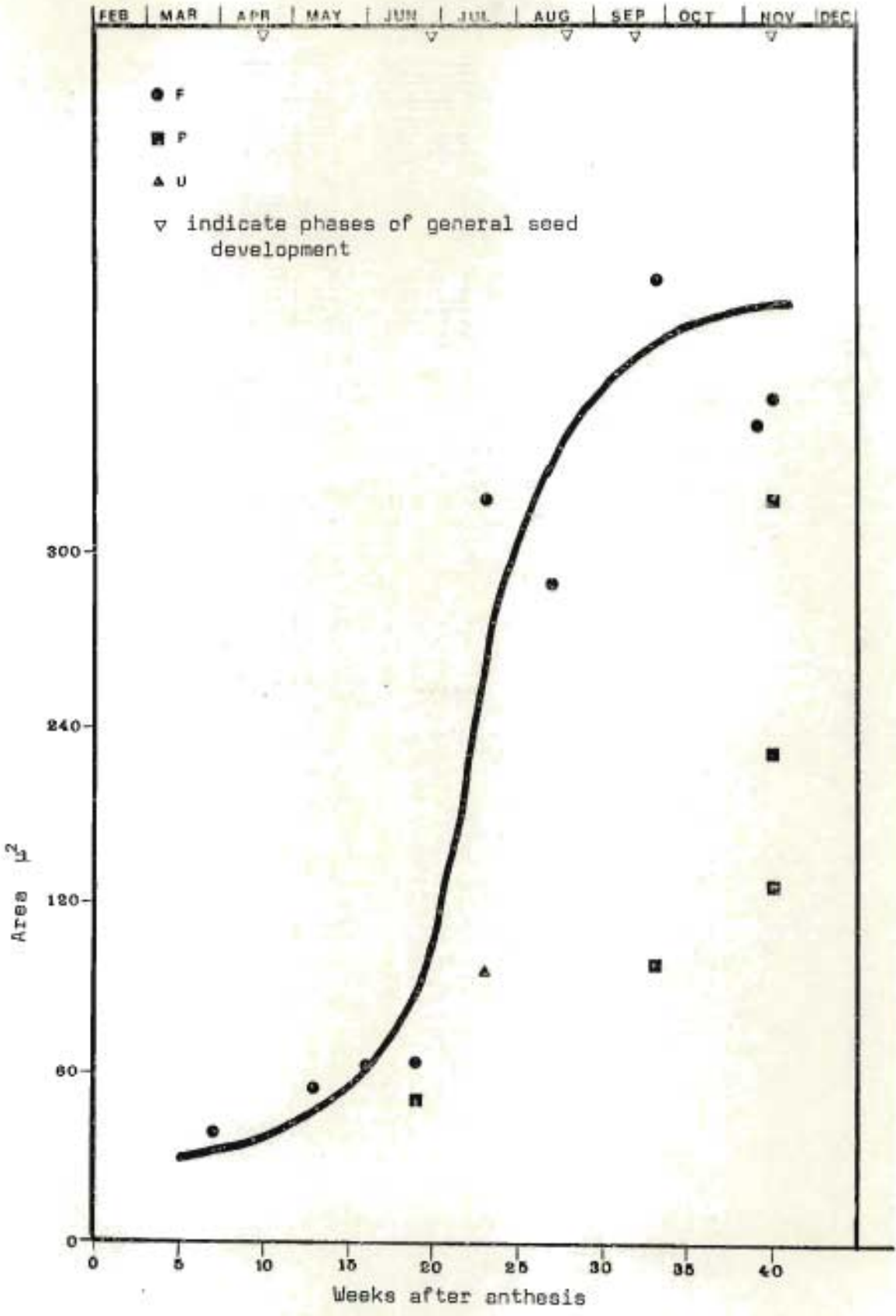

FIGURE 13 Cross-sectional area of embryo cells within the protoderm of the cotyledons in longisection (summer, 1970).
See ABBREVIATIONS for F, P and U .

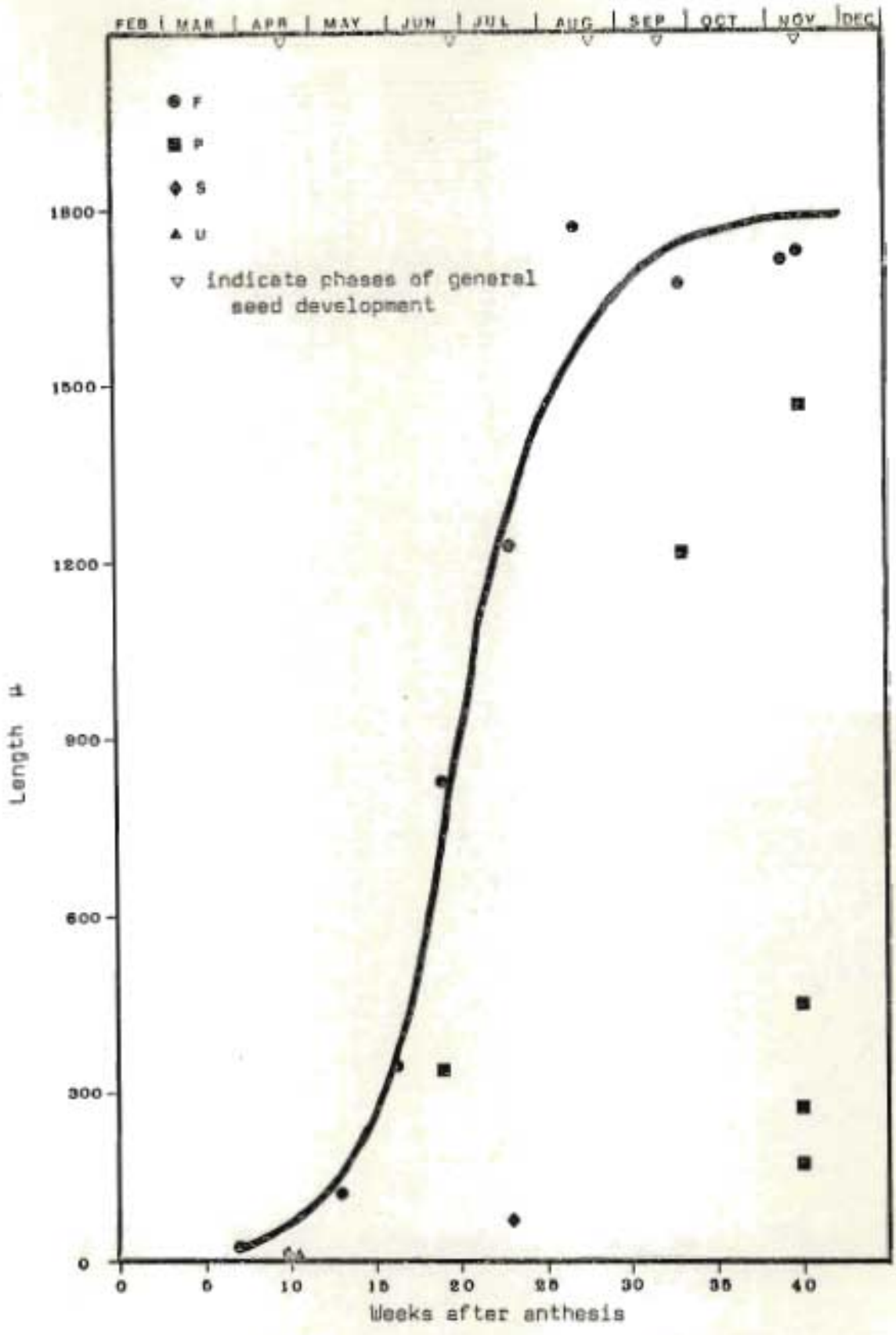

FIGURE 14 Embryo length of seeds in fruits set in summer, 1970.
See ABBREVIATIONS for F, P, S and U .

in the latter the connection with the testal tissues appears to be practically obliterated by heavy tannin deposition. In some seeds this obliteration appear to have occurred much earlier, whereas in others, as shown in Plate 14a, the pollen tube tip still extends through the tannin layer towards the micropyle.

Figure 13 shows the growth curve of expansion of cells found within the protoderm layers of the cotyledons. Maximal rate of expansion occurred at abou the 24th week, and the rate began to decline after about the 30th week. From approximately the 35th week onwards, such embryo cells showed little expansion. As mentioned before, in reference to the discussion on the endosperm, most embryo and endosperm cells had entered the maturation phase by the 33rd week sample.

Figure 14 depicts the growth in length of the embryo as measured from the base of the hypocotyl region to the tip of the cotyledons. The initial growth of the embryo was delayed (as mentioned also by Foster, 1943), and only became marked from about the seventh week. The maximal rate appears to have been reac ed by the 18th week, with a diminishing rate setting in after about the 22nd week. Final length seems to have been reached by about the 35th week, i.e. during the final maturation.

In comparing Figures 12, 13 and 25j, k , it appears that the maximal rate cell expansion in the embryo cotyledons and the endosperm was reached at about the same time (24th and 26th weeks). The embryo length (Fig. 14), on the other hand, reached its maximal rate before the above described cell expansions, i.e. by the 18th week. During the phase of rapid growth of the embryo, most of this growth occurred in the cotyledons. This suggests, then, that the process of ce division was contributing more to embryo growth before the 20th week, and that thereafter embryo cell expansion was more important. This relative contributio from cell division also appears to be confirmed by the data in Table 8. The latter shows that the number of cells along the protoderm had virtually reached its maximum by the 23rd week.

1.3.3.4 Testal tissues derived from outer integument

(a) Outer epidermis

From the fourth week, i.e. beginning of this study, the rate of cell expan sion of epidermal cells above the endotestal ridges was declining slightly (Fig. 15). This changed into an accelerating rate by about the 11th week, reac ing its maximal rate at about the 22nd week, whereupon it again started to decelerate. The latter maximal rate occurred slightly after that of the under-lying large-celled endotestal e(L) cells (19th week, Figs. 15, 16 and 25a, d).

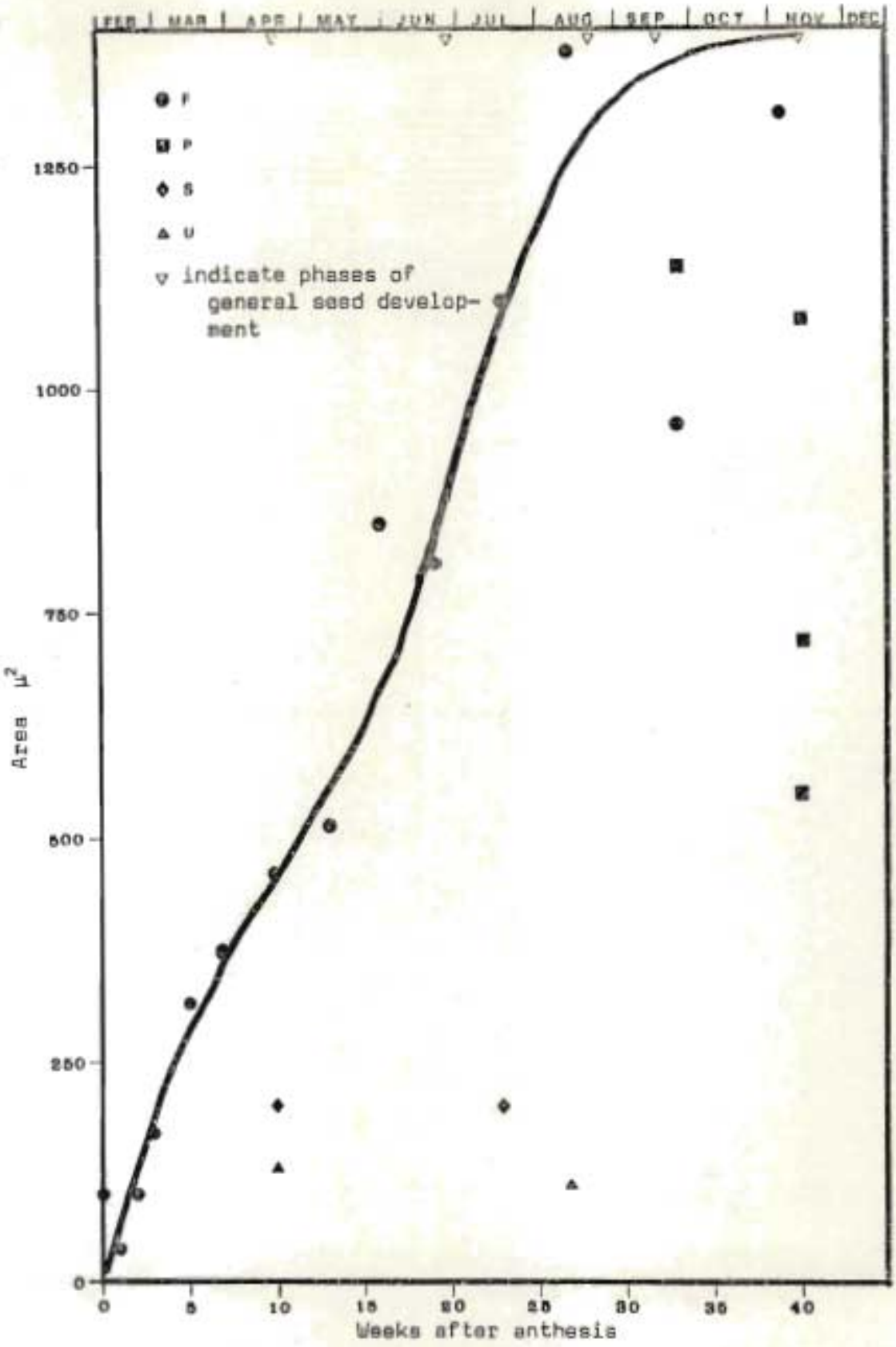

FIGURE 15 Cross-sectional area of cells of outer epidermis of outer testa above endotestal ridges (summer, 1970).
See ABBREVIATIONS for F, P, S and U .

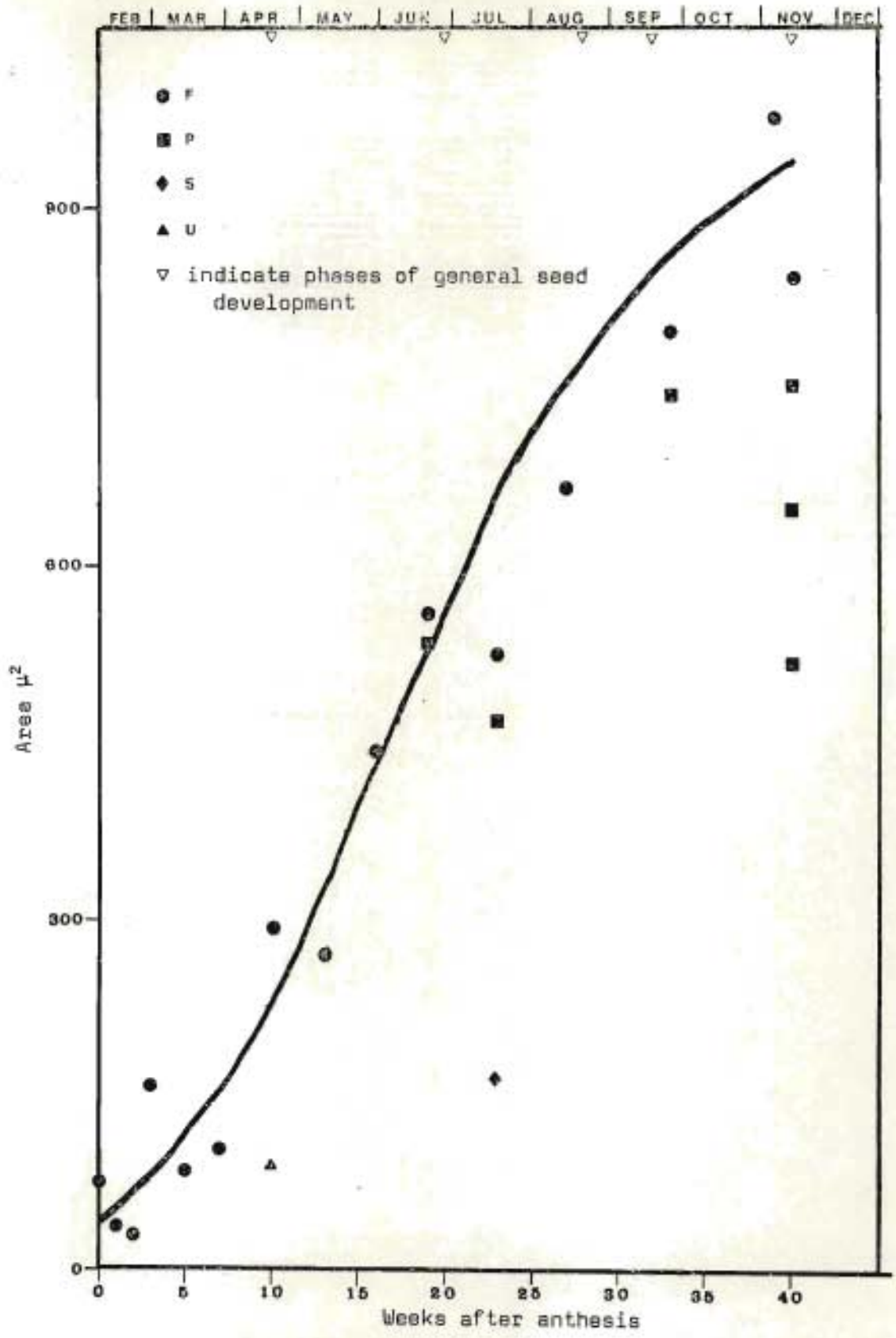

FIGURE 16 Cross-sectional area of cells of large-celled endotestal tissue [e(L)] (summer, 1970).

See ABBREVIATIONS for F, P, S and U .

The epidermal cells situated between the endotestal ridges started off at accelerating rate, reaching their maximal rate after about 15 weeks (Fig. 17), i.e. slightly ahead of that of the e(L) tissue. The rate of expansion of epidermal cells between the ridges only began to decline from about the 34th week (Fig. 17), i.e. at the onset of seed maturation. The epidermal cells above the ridges, on the other hand, had already begun to enter a marked decline in expansion by about the 29th week (Fig. 15). From Figures 15 and 17 it is clear that the epidermal cells situated between the endotestal ridges were larger tha those situated above these ridges. This is in agreement with Singh's (1960) report. Finally, during the final maturation phase (after 34 weeks), the cells of the epidermal layer were still seen to remain nucleated.

(b) Sub-epidermal sarcotestal tissues

The sarcotestal component below the outer epidermis consisted of two to three layers, as reported by Singh (1960). There was a substantial deposition of mucilage into these layers after the fourth week. This was particularly the case in the 2nd layer, as can be seen in Plate 14b. However, from the 16th wee onwards these cells appeared to have less mucilage. Whether this was because the cells had expanded with little or no further mucilagenous deposits, or whet the seeds started to utilize some of this, was not ascertained.

Figures 18 and 25c show the cell expansion of the uppermost layer of this tissue. The form of this growth curve resembles that of the epidermal cells above the endotestal ridges, with the accelerating period setting in at about the 17th week. The maximal rate was reached at about the 27th week, followed b a declining rate, tending towards a plateau from about the 34th week.

From after the 33rd week's sample until fruit ripening, the sarcotestal tissues (including the outer epidermis) were virtually the only testal tissues retain nuclei. The exceptions seen were in some cells associated with the vasc lar bundle running through the inner endotestal tissue e(s). This persistence of nuclei in the sarcotestal tissues during seed maturation is interesting from the point-of-view of the colouration of seeds. From Singh's (1960) report, it appears that the colour of mature seeds is due to the thickened endotestal tiss underlying the sarcotesta. This would appear to have been the case here too (Plates 16a and b). However, the mature normally developed seeds were either dark grey or black in colour. When fruits were kept in a deep freezer, the dar grey seeds took on an olive green-appearance, whereas the black seeds remained black. On thawing out, the "green" seeds reverted to a grey colour. On remova of the sarcotestal tissues from the grey and black seeds, differences could be seen in the colouration of these tissues themselves. Therefore some of the

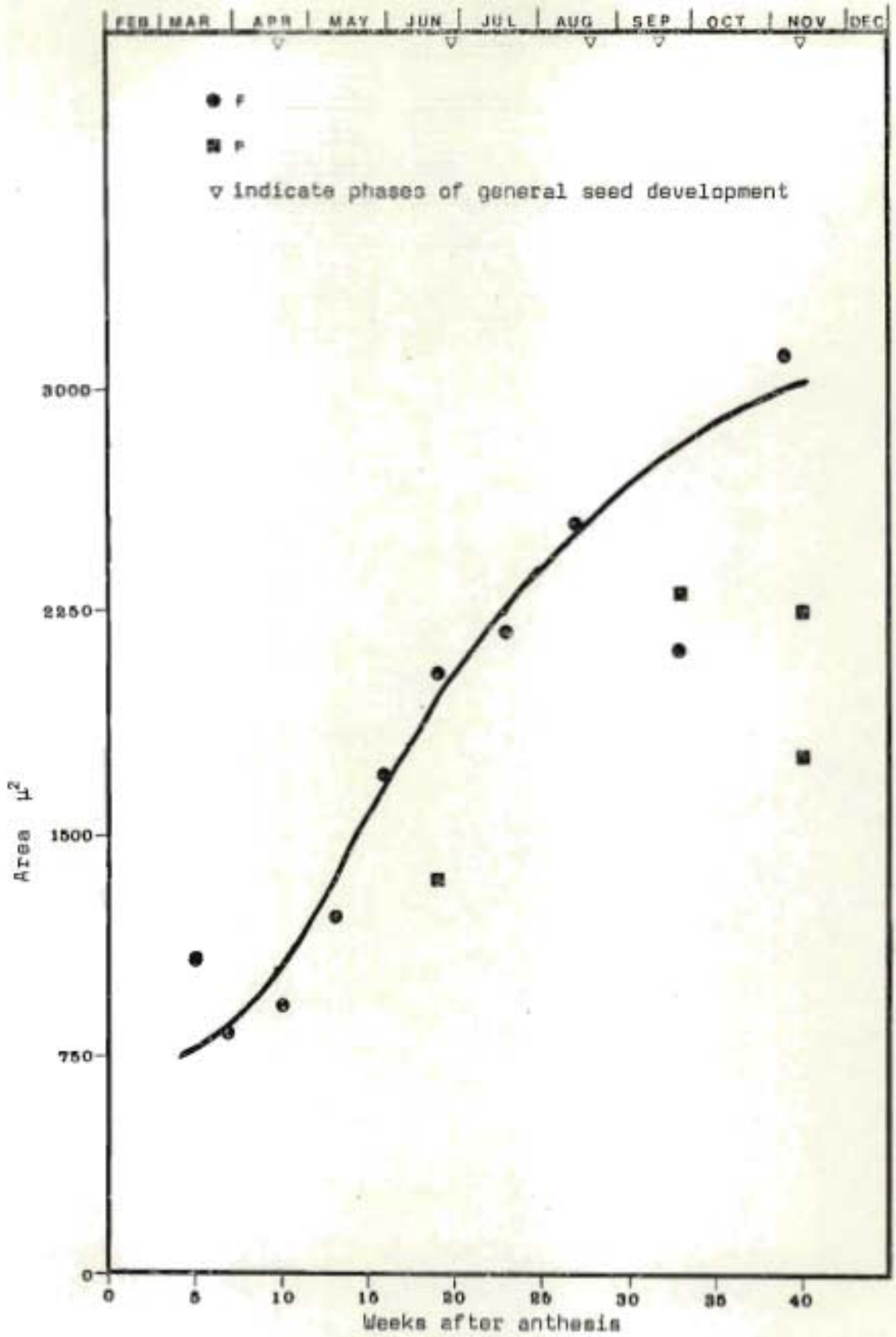

FIGURE 17 Cross-sectional area of cells of outer epidermis of outer testa between endotestal ridges (summer, 1970).
See ABBREVIATIONS for F and P .

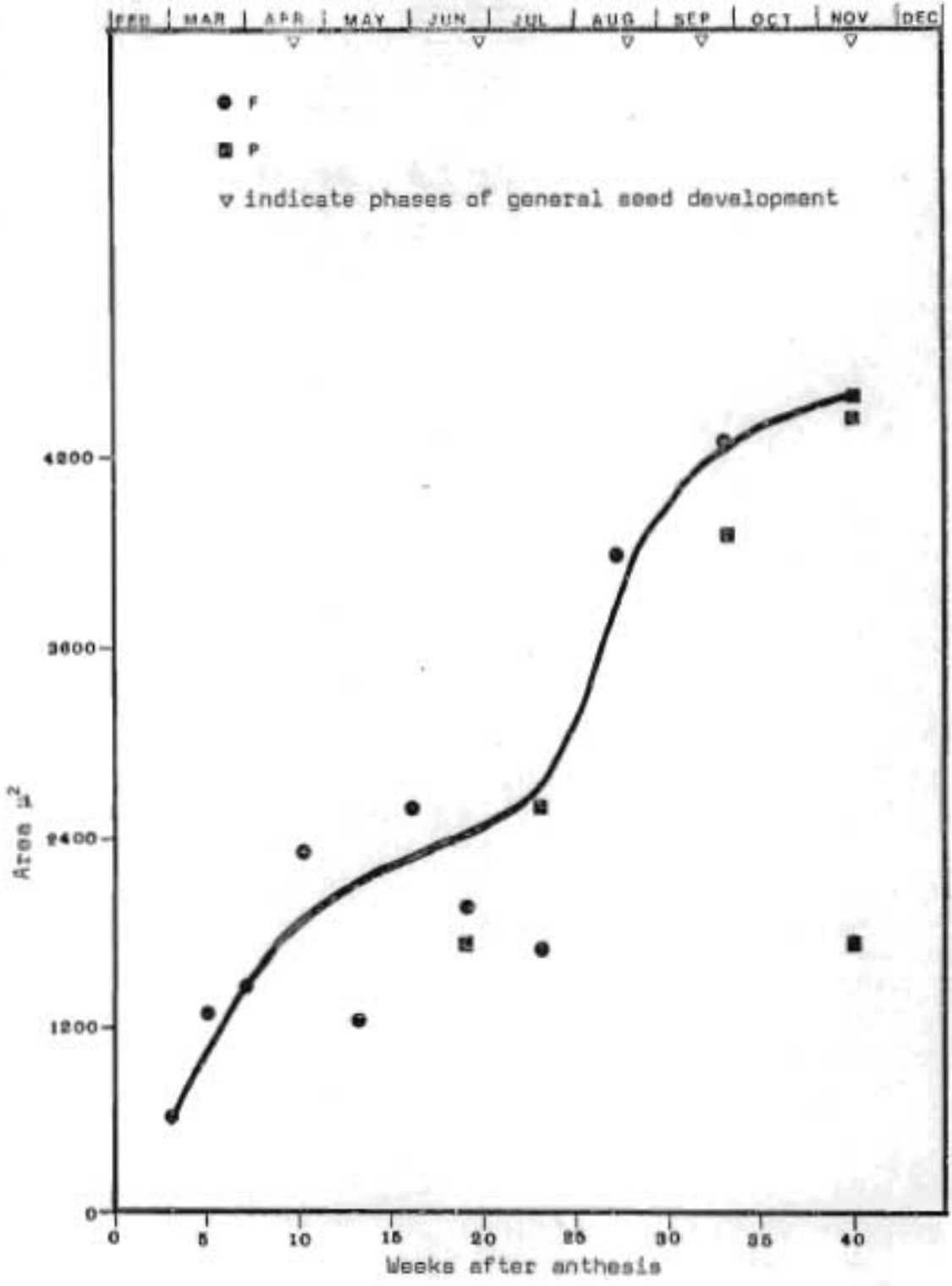

FIGURE 18 Cross-sectional area of cells of outer layer of sub-epidermal sarcotestal tissue (summer, 1970).
See ABBREVIATIONS for F and P .

Finally, a comment on the derivation of the sarcotestal tissue. In the discussion on ovule and early seed development, Singh's (1960) contention that the bottom layer was derived from the endotesta rather than the outer epidermis was supported. Plates 14c, d and 15a would appear to support this claim as wel It is, however, understandable that this layer has been thought of as being derived from the epidermis, since its features resemble that of the overlying sarcotestal layers. Furthermore, the upper portion of this single layer dries off with, or is removable with the rest of the epidermally derived sarcotesta.

(c) Large-celled endotestal tissue e(L)

Apart from increasing in cell area during seed development, the e(L) and the underlying small-celled e(s) endotestal tissues shared the feature of being the only testal tissues to increase in number of layers perpendicular to the longitudinal axis. Periclinal cell divisions occurred at quite a steep but diminishing rate during the early part of seed development. Figure 19 shows th these cell divisions finally ceased from about the 20th week onwards, with the final number of layers being about 28. It was by means of these cell divisions and expansion that the e(L) produced the seed's characteristic ridged coat (as seen in the dried state).

With regard to cell expansion, Figure 16 shows that this growth was of a simple sigmoid form. The maximal rate of increase occurred at about the 19th week. Cell expansion tended to cease after about the 35th week.

Mention was made above of the ridged appearance of dried seeds. During development, however, and in the freshly cut ripe fruit, the seeds have a rathe smooth appearance. From an examination of Figures 25b, c and d it may be appreciated that the increases and decreases in growth rate of the sarcotestal tissues between the e(L) ridges dovetailed sufficiently with that of the growth pattern of the e(L) tissue.

The "qualitative" features of e(L) development were as follows. At about the time of onset of endosperm cellularization (10th week), the first appearanc of a "buckling" of e(L) cell walls became evident (Plate 15b). This condition persisted until about the 23rd week (i.e. after the maximal rate of cell expans and also cell division stages), and some seeds even showed this condition at th 27th week. When the e(L) cell walls began to thicken considerably after the 27th week, the buckling disappeared in normally developing seeds. Plate 15c shows e(L) cells, still nucleated, but having begun to thicken and lose their buckled-wall appearance. The buckling might have been the result of the microtome sectioning or dehydration processes, but then that would suggest a conditi of weakness or susceptibility over the period concerned.

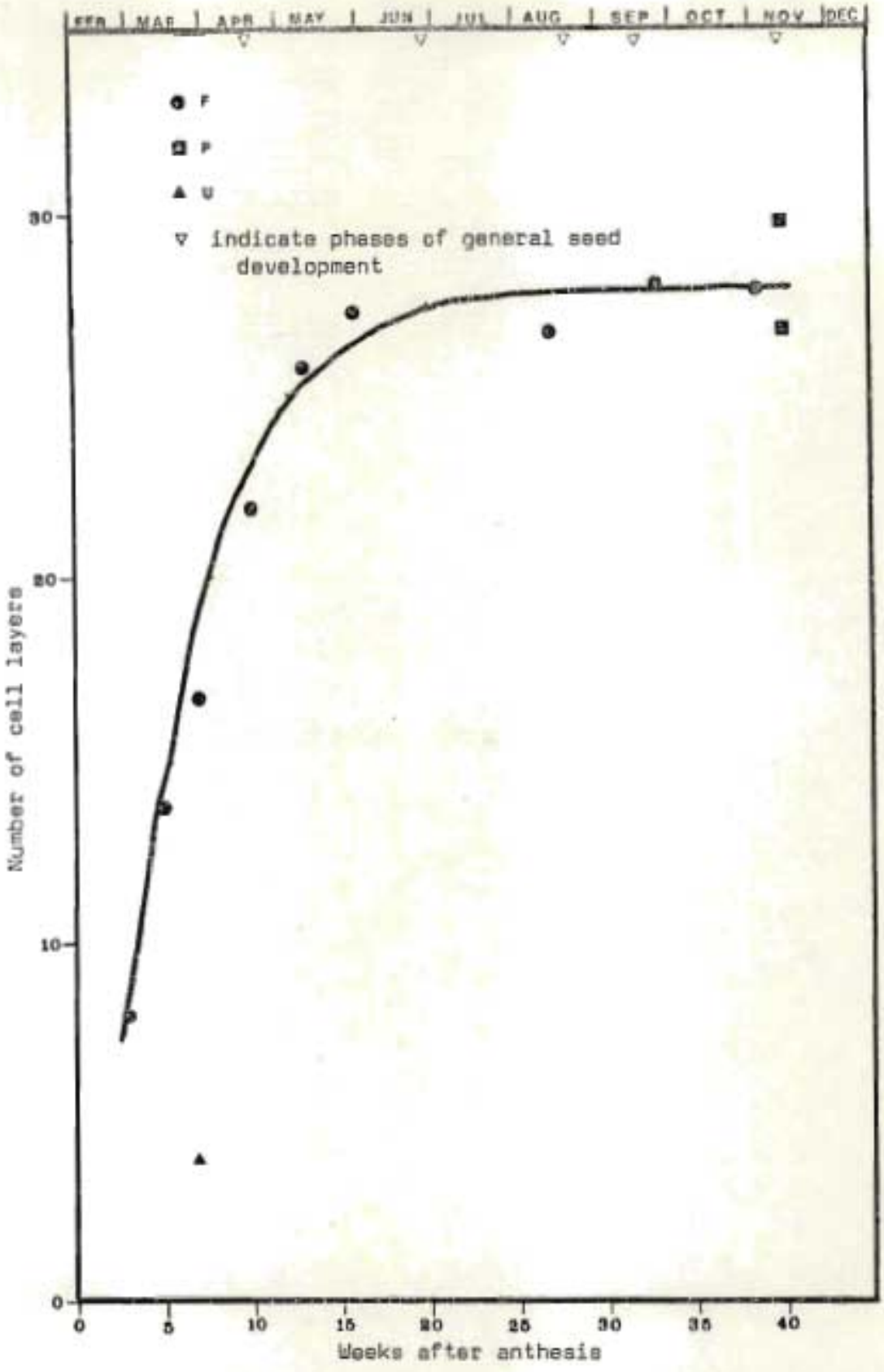

FIGURE 19 Cell count perpendicular to longitudinal axis in large-celled endotestal tissue [e(l)] (summer, 1970).
See ABBREVIATIONS for F, P and U .

At the 33rd week the e(L) tissue of most seeds examined were still nucleated. Seeds varied as to how much of this tissue had begun to thicken. Thickenings appeared to start from the base of this tissue, i.e. in the layers adjacent to the e(s) tissue. Correlated to this, seeds in which thickening had just begun still showed buckling of walls nearer the tips of the endotestal ridges. The thickenings of the cell walls began at the corners, as shown in Plate 15c, and as reported by Singh (1960).

During the final maturation phase the e(L) cell walls had thickened considerably (Plates 16a, b) and darkened. At the inception of the latter, fresh seeds still appeared white, but these coloured up in the following weeks. The colour and thickening of these cell walls no doubt contribute to the characteristic colour of dried (whole) mature seeds.

(d) Small-celled endotestal tissue e(s)

Periclinal cell divisions occurred in this tissue, as mentioned in the previous section. From Figure 20 it is evident that this activity followed the same pattern (and virtually the same final number of layers, about 29) as that of the e(L). There was greater variability in the counts on this tissue as compared to that of the e(L), so that the time the cell divisions ceased is less clear. From Figure 20 it seems that cell divisions ceased by about the 23rd week, i.e. possibly a little later than that of the e(L) tissue.

Figure 21 depicts the pattern of cell expansion in e(s) tissue. From the start cell expansion proceeded at an accelerating rate, the maximal rate being reached at about the 8th week. Unlike the outermost tissues already discussed, a period in which further cell expansion ceased to occur took place, starting at about the 20th week and lasting until about the 26th week. Thereafter there was again an accelerating rate, reaching a second maximal rate at about the 30th week. A marked slowing down had set in by about the 35th week.

The "qualitative" features of development were as follows. At about the time this tissue was reaching its first maximal rate of expansion (11th week), cell walls were relatively thin, as shown in Plate 18a. With the start of the second spurt of growth (27th week) these cells were larger, but still relatively thin-walled (Plate 17a). The buckled condition of the e(L) tissue did not occur in this tissue, as can be seen in Plate 15b.

Soon after this both e(s) and e(L) cells began to thicken their walls, although still nucleated in the way shown in Plate 15c. After the 33rd week, most of the seeds examined had e(s) cells with no nuclei. In such seeds, the walls were beginning to develop pitted, thickened walls (Plate 17b). At this

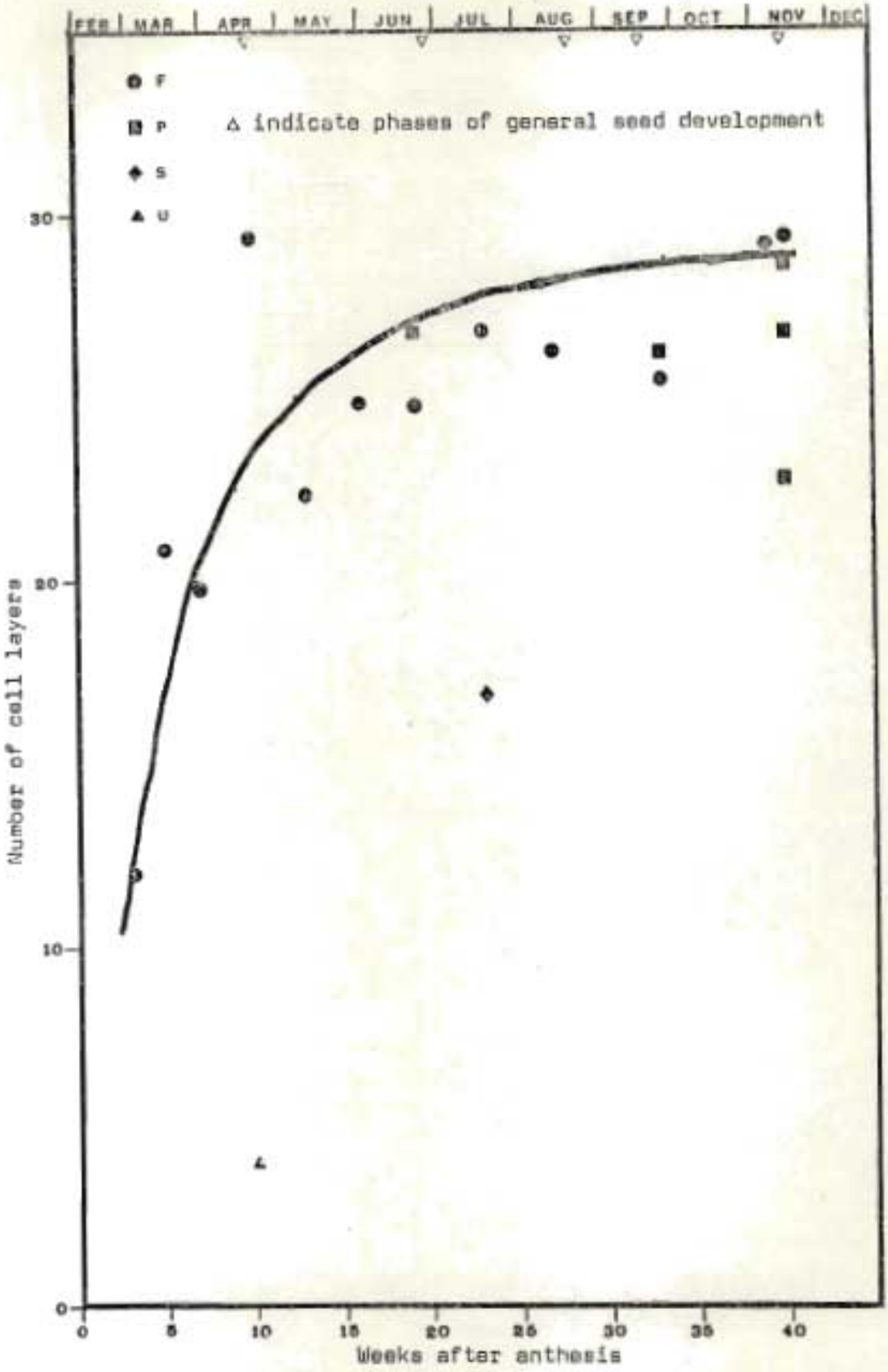

FIGURE 20 Cell count perpendicular to longitudinal axis in small-celled endotestal tissue [e(s)] (summer, 1970).
See ABBREVIATIONS for F, P, S and U .

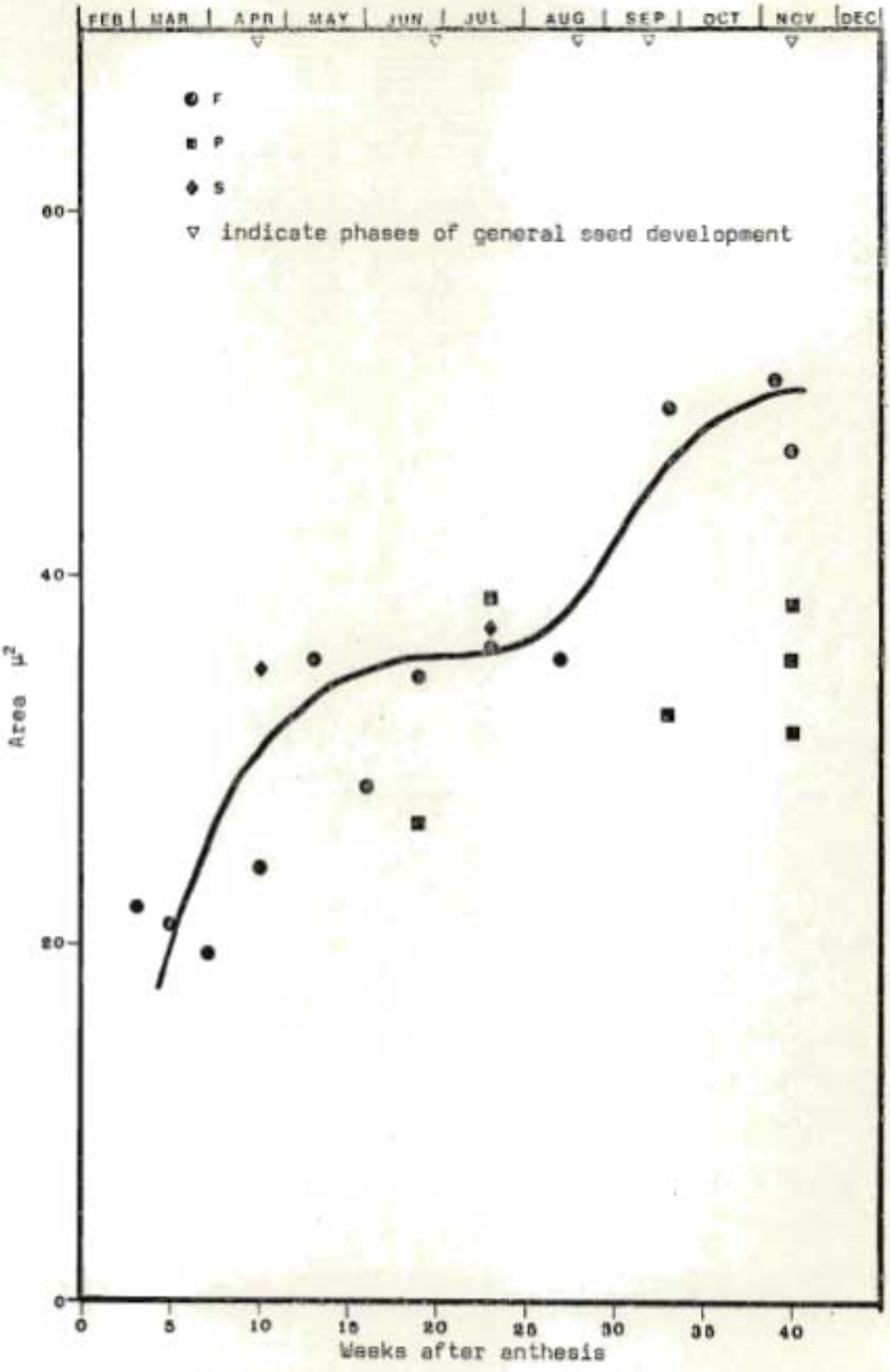

FIGURE 21 Cross-sectional area of cells of small-celled endotestal tissue [e(s)] (summer, 1970).

See ABBREVIATIONS for F, P and S .

time, these cells appeared light brown, although the whole (fresh) seeds were still white in appearance. But even at this time (33rd week), a few seeds had e(s) tissue in which cell walls were only slightly thickened, were not pitted, and had not begun to colour brown. (Incidentally, the difference in time to fruit maturity of fruits set at the same time in this study ranged over about four weeks.) Some cells were even nucleated. But finally, at the time of a fruit ripening, e(s) cells lacked cytoplasmic content, were very thick-walled and black, as can be seen in Plates 16a and b.

(e) Inner epidermis

This innermost layer adjecent to the e(s) also had a pattern of cell expan sion like that of the e(s) tissue (Figs. 22 and 25f, e). The first maximal rat was reached at about the fifth week; a short period during which cell expansio ceased occurred between the 14th and 20th weeks; the second maximal rate of expansion occurred at about the 30th week, and by the 35th week onwards, the ra of cell expansion was slowing down. As can be seen from figures 25f, e, the ke sequences just enumerated occurred a good deal earlier in this epidermal layer than in the adjacent e(s) tissue, and the period of quiescence in cell expansio was much shorter.

The "qualitative" features in the development of this layer were as follow At about the time of endosperm cellularization (10th week), calcium oxalate crystals began to appear in these cells (Plate 19c). Even in cells in which a crystal had not yet appeared the cytoplasm was often seen to arrange itself around (presumably) a vacuole which itself had the shape of later crystals (Plate 18a). Several weeks later, when cellular endosperm had virtually fille the centre of the embryo sac, calcium oxalate crystals had started to become conspicuous (Plate 18b). Plate 20a of a LCPCX-cleared segment of a seed at a later stage than above shows the extent of crystal deposition at the micropylar end of the seed. However, some seeds as late as the 23rd week's sample showed no crystal formation. The occurrence of conditions conducive to crystal forma had presumably not occurred or were not present in these last-mentioned seeds.

This spread in the time taken to reach this developmental sequence was surprising to the author. The fact that cessations in cell expansion growth occurred in this tissue and the tissues immediately adjacent to it on either si during this period (10th to 23rd weeks) might possibly contain a clue to this phenomenon.

By the time at which this tissue reached its second maximal rate o expansion (30th week), its inner wall was seen to be rather thicker (Plate 18c) Although not shown here, this tissue was still nucleated. Even by the 33rd wee

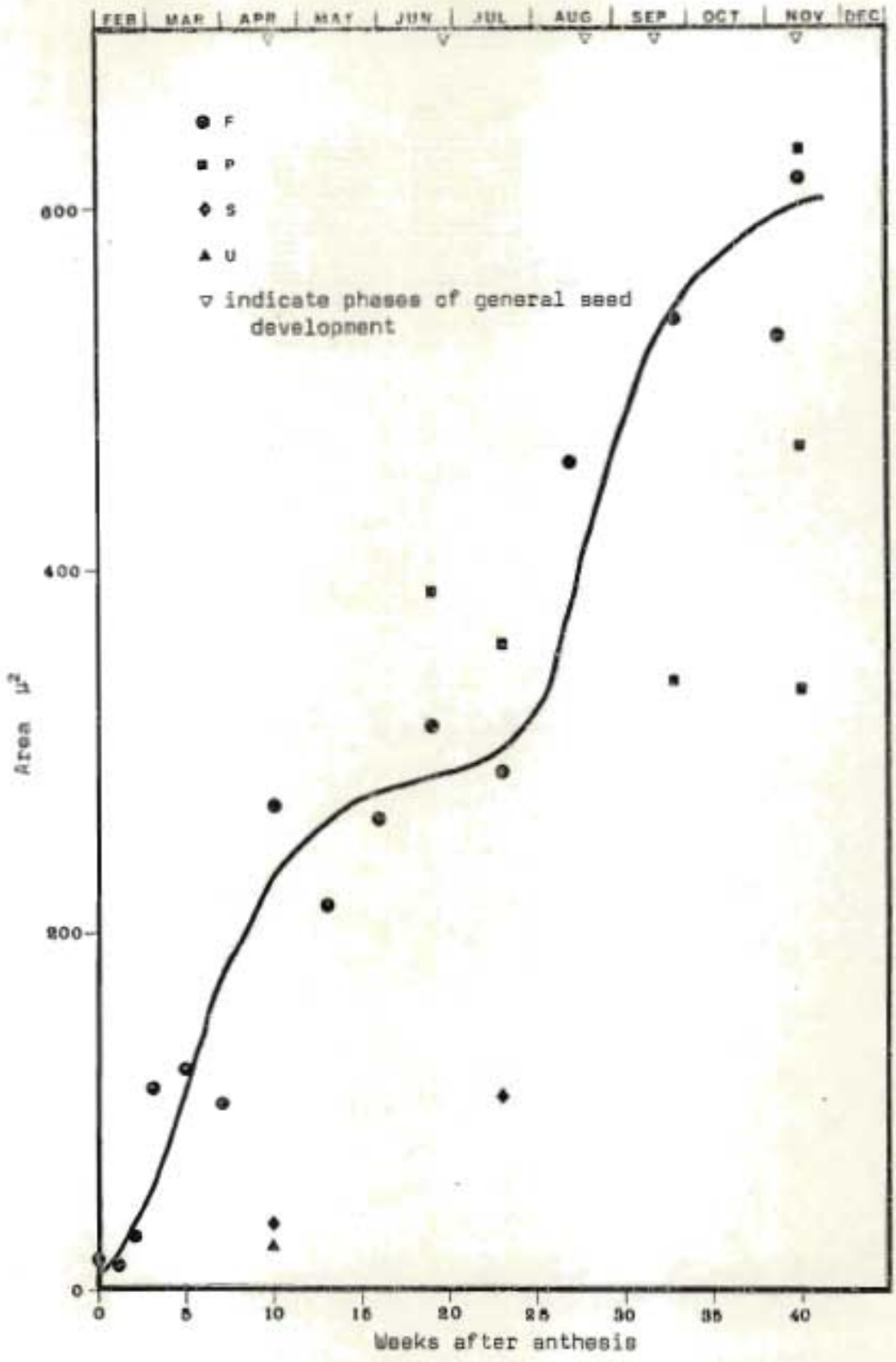

FIGURE 22 Cross-sectional area of cells of inner epidermis of outer testa (summer, 1970).

See ABBREVIATIONS for F, P, S and U .

present in some cells. By the time the fruits were ripe, the crystals virtuall filled these large, thick-walled cells (Plates 13d and 16c, d).

1.3.3.5 Testal tissues derived from the inner integument

(a) Outer epidermis

Figure 23 depicts the width or depth of the outer epidermis as seen in longitudinal sections. The cross-sectional areas have not been shown because i was often difficult to find the tapering cross walls of these greatly elongated cells. Due to this shape, the cross-sectional areas of these cells were mostly a function of their longitudinal (tangential) axis, so that it was unfortunate that this major dimension could not be measured in most of the tissue examined. However, in those cells in which it was possible, the pattern of expansion grow as expressed by the calculated cross-sectional areas (not shown here) appears t fit in with the pattern of growth in the width of this layer.

From Figure 25g it appears that after an initial phase of growth in this dimension, a period of quiescence set in at about the 10th week (the time of endosperm cellularization), and a second phase of growth only commenced at abou the 19th week, although it might have been later (see Fig. 23), i.e. a period o 9 to 13 weeks. Of all the testal tissues examined, this tissue's period of quiescence was the longest.

The maximal rate of growth in width of this layer occurred at about the 28th week. What was quite marked is that virtually 70% of the growth in width was made in the period following its quiescence (Fig. 25g).

The "qualitative" features follow. Plate 19c of the 10th week shows this layer as a rather narrow one, whilst Plate 17c of the 23rd week shows a conside ably wider layer with somewhat thickened longitudinal walls. Cytoplasm was sti evident. Plate 15d of the 27th week shows the appearance of this tissue in the region of the micropyle, with nuclei still having been quite prominent.
Plates 18c, d taken of other more advanced seeds of the 27th week show walls as having become thicker and pitted. A tapering cross-wall can be seen in Plate Plate 17d gives some impression of the thickening as seen in seeds taken at fru ripening (44th week). As Singh (1960) put it, this layer forms the main mechan cal layer of the mature seed coat. In further reference to the literature, thi tissue as found in this study appeared more like that described by Winton and Winton (1935), i.e. longitudinally elongated fibres. However, in the regions o the micropyle it was more like that described by Foster (1943) and Singh (1960) viz. stone cells. Perhaps these different interpretations were due to either looking at and describing cells taken from either the central versus micropyla

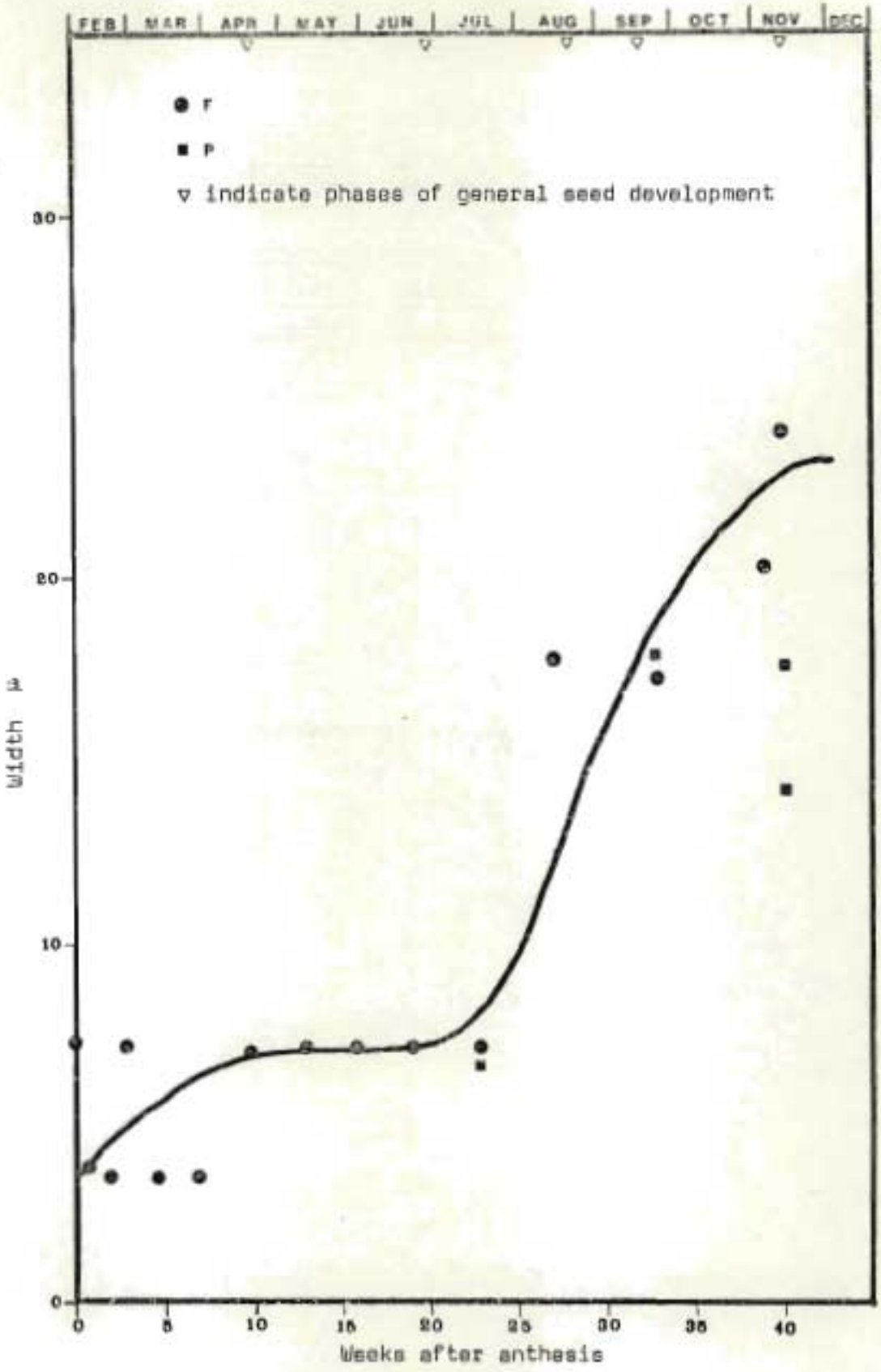

FIGURE 23 Width along perpendicular to the longitudinal axis of outer epidermal cells of inner testa (summer, 1970).
See ABBREVIATIONS for F and P .

regions (or chalazal) - or possibly from longitudinal versus transverse section. Furthermore, this study was confined to one clone, i.e. there may be clonal differences.

(b) Inter-epidermal tissue

With regard to the tissues lying between the two epidermises, it appears that another two to three layers were laid down during seed development. The final number of layers seen thus varied between four and six. Figure 24 indicates that the individual cells reached their final cross-sectional size as early as the 12th to 16th weeks.

Plate 19c shows the relative thinness of the cell walls at the 10th week, whereas in Plate 17c (23rd week) the cells of the outer layers had begun to thicken. Plates 18c, d (27th week) show further advancement in this, although the cells were still nucleated. By the 33rd week, their walls were yet thicker, showing some pitting, and they no longer had nuclei. Plate 16c of the 44th week shows the degree of thickening seen in this tissue in seeds of ripe fruit.

(c) Inner epidermis

Figure 24 indicates that the longitudinal cross-sectional area of this layer increased rapidly but at a declining rate during the first half of seed development. Final cross-sectional size was reached between the 20th and 25th weeks.

Plate 19a (5th week) shows that in a section of this layer near the chalazal end there had been no tannin deposition, whereas Plate 19b of the same seed shows tannin deposition in some cells nearer the micropylar end. Thereafter, tannin deposition followed a variety of forms. In some seeds the deposition appears to have occurred in the centre of the cell, resulting in a smooth deposit which followed closely the shape of the cell (Plate 18c). Some were not so smooth, having irregular edges (Plate 19c). The colour of the deposit also varied: from a light, yellowish-brown to dark brown to reddish-brown, sometimes even in the same seed. In some seeds the deposition appeared to have started along the cell walls rather than in the centre of the cell (Plate 19d). These two types of deposition, viz. along the walls or else into the centre of the cell, have already been noted during the discussion of the disc region of the nucellar tissue. The inner epidermal layer often appeared compressed indicating that the tannin deposition was fairly pliable under the pressure of either the expanded inner tissues (especially the endosperm), or of the force of the microtome sectioning (or of both). Plate 16c shows the compressed condition of this layer in a seed from a ripe fruit.

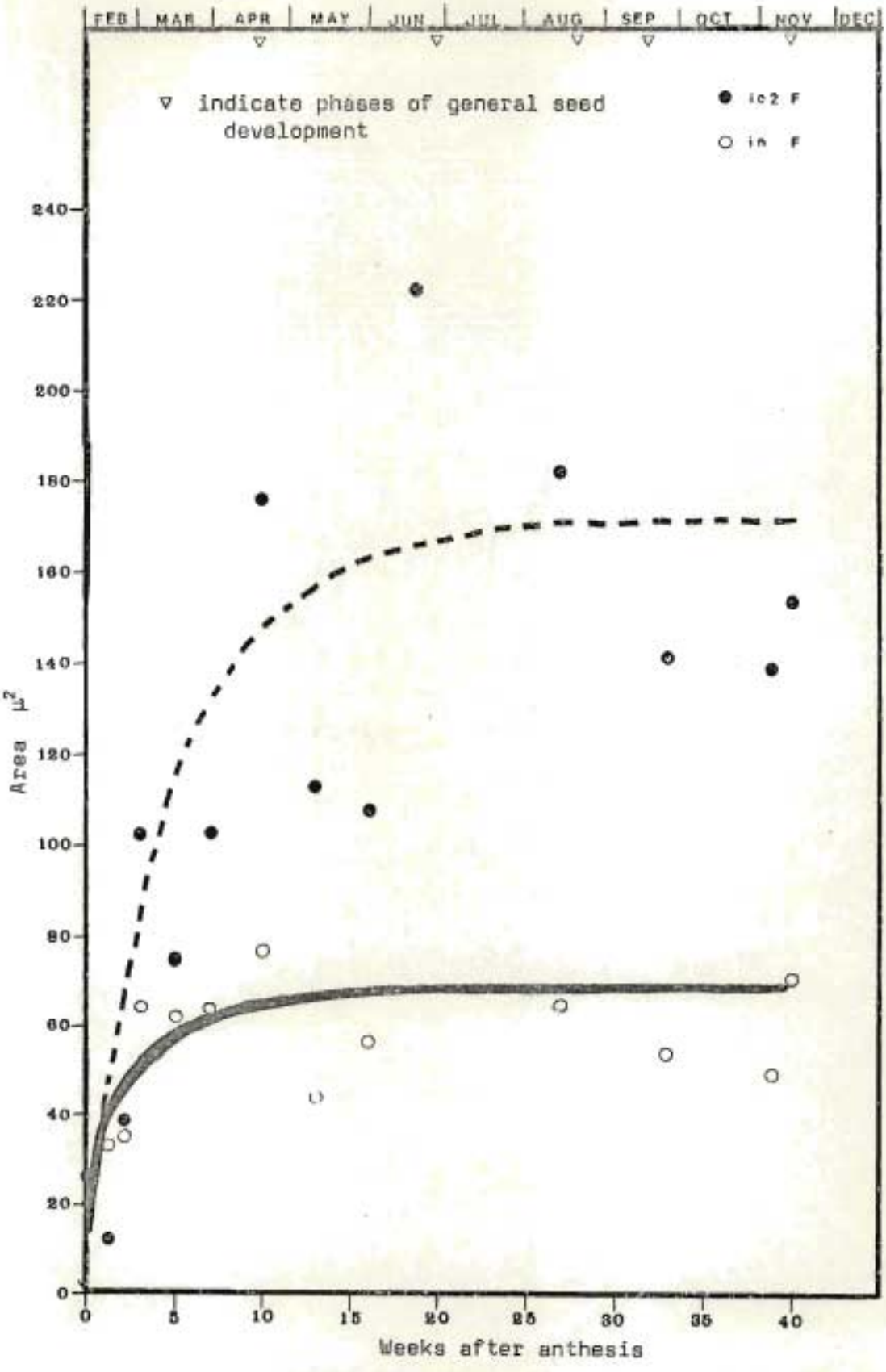

FIGURE 24 Cross-sectional areas of cells of inner- and inter-epidermises of inner testa (summer, 1970).
See ABBREVIATIONS.

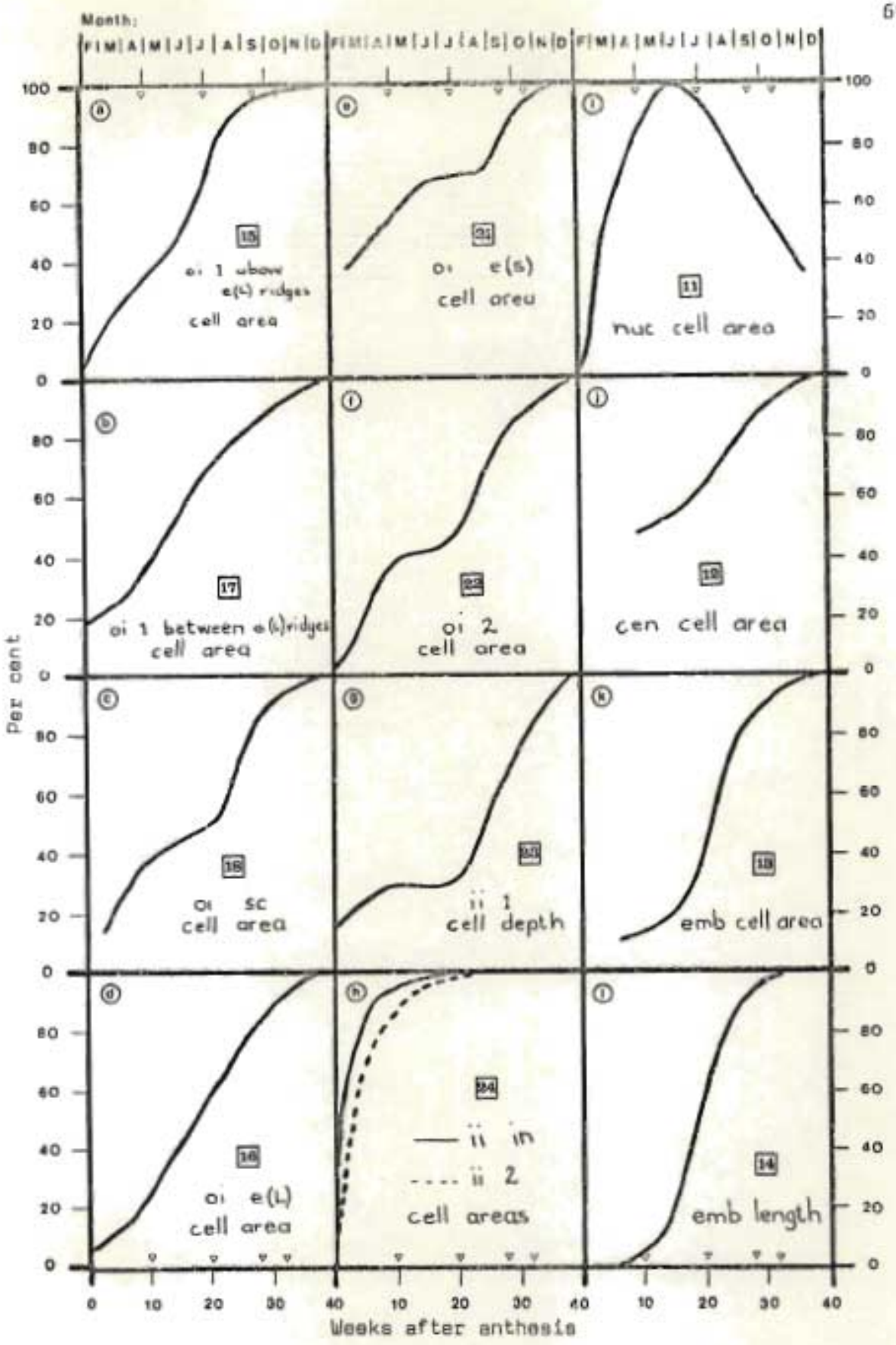

FIGURE 25 Percentage of final or greatest size of various seed tissues in normally developing (F) seeds from fruit set in summer, 1970. Based on measurements of figures referred to in squares. The order, a to l (encircled), corresponds with that of outermost to innermost tissues.

▽ indicate phases of general seed development.

1.3.3.6 Vascular supply. The limit to which the vascular bundle or umbrella extended was about that shown in Plate 20b. If one regards the region where the inner epidermis of the inner integument meets the "disc" (shown in the above Plate and discussed in the section on the nucellus) as the transition zone between the inner integument and the chalaza, then the vascular supply did not extend into the inner integument. Singh (1960) stated this to be the case whereas Foster (1943) implied (it seems) that the vascular supply did enter the inner integument.

1.3.4 Comparative normal seed development: Autumn

Anatomically, the mature normally developed seeds from fruit set in autumn were identical in appearance to those set in summer as just described. Microtome-sectioned, as well as additional hand-sectioned material from both autumn and summer-set fruits at the time their respective endosperms became cellular revealed that all their testal tissues were at comparable stages of development. At other periods, the correlation between various tissues within a particular seed appeared much like that of seeds from summer-set fruit.

The differences between the sets appear to have been in terms of the time pattern at which various stages were reached. For example, whilst it took seeds from the 1970 summer set (early February) 10 weeks for the endosperm to become cellular, seeds from the carpellary margin of fruits set in April, 1969, took 18 weeks, those along the placentary edge of the same fruits, about 23 weeks. Seeds from fruits set in the last week of April, first week of May (autumn), 197 took on the average 19 weeks. Those from fruit set in the second week of May (autumn), 1971, took about 23 weeks. Whilst the post-endosperm-cellularization phases were spread over 30 weeks in the summer set, these same phases were relatively compressed into 15 to 20 weeks in the autumn sets (depending on the time taken for endosperm cellularization, and fruit ripening).

In the 1970 summer set, the onset of endosperm cellularization was occurrin virtually at the time the 1970 autumn fruits were being set (end of April, beginning of May), and the further developments of the former were spread out through the winter months and finally early summer (November). On the other han the seeds of the autumn sets had to go through the winter months and even into spring (September/October) before their endosperm became cellular, after which their further developments occurred during the warm months (up to February/March The latter conditions help to explain why the post-endosperm-cellularization phases were compressed into fewer weeks in the autumn sets.

With regard to the number of layers in the endotestal tissues, the autumn fruit-set seeds appeared to have about five less in each of the e(L) and e(s) tissues, i.e. 23 layers each, in comparison to approximately the 28's of the summer set. This difference then, was in the order of 20%. Individual cross-sectional cell areas of all the various tissue types discussed before were about 80% of the size of the corresponding tissues of summer fruit-set seeds when both were at the cellularization of endosperm stage. Again, final sizes in tissues of mature seeds were in the order of 70 to 80% of those of the corresponding summer fruits' seeds.

So although the autumn fruit-set seeds had grown for a period twice as long as that of the summer set by the time the endosperm became cellular (and the embryos began their rapid growth), the autumn-set ones had not yet caught up in cell sizes. Neither did they finally catch up in size in the remaining warmer (although fewer) months. Further data related to the above results will be presented in the section that follows.

1.3.5 Whole seed and fruit growth

Figure 26 shows the growth in volume of seeds growing in the c.m. and p.e. regions of fruits set in autumn, 1969. A growth curve for fruit volume based on the sub-set of 18 fruits is also depicted. Peak fruit growth rate was reached at about the time the c.m. seeds' endosperm began to cellularize (about the 18th week, beginning of September). By the time the endosperm of the p.e. seeds had cellularized (23rd week) and the embryos had entered the rapid growth phase (by the 26th week, end of October) the fruit volume growth rate had begun to decline. The inflexion in the sigmoid form of the fruit growth occurred about halfway through the growth period (21st week, mid-September).

The seed volume growth patterns were virtually parallel to that of the fruit, with the seeds in the c.m. region remaining larger than those of the p.e. Their inflexion points, however, appear to have been a little later than that of the fruits. The growth patterns of the seeds from the c.m. and p.e. regions were also virtually parallel to each other.

Figure 27 depicts the growth in volume of seeds from the c.m. and p.e. regions for both the summer and autumn sets of 1970. Within a given fruit-set, the pattern of growth of c.m. and p.e. seeds were again parallel, with the c.m. seeds again remaining larger throughout. All four curves are sigmoid in form, but obvious differences existed between the summer and autumn sets.

Whilst both sets grew over 40 - 45 weeks, the seed growth of the summer set reached their maximal rates (inflexion point) at about the 10th week (mid-April)

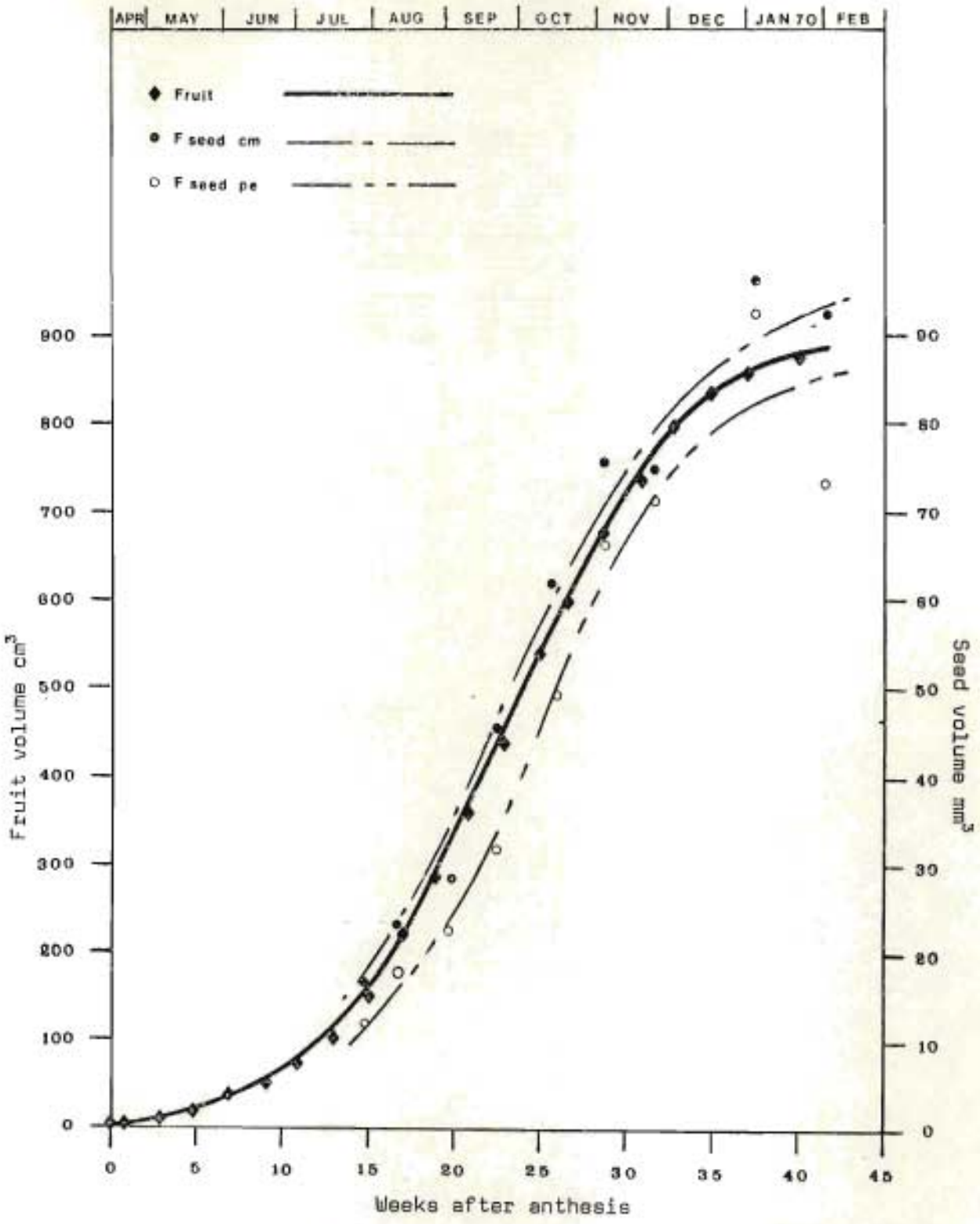

FIGURE 26 Mean fruit and individual seed volumes during development, autumn set, 1969.

See ABBREVIATIONS for F, cm and pe.

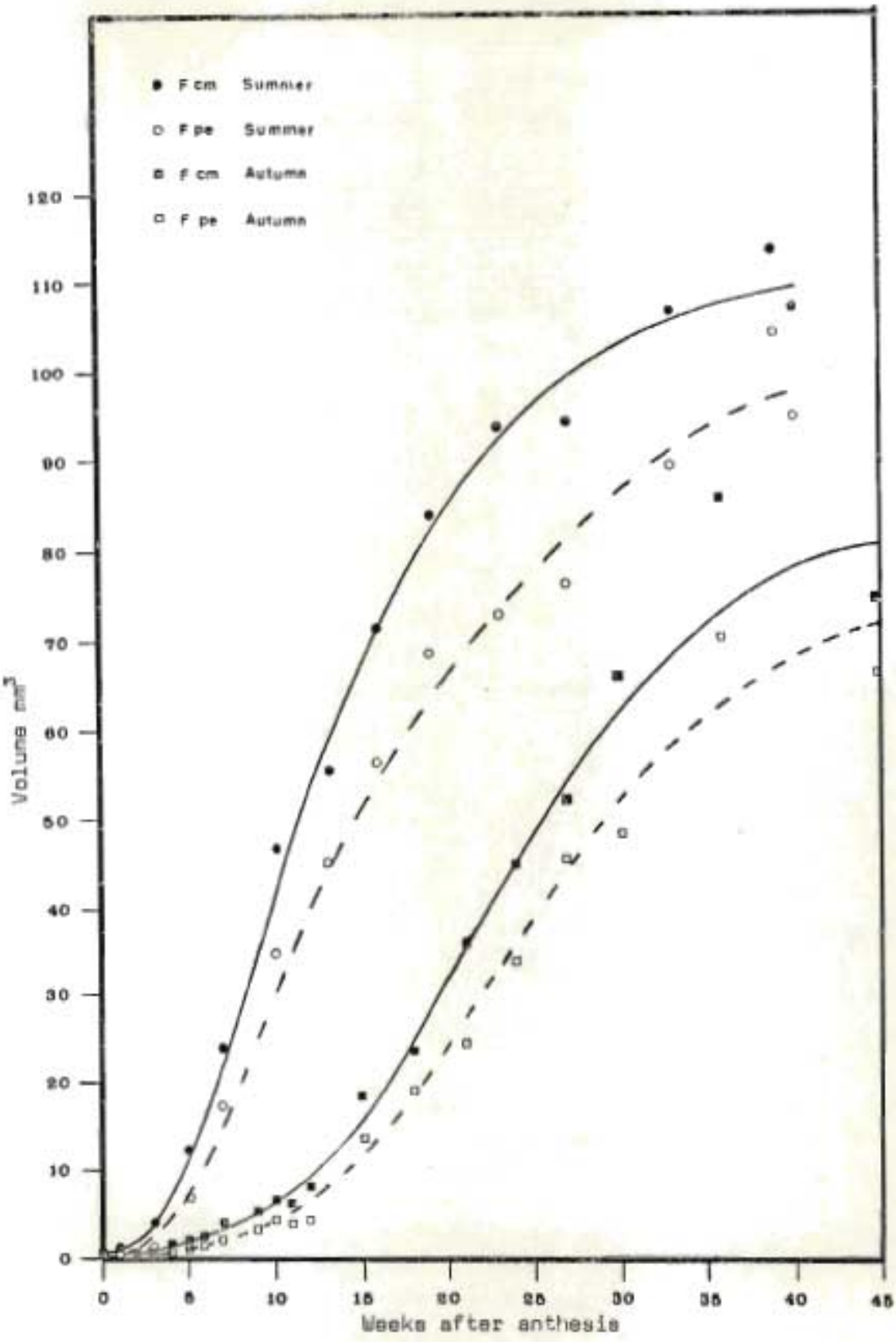

FIGURE 27 Mean individual volumes of fully developing seeds (F) from carpellary margin (cm) and placental edge (pe) regions (summer and autumn sets, 1970).

i.e. about a quarter of the developmental period, and also at the time of endosperm cellularization. In the case of this (1970) autumn set, the inflexion point was again about half-way through the development period (20th week, mid-September), and again during the transition of free nuclear to cellular endosperm.

So whilst the summer-set seeds had reached their maximal rate before the winter set in, that of the autumn set did so only after the winter months. At fruit ripening, i.e. after 10 months in both sets, p.e. seeds were approximately 90% the size of their c.m. counterparts in both sets. On the whole, the autumn-set seeds were about 70% the size of those of the summer set. This proportion matches that found between the cross-sectional areas of respective individual cell types of these two sets (cf. anatomy sections of this chapter). Similarly, at the time of their respective endosperm cellularization phases (10th week, mid-April and 20th week, mid-September, summer and autumn sets respectively), th autumn-set seeds were about 80% the size of that of the summer set's. This was also the case with the individual cell type sizes, as would be expected.

The summer set's seed growth, then, does not appear to have been affected by the winter conditions, whereas the autumn set's seed growth accelerated only after the coldest months (June/July) had passed. These findings (on growth in volume) for individual normally developing seeds parallels those found by Kuhne and Allan (1970) for fruit (volume) growth of summer and autumn sets.

Figure 28 shows amongst other things, the fruit and seed growth (measured as fresh mass) for both the summer and autumn sets of 1970. The mean seed mass patterns followed much the same patterns as those of the mean seed volumes, as would be expected. In both the summer and autumn sets the inflexion in the growth curves of the fruits seems to have occurred slightly before those of thei individual seeds. After the period at which the inflexions in the growth curves of both seed and fruit occurred, there were divergencies in relative growth rate Fruit growth rate appears to have proceeded at a relatively faster rate than tha of the normal seeds in the summer set, whereas the reverse seems to have occurre in the autumn set.

Now that normal ("F") seed development in the clone 'Honey Gold' in relatio to its fruit growth has been dealt with, it will be possible to make a comparative examination of the "development" of abortive or underdeveloped ovules and seeds in the following chapter.

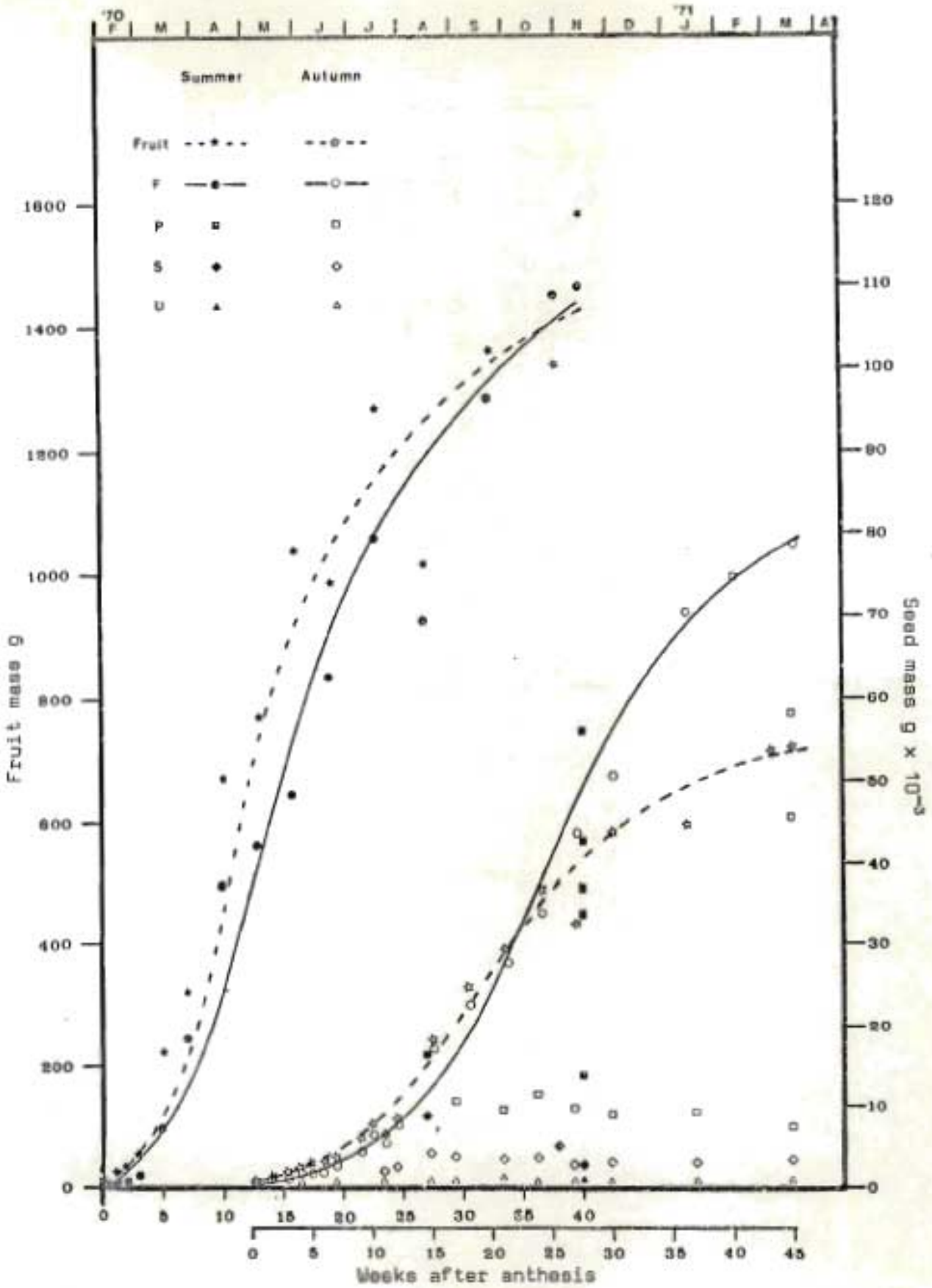

FIGURE 28 Fruit and individual seed masses during development, summer and autumn sets, 1970.

See ABBREVIATIONS for F, P, S and U .

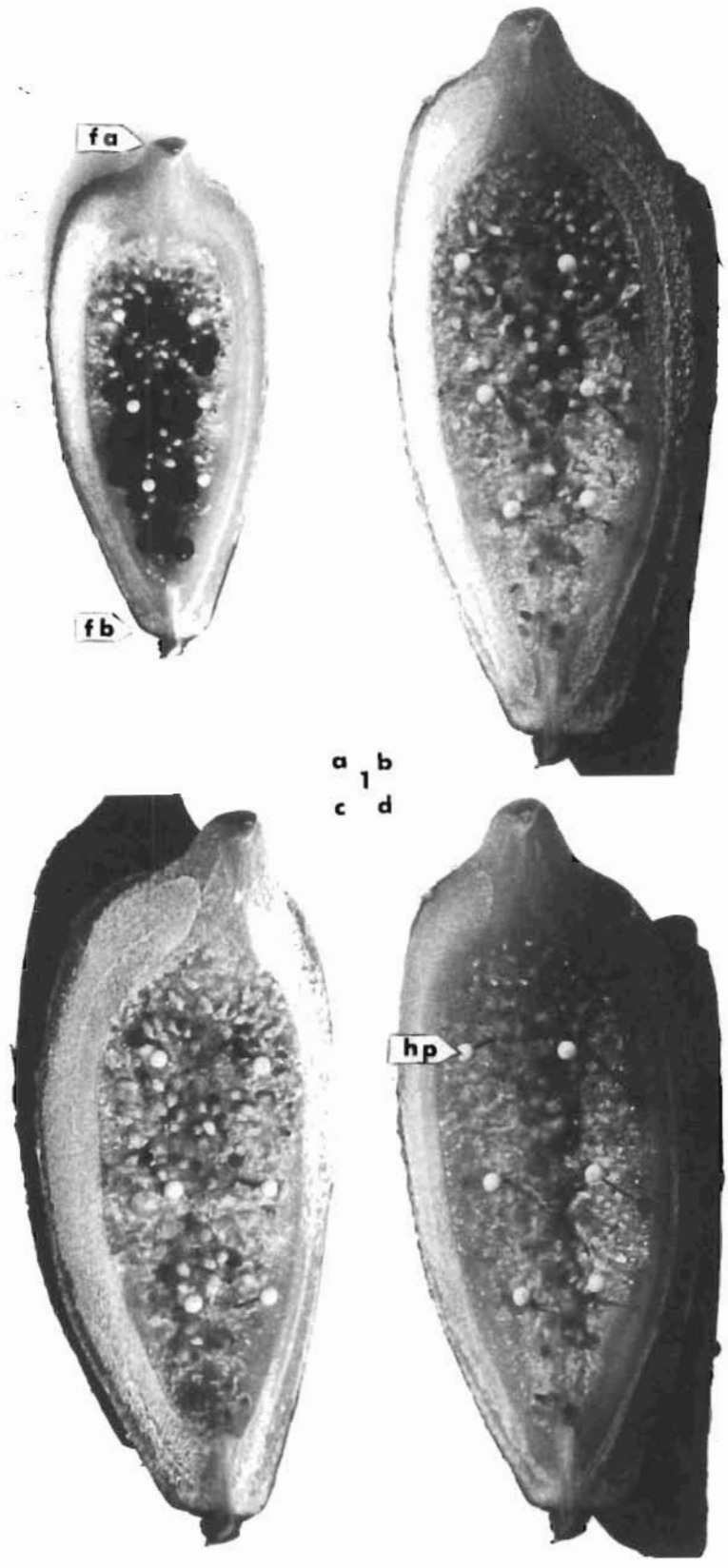

PLATE 1 One-fifth longitudinal portion of fruit with various complements of seeds.

(a) Full complement of F + P + S seeds and U ovules.

(b) P + S seeds and U ovules.

(c) S seeds and U ovules.

(d) U ovules only.

See Abbreviations and Plate 2b.

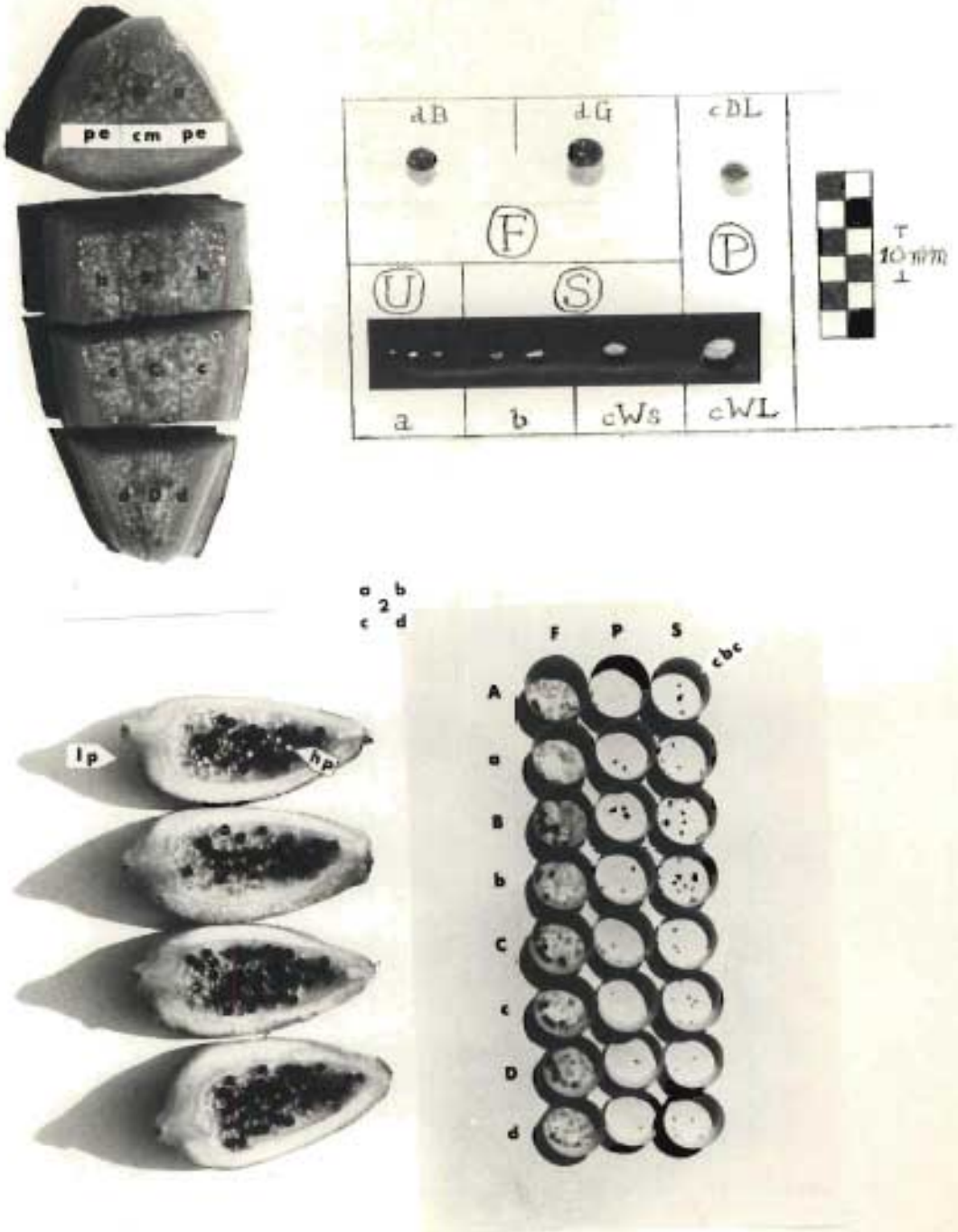

PLATE 2 (a) Divided fifth longitudinal fruit portion after seeds removed.
(b) Two notational keys for seeds and ovules found in mature fruits.
(c) Four of five longitudinal portions of fruit with seeds.
(d) Seeds sorted into type and intra-fruit subregion.
See Abbreviations.

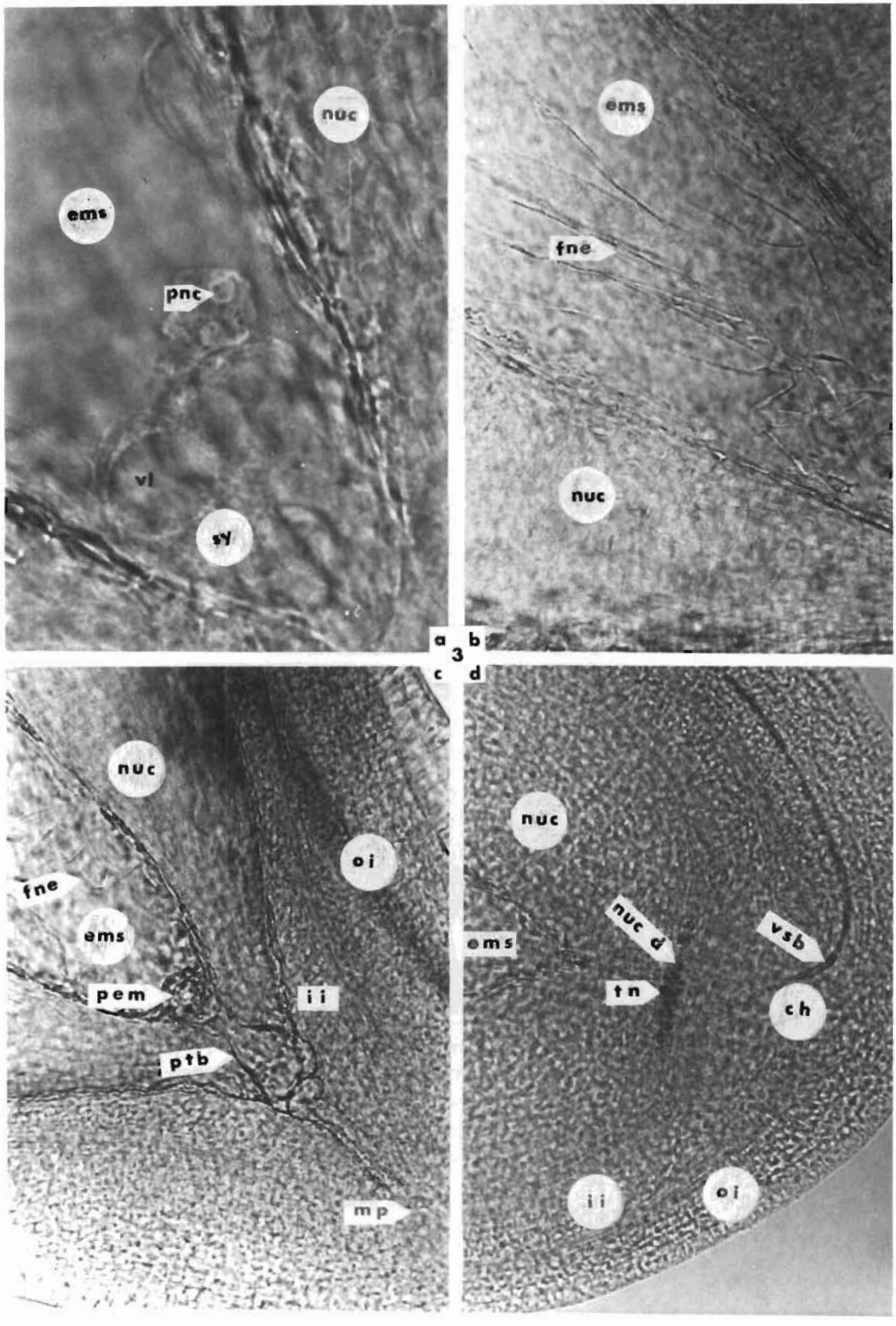

PLATE 3 (a) Micropylar end of mature megagametophyte (cleared, x 1880).

(b) Centre of 6-week seed, autumn set (cleared, x 470).

(c) Micropylar end of 6-week seed, autumn set (cleared, x 470).

(d) Ovule two weeks after anthesis in autumn, with tannin at chalaza (cleared, x 470).

See Abbreviations.

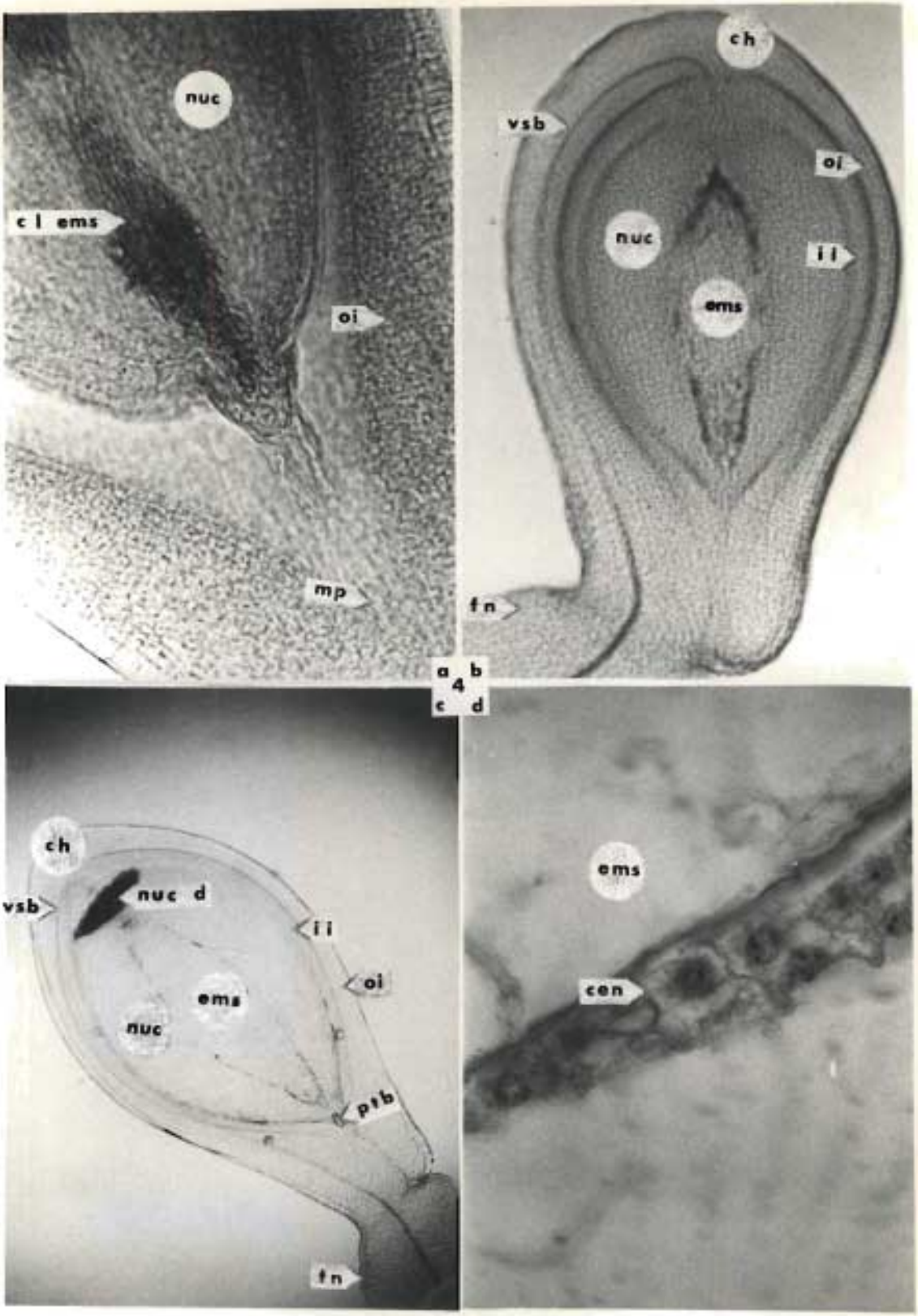

PLATE 4 (a) Collapsed embryo sac at anthesis, autumn (cleared, x 470).

(b) Ovule two weeks after anthesis, autumn, without tannin at chalaza (cleared, x 470).

(c) Week-2 seed with pollen tube and tannin, autumn (cleared, x 120)

(d) Cellular endosperm bordered by nucellar sheath, 13-week seed, summer set (x 1880).

See Abbreviations.

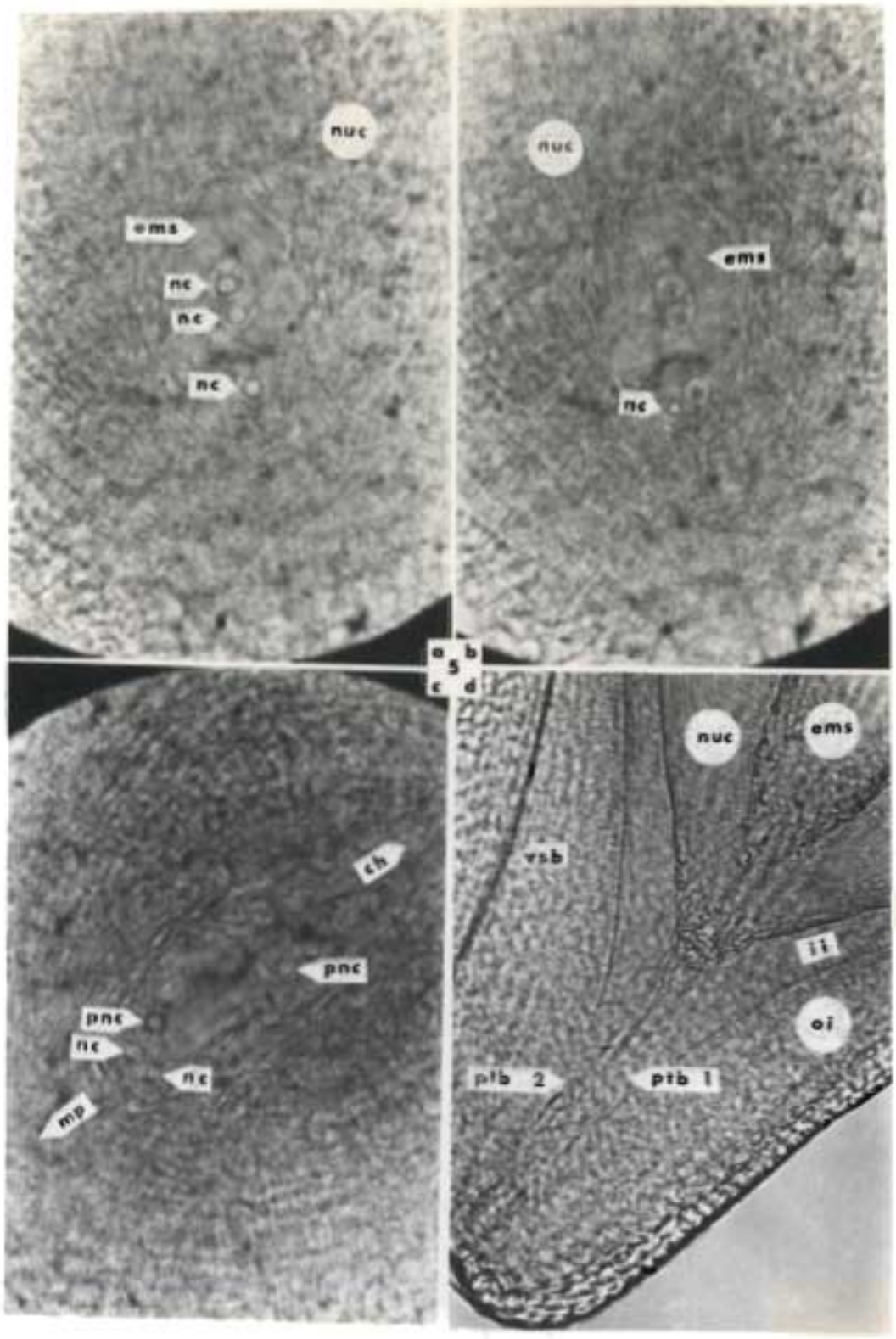

PLATE 5 (a) Four-nucleate megagametophyte, three nuclei in focus; anthesis, autumn (cleared, x 1680).

(b) Same as (a), different focal plane.

(c) Eight-nucleate megagametophyte; four nuclei in focus (cleared, x 1680).

(d) Week-6 seed with two pollen tubes, autumn set (x 470).

See Abbreviations.

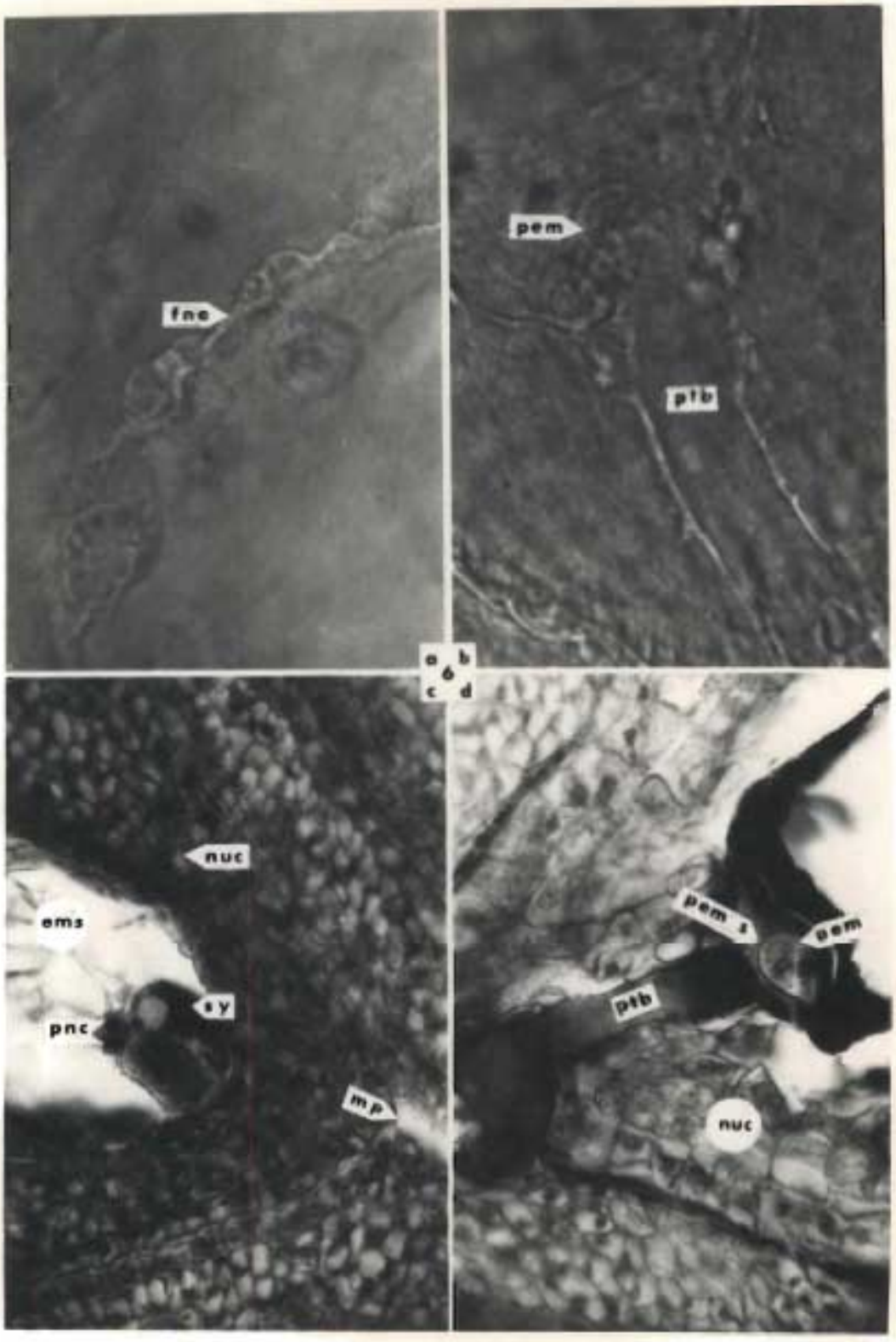

PLATE 6 (a) Free nuclear endosperm; week-6, autumn (cleared, x 1880).

(b) Pro-embryo, at pollen tube tip; week-6, autumn (cleared, x 1880).

(c) Mature megagametophyte, autumn (x 1880).

(d) Ensheathed, two-celled pro-embryo; week-8, autumn (x 1880).

See Abbreviations.

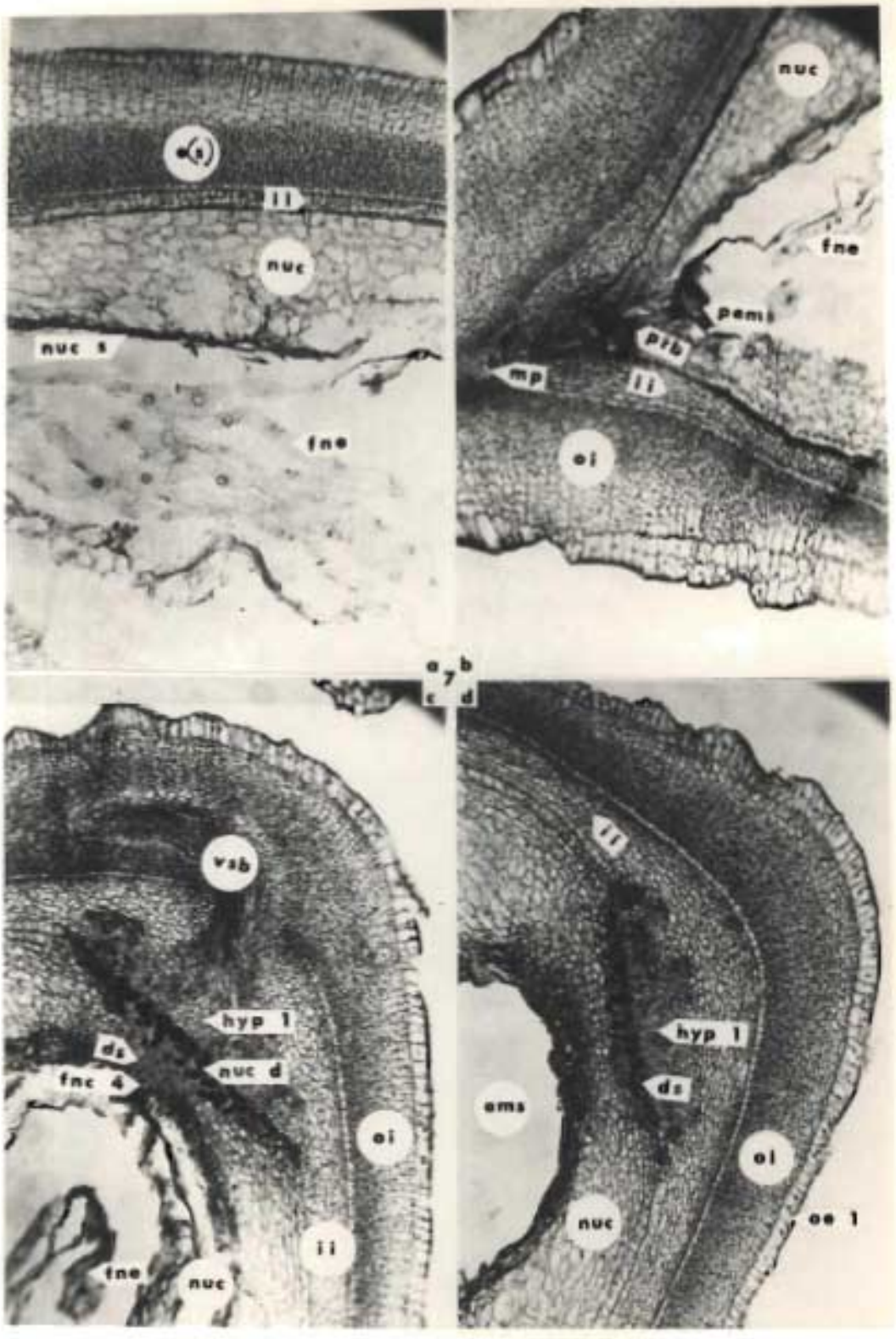

PLATE 7 (a) Week-3 summer seed.

(b) Micropylar end; week-8 seed, autumn.

(c) Disc and hypostase region at chalagal end, week-8, autumn seed.

(d) As for (c), but without finger-like nucellus (fnc 4).

All (x 470). See Abbreviations.

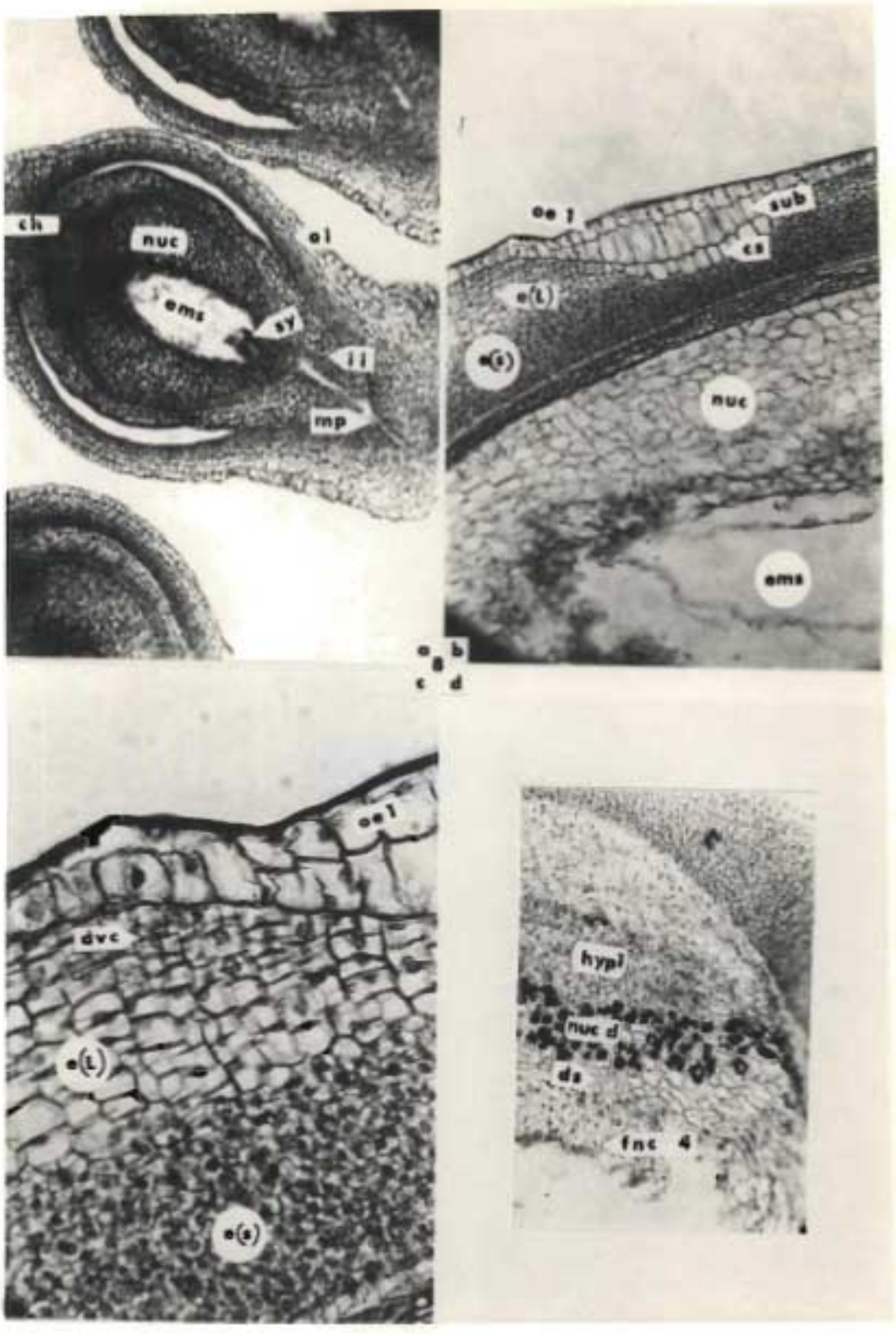

PLATE 8 (a) Ovule with mature megagametophyte; anthesis, autumn (x 470).

(b) Week-8 autumn seed coat (x 470).

(c) Same as (b) (x 1880).

(d) Relative positions of specialized nucellus at chalaza (x 470).

See Abbreviations.

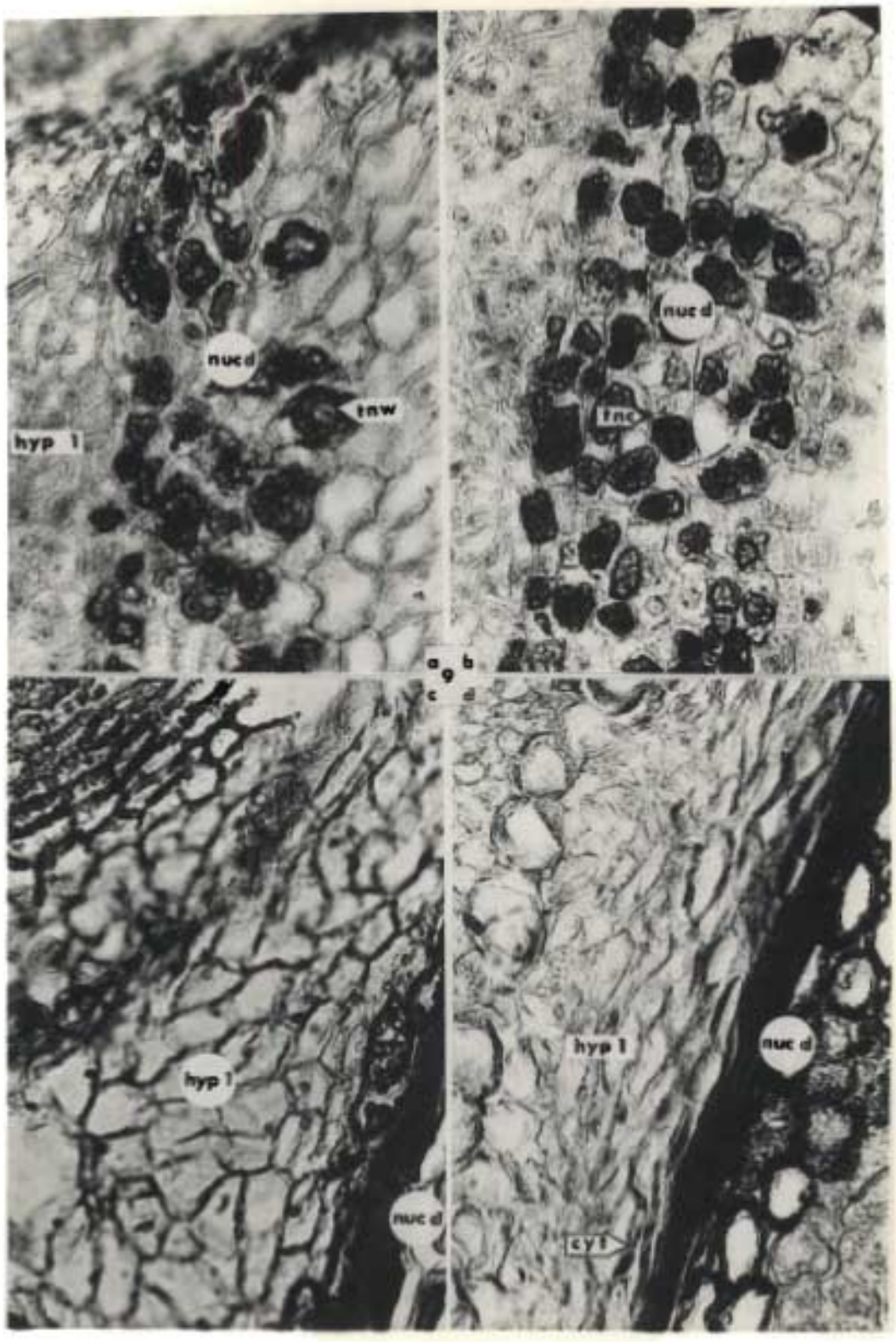

PLATE 9 (a) Tannin deposited along walls in nucellar disc region.

(b) Tannin deposited into cells of disc region.

(c) Wall thickening of hypostase cells.

(d) Cytoplasm along walls of hypostase cells.

All (x 1880) and from week-33 summer seeds.

See Abbreviations.

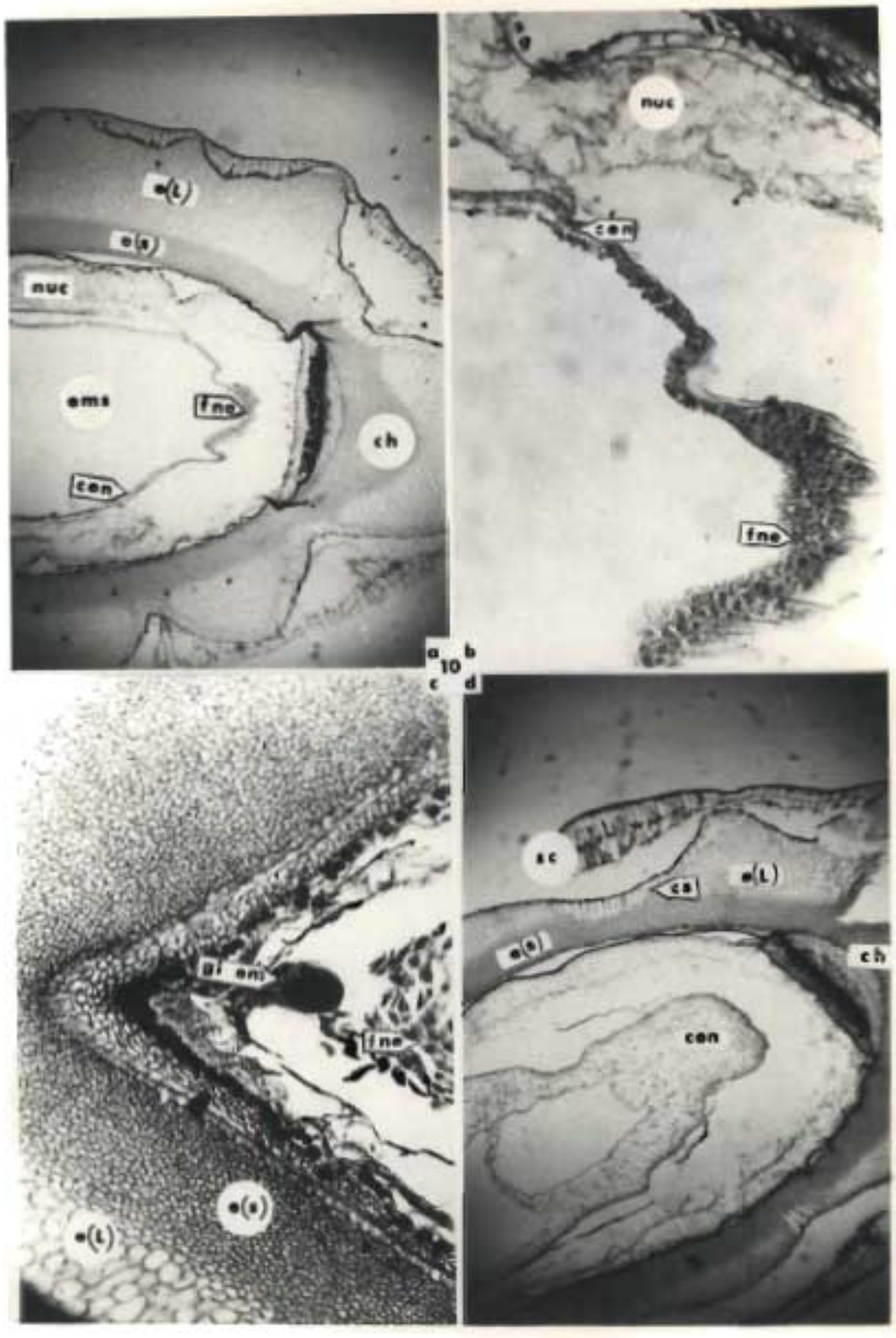

PLATE 10 (a) Cellularization of endosperm from micropylar to chalazal end (x 120).

(b) Same as (a) (x 470).

(c) Free nuclear endosperm near bulbous embryo (x 470).

(d) Cellular endosperm (x 120).

All from week-13 summer seeds.

SeeAbbreviations.

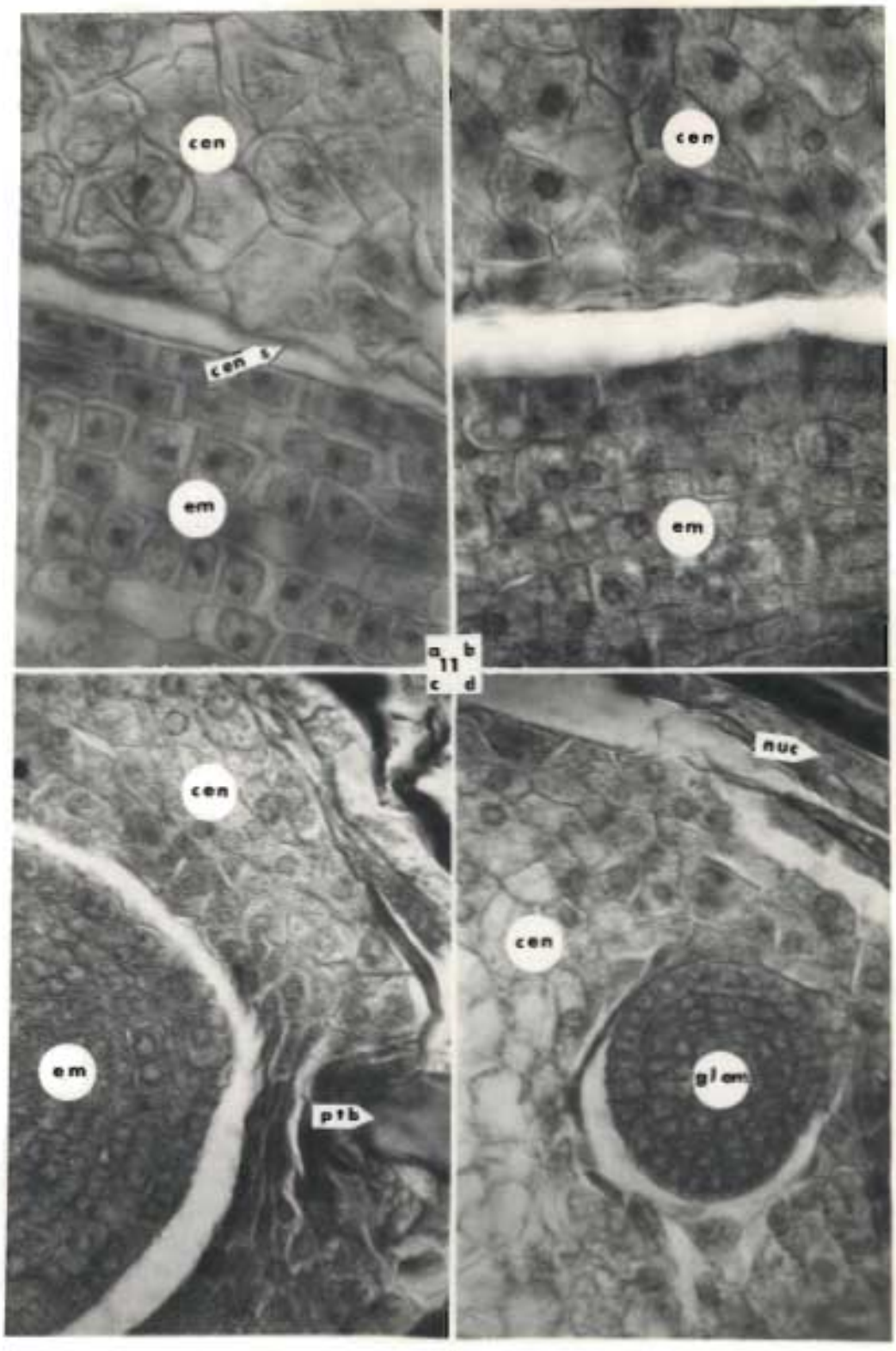

PLATE 11 Embryo and endosperm tissue in summer seeds.

(a) During early maturation, week-27.

(b) Prior to early maturation, week-27.

(c) At week-16.

(d) Globular embryo, week-13.

All (x 1880). See Abbreviations.

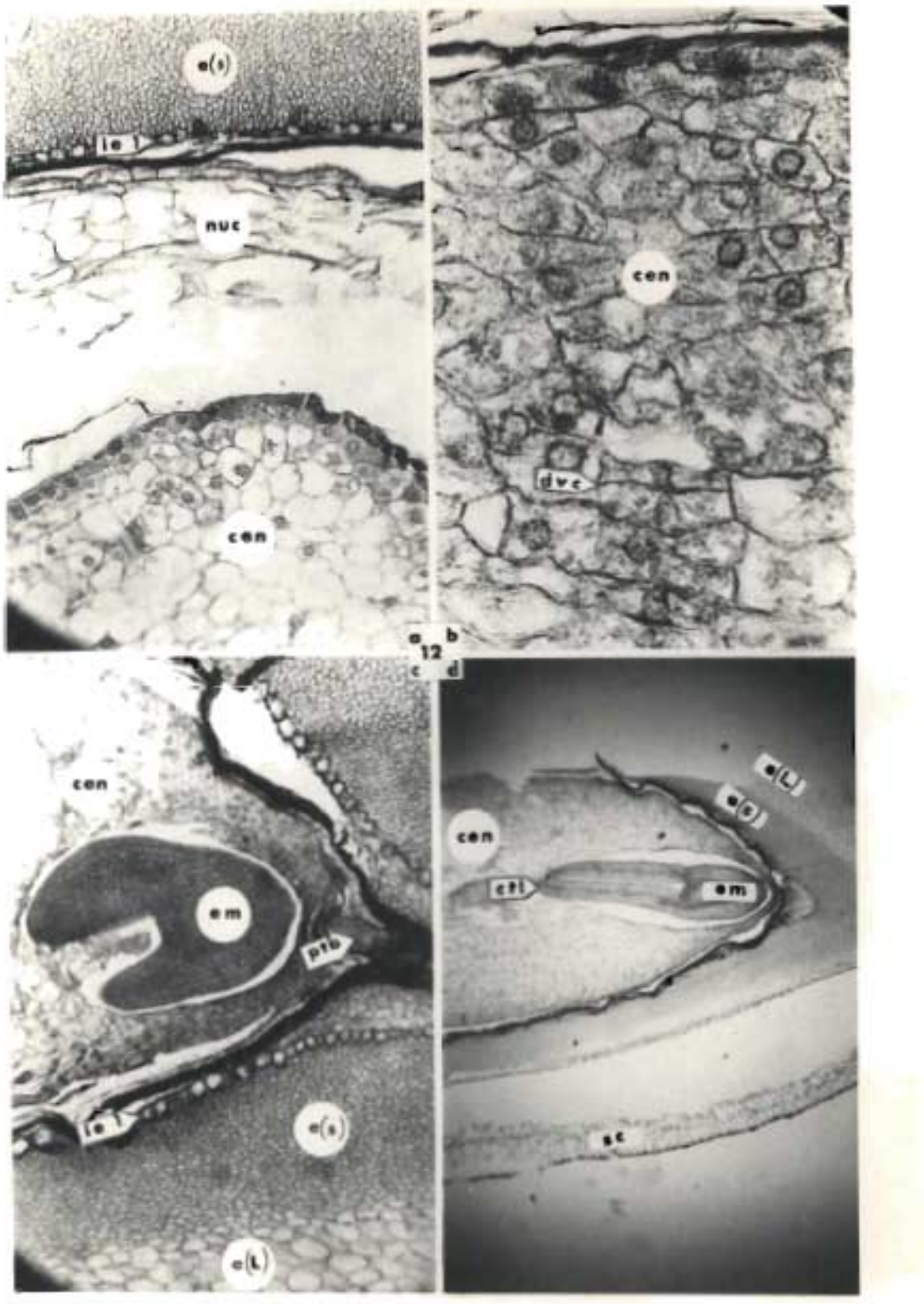

PLATE 12 (a) Cellular formation of endosperm; week-13, summer seed (x 470).

(b) As for (a), week-19 (x 1880).

(c) Heart-shaped embryo, week-16, summer seed (x 470).

(d) Final torpedo-shape of embryo; week-19, summer seed (x 120).

See Abbreviations.

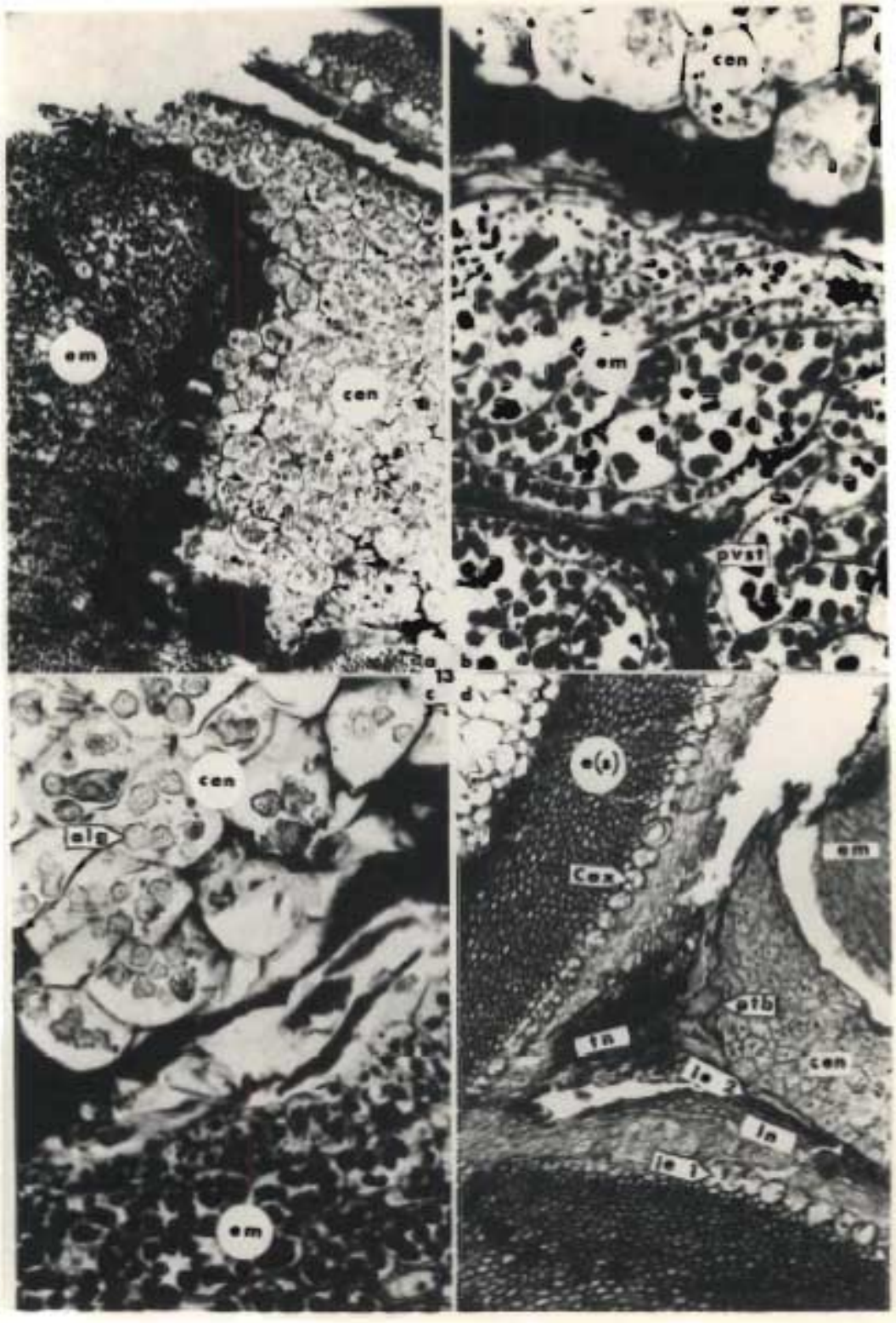

PLATE 13 From matured seeds in ripe summer fruits.

(a) Endosperm and embryo (x 470).

(b) Provascular strand in cotyledon (x 1880).

(c) Aleurone grains in endosperm (x 1880).

(d) Persistent pollen tube tip (x 470).

See Abbreviations.

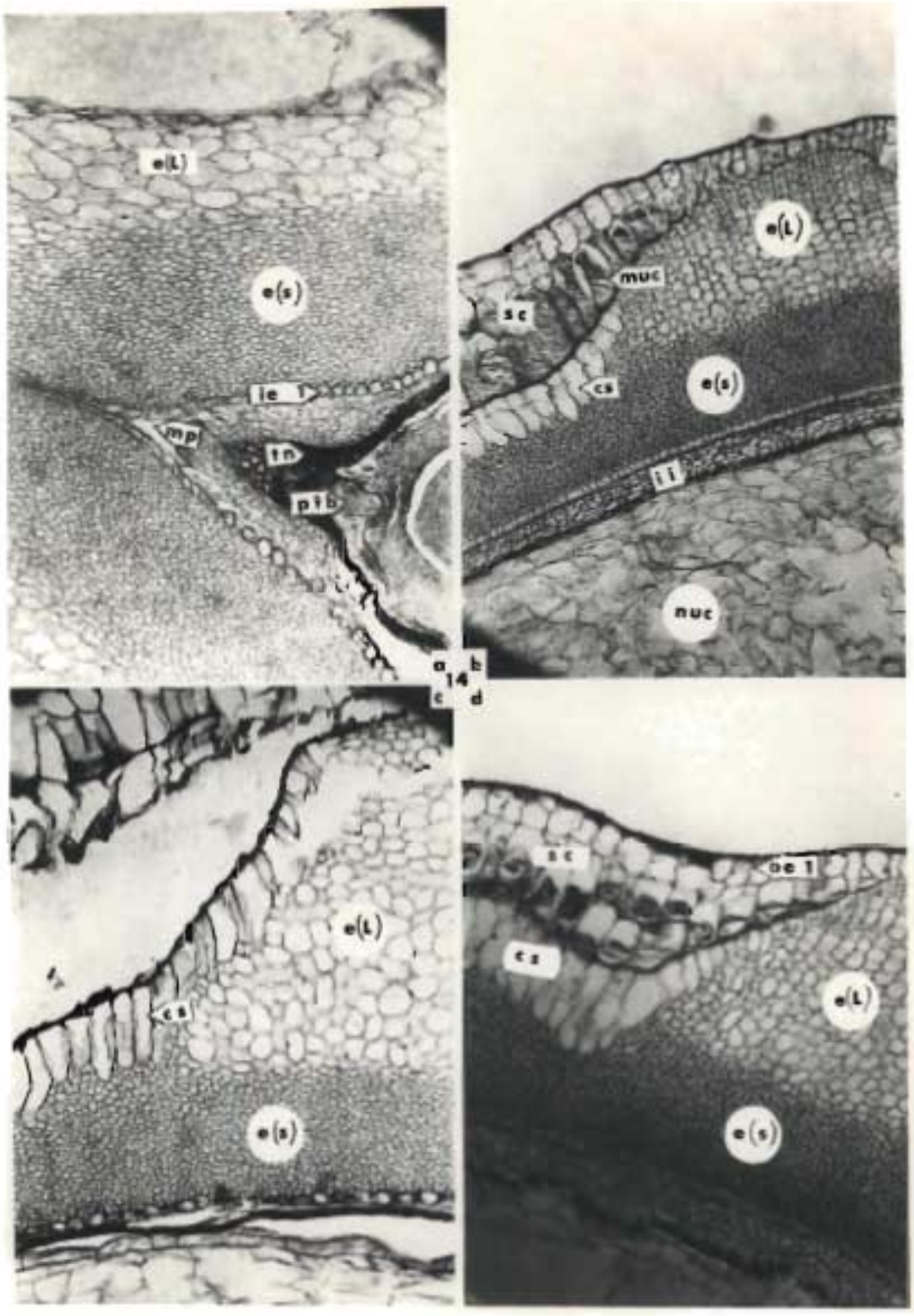

PLATE 14 (a) Persistent pollen tube tip, week-16.

(b) Mucilage in sarcotesta, week-6.

(c) Contiguous endotestal layer (cs), week-13.

(d) Same as (c), different seed.

All from summer seeds, all (x 470).

See Abbreviations.

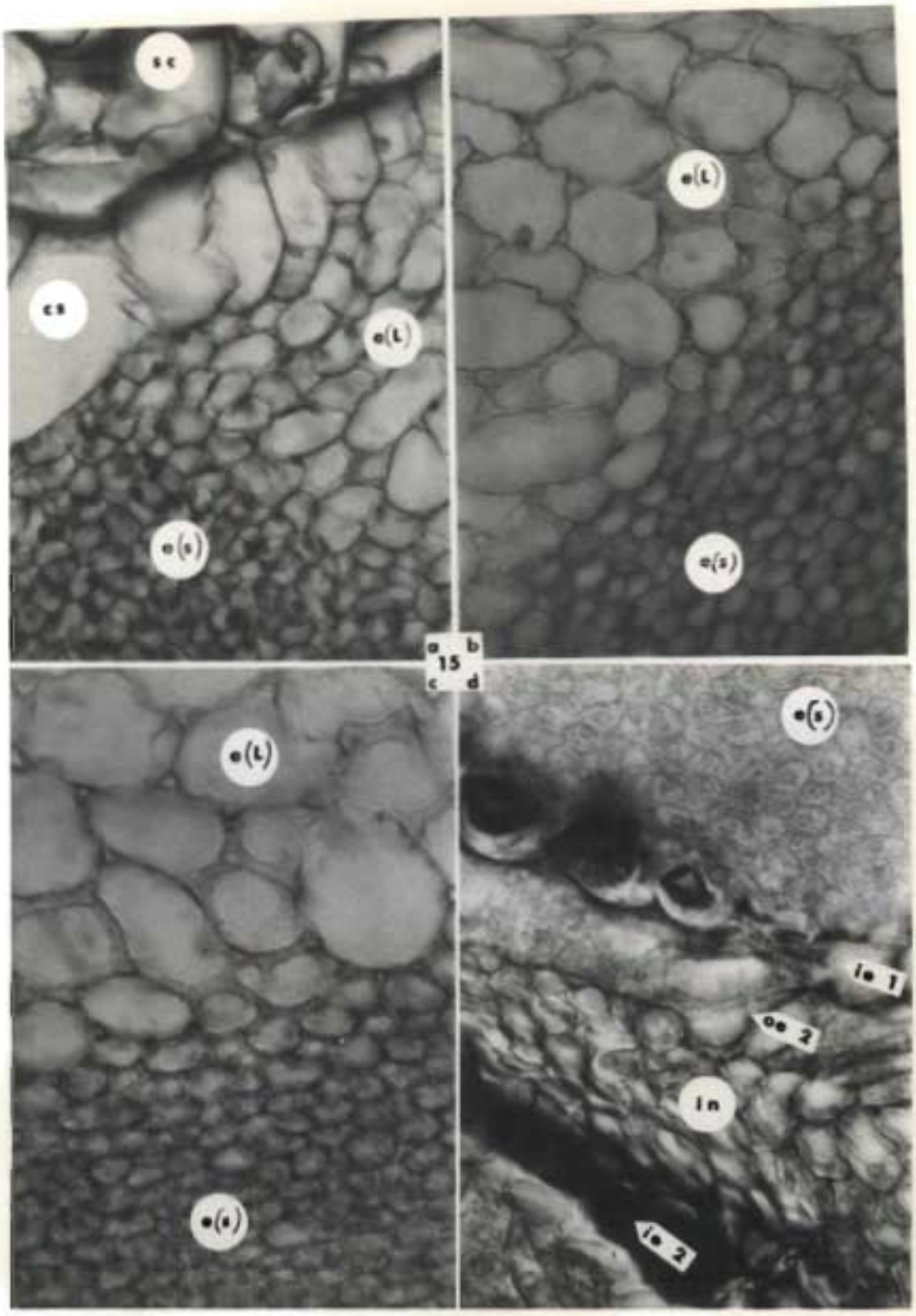

PLATE 15 (a) Contiguous endotestal layer (cs), week-13.

(b) Buckled endotestal ⌈e(L)⌋ cell walls, week-13.

(c) Buckling of ⌈e(L)⌋ disappearing with onset of thickening, week-27.

(d) Outer epidermis of inner testa (oe 2), week-27.

All summer seeds, all (x 1880).

See Abbreviations.

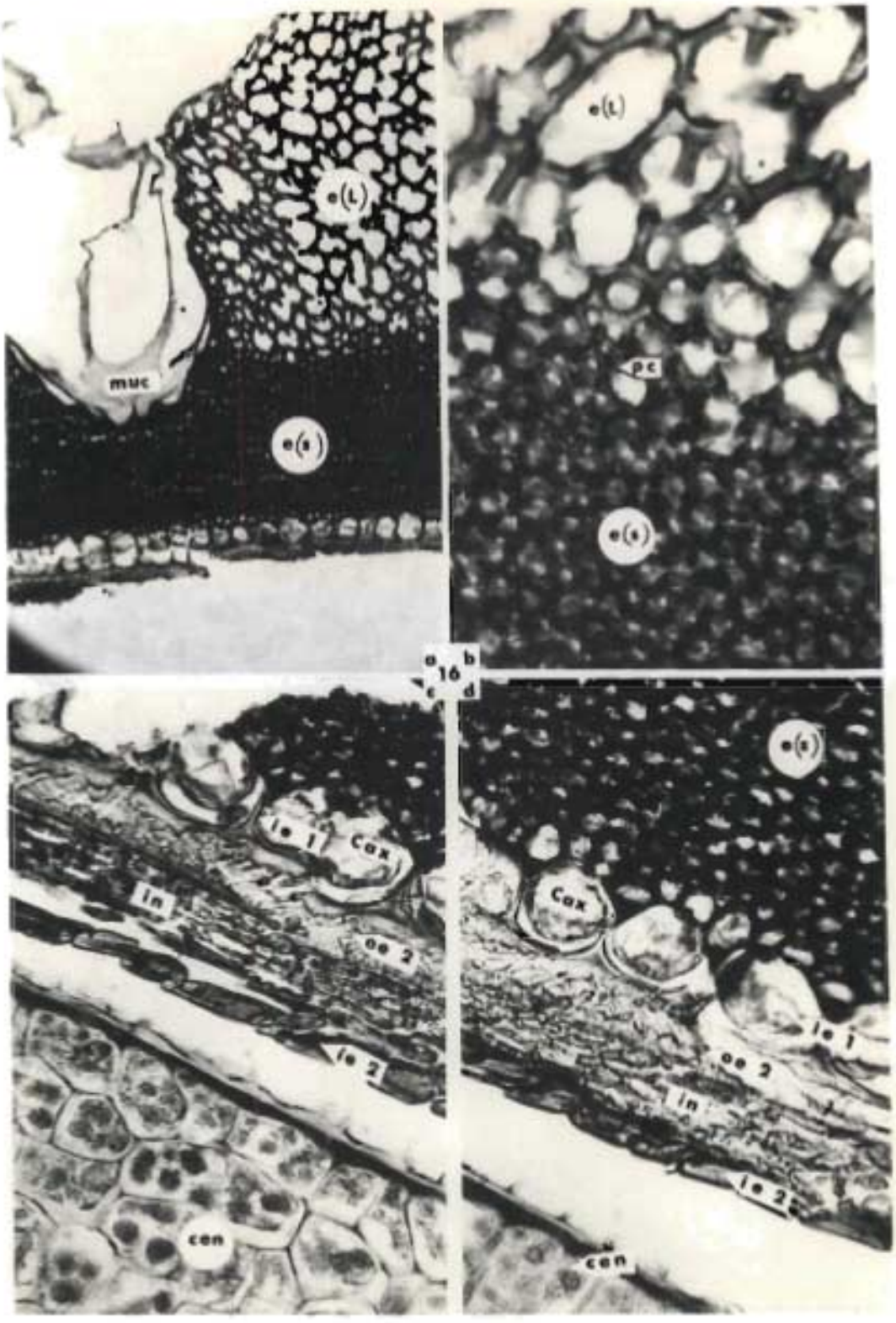

PLATE 16 (a) Endotestal tissue (x 470).

(b) Same as (a) (x 1880).

(c) and (d) Inner testa and adjacent tissues. Both (x 1880).

All from seeds of ripe summer fruits.

See Abbreviations.

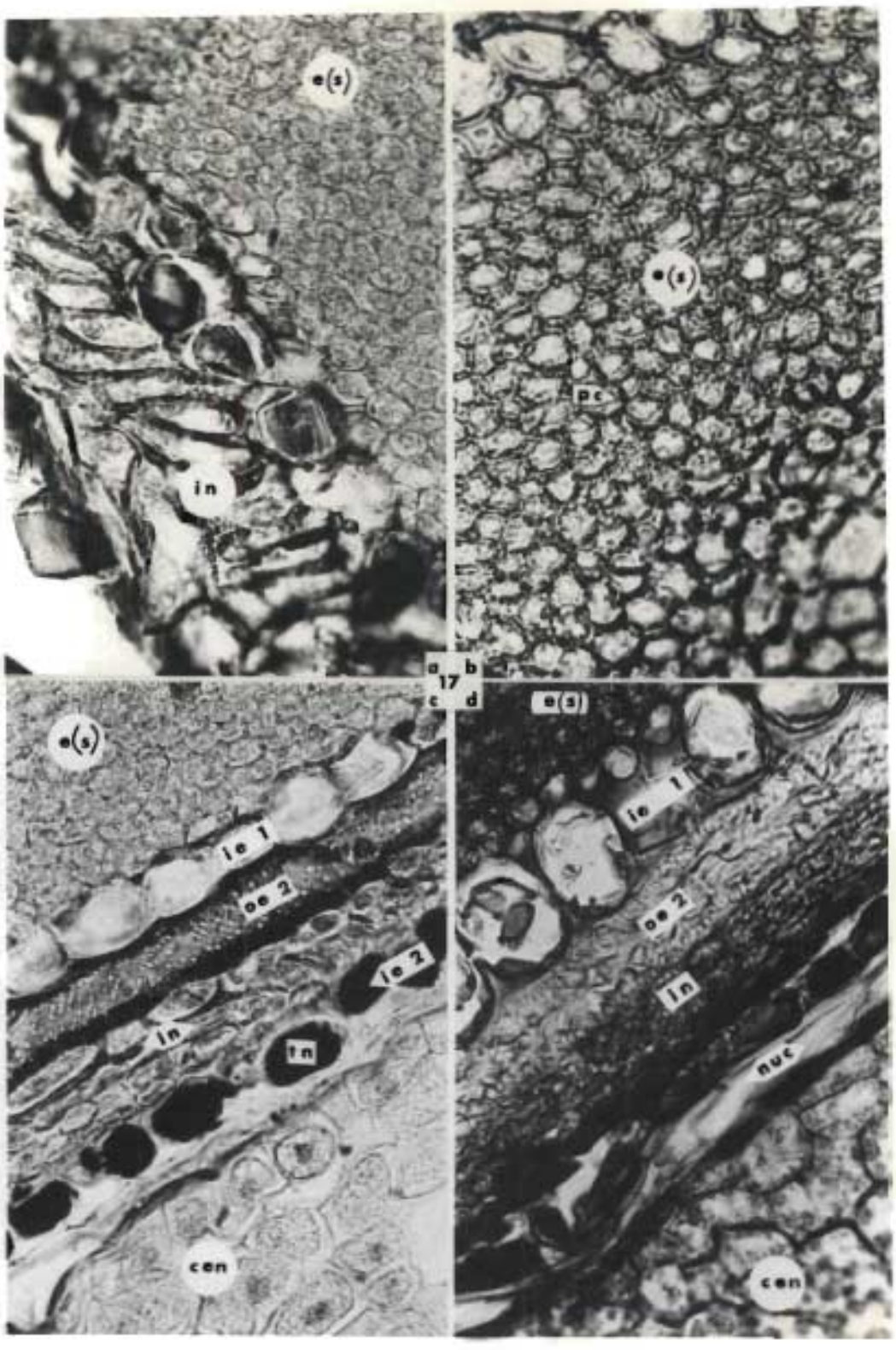

PLATE 17 Inner testa and adjacent tissues, summer seeds.

(a) Week-27.

(b) Pitting of [e(s)] endotestal tissue, week-33.

(c) Tapered walls of outer epidermis (oe 2), week-27.

(d) Extent of general thickening, week-40.

All (x 1880). See Abbreviations.

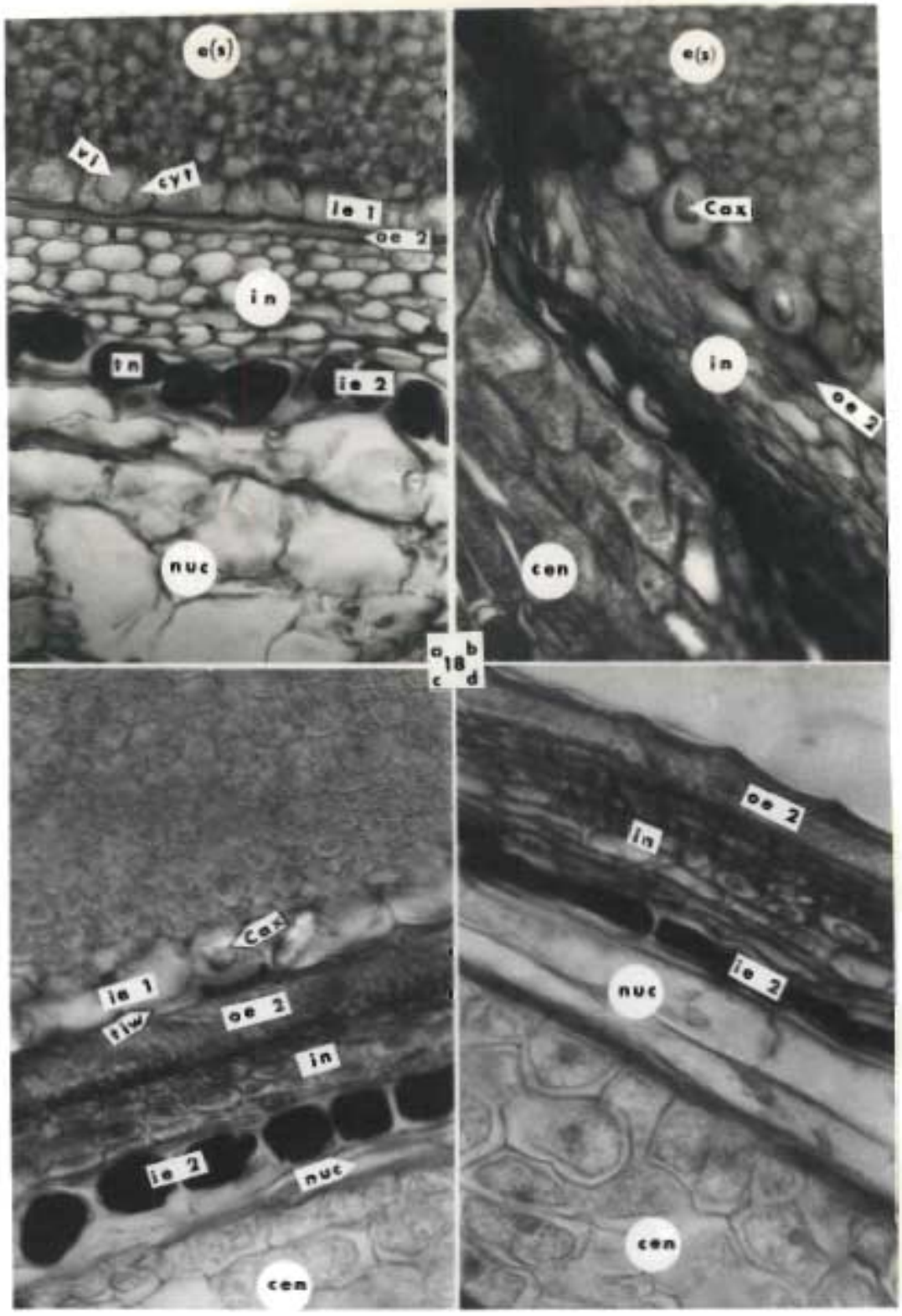

PLATE 18 Inner testa and adjacent tissues, summer seeds.

(a) Week-13.

(b) Week-27.

(c) and (d) Week-23.

All (x 1880). See Abbreviations.

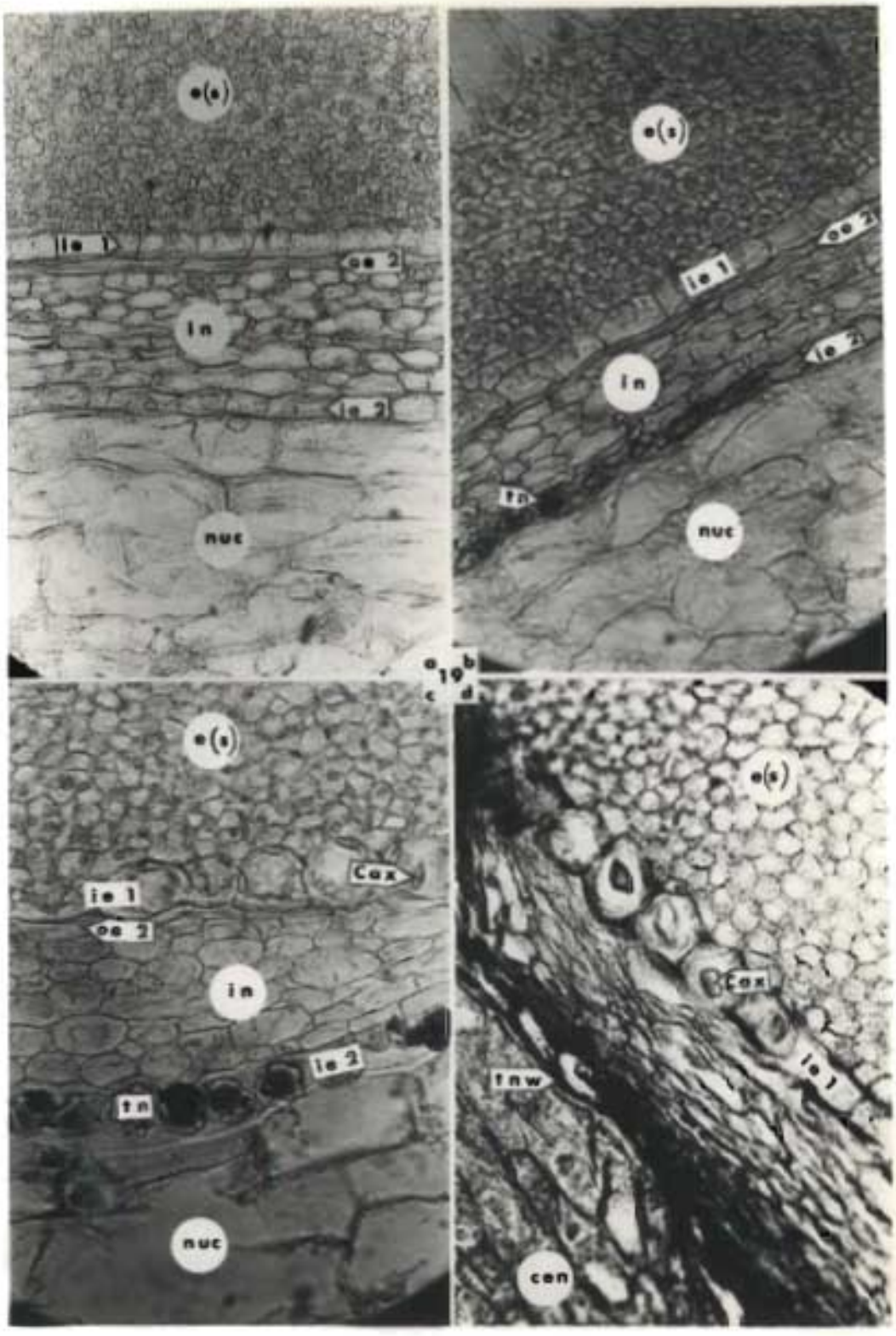

PLATE 19 Inner testal tissue, summer seeds.

(a) Same as (a), with some tannin.

(c) Week-11, with Calcium oxylate crystal in epidermis of outer testa (ie 1).

(d) Tannin deposition along walls of (ie 2).

All (x 1880). See Abbreviations.

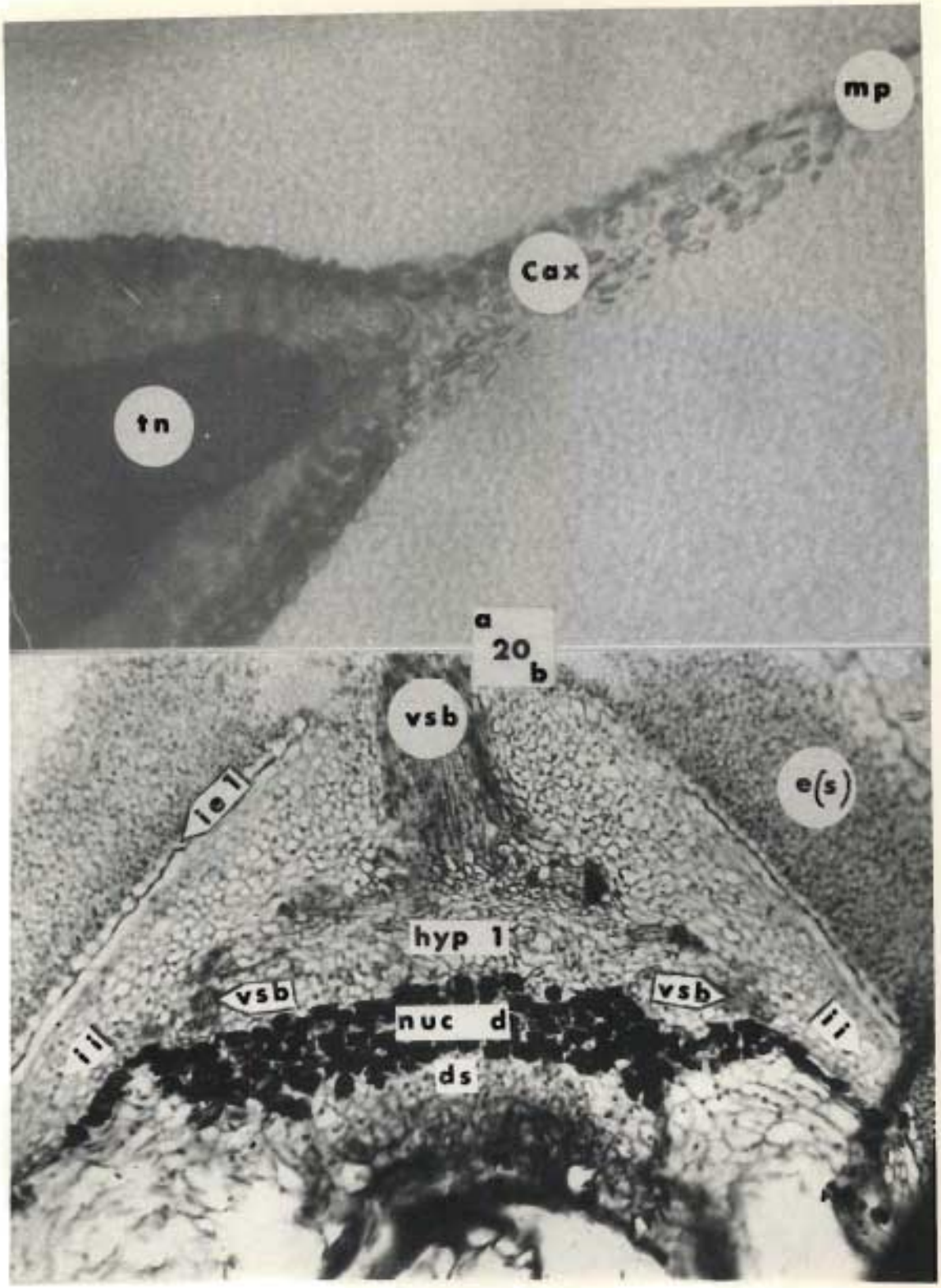

PLATE 20 (a) Calcium oxylate crystals in micropylar region, week-27. (Whole mount, cleared; x 235).

(b) Vascular supply and specialized region of nucellus at chalazal end, week-13 (x 940).

Both from summer seeds. See Abbreviations.

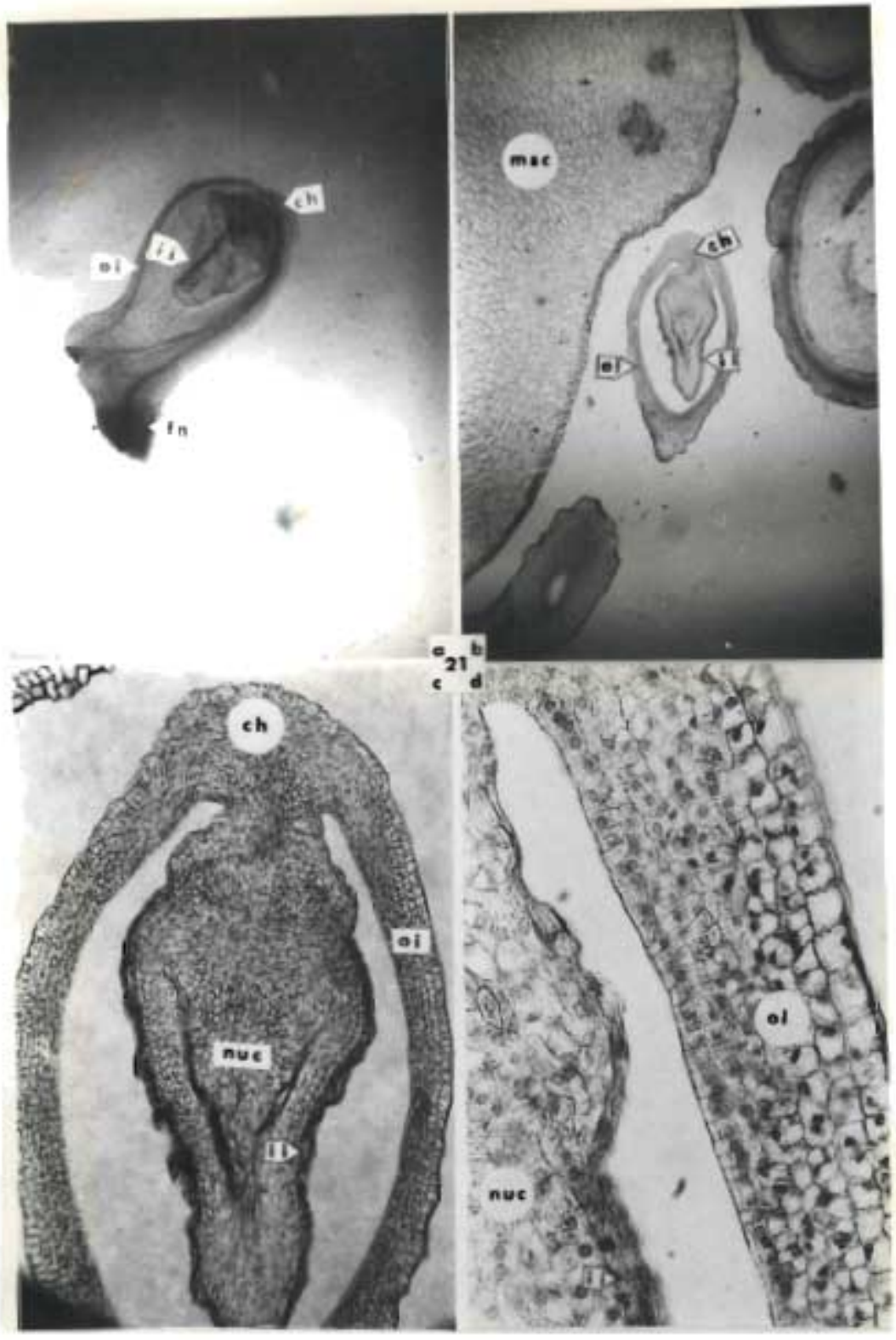

PLATE 21 (a) Unfertilized ovule, eight weeks after anthesis, autumn (cleared, x 120).

(b) Same kind and age as (a) (sectioned, stained; x 120).

(c) Same as (b) (x 470).

(d) Same as (b) (x 1880).

See Abbreviations.

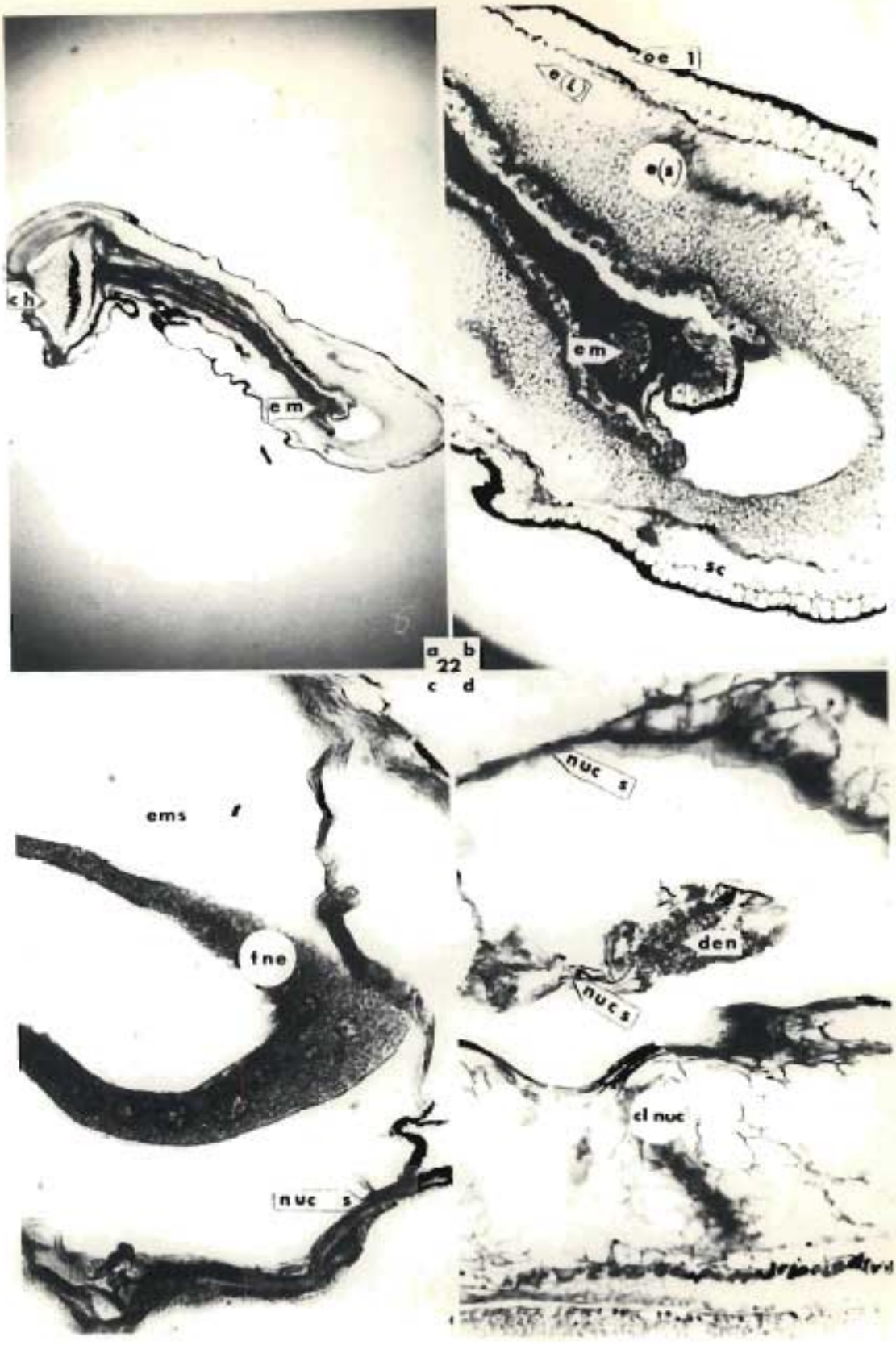

PLATE 22 (a) Aborted autumn "b" seed, week-23 (x 120).

(b) Same as (a) (x 470).

(c) Endosperm of autumn "cWL" seed, week-23 (x 1880).

(d) Endosperm and nucellus of autumn "cWs" seed, week-23 (x 1880).

See Abbreviations.

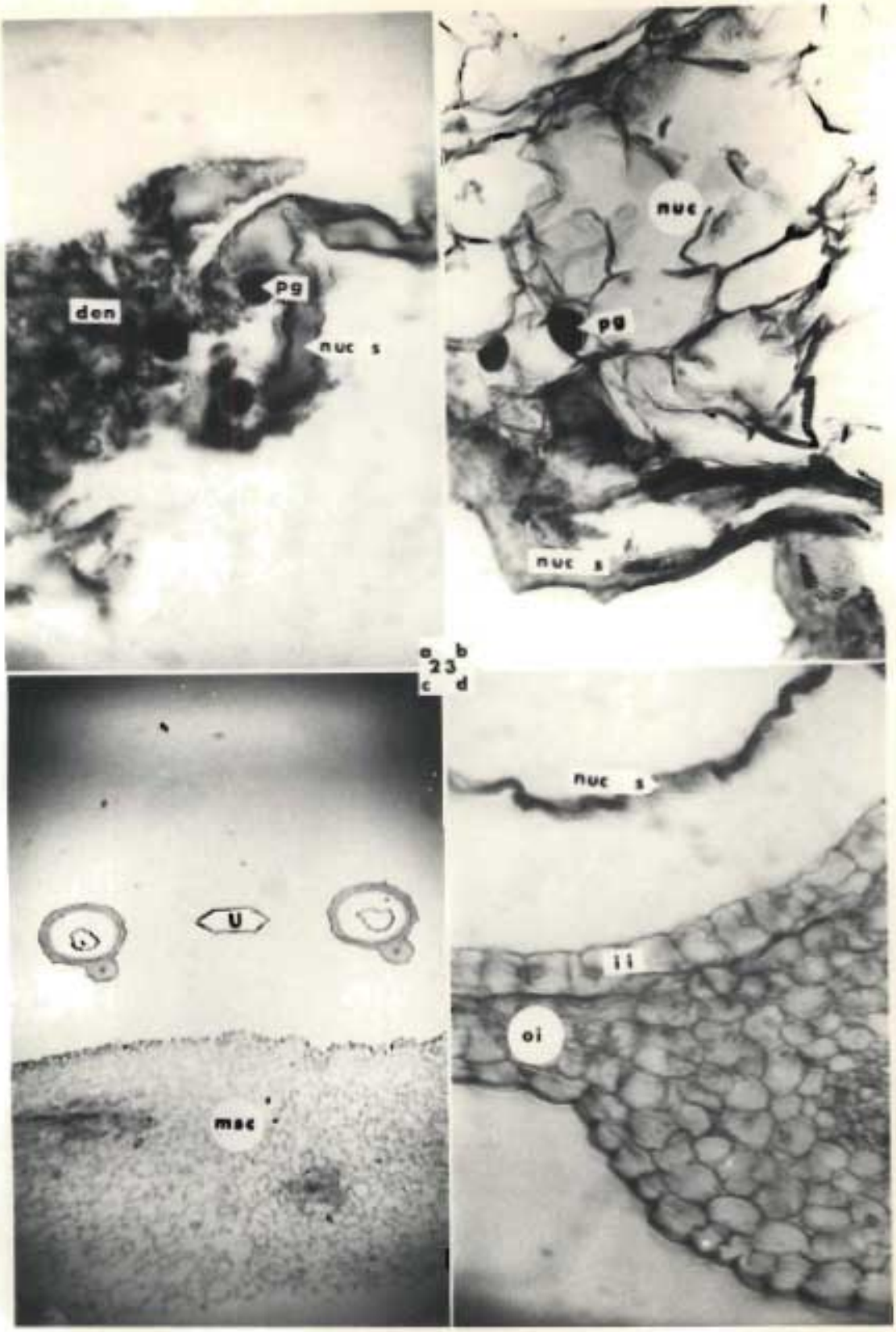

PLATE 23 (a) Endosperm, autumn "cWs" seed, week-23 (x 1880).

(b) Nucellus of (a) (x 1880).

(c) Unfertilized summer ovules, week-23 (x 120; transverse section).

(d) Same as (c) (x 1880).

See Abbreviations.

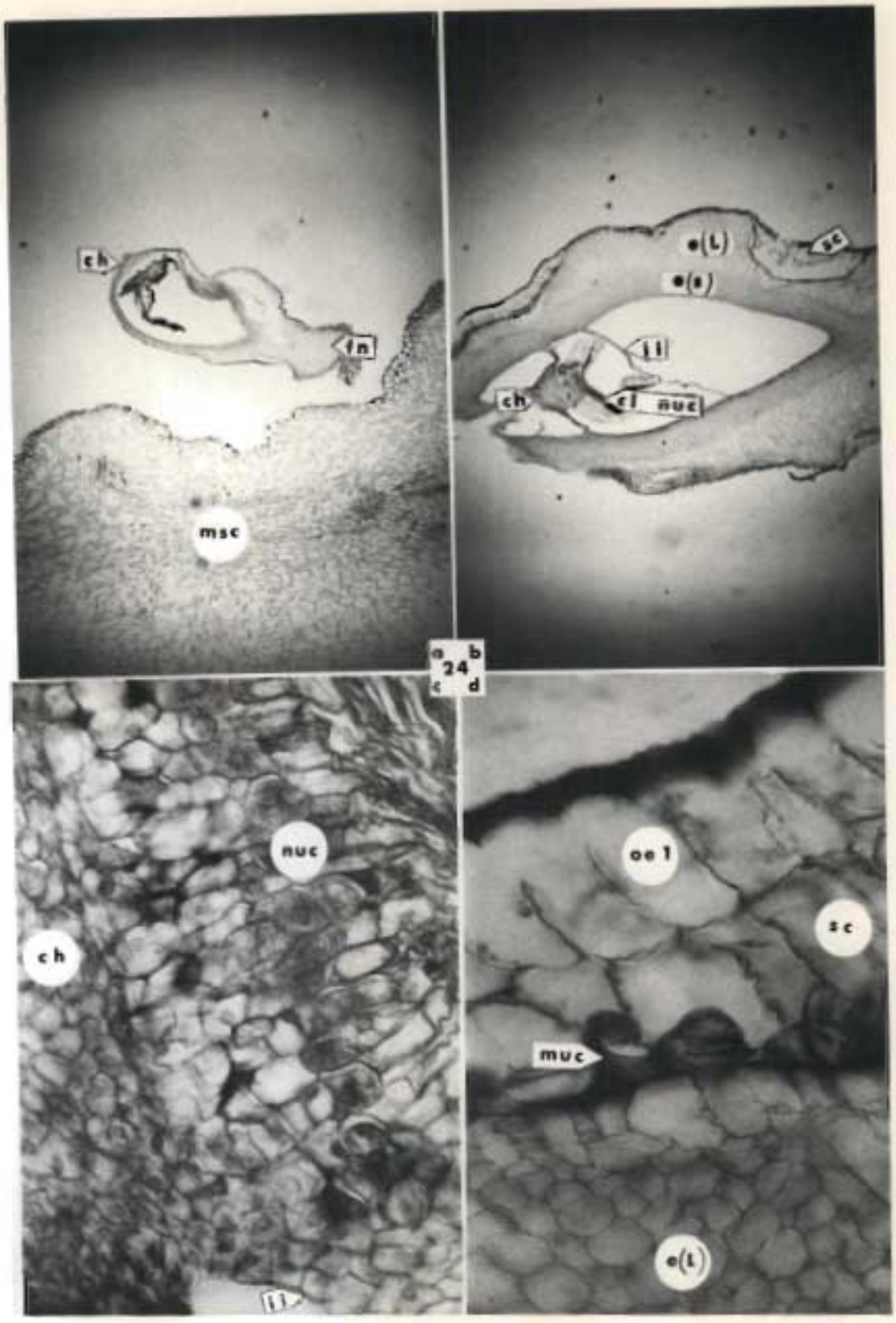

PLATE 24 (a) Unfertilized summer ovule, week-23 (x 120).

(b) "Empty cWs" summer seed, week-23 (x 120).

(c) Chalazal region of (b) (x 1880).

(d) Endotestal and sarcotestal tissues of (b) (x 1880).

See Abbreviations.

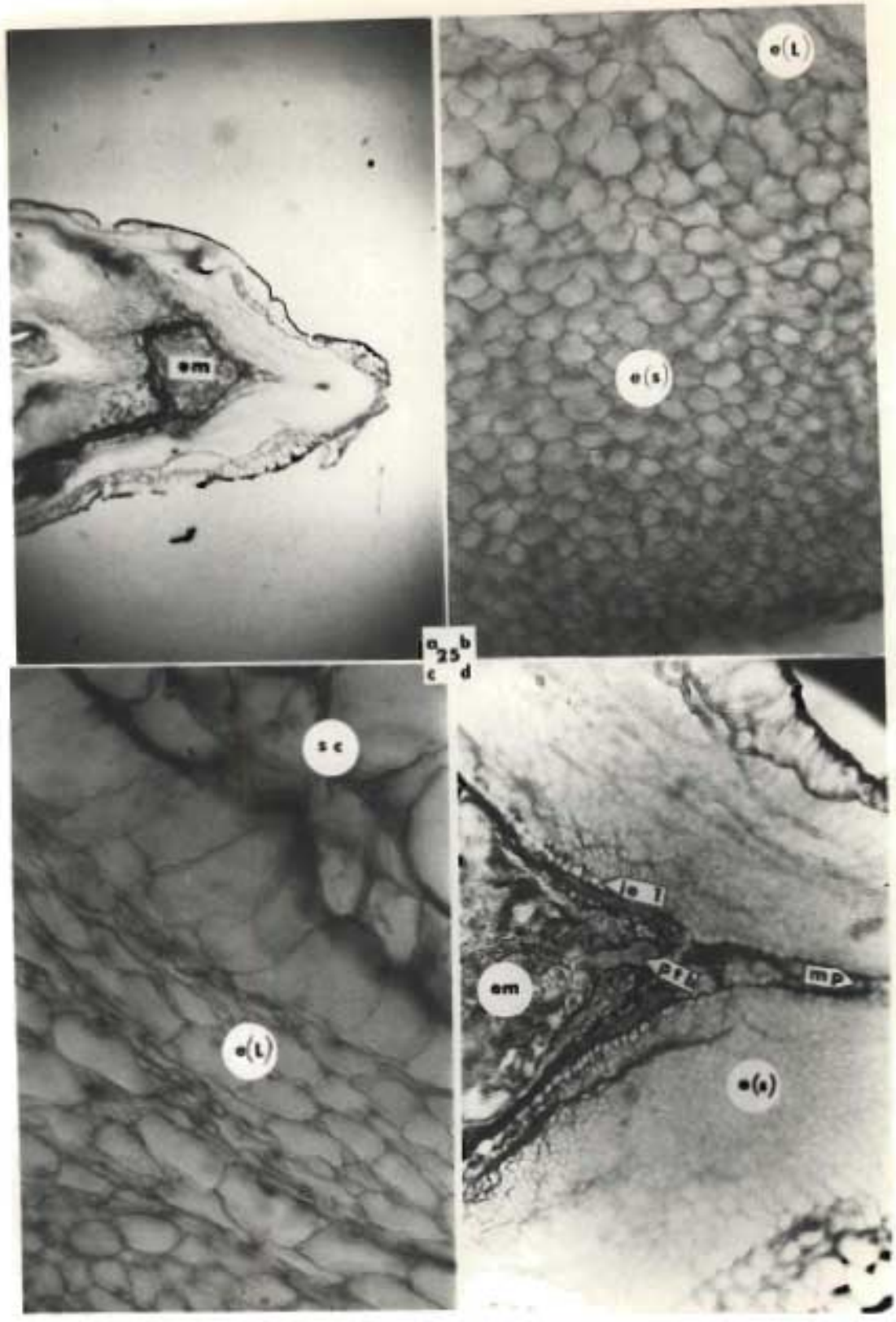

PLATE 25 (a) Micropylar end, "b" autumn seed, week-44 (x 120).

(b) Endotestal tissue, summer "empty cWs" seed; week-23 (x 1880).

(c) Sarcotestal and endotestal tissue of (a) above (x 1880).

(d) Same as (a) (x 470).

See Abbreviations.

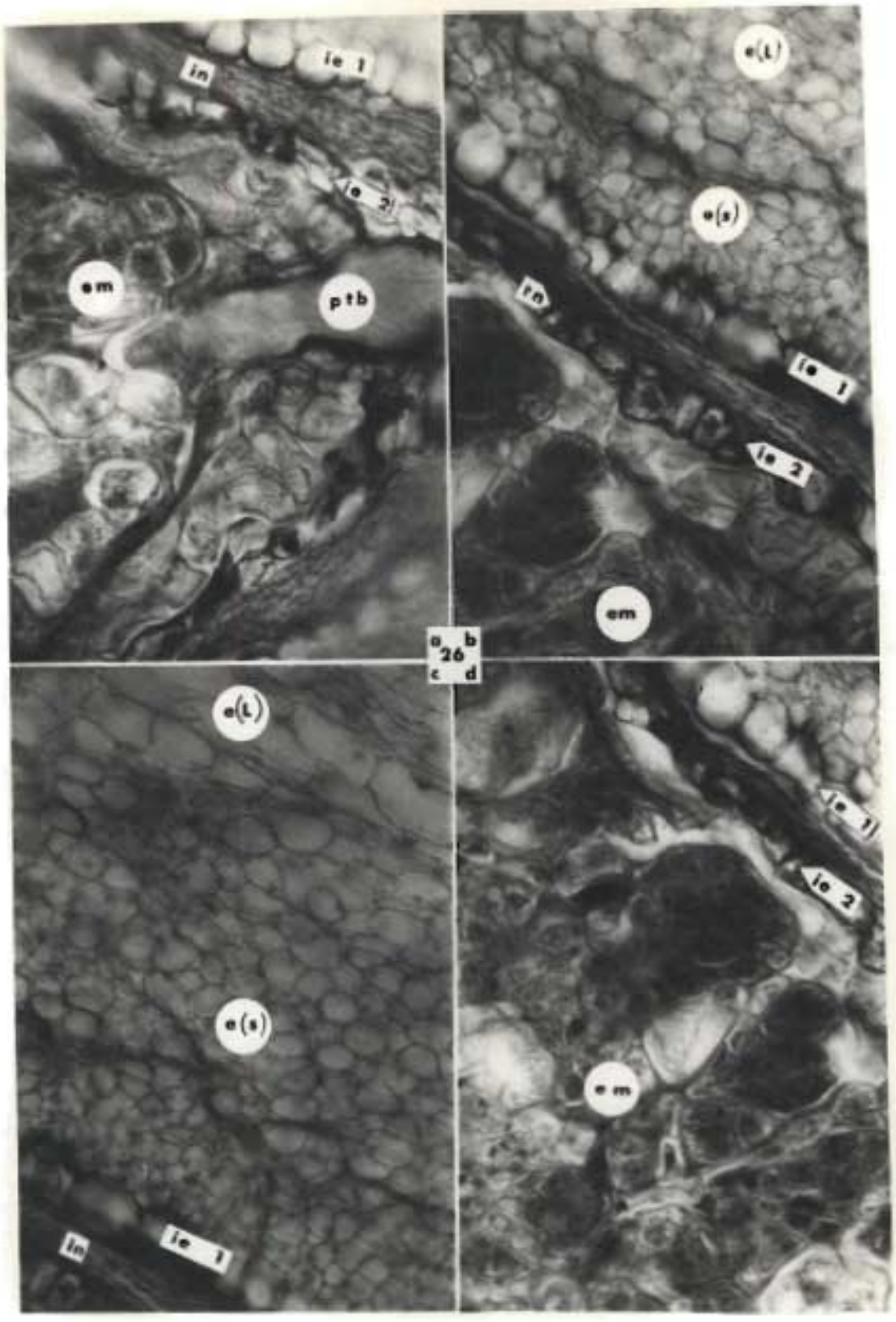

PLATE 26 (a) Pollen tube tip, "b" autumn seed, week-44.
(b) Inner testal tissue of (a).
(c) Endotesta of (a).
(d) Embryo tissue of (a).
All (x 1880). See Abbreviations.

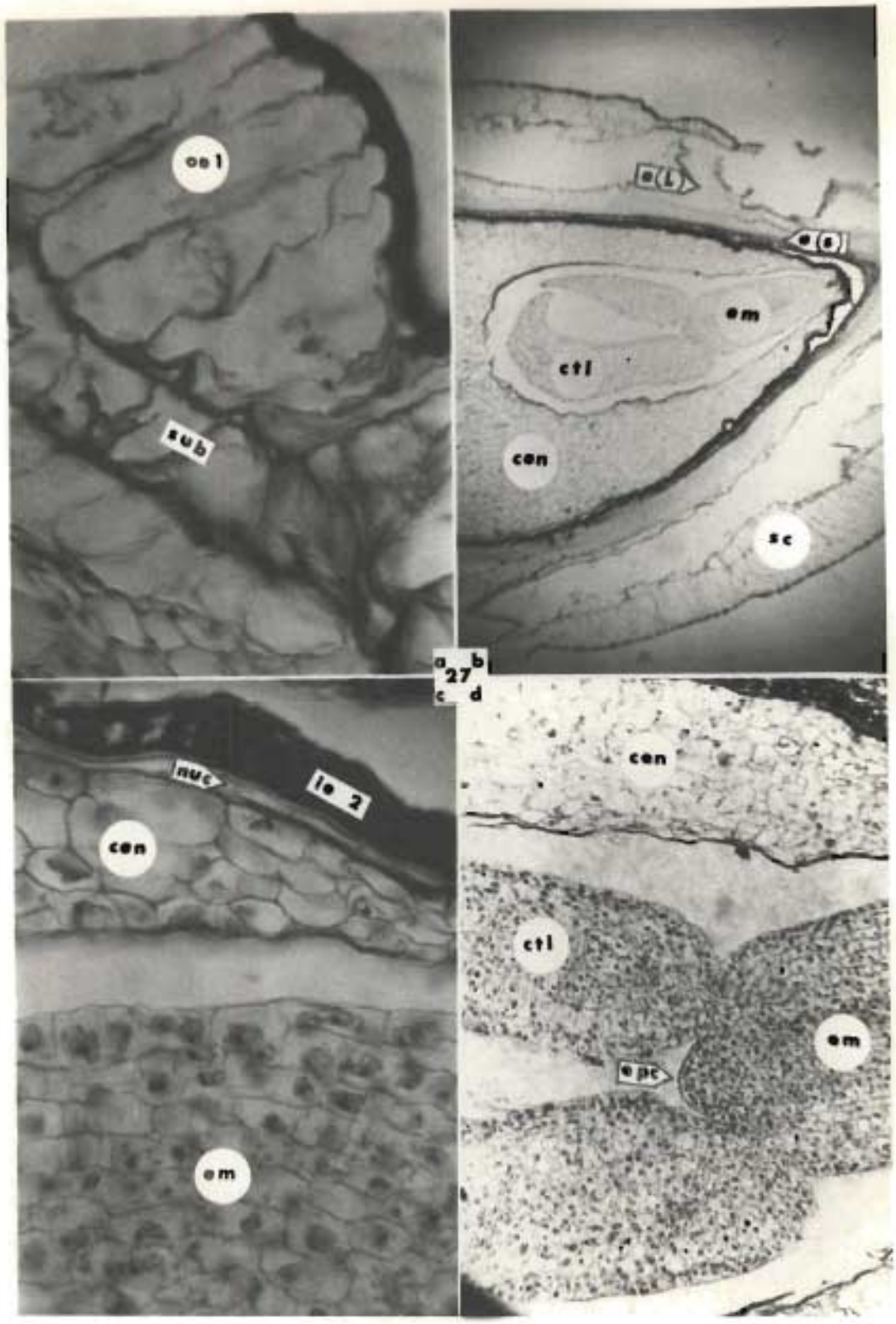

PLATE 27 (a) Sarcotesta, "b" autumn seed, week-44 (x 1880).

(b) Filled "cWs" summer seed, week-40 (x 120).

(c) Embryo, endosperm tissue of (b) (x 1880).

(d) Epicotyl region of embryo of (b) (x 470).

See Abbreviations.

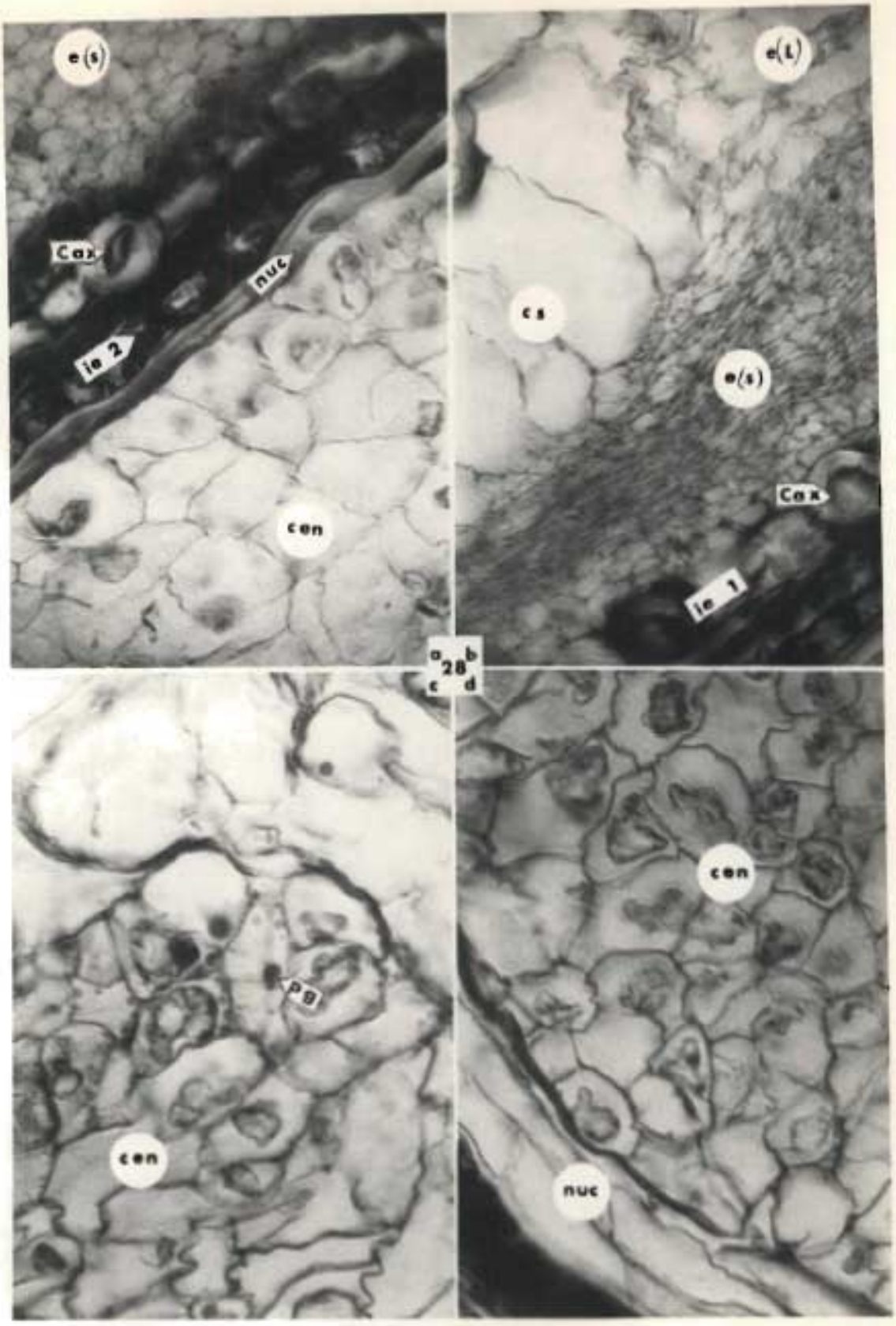

PLATE 28 (a) Inner testal tissue, filled "cWs" seed.

(b) Endotesta of (a).

(c) Phytin globoids, endosperm of filled "cWL" seed.

(d) Endosperm of (c).

All summer seeds, week-40. All (x 1880).

See Abbreviations.

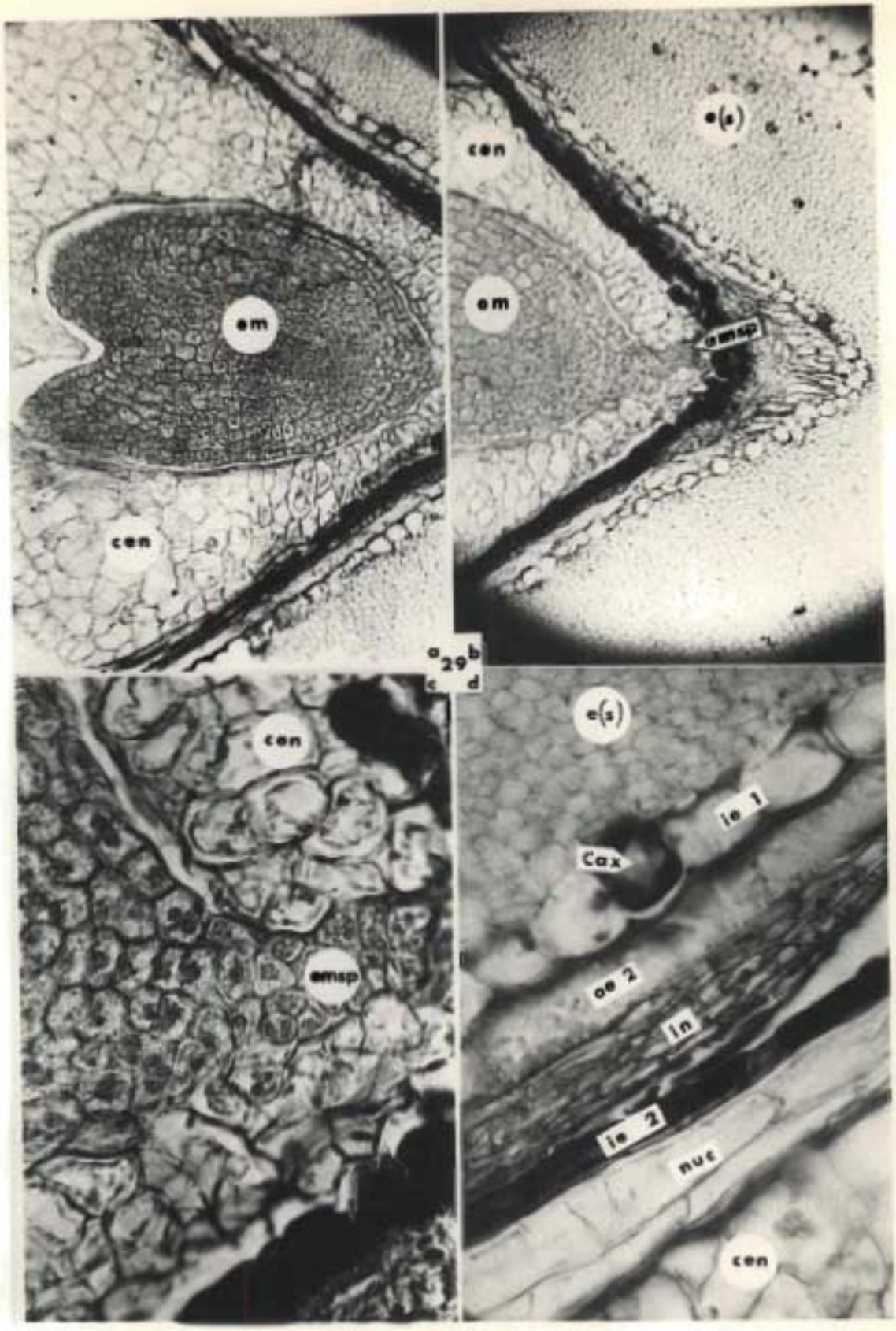

PLATE 29 (a) Embryo, filled summer "cWL" seed, week-40 (x 470).

(b) Suspensor of embryo in (a) (x 470).

(c) Same as (b) (x 1880).

(d) Inner testal tissues of (a) (x 1880).

See Abbreviations.

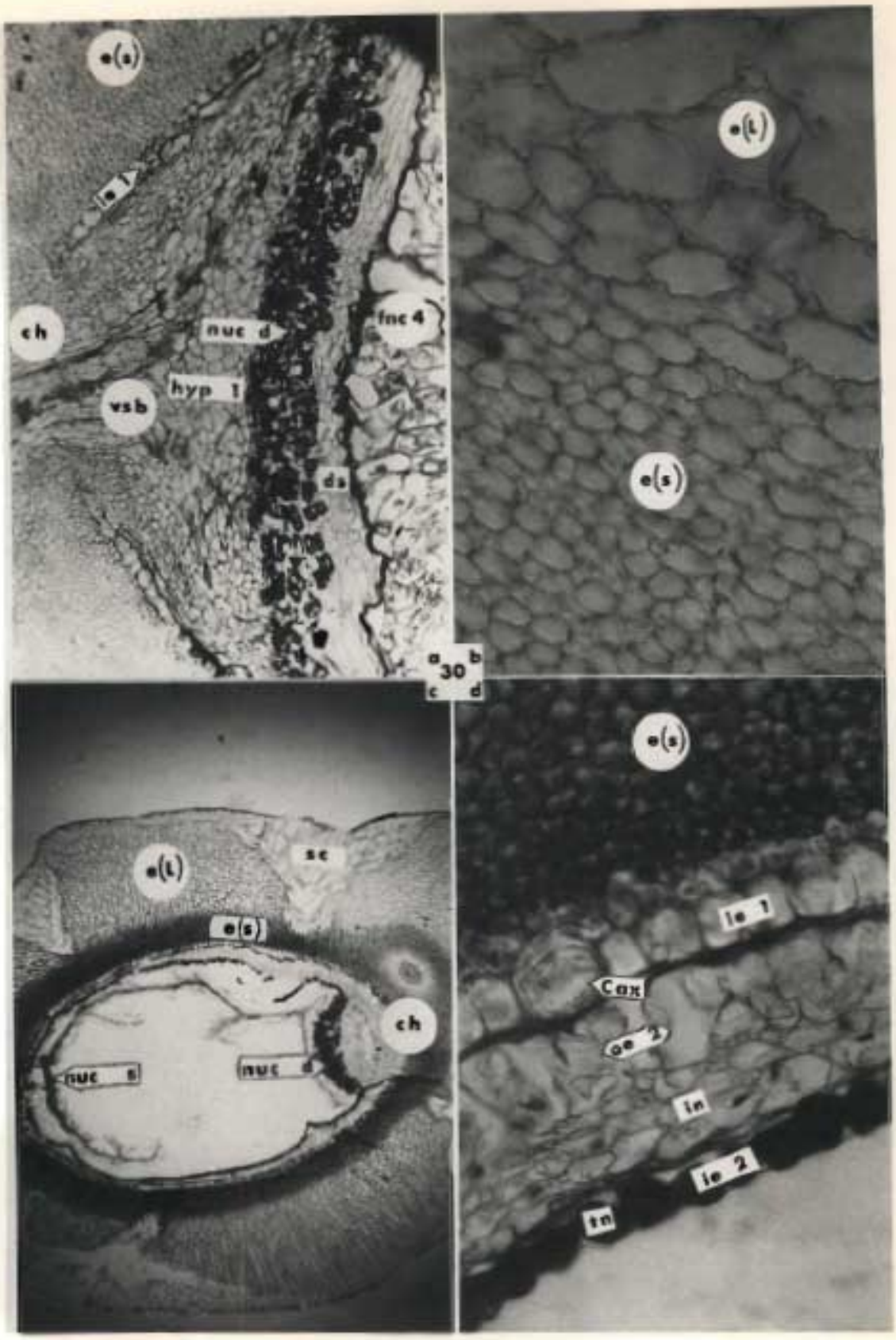

PLATE 30 (a) Chalazal region, filled "cWL" seed (x 470).

(b) Endotestal tissue of (a) (x 1880).

(c) Empty "cDL" seed (x 120).

(d) Inner testal tissues of (c) (x 1880).

All summer seeds, week-40. See Abbreviations.

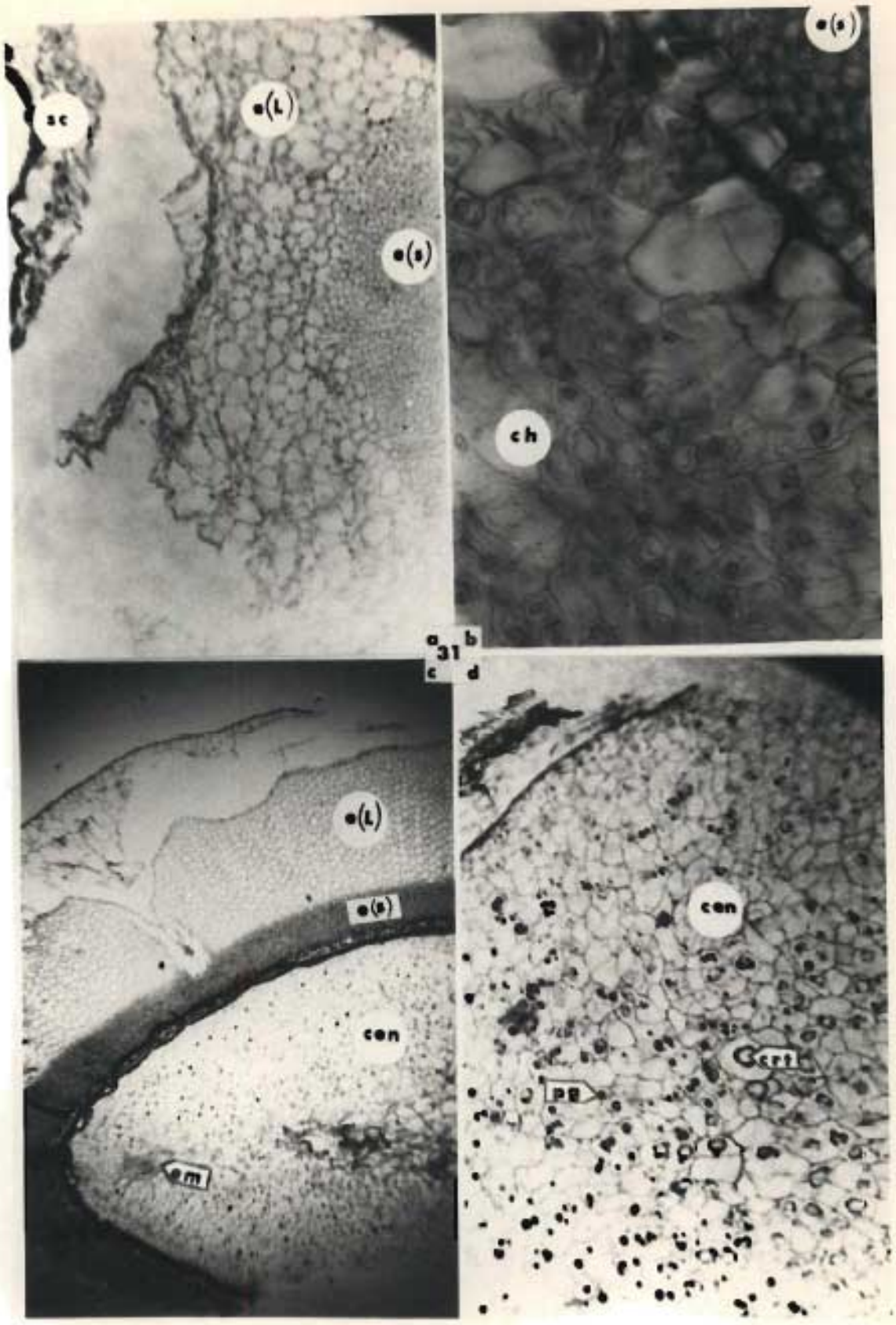

PLATE 31 (a) Collapsed endotestal ridge, filled "cWL" seed (x 470).

(b) Chalazal tissue, empty "cDL" seed (x 1880).

(c) Filled "cDL" seed (x 120).

(d) Endosperm of (c) (x 470).

All summer seeds, week-40. See Abbreviations.

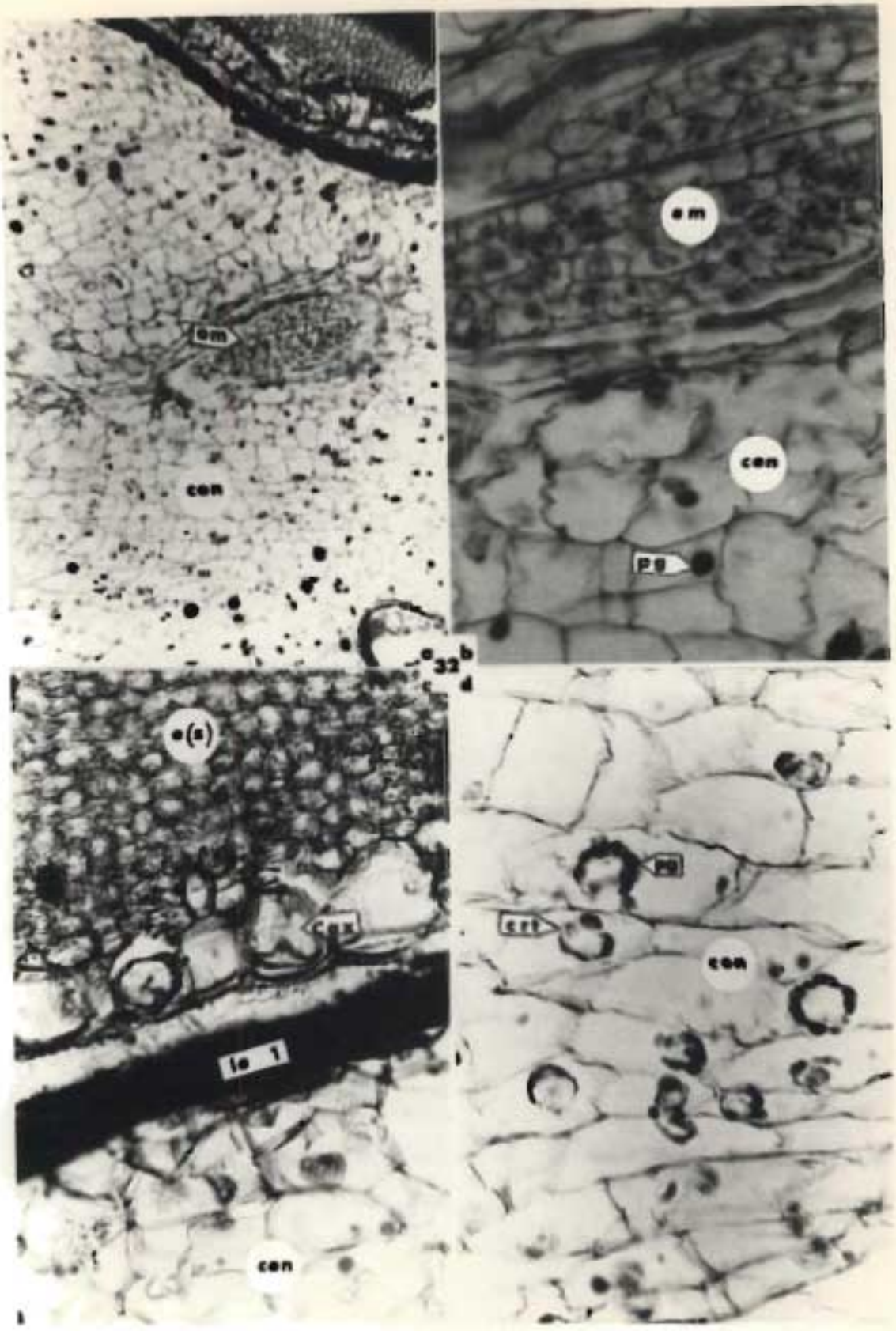

PLATE 32 (a) Endosperm, embryo; filled summer "cDL" seed, week-40.

(b) Same as (a) (x 1880).

(c) Inner testal tissues of (a) (x 1880).

(d) Phytin globoids and crystaloids of endosperm of (a) (x 1880).

See Abbreviations.

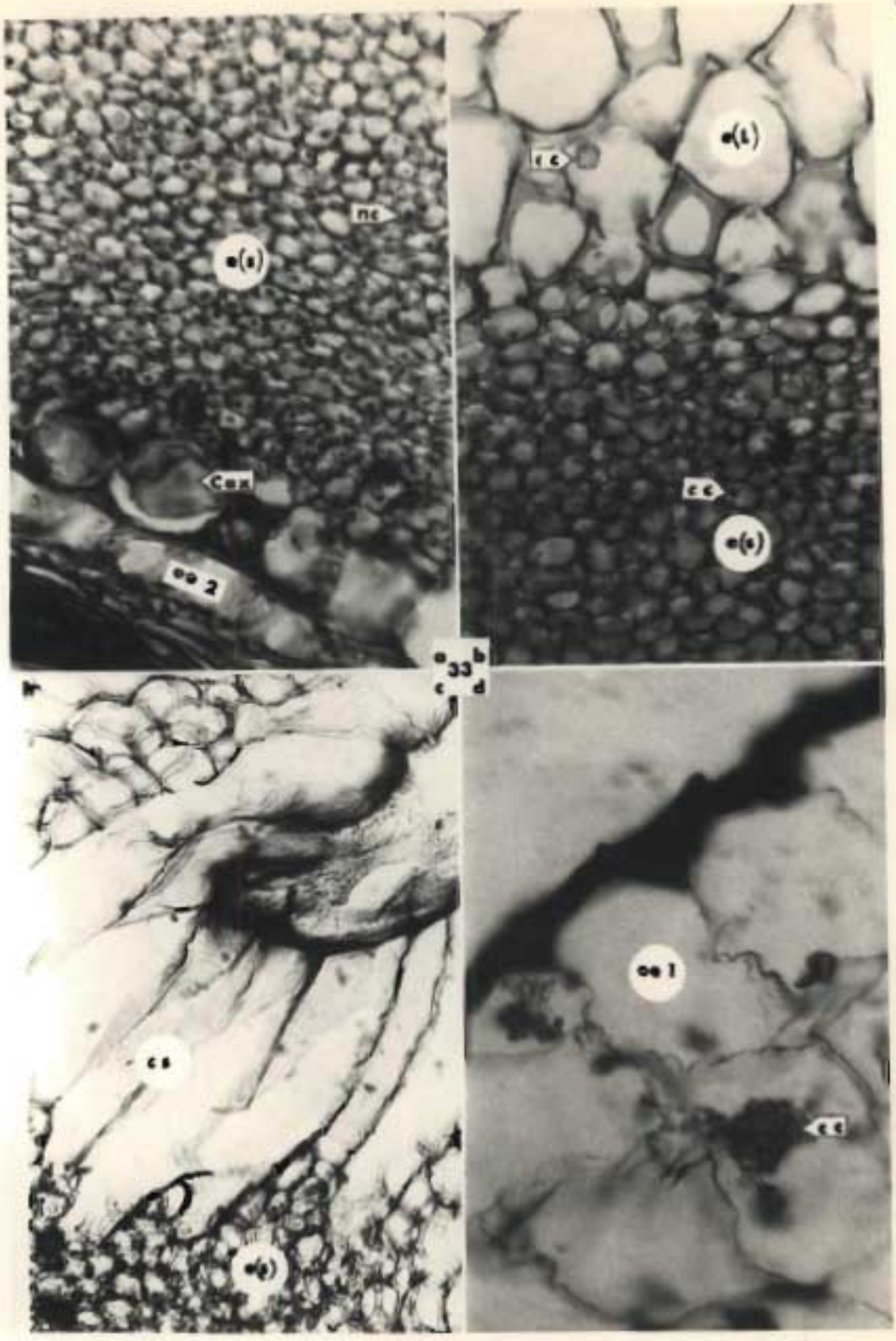

PLATE 33 (a) Inner testal and endotestal tissue; filled summer "cDL" seed, week-40.

(b) Endotestal tissue of (a).

(c) Contiguous layer of endotesta of (a).

(d) Outer epidermis of outer testa of (a).

All (x 1880). See Abbreviations.

CHAPTER II

OVULE AND SEED ABORTION

2.1 LITERATURE REVIEW

Both Agnew (1948) and Allan (1969) report the incidence of parthenocarpic and near-seedless fruits in papaya. This tendency is more marked in pistillate plants. According to Allan (1969) there are several types of normal and underdeveloped (aborted) seeds, with the latter being more noticeable in fruits set in autumn in the cool subtropical conditions of Pietermaritzburg, South Africa. He carried out a preliminary anatomical study on these underdeveloped ovules/seeds, comparing them with Foster's (1943) findings on seed development.

He described his findings as follows. The smallest of these were obovate, white to off-white ovules, which are found in both fertilized and parthenocarpic papaya fruits. In Pietermaritzburg the latter fruits are sometimes set on plant carrying few fruits in spring, when leaf cover and new vegetative growth are at a minimum. He presumed that these "ovules" were unfertilized. They consisted of the outer and inner integuments, of two to four layers only, some cells of which had shrivelled, and the remains of the nucellus. In terms of Foster's (1943) findings, he suggested that these "ovules" had shown no further development after anthesis.

The next type were small, brown, slightly-developed "ovules" which he presumed to be the same as the "ovules" Foster (1943) described as having a queer "digested" appearance. These showed limited development of the "integuments" such as a few large cells in the region of the normal sarcotesta, and only sligh ridges for the endotesta. Crystals were found in the inner epidermis of the "outer integument" and tannin in that of the "inner integument". Nucellus was found in some cases.

Another group comprised small partially-developed "seeds" and also fairly large, unfilled "seeds". These whitish "seeds" were found to have "progressivel greater development of the integuments, but generally with only small pointed ridges of the endotesta and a little sarcotesta". Their "integuments" showed th development reached by Foster's (1943) normal seeds after three to nine weeks. Nucellus cells, some of them said to contain deposits, were present, and occasio ally, partially developed embryos and free nuclear endosperm were found. Allan (1969) suggested that the latter would compare with Foster's (1943) normally

developing seeds between the sixth and eleventh weeks. Foster (1943) also stat that she found many aborted seeds with "well differentiated seed coats" (9th week). To sum up, then, Allen's (1969) findings suggested that abortion of ovules and seeds occurred either soon after anthesis, or else over a period of four to twelve weeks after pollination.

Allan (1969) considers that apart from the small undeveloped ovules (presu "not fertilized") and the small, brown, slightly-developed "ovules" (presumed t be the "results of stimulative parthenocarpy"), the cause of the abortions was competition of the earlier (summer-set) fruits and less favourable environmenta conditions of the autumn-set fruits. The latter two conditions were thought to have affected "fertilization and embryo growth".

According to the extensive reviews of Brink and Cooper (1947) and Rangaswa (1963) endosperm development (which is invariably prior to that of the embryo) obligatory for embryo development. Much of the evidence for this is based on hybridization experiments. Rangaswamy's (1963) review also points to evidence that implies that endosperm development controls not only that of the embryo (nutritionally and hormonally), but that of the seed coat as well. Degeneratio of the endosperm appears to lead to poor development of the seed coat.

Nevertheless, in Allan's (1969) work, the pollen source was presumably of compatible type, and it did lead to development of normal seeds. The stress conditions of inter-fruit competition plus that of unfavourable climate may wel have been major predisposing factors. Sarvas (1968) and Sweet (1973) in their work and reviews on ovule development in the conifers (gymnosperms) suggest tha apart from lack of pollination, abortion may also result from competitive effec

In angiosperms too, lack of pollination and fertilization, and competitive and environmental stresses on seed development, have all been noted. A number examples will suffice. In Clarkia, if fertilization occurs, petals abscise shortly afterwards (40 hours). If fertilization does not occur, petals remain for many days. Related to this, if embryos fail to develop, ovulary tissues abscise, whereas if the embryos develop, the "ovulary" remains attached until maturity (Lewis, 1946).

Environmental stresses on seed development have been associated with the following: with excess temperature in wheat (Hoshikawa, 1962), and low tempera ture in apples (Hayashi, Naito, Bukovac & Sell, 1968); drought in corn (Rowe & Andrew, 1964), and excess soil moisture in wheat (Campbell, McBean & Green, 196 and deficiencies of manganese in peas (Heintze, 1956), and of boron and calcium in peanuts (Cox & Reid, 1964; Harris & Brolmann, 1966, respectively).

Adams (1967) has found that with field bean (Phaseolus vulgaris) plants, there is a "peck order" such that if the plant is exposed to environmental stress, it will suffer abortions in the following order:-

(i) "... freshly pollinated embryos and very young pods;

(ii) young fertilized ovules in developing pods;

(iii) open flowers;

(iv) unopened flowers; and

(v) rapidly developing young pods."

Pollock and Roos (1972) state that although the "peck order" concept of Adams (1967) was not supported by experimental evidence, they feel that "... under conditions of stress, the plant will tend to produce a minimum number of seeds of the highest possible vigour, rather than a large number of low vigour ... this interpretation of vigour (quality) relative to seed production (quantity) would be compatible with maximum potential for survival of a species under unfavourable environmental conditions ...."

To get back to papaya, the photographs of normal and aborted seeds in fru shown in Agnew (1948) and Allan (1969) could suggest that ovules closer to the stigma and have a greater chance of developing into normal, mature seeds than those at the base of the flower/fruit. In conifers it sometimes happens that the ovules further away from the apex of the strobilus ("flower") are under-developed, and fail to develop any further during the long period required for pollen tube growth and syngamy in conifers (Sweet, 1973). Thus the relative position of ovules in the flower or strobilus may affect the incidence and spatial distribution of abortion in these maternal structures.

In apples, effective pollination and fertilization of ovules is essential for adequate fruit-set (Williams, 1969). Subsequent to this, partially develo ed fruits may be shed at the (physiological) "June drop", a period during whic growth-hormone content of seeds is low, and fruits with the lowest complement of fertile seed are the most frequently shed (Luckwill, 1948). The shedding o apple fruit is also a competition phenomenon amongst and between vegetative shoots and fruits for metabolites (Abbot, 1960; Luckwill, 1970). The latter author, amongst others, postulates that in this competition, hormone-directed transport plays a major role. "The relative strength of the hormonal stimuli from shoot tips and seeds ... determine the general direction of metabolites.. (Luckwill, 1970).

But how is this possibly seen as relating to ovule or seed abortion? There has been some controversy as to the relationship of "seed degeneration" to abscission of immature apple fruit (Weinbaum & Simons, 1974 a). The latter workers' histochemical and ultrastructural evaluations (1974 a, b) suggest that the "embryo degeneration which has been associated with fruit abortion occurs subsequent to the commitment of the fruit to abscise". Stembridge and Gambrell (1972) work on peaches is also supportive of the above. The latter authors have suggested that *if* seed abortion *is involved* in fruit abscission, *then* "... it most likely promotes fruit abscission actively, by ethylene release ... rather than passively, by depriving the fruit of an essential hormone supply from the seed".

In Weinbaum and Simon's (1974 a) work, however, aborting seed did have less starch in the maternal tissues (funiculus, integuments and nucellus) as compared with as yet normally developing, larger seeds. (Both these types of seeds were from "potential drop fruit".) There was, however, no evidence of starch utilization in either the embryo or the free nuclear endosperm at this stage (two to three weeks). This ties in with the finding that in apples, gibberellic acid, which is involved in *de novo* synthesis of α-amylase which in turn acts on starch (Paleg, 1960) is only detectable after four to five weeks after bloom (Luckwill, Weaver & MacMillan, 1969). This is also about the time the cytokinesis of the endosperm is about to begin (Murneek, 1954).

The above papers were focused on *fruit* abscission, and they seem to suggest that endosperm and embryo abortion may not be the usual cause of apple fruit abscission. In the context of an enquiry into seed abortion itself, however, it seems that lack of metabolites as suggested by a lower accumulation of reserves (such as starch in the above examples) may be correlative to and further predisposing to seed abortion. This will be borne in mind when attempting to understand the occurrence of seed abortion in the *Carica papaya* L. material investigated by the author.

2.2 MATERIALS AND METHODS: COMPARATIVE ANATOMY AND MORPHOLOGY

2.2.1 Types of ovules and seeds

Allan's (1969) preliminary classification of ovules and seeds found in (ripe) papaya fruits was:-

(i) undeveloped "ovules";

(ii) slightly developed "ovules";

(iii) partially developed "seeds"; and

(iv) fully developed seeds.

For the purposes of the studies that follow, the author has labelled the above as: (i) "U" ; (ii) "S" ; (iii) "P" ; and (iv) "F" types. A second, more detailed typology related to the above is also used. Plate 2b shows the relationship, viz:-

(i) U = a ;

(ii) S = b + cWs ;

(iii) P = cWL + cDL ; and

(iv) F = dG + dB .

The further differentiation is as follows:-

b = flattened type of "S", small;

cWs = uncollapsed type of "S", white and small;

cWL = white, larger than cWs, and type of "P";

cDL = darkened, but not black or grey, type of "P"; and

dG = grey and dB = black types of "F".

At the time the author made and used this second typology, he was of the opinion that: 'a' were unfertilized ovules which showed no further development after anthesis; 'b' were unfertilized ovules that had developed further; 'c [Ws + WL + DL]' were partially developed seeds ranging in size and colour and 'd [G + B]' were fully developed seeds differing in colour. All of the abo were from or applicable fully to ovules and seeds of ripe fruit.

The reason "cWs" was placed with "b" in Allan's (ii) = "S" was that in many fruits "b" and "cWs" were of very similar size, apparently differing only in the degree of collapse of the structure as a whole, and of the surface layer too. (In other fruits "b" were smaller than "cWs".)

The above typologies were of course more difficult to apply the earlier th stage of fruit development. It was initially not possible to differentiate ovules/seeds into normally developing versus unfertilized or aborting ovules/ seeds. As the fruits developed over time, more and more types could be used. The initial classifications were into "F" ('fully developed') and "U" ('undevel ed'). Later, "P" ('partially developed') and "S" ('slightly developed')

categories were applied, merely on size. It was only with the onset of fruit ripening and colouration of seeds that the more detailed typology could be used (and was then initially applied).

2.2.2 Anatomy

Anatomic material for the different types of (abortive) ovules and seeds were available from the fruits of the autumn sets of 1971 (1.2.2.1) and 1970 (1.2.3.2); and the summer set of 1970 (1.2.2.2 and 1.2.3.1). Materia was also available for whole seed growth measurements (seed mass), viz. from the autumn sets of 1969 and 1970; and the summer set of 1970 (1.2.3.3). The microtechnique and sampling procedure used was basically the same as that used on fully developing "F" seeds (1.2.4). One difference was that there were not always 50 ovules or seeds for a given type for the 'mass' measurements. (The lowest number used was 15.)

The measurements on the dimensions of individual cell types (1.2.4.6) of abortive ovules and seeds were carried out on selected sample periods from the 1970 summer set (in order to compare these with those of the normally-developin "F" seeds of the same period - [1.3.3]). Measurements were also carried out on the cross-sectional area of whole tissues (as seen in the median longitudinal plane) of selected normal and abortive seed types from the summer set of 1970 and the autumn set of 1971. These measurements were done by means of a calibrated Reichert visopan (projection microscope).

In order to demonstrate the anatomic features of abortive ovules/seeds, photographs were taken of slides from the summer set, 1970. However, where mor presentable slides of comparable development were available from the other sets these have been used.

2.2.3 Contents of dissected seeds

At the end of the growth periods of the summer and autumn sets of 1970, ovules and seeds of the different types (2.2.1) were removed from the remaining ripe fruits. These were counted according to ovule/seed type and intra-fruit regional distribution, as described in a later section (2.4). A variable number of seeds from each of these types were dissected and their internal contents examined. The presence or absence of endosperm, embryo and nucellus, together with their appearance, was tabulated.

2.2.4 Method of presentation

Reference has already been made to typologies of abortive ovules or seeds in 2.2.1 and Plate 2b. Table 9 sets out a framework by means of which further plates on their anatomic features can be described and discussed. These plates constitute a selection of the extent of seed development in various abortion types at four selected periods.

The first period is the eighth week in the autumn set of 1971. This was th latest time at which the clearing technique of 1.2.4.4 could be applied to whole ovules/seeds. (Conventional microtechnique was also used, and nearly all of the photoplates are from this technique.) The equivalent developmental stage of normal "F" seeds in the summer (1970) set was about that at four weeks.

The second period refers to the 23rd week of the 1971 autumn set. This was approximately the time normal "F" seeds began developing cellular endosperm in that set. The equivalent period for the 1970 summer set was the 10th to 13th week.

The third period refers to the 23rd week of the 1970 summer set, i.e. approximately halfway through the growth period of both summer and autumn-set fruit. Developmentally, however, normal "F"-type seeds of the autumn sets only reached this stage of the summer sets after about 30 weeks.

The final period refers to the final month of both summer and autumn sets during which fruits were ripening, viz. 40 - 44 weeks after anthesis. Normal "F" seeds of both sets were at the same developmental stage, if not the same size (Chapter I).

Some of the anatomic features will be described and discussed by referring to the plates along each row (i.e. each period) and comparing them with features referred to in normally developing "F" seeds in Chapter I. (Use will also be made of notes taken from other slides not displayed in these plates.) Figures and tables already presented in Chapter I, but which contain information pertaining to this chapter, together with some additional figures, will form the basis of 2.3.1 (anatomy). Figures related to whole ovule/seed growth (2.3.2) and tables for the contents of dissected seeds at fruit ripening (2.3.3) will compl the first part of this chapter. They constitute three approaches providing a basis for comparing the extent of the anatomic and morphological development of the various ovule/seed types.

TABLE 9 Plate numbers referring to abortive ovule and seed types and their development

Equivalent developmental weeks after anthesis		ABORTIVE OVULE/SEED TYPE ‡					
		U‡	S‡		P‡		
Summer set 1970	Autumn sets 1970/71	a	b	cWs	cWL	"Empty" cDL	"Filled" cDL
4	8*	21a, b, c, d	-	-	-	-	-
10 - 13	23*	-	22a, b	22d 23a, b	22c	-	-
23*	30	23c, d 24a	-	24b, c, d 25b	-	-	-
40 - 44*	40 - 44*	-	25a, c, d 26a, b, c, d 27a	27b, c, d 28a, b	28c, d 29a, b, c, d 30a, b 31a	30c, d 31b	31c, d 32a, b, c, d 33b, c, d

* indicates actual fruit set from which photomicrographs were taken.

‡ for ovule/seed type, see Plate 2b.

2.3 RESULTS AND DISCUSSION: COMPARATIVE ANATOMY AND MORPHOLOGY

2.3.1 Anatomy and tissue growth

The entry in the first row of Table 9, viz. Plate 21 b, c, d refers to an unfertilized ovule at the eighth week (autumn set). It apparently never developed an embryo sac. Another possibility is that the embry sac had collapsed, judging from the mucilagenous-like region within the nucellu The mucilagenous regions could also be due to the digestion of nucellus tissue as the rest of this ovule "tried" to meet its ongoing metabolic requirements.

Compared with Plates 4a (ovule definitely with no embryo sac at anthesis) and 4b (unfertilized ovule with an embryo sac at week two), the ovule of Plate 21b, c, d is more like the former. The ovules of Plates 4a and 21b, c, d also show a loosening and shrinking away of the nucellus from the surrounding integuments. The mucilagenous-like regions (within the nucellus and surroundin or in place of the inner integument) suggest the first regions to have been digested away as the unfertilized ovule degenerated.

This ovule, and that of Plate 21a, a cleared ovule from the same sample, had not yet deposited tannin in the "disc" region of the chalaza (cf. the fertilized ovule at week two, Plate 4c). The outer integument of the ovule of Plate 21d (week eight) was at about the same stage of development as that of th mature but unfertilized ovule of Plate 8a (week two). It had not developed the same number of layers nor differentiated the integuments as those of Plates 7c, d and 8b of a comparable (normal) developmental age.

The above Plates were of unfertilized ovules. Reference has already been made in 1.3.1.5 to the proportions of (fertilized) seeds which showed normal endosperm and (pro-) embryo development at the sixth week after anthesis (autum set, Fig. 8). Reciprocally, about 20% of all fertilized seeds in each sub-region (except "d") had flimsy-looking free nuclear endosperm. These would appear to have been the likeliest candidates for early seed abortion. With the exception of fruit sub-region "d", all sub-regions appeared to carry the same proportion of potential early abortants.

From Appendix 1 it is evident that larger developing seeds tended to have a greater number of free nuclear endosperm nuclei. The author also teased open some abortive-looking (i.e. markedly smaller) cleared seeds of samples from, for example, the twelfth week after anthesis in the autumn set. These often ha free nuclear endosperm, but this sometimes appeared flimsy, or somewhat clumped and flimsy; and the number of nuclei were noticeably fewer than that in their 'normal' sized counterparts. Mention has also been made in 1.3.1.9 to the

observation on Figure 9 that seeds with non-normal endosperm produced less nucellus tissue.

Row two of Table 9 is of abortive seeds at the time of endosperm cellularization in normal "F" seeds. Plates 22a, b are of one and the same "b" type of seed. In comparison with Plate 10a (an "F" seed at a comparable time, and at the same magnification as that of Plate 22a), the "b" seed showed a very limited development of e(L) endotestal tissue. It was of course collapsed (as is typical for "b" seeds). The "disc" region of the chalazal nucellus was present - as is the case in normal "F" seeds too. Whatever nucellus and endosperm there may have been appears to have been reduced to an amorphous mucilagenous mass which has stained deeply. A globular embryo not very much smaller than that shown in Plate 10c (same magnification) and of a comparable age was also present. The inner integumentary-derived part of the testa had also pulled away from the endotestal tissue at the micropylar end.

Plates 22d and 23a, b are of a nucellus and endosperm from a likely "cWs" type seed of the 23rd week. Compared with Plates 10b, d and 12a, the nucellus contained more mucilagenous-like material. The phytin globoids shown in the nucellus in Plate 23b and in the remains of endosperm and nucellar sheath (Plate 23a) were never seen in normally developing seeds. There was a close contact between the nucellar breakdown sheath and the degenerated endosperm (Plate 22d).

Plate 22c is of the free nuclear endosperm at the chalazal end of an apparently "cWL" type of seed of the same age (23 weeks, autumn set). It is not clear to the author whether the rather prominent nuclei seen in the endosperm is a sign of degenerating endosperm, as some apparently normal "F" seeds also showed this feature. (The latter, of course, may have been incipient abortive seeds, too). The appearance of this endosperm was not quite like that of the "nucleated cytoplasmic nodules" referred to by Singh (1961) and mentioned in 1.3.3.2.

In contrast with the appearance of free nuclear endosperm still present in normal "F" seeds of this sample (e.g. Plate 10b), this seed's (Plate 22c) endosperm and its closely associated nucellar breakdown sheath was more granulated. Plate 23a of the previously mentioned "cWs" seed also showed this granulated appearance of the degenerating nucellar sheath, particularly at its edges.

Plate 23c, d is of a transverse section through an unfertilized ovule 23 weeks after anthesis in summer (row 3, Table 9). Plate 24a is of a longitudinal section through this kind of ovule too. They consisted virtually of tissue derived from the outer integument and the breakdown sheath of the nucellus (Plate 23c, d) and the inner integument (Plate 24a).

These aborted, unfertilized ovules of Plate 23c, d (23 weeks) appeared shrunken in size in comparison with the unfertilized and abortive ovule of Plate 21a (equivalent to week four) and the fertilized ovule of Plate 4c (week two) - all photographed at the same magnification. There appears to have been a very slight differentiation of an endotesta /e(s)/e(L)/ along the lower half of the ovule of Plate 24a - to about the same extent of that of the aborted ovule of Plate 21b, c, d (equivalent to four weeks after anthesis). The contras in differentiation with normally developing "F" seeds is in Plate 8b (four weeks after anthesis in summer). Aborted, unfertilized ovules taken from ripe fruit were very much like the one shown in Plate 24a. Thus, at fruit ripening, "U" or "a" ovules showed very little testal development beyond what they had completed by about the fourth week after anthesis. They also lost most of the material of their nucellus and inner integuments, together with some of the material of their outer integuments.

Plates 24b, c, d and 25b depict an "empty" "cWs" type of seed 23 weeks afte anthesis (summer, 1970). The appearance of its outertestal tissue (Plate 24b) resembles that of Plate 10a (an "F" seed at 13 weeks), although it was a good deal smaller than the latter (Plates 10a and 24b at the same magnification). Apart from the nucellus of the specialized region at the chalaza, the bulk of t nucellus had been digested away. The one time inner integument has pulled awa from the outer testal tissue (Plate 24b). There was little tannin deposition. The hypostase nucellar tissue on the testal side of the "disc" region at the chalaza (Plate 24b, d) appears normal. Two of the endotestal tissues /e(s)/e(L)/ and the sarcotestal tissues of Plate 24c and 25b show a developmen stage somewhat between those of Plates 15a, b (both at week 13, the time of end sperm cellularization). The more marked buckling of the walls of e(L) tissue, and also the thickening at corners of the walls of these cells (Plate 15b) in seeds beginning to form cellular endosperm was not present in this "cWs" seed at week 23. The endotestal /e(s) and e(L)/ tissues of the latter certainly di not have the degree of cell wall thickening of normal "F" seeds of the same age (Plate 15c). Thus the <u>testal</u> development of this "empty" "cWs" seed at week 23 had the developmental age of normal "F" seeds just before endosperm cellulari-zation (weeks 10 - 13). And it was noticeably smaller than the latter. The difference between this "empty" "cWs" seed and the flattened, "empty" "b" type seeds appeared to be the relatively greater degree of stable rigidity of the testal tissues in the "cWs" type.

There was no sign of pollen tube penetration in this "cWs" seed, but by that time remains of a pollen tube <u>may</u> have been digested away, or else lost in the sectioning process. On the other hand, perhaps there had been <u>no</u> pollen tu

penetration. The author surmises that factors necessary for testal development prior to that found in seeds beginning to develop cellular endosperm may be produced in the occasional "ovule", or else these factors may be transferred through a favourably associated vascular supply of an adjacent normally developing seed. But from further data still to be presented in 2.5, (which will show that a greater proportion of "b" and "cWs" seeds occurred closer to the stigma end), the author is of the opinion that most "b" and "cWs" seeds owed their limited development to some such stimulus as pollen tube penetration and/or some endosperm or embryo development. Besides, from Figure 6 it is evident that a relatively high proportion of ovules in hand-pollinated fruit are fertilized; and from Figure 8, that a large proportion of these show apparently normal endosperm development in the first few weeks after that.

The fourth row of Table 9 refers to aborted seeds taken from ripe fruit. Plates 25a, c, d and 26a, and Plates 26b, c, d and 27a are from a "b" type seed. Typically, the "embryo sac" was again collapsed (Plate 25a). A persistent pollen tube can be seen in Plates 25d and 26a. A globular but rather disorganized embryo is shown in Plates 25a, d and 26a, b, c. The nuclei of some cells were still quite prominent (contrasted with the dehydrated embryo cells of, say, Plate 13a, b, c of an "F" seed of the same age). Other cells were rather hypertrophied, with less cellular content. It is not clear whether any endosperm or nucellus remained, as the disorganization and breakdown of some of the embryo tissue obscured its boundaries. The layer of tissue adjacent to the inner epidermis of the inner integument in Plate 26b is possibly nucellar. The inner epidermis of the inner integument is itself poorly developed, with little tannin deposition. The remaining tissues of the inner integument are also poorly developed - contrast with, say, Plates 16c, d; 17d of "F" seed of this age.

The inner epidermis of the outer integumentary tissue was hardly more developed than that of a "F" seed at the cellularization of endosperm (Plate 18). It was a little thicker along the inner walls. The e(s) cells are about as hyline as those of Plate 18a again, with regions of collapse. The e(L) tissue is also collapsed in places. With the exception of the inner integumentary tissue and the inner epidermis of the outer "integument", the tissues are all still clearly nucleated. In "F" seed at fruit ripening, this is so only for sarcotestal tissue. There, the other testal tissues lose their cellular content when the walls thicken greatly, and the nuclei of endosperm and embryo cells are not readily distinguishable amongst the amorphous deposition of cellular content in dehydrated cells. In short, differentiation and development of the testa did not appear to have gone beyond that of "F" seed at the onset of the cellularization of endosperm.

Plates 27b, c, d and 28a, b show a "filled" "cWs" type of seed having a half normal sized embryo with distorted cotyledons. There was again a considerable collapse of endotestal tissue and development was not beyond that of "F" seeds at endosperm cellularization. Calcium oxylate crystals were present in some of the cells of the inner epidermis of the outer "integumentary" tissue. The cellular endosperm and embryo are much more like that of "F" seed in comparison with what has been described of aborted seeds so far. Nevertheless, a striking feature is the relative lack of cellular content (contrast with Plate 13a, b, c, d) of the endosperm and embryo tissue. These cells appear to be in a dehydrating condition somewhat beyond that shown in Plate 11a (week 23, "F" seed), but certainly not like those of Plate 13a, b, c ("F" seed, ripe fruit).

To sum up, the endotesta was in a collapsed form of "F" seed at endosperm cellularization (10 - 13 weeks, summer set). The inner "integumentary" tissue was equivalent to that of "F" seed between weeks 23 and 27, and the endosperm and embryo development somewhat like that of "F" seed between weeks 23 and 30.

Plates 28c, d; 29; 30a, b and 31a are of a "filled" "cWL" type of seed with a small "heart-shaped" embryo. (Plate 12c shows an "F" seed at that stage at week 16.) The embryonic suspensor is nicely visible in Plate 29b, c. The embryo cells look quite normal, although not dehydrated to the extent of "F" seed in ripe fruit - this embryo is more in the condition of "F" embryos at abo week 30 (summer set).

The endosperm cells are more dehydrated. They also have less cellular content, and the form of deposition is unlike that of "F" seeds. Phytin globoi can be seen in Plate 28c, a form of deposition not seen in "F" seeds. But apar from the form of the deposited reserves, the endosperm and embryo <u>developmental phase</u> of this "cWL" seed was closer to that of "F" seed than those described before. The endotesta, however, was still not beyond that of "F" seed at endosperm cellularization (weeks 10 - 13). In Plates 30b and 31a the buckled form of the e(L) cells of "F" seed at that stage can be seen (viz. Plate 15b). The inner "integumentary" tissues plus the inner epidermis of the outer "integument tissue (Plate 29d), however, was much like that of "F" seed in summer fruit at week 23 (Plate 18c, d). The specialized chalazal region of the nucellus (Plate 30a) looked much like that of an "F" seed at endosperm cellularization (weeks 10 - 13, Plate 20b).

To sum up: this "cWL" seed from a ripe fruit had an endotesta of a "F" seed at 10 - 13 weeks (summer); an inner "integument" of an "F" at 23 weeks; an embryo of the shape of one at 16 weeks but with cellular content of about week 30. The endosperm was dehydrated like maturing "F" seed, but had less content and contained phytin globoids.

Plates 30c, d and 31b are of an "empty" "cDL" seed. The outer "integumentary" tissues are relatively well developed - about that of an "F" seed at week 33 (summer). The e(s) tissue shown in Plate 30d is equivalent to that of the "F" seed at week 33 of Plate 17b. Interestingly enough, the inner "integumentary" tissues of this "empty" seed are rather hyline and nucleated, much like that of an "F" seed at weeks 13 to 16 (like Plate 18a but with calcium oxylate crystals). Thus the presence of endosperm or embryo appears to affect the development of the inner "integument".

The chalazal nucellus of Plate 31b is much like that of the "empty" "cWs" seed at week 23 in Plate 24d - and that of "F" seed at 13 weeks. As for the central ("embryo sac") cavity, all that remained was a thin nucellar breakdown sheath, probably utilized by the developing testal tissue.

Plates 31c, d, 32 and 33 are of a "filled" "cDL" seed at fruit ripening. The "embryo" was very small, and both embryo and endosperm were dehydrated. Both had also relatively less cellular content than that of comparable "F" seeds. This relatively sparse cellular content of endosperm and embryo in this and the other abortive seeds already shown is quite apparent even in dissected whole seeds (section 2.3.3). The endosperm and embryo of "F" seeds from ripe fruit i opaque when dissected out, whereas most of the aborted seeds that have any noticeable amount of endosperm are translucent. The endosperm reserves of this "cDL" seed was deposited in the form of crystalloids and phytin globoids (Plate 31d; 32a, b, d). As mentioned before, this type of deposition was not seen in "F" seeds.

The testal tissues (Plate 31c) were quite extensive in size. The e(s) tissue (Plate 33a) still contained cellular contents, although the process of thickening had already begun (Plate 33a, b), particularly in the e(L) tissue. The sarcotesta (Plates 31c; 33d) was much like that of "F" seeds of the same a Plate 33c shows a section of the endotesta next to an endotestal furrow to show the large cells contiguous with the rest of the endotesta - as demonstrated als for "F" seeds (Plate 14b, c and the discussion in 1.3.3.4 (b)). Overall, this "filled" "cDL" seed had endotesta comparable to "F" seeds between weeks 23 and 40; and inner "integumentary" tissue (Plate 33a) like that between weeks 23 an 27 (Plates 18d; 17c; 15d).

The foregoing accounts give one sketch of the developmental details and differences of the various ovule/seed types as seen under the microscope. One can get a further view by looking at the cell measurements of separate tissues of these ovule/seed types.

Figure 11 shows that the cross-sectional area of individual nucellar cells of "U" and "S" ("b" and "cWa") types never reached the size of "F" seeds. The size in "P"-type seeds, on the other hand, rose and fell in the same manner as that of "F" seeds and for similar reasons (1.3.3.1). The presence of greater endosperm development and quantity, approaching that for "F" seeds, would seem to explain the difference between "P" ("cWL" and "cDL") and "U"/"S" types.

The cross-sectional area of individual cellular endosperm cells of "P" type showed a wide variation at fruit ripening, whereas it was rather similar to that of the "F" type soon after cellularization (Fig. 12). This is parallel (if not necessarily causally related) to the spread in developmental stages of development previously described for this tissue.

There is likewise a wide spread in the cross-sectional areas of individual embryo cells for the "P" types at fruit ripening (Fig. 13). The smallest of these was no larger than that of "F" seed soon after the rapid phase of cell enlargement occurred in this tissue (about two months after endosperm cellularization). The spread in embryo length is even more marked (Fig. 14). "S" and "U" embryos hardly got beyond the globular stage and this is reflected here in their very limited extension. The fact that embryos of some "P" type seeds at fruit ripening were only at the "heart" stage, i.e. at the beginning of cotyledonary extension, ties in with this wide spread shown in this figure.

Turning now to the testal tissues, and firstly to that of the endotestal tissues e(L) and e(s) (Figs. 16 and 21) there is again a spread in "P"-type seeds. This appears to have been correlated with the spread in developmental stages reached by individual "P"-type seeds. Thus if a "cWL" type of "P" seed concluded its endotestal development at the level reached by normal "F" seeds at the cellularization of endosperm (weeks 10 to 13) such a seed did not expand the cells and thicken the walls of its e(L) tissue as was characteristic of "F" seeds after week 13. To illustrate this, the lowest type "P" value at fruit ripening in Figure 16 refers to a "cWL"-type seed whose e(L) cells did not expand much beyond that of "F"-type seeds between weeks 10 and 15.

Figure 21 of cell expansion in e(s) is interesting in that the second and quite extensive spurt of growth in this tissue occurred after week 25. Now the spread in developmental stages reached for "P"-type seeds ranged from that at week 12 for some "cWL" seeds to those at week 23; to others at week 30 for "cWL" and "cDL" seeds, and to yet others at maybe week 35 in some "cDL" seeds. Furthermore, as previously described in 1.3.3.4 (d) and evident in Figure 21, e(s) tissue of "F" seeds had a relatively long period of quiescence starting with the onset of endosperm cellularization (week 10 in the summer set). Not surprising then, the spread in sizes of "P"-type seeds, and even "S" types (viz. testal

development up to the period of endosperm cellularization in "F" seeds) formed a narrow band at and above the size of "F" at weeks 10 to 15.

As previously described in 1.3.3.4 (c) and 1.3.3.4 (d), cell divisions perpendicular to the longitudinal axis in e(L) and e(s) (Figs. 19 and 20, respectively) ended soon after all the endosperm became cellular, viz. at about week 20. As may be expected, the counts for "P"-type seeds in Figures 19 and 20 suggest that cell division in e(s) and e(L) was not affected by the varying abortive arrest that occurred in the endotesta after week 20. "S" and "U" ovul and seeds, on the other hand, whose development did not go beyond that of "F" at endosperm cellularization (weeks 10 - 13) were evidently severely affected by an arrest of cell division in e(s) and e(L) tissue (Figs. 19 and 20). This, together with the later progressive collapse of the e(L) ridge and even e(s) layers in "S"-type seeds explains their "queer, digested appearance" (Foster, 1943; Allan, 1969).

Sarcotestal tissue in "F" seeds appeared to expand at a compensatory rate that enabled such seed to maintain a relatively smooth outer cover. Deeper endotestal "furrows" fill up with more sarcotestal tissue, and shallower endotestal furrows with less, resulting in the undulating yet smooth appearance of fresh seed (Plate 2b). Likewise, "P"-type seeds with varying amounts of endotestal tissue had a correspondingly varying amount of sarcotesta. This complementary correspondence could be observed in empty, uncollapsed "cWs" ("S") seeds as well as in ("empty") "cOL" ("P") seeds, e.g. Plates 24b and 30c. The spread then in the cross-sectional areas of individual cells in sarcotestal tissues (Figs. 15, 17 and 18) for "P"-type seeds follows the pattern for that o the endotestal tissues e(L) and e(s). Interestingly, "U" and "S" ovule/seed types showed only the expansion of outer epidermal cells of "F"-type seeds before endosperm cellularization (week 10, Fig. 15), again consistent with thei earlier abortion.

In 1.3.3.4 (e) and 1.3.3.5 (a) it was pointed out that the "F"-type growth pattern of the outer epidermis of the inner integumentary tissue (Fig. 23) and the adjacent inner epidermis of the outer integumentary tissue (Fig. 22) had a similar pattern to that of the (next adjacent) e(s) endotestal tissue (Fig. 21) similarly for "P"-type seeds. And likewise, "U" and "S" types had cell sizes for these tissues consistent with those found in "F" seeds at the stage the former stopped developing.

Figure 30 of intra-integumentary tissues and Figure 31 of actual "integumentary" tissues from seeds of autumn-set fruit illustrate the relative quantit of these tissues for "F", "P", "S" and "U" types up to endosperm cellularizatio From the former figure, at the 23rd week, it is interesting to note that the

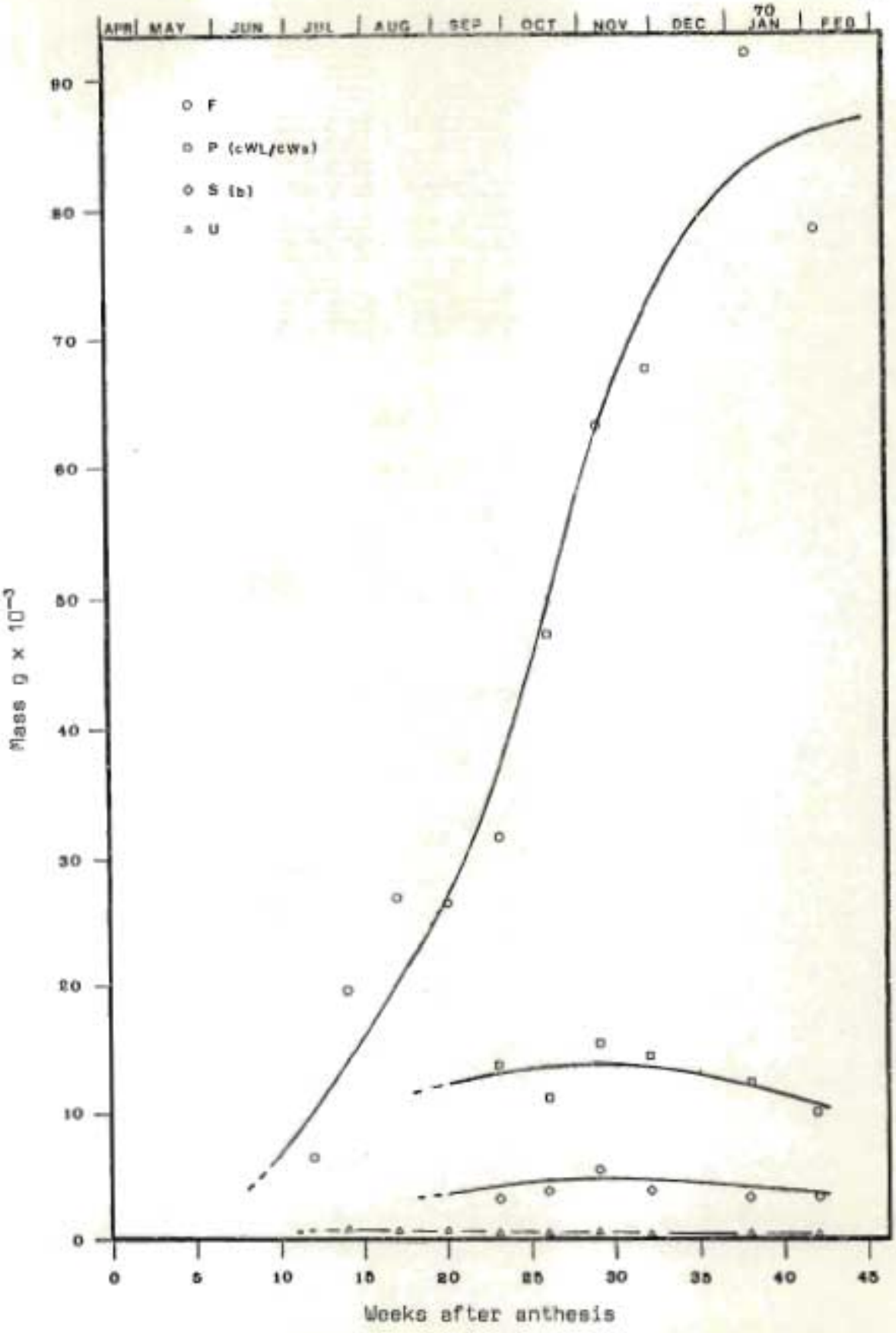

FIGURE 29 Mean individual masses of different seed types during development, autumn set, 1969.

See ABBREVIATIONS for F, P, S, U, cWL, cWs and b .

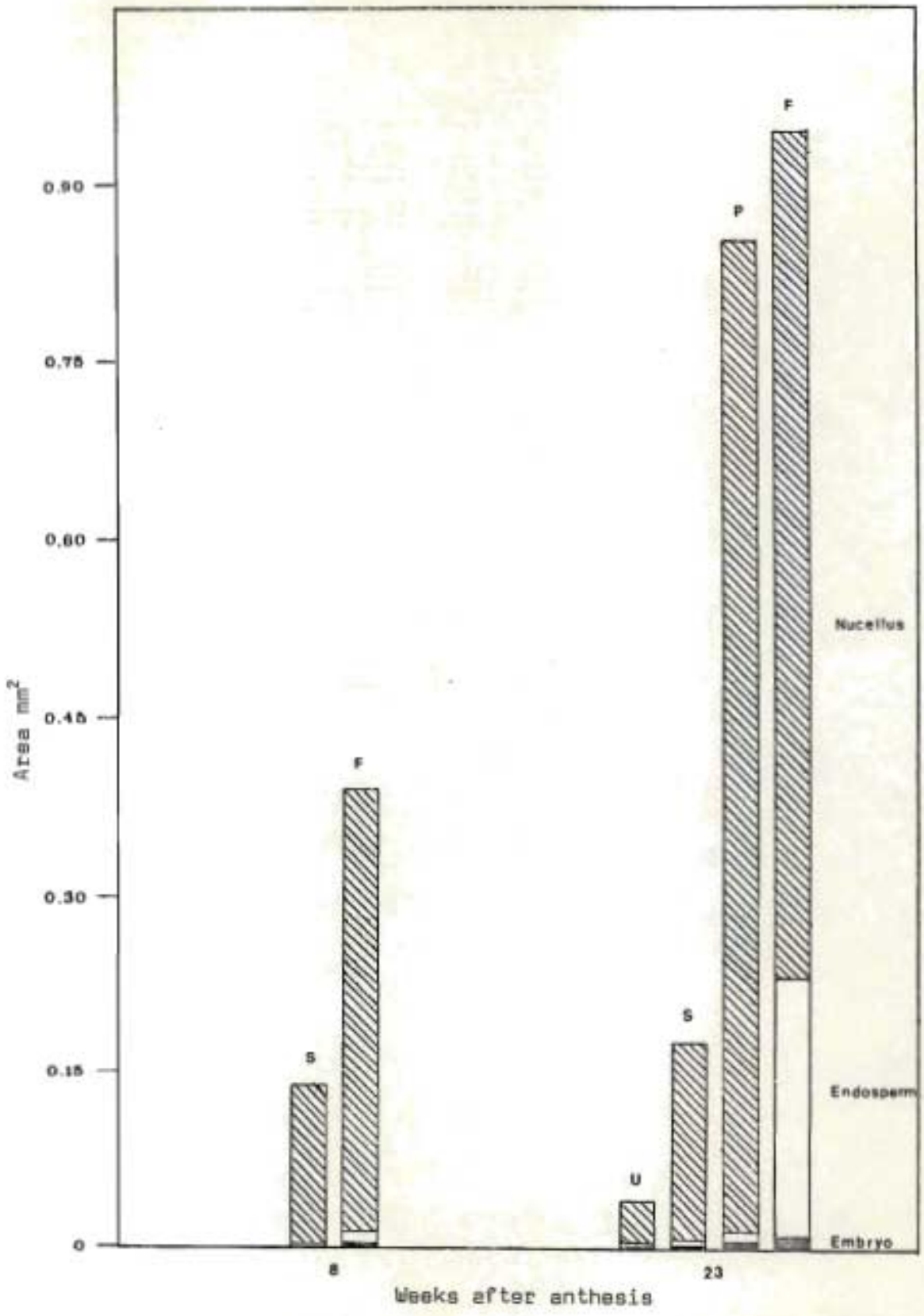

FIGURE 30 Mean cross-sectional areas along median longitudinal planes of intra-testal tissues of various seed types at weeks-8 and -23 (autumn, 1971).

See ABBREVIATIONS for F, P, S and U .

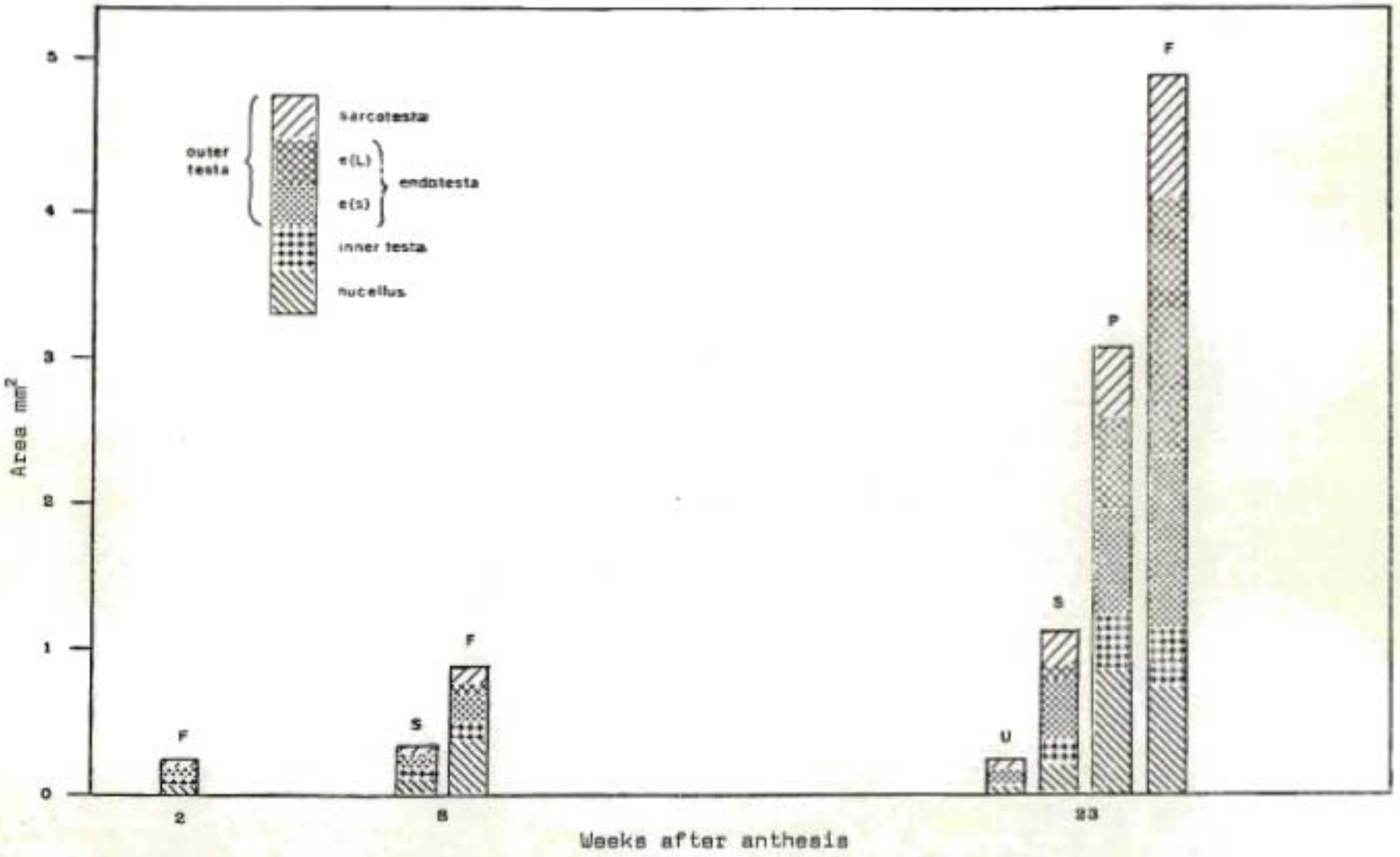

FIGURE 31 Mean cross-sectional areas along median longitudinal planes of tissues external to embryo and endosperm of various seed types at selected times (autumn set, 1971).
See ABBREVIATIONS for F, P, S, U, e(L) and e(s) .

"P" type of seed, which would not yet have had serious testal abortion, had the largest amount of nucellus. It would appear that the greater quantity of endosperm in "F" seeds had begun to consume more of their nucellus - as would be consistent with the discussion on the size of individual nucellus cells of Figure 11 in 1.3.3.1. There certainly was quite a change in the relative amoun of nucellus between "F" and "P" seeds from the eighth to the 23rd week (autumn).

From Figure 31 it is clear that at week 23, (the time of endosperm cellularization in this set), "F" seeds already had more extensive endotestal tissue than that of "P" seeds, and of course even more than that in "S" and "U" seeds. The extent of endotestal tissue appears to be correlated with the extent of endosperm and embryo development. At the time of endosperm cellularization, too, little difference existed in the amount of inner "integumentary" tissue between "F" and "P" seeds, but the latter two obviously had more than that in "S" seeds "U" ovules had relatively little e(s) tissue and virtually no e(L) and inner integumentary tissue - as was previously illustrated with the photoplates.

Figure 32 shows the relative quantities of seed tissues for various "F" and "P"-type seeds taken from ripe fruits of the 1970 summer set. As previousl mentioned, the amount of sarcotesta appears correlated with that of the e(L) endotestal ridge tissues. The latter in turn appears correlated with the quant of endosperm and embryo tissue. The difference in e(s) was not marked (they ha presumably similar numbers of layers as shown in Figure 20, with little differe in cell size for this sample). The measurement of inner "integumentary" tissue is not very satisfactory because of the susceptibility to crushing of the pliab inner epidermis. The largest differences noticeable then, were in e(L) endotestal tissue on the one hand, and the quantity of endosperm and embryo tissue on the other.

2.3.2 Whole ovule/seed growth

Figure 28, already introduced in 1.3.5, shows the pattern that t mass of ovules/seeds from summer and autumn (1970) fruits took. Again, as poin ed out in 2.3.1, there was a spread in the size of "P"-type seeds probably correlated with the time and stage at which tissue development ceased or was arrested.

Most of the "P" seeds measured were actually "cWs" to "cWL" seeds - as wil be clearer from the sections on intra-fruit distribution of abortion in 2.5. Similarly, the bulk of the mass of "S" seeds was actually made up of "b" seeds rather than an even mixture of "b" and "cWs" seeds. This was because these ("b" and "cWs") were the most abundant of the types and there was a tendency to sample from these when the larger-sized types were used up.

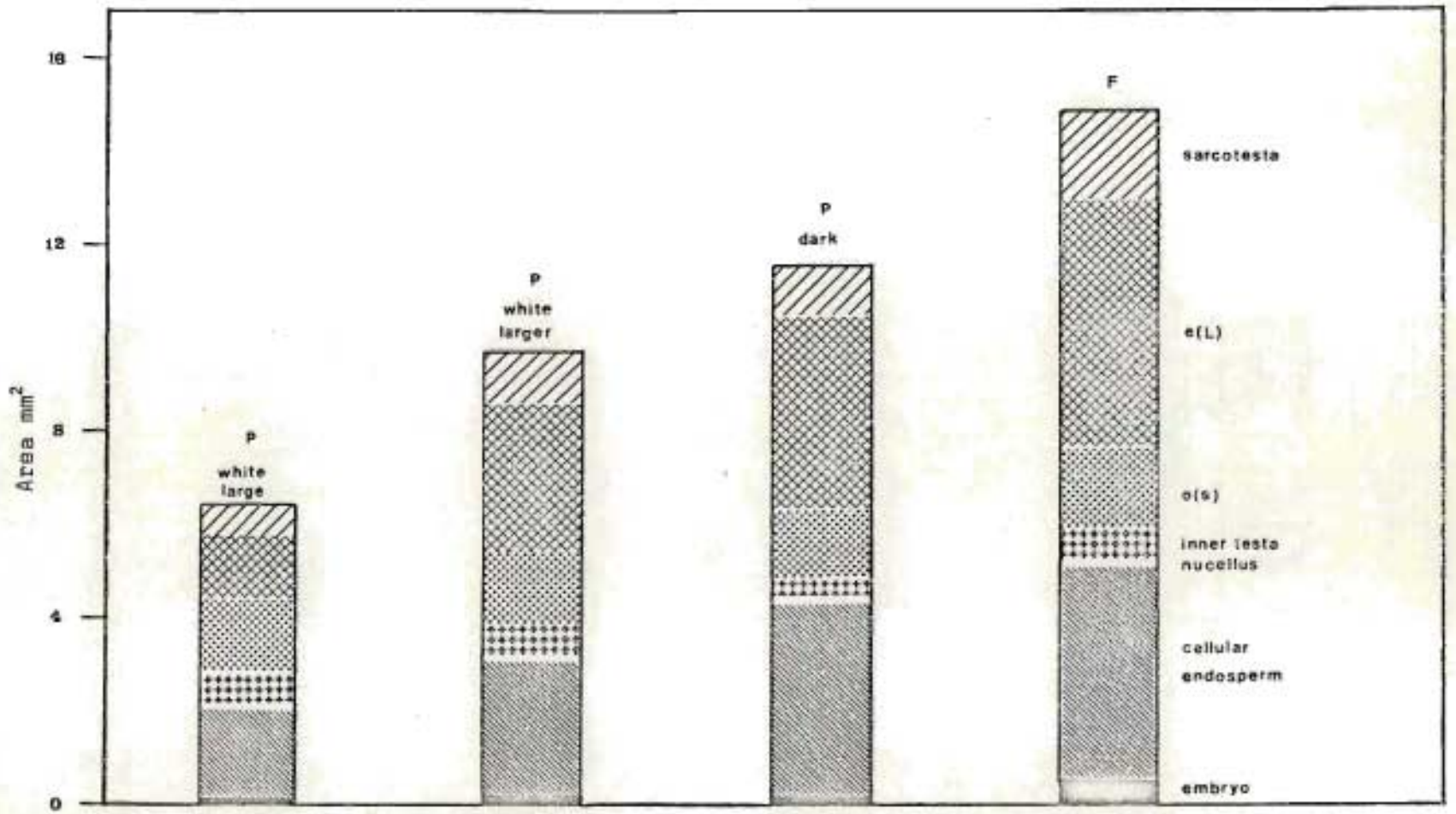

FIGURE 32 Mean cross-sectional areas along median longitudinal planes of selected normal (F) and partially developed (P) seeds from ripe fruit 'summer set, 1970).
See ABBREVIATIONS for e(L) and e(s) .

It is evident that "cWs" and "b" seeds showed little quantitative growth from between the 10th and 20th weeks after anthesis in the autumn set, i.e. before the free nuclear endosperm of "S" seeds began to cellularize. From this Figure (28) it is also evident that "cWs" and "b" seeds only became noticeable when their sizes became sufficiently different from that of "f" seeds - i.e. when the latter slowly started to accelerate in size after the initially slow growth through the cold months up to July (autumn set).

The "f" seeds of the summer set of course, grew more rapidly from the star and sustained this even in the coldest months. Abortive types should have been picked out much earlier than they were. However, there were so few of them tha the author overlooked them, assuming them to be the largest of the unfertilized ovules. It was only when the higher frequency of abortions in the autumn set samples focused the attention of the author again that he began to look for and to measure abortive seed types in the summer set. (The two sets were being sampled from over the same months at this stage.)

The author had first become aware of abortive seeds in the later half of growth in an autumn set survey of the previous year. Measurements begun in tha set are shown in Figure 29 (see p. 125). The results are confirmative of those of the previous figures already discussed.

2.3.3 Contents of dissected seeds

Tables 10 and 11 show the relative frequency of various combinations of "intra-integumentary" tissues dissected out of different seed types (Plate 2b) from ripe fruit. From Table 10 of the 1970 summer set, the greatest frequency of normal endosperm and embryos (row 1) was in the "dG" seeds, follow by that in the "dB" seeds. A small percentage of "cDL" seeds (13,3%) had this "normal" or "fully developed" complement. No "cWL" nor "cWs" seeds had this. A small percentage of the latter two seed types (12 and 8 per cent respectively had the next best category of row 2, i.e. "normal" opaque endosperm but small embryos. All "dG" and "dB" seeds had endosperm and embryos. The other three categories ("cDL", "cWL" and "cWs") had a good deal less of these tissues, and they also had a higher frequency of endosperm than of embryo tissue.

The most frequent complement of the "cDL" seeds was (surprisingly) "nucell only", followed by that of normal, opaque endosperm and small embryos. The mos frequent complement of both "cWL" and "cWs" seeds was that of "apparently empty" These are surprisingly high figures, but it must be remembered that whatever nucellus and endosperm there probably was during the first half of the developmental period, was probably consumed by the time of fruit ripening. The data

TABLE 10 Internal contents of dissected seeds from ripe papaya fruit set in summer, 1970

INTERNAL TISSUES		SEED TYPE				
		dB	dG	cOL	cWL	cWs
Opaque endosperm plus normal embryo	No.	314	615	40	-	-
	%	84,2	90,2	13,3		
Opaque endosperm plus small embryo	No.	57	67	67	35	24
	%	15,3	9,8	22,3	11,9	7,9
Opaque endosperm but no embryo	No.	-	-	7	3	1
	%			2,3	1,0	0,3
Translucent endosperm plus small embryo	No.	2	-	42	27	1
	%	0,5		14,0	9,2	0,3
Translucent endosperm but no embryo	No.	-	-	28	17	10
	%			9,3	5,8	3,3
Little translucent endosperm, no embryo	No.	-	-	2	8	12
	%			0,7	2,7	4,0
No endosperm, little nucellus, small embryo	No.	-	-	-	3	1
	%				1,0	0,3
Nucellus only	No.	-	-	113	20	11
	%			37,5	6,8	3,6
Apparently empty	No.	-	-	2	180	242
	%			0,6	61,4	80,1
$\sum$	No.	373	682	301	293	302
	%	100	100	100	100	100
Σ% endosperm		100	100	61,9	30,6	15,8
Σ% embryos		100	100	49,6	22,1	8,5

TABLE 11 Internal contents of dissected seeds from ripe papaya fruit set in autumn, 1970

INTERNAL TISSUES		SEED TYPE				
		dB	dG	cOL	cWL	cWs
Opaque endosperm plus normal embryo	No.	–	175	–	–	–
	%		97,2			
Opaque endosperm plus small embryo	No.	13	–	5	–	–
	%	17,3		20,8		
Opaque endosperm but no embryo	No.	–	–	–	–	–
	%					
Translucent endosperm plus small embryo	No.	61	5	13	5	–
	%	81,3	2,8	54,2	26,3	
Translucent endosperm but no embryo	No.	–	–	–	–	–
	%					
Little translucent endosperm, no embryo	No.	–	–	1	–	1
	%			4,2		1,1
No endosperm, little nucellus, small embryo	No.	–	–	–	–	–
	%					
Nucellus only	No.	1	–	3	6	10
	%	1,3		12,5	31,6	10,8
Apparently empty	No.	–	–	2	8	82
	%			8,3	42,1	88,2
$\sum$	No.	75	180	24	19	93
	%	100	100	100	100	100
Σ% endosperm		98,6	100	79,2	26,3	1,1
Σ% embryos		98,6	100	75,0	26,3	0,0

for Figures 4 and 30 at the earlier developmental periods were also based on a large number of ovules/seeds. (These show that nucellus and endosperm were present.)

Table 11 is of the same categorization of the seeds of the autumn-set frui In comparison with the summer set, there was a considerable shift in the highes frequency for "dB" seeds, viz. to 'translucent endosperm plus small embryo'. One "dB" seed even had nucellus alone. None had 'normal opaque endosperm plus normal embryo'. (It might appear from the foregoing that black seeds are inferior to grey seeds. However, in riper fruits the grey seeds might actually become black. Thus some of the 'inferior' smaller black seeds may have been 'prematurely ripened seeds' - the way injured fruits can ripen prematurely.)

In contrast to the summer set again, the most frequent complement in the "cDL" seeds was 'translucent endosperm plus small embryo' followed by 'normal, opaque endosperm plus small embryo'. There were again no 'normal, opaque endosperm plus normal embryo' in the "cDL" seeds examined. The "cWL" seeds were ma up of only three categories, viz. 'translucent endosperm plus small embryo', 'nucellus only' and 'apparently empty'; with an increasing frequency towards t latter contents. The "cWs" were also concentrated around 'apparently empty' and 'nucellus only' categories. All "b" seeds examined in both the autumn and summer sets were 'apparently empty'.

The summer set's "cDL" to "cWs" seeds covered a far wider spectrum of comp ments. In contrast, one can consider the autumn set's "cDL" seeds to have centred around 'translucent to opaque endosperm, plus small embryos'; a quarte of "cWL" seeds around 'translucent endosperm plus small embryos' and the rest 'virtually empty'; and the "cWs" and "b" seeds as 'apparently empty'. The The abortions in the 1970 autumn set of "b", "cWs" and (three-quarters of) "cWL seeds thus appear to have occurred in the period before the cellularization of free nuclear endosperm. That is, the bulk of these three types began aborting from the end of May until the end of July, the coldest months. From Figures 6 and 8 (weeks 4 and 6) relating to the following year's autumn set, it would appear that only a small proportion of ovules/seeds would have started aborting before the end of May.

In the sections that follow (2.5 onwards) more data and analyses will be presented which may further clarify the time and extent of ovule and seed abort in autumn-set fruits, and also some of the possible predisposing factors.

2.4 MATERIALS AND METHODS: INTRA-FRUIT DISTRIBUTION OF ABORTION

2.4.1 Materials

The following groups of fruit sets were made use of in a detailed examination and analysis of the distribution of seed abortion within the fruit. These included:-

(i) all the ovules and seeds of 14 ripe whole fruits of the hand-pollinated autumn set, 1970;

(ii) 50 ovules/seeds for each of eight fruit sub-regions (A, a, B, b, C, c, D, d) of fruit sampled at the sixth week after anthesis, autumn set, 1971; and

(iii) all the ovules and seeds of 24 ripe whole fruits of the hand-pollinated summer set, 1970.

Reference has already been made to these sets [(i), (ii) and (iii) above] in 1.2.3.2, 1.2.2.1 and 1.2.3.1 respectively. In addition,

(iv) 21 ripe fruits randomly chosen from a larger number picked from the bottom end of fruit stems in November, 1973, were used for this study after being kept in a deep-freezer. These fruit were judged to have set in the early to mid-summer period of 1972/73. These had not been hand-pollinated; and finally,

(v) 15 ripe fruits, randomly chosen from a larger number picked from the top end of fruit stems in April, 1974, were also used for this study after being kept in a deep-freezer. These were judged to have set in the previous autumn of 1973. They had also not been hand-pollinated.

(Measurements on the seed and fruit flesh mass of the above (iv and v), and also on the other fruits from these two sets were also taken. These were used for a correlation study presented in Chapter III.) The fruits for (iv) and (v) were on trees somewhat similar in vigour and age to those picked for the sets of (i) and (iii) at their time of harvesting.

In contrast to the autumn and summer sets of 1970 [(i) and (iii) above], in which all the ovules and seeds of the fruits used were removed and classifi seeds and ovules were removed from only some longi-portions (Plate 2c) of the fruits used for the 1972/73 summer- and 1973 autumn-set groups (iv and v above

For the summer set of 1972/73, 2/5 longi-portions of 21 of the fruits were used for this study.

From the autumn set of 1973, 2/5 to 4/5 longi-portions were used. In connection with the use of only portions of fruits of the 1972/73 sets, it had previously been observed that 2/5 or greater portions gave reasonable estimates for the pattern of seed type distribution for whole fruits. (There were a few fruits in which the character of one 2/5 portion was quite dissimilar to that of the other 2/5 portion of the same fruit. The remaining 1/5 portions of the five-carpellate fruits were of course, discarded because the positions of some of the seeds were invariably displaced in the act of cutting the fruit.) Furthermore, the selection (from one of five) of the longitudinal plane between two adjacent placental edges to cut along can be considered to have been a random one. The resulting analyses on the distribution of ovule/seed types along the longitudinal placental regions of two to four longi-portions can be considered to be representative of the patterns in the whole fruits (5/5).

Once the author was ready to process a given fruit, he would allow it to thaw sufficiently for it to be cut into the desired longi-portions. These were then re-frozen in the deep-freezer. The portions used for the intra-fruit distribution of abortion study were processed as follows: all the seeds of the types "F", "P" and "S" for each of the eight intra-fruit sub-regions were removed with tweezers, transferred to cardboard cups and counted (Plate 2d). The remaining fruit flesh (Plates 1d, 2a) was then cut into the separate A, a, B, b, C, c, D, d sub-regions, and each was examined under a dissecting microscope in order to count the "U"-type ovules. It proved important to do this, because inaccurate, underestimated counts for these relatively tiny ovules were obtained when they were counted with the naked eye. Their smallness, and the relative largeness of adjacent seed stalks of the fully developed "F" seeds tended to obscure the presence of quite a number of them. They were also difficult to count accurately in unfrozen, over-ripe fruit, and in over-thawed fruit.

In the case of the autumn and summer sets of 1970, all the ovules and seeds (i.e. for the entire fruits) were counted, but only relative to the intra-fruit quarters Aa, Bb, Cc, Dd and not the eight sub-regions, viz. A, a, B, b, C, c, D, d. With regard to the sampling for the autumn set of 1971, this has already been dealt with in 1.2.2.1.

2.4.2 Rationale and statistical methods

One of the ways of approaching the problem of ovule/seed abortion is to make a comparative study of seeds in fruits set and developed over different seasons, e.g. late autumn versus mid-summer sets. Any differences in abortion

pattern could be further examined against differences in the seasonal climatic and physiological conditions associated with such sets.

Another approach can be to examine the distribution pattern of abortion within fruits for any given set of seasonal conditions. Some of the possible factors involved in abortion can be sought from differences present within the fruits. The effect of different levels or methods of pollination can also be considered. In addition, all three mentioned approaches can be combined and th determining factors sought in an interactional framework.

In order to advance such a study of abortion, more specific, likely factor contributing to seed abortion need to be formulated, together with predictions their likely effects. When these factors have been measured in some appropriat way, the effects predicted by theory or hypothesis can be compared and, where appropriate, statistically tested against actual measured data.

From the literature review of this chapter and from the anatomical studies already surveyed, a number of possible causes of ovule/seed abortion in develop ing papaya fruit were postulated.

Firstly, ovules and seeds that experience colder subtropical conditions during the first phases of growth are more likely to abort than those developin under more tropical-like conditions, such as are approached in summer. The extent and timing of the onset of abortions should reflect the timing and onset of the cold conditions.

Differences in the maturity of ovules at anthesis and when fertilization i occurring should be reflected in differences in abortion. Thus, if there are differences along the fruit stem-apex axis, or else between carpellary margin versus placental edge regions, then such regions with greater proportions of immature ovules should have a greater proportion of abortions, if these immatur ovules are fertilized.

The pattern of pollen tube penetration may be inter-related with the above If immature ovules receive pollen tubes too early, then regions of the fruit wi the greater likelihood of such events should reflect an increase in abortions due to this. Conversely, those regions furthest from the entering pollen tubes may receive pollen tubes too late, i.e. such ovules may start degenerating by the time they are fertilized, resulting in an increase in the proportion of abortions. (In connection with this postulate, it must also be borne in mind that pollen tubes may only enter mature ovules - see 1.3.1.3.)

Another set of differences could be attributed to differences in avail- ability of hormones or metabolites from the rest of the plant, or the fruit its

supply: ovules along the carpellary margin are closer to the main vascular supply than those along the placental edge. Similarly, within the carpellary or placental edge regions, those ovules closer to the base of the flower/fruit may be closer to the incoming materials from the rest of the plant. That is, a competition for metabolites on the basis of the location of the placental vascular supply may exist.

Differences in the degree of intra-fruit competition of another sort may also exist. Developing seeds may compete against each other for the scarce supp of metabolites, particularly during the stressful coldest months, and/or the stress of competition of other fruits. Such intra-fruit regions with the highe degree of initial seed growth and development may suffer greater rates of abort during such periods. Finally, differences may exist in definite localized regi of the fruit for reasons other then those already suggested. If such definite sub-regions can be identified, their localized characteristics can be studied further.

In order to test most of the above postulates and related predictions, use will be made of a 'battery' or series of statistical tests. These tests are meant to complement each other. They vary from each other

(i) with respect to the kind of score or measurements with which they can appropriately be used;

(ii) in the kind of prediction they can test; and

(iii) in terms of the underlying assumptions upon which they operate.

These tests are not physiological proofs. Rather, they are meant to be logical (statistical) tests of inferences based on physiological assumptions and hypotheses. As such they may

(i) lend supportive (or a contradictory) weight to developing theory; they may also

(ii) highlight areas for further research.

It is in the spirit of (i) and (ii) and in the light of the anatomical and morphological results already presented that these statistical tests have been applied. An overview will now be given of the tests that will be used, the material and thesis sections to which they are applied, the hypotheses tested and the statistical models assumed.

A. The sections have been divided into two main parts: 2.5.1 for data from autumn sets; and 2.5.2, from summer sets. Each of the autumn and summer sections, in turn, includes studies on hand-pollinated and non-hand-pollinated sets. Tabulated data from these four sources provide an initial indication of the effects of season and method of pollination on abortion levels and patterns. These sources of data have been enumerated under 2.4.1.

However, many of the statistical approaches of the sub-sections that follo involved chi-square tests. These in turn required that the expected frequencie on which the tested proportions were based were not less than five in more than 20 per cent of the proportions in any one chi-square test (Cochran, 1954). Con sequently, of the 15 fruits in the 1973 autumn set, only 11 were subjected to further statistical analysis. Similarly, of the 21 fruits of the 1972/73 summe set, 20 of these were subjected to some tests and only a sub-set of five of the to further tests. The various procedures and their rationale follow.

B. In section 2.5.1.1 for autumn sets, and 2.5.2.1 for a summer set, the con- sistency of the distribution pattern within the fruit for each of the ovule/see types is tested. The null hypothesis is that the distribution pattern within the fruit for each of the ovule/seed types was one of randomness, i.e. no differences existed in the proportion of each type between fruit sub-regions, o between any sub-region and the total fruit.

The research hypothesis was that differences in proportions for each ovule seed type did exist. These differences could have been brought about by:

(i) a differentiated pattern of pollen tube penetration which, in turn, led to a differentiation in the pattern of proportion of ovules fertilized. From the latter, there could have been

(ii) a sufficient differentiation in the pattern of sub-regional intensity of inter-seed competition for metabolites;

(iii) an inter-action between the differentiated pattern of pollen tube penetrations and a differentiated intra-fruit pattern of the level of maturity of ovules could also have contributed to a subsequent differentiation in the intra-fruit pattern of proportion of ovule/seed types.

It was postulated that the net effect of (i), (ii) and (iii), enumerated above, would have been in the same direction, i.e. (i) and (ii) would be correlated whilst (i) and (iii) would be interactional, or the product of the two pattern Differences between types of ovules/seeds could be due to the spread in time of

development over which abortions set in, with the more numerous type(s) reflecting the time at which peak abortion occurred.

The statistical method used for this section was the Kendall co-efficient of concordance, W. This W can be used to measure the correlation among several rankings of N objects or individuals. "When we have k sets of rankings, W expresses the degree of association among k such variables." (Siegel, 1956).

In other words, W expresses the degree of association among several (k) variables measured as, or transformed to, ranks (Siegel, 1956). "Imagine how .. data would look if there were no agreement among several sets of rankings, and then ... imagine how it would look if there were perfect agreement among several sets. The co-efficient of concordance would then be an index of the divergence of the actual agreement shown in the data from the maximum possible (perfect) agreement, ... Roughly speaking, W is just such a co-efficient." (Siegel, 19 Translated into the framework of sections 2.5.1.1 and 2.5.2.1, each fruit sampl can be considered to have had ranked (.. the pattern of ..) the proportion of a particular ovule/seed type within that fruit, e.g. the rank order from the highest to the lowest proportion amongst the intra-fruit sub-regions in that fruit. W measures the consistency of such a ranking of the intra-fruit sub-regions (with respect to the proportion of a given ovule/seed type) over several (k) fruits. In terms of the level of measurement required for W, they may be merely in the ordinal scale. Siegel (1956) provides tables of critical values for testing W for small samples - (N = number of entities to be ranked, i.e. number of intra-fruit sub-regions = 7 or less) and χ^2 with df = N - 1 can be used for N larger than 7.

C. In sections 2.5.1.2 and 2.5.2.2 for autumn and summer sets respectively, t differences in abortion rates between intra-fruit sub-regions along the carpell margins versus those along the placental edge are tested. For the purposes of these sections, the abortion rate, p_i , for a given intra-fruit sub-region (i) was measured to be the proportion

$$\left(\frac{P + S}{F + P + S}\right)_i \quad .$$

That is, using the overall findings of the anatomy and morphology studies, it was assumed that the majority of "U" "ovules" were not actually fertilized and so never developed as seeds. For practical purposes, then, the seed abortion r would have been the proportion of [partially developed ("P") plus slightly developed ("S") seeds] to the total of [fully developed ("F") plus "P" plus "S" seeds] for a given intra-fruit sub-region, (i).

The null hypothesis was that no differences existed in abortion rates betwe the intra-fruit sub-regions along the carpellary margin and those along the placental edge. For a given fruit, the abortion rates of both simply reflected the abortion rate for the whole fruit. The research hypothesis was that differences existed by virtue of differences between these regions in (i) maturity of ovules at fertilization, and (ii) closeness to the main placental vascular supply and hence accessibility to available significant substrates. Both (i) and (ii) would have a similar pattern of intra-fruit sub-regional location.

Statistically the tests on these hypotheses involved finding the "total" χ^2 for all sub-regions for a given fruit, followed by a χ^2 "differences" test between carpellary margin (A, B, C, D) and placental edge (a, b, c, d) sub-regions if the "total" χ^2 test was significant (Fleiss, 1973). When this had been done for each fruit, a "total" χ^2 for the <u>whole series</u> of fruits was done. "Pooled" χ^2 and "heterogeneity" (or homogeneity) χ^2 were then calculated to see if the probability for the "total" χ^2 for the whole series could be accepted, or whether the fruits were too heterogeneous with respect to individual abortion rates. Anticipating the latter, and as a separate test for the <u>whole series</u> from that given above, <u>probability values</u> (corresponding to a χ^2 value with two degrees of freedom), viz. $e^{-\frac{1}{2}\chi^2}$ or $-2 \ln p$ were calculated for each fruit (where p = the probability value of "total" χ^2 for the <u>given fruit</u> and ln is the natural log). The combined probability value for a χ^2 of the whole series of fruits (irrespective of a finding of significant heterogeneity) was then calculated; this χ^2 being equal to $\left[\Sigma - 2 \ln p\right]$ with two degrees of freedom for each individual fruit's χ^2, i.e. with total df = twice the number of fruits in the series (Rayner, 1969). (This useful overall χ^2 test was also applied to other series of independent probability values, such as t-test probability values on parameters of individual fruits of a series, e.g. of a particular fruit set. This latter χ^2 test is of course more cumbersome than that found by simply addi up individual χ^2 values where these tests provide the original probability valu It is nevertheless included as a separate check.)

D. <u>In sections 2.5.1.3 and 2.5.2.3 for autumn and summer sets respectively</u>, t consistency of intra-fruit patterns of (i) the abortion rate, and (ii) a postulated competition factor, are tested. For (i), the abortion rate for any intra fruit sub-region i was estimated as

$$\left(\frac{P + S}{F + P + S}\right)_i$$

as mentioned in the previous sub-section C of this section (2.4.2). For (ii), a competition factor,

$$x_i = \left[(F + P + S)/(F + P + S + U)\right]_i \%\ ,$$

for each intra-fruit sub-region, was used. This x_i based on the proportions of the various ovule/seed types ("F" , ... "U") , was taken as an index of early seed development. More specifically, this proportion, x_i , measures the probab proportion of the total ovules/seeds per sub-region that were actually fertiliz and subsequently underwent normal to near-normal early seed development up to the period before or soon after abortion set in. It has been assumed that the degree or intensity of quantitatively measurable physiological inter-seed "competition" within a given intra-fruit sub-region will be found to be correlated with this index. By 'quantitatively measurable' is meant measurement in the interval scale (Siegel, 1956). Alternatively, the index used here is a measure of inter-seed competition, although, without the above postulated correlation, remaining entirely at the ordinal level (Siegel, 1956). [This distinct between levels of measurement has a bearing on the validity of various significance tests (Siegel, 1956).]

In these sections, viz. 2.5.1.3 and 2.5.2.3, x_i was taken to be at least a the ordinal level, and concordance (W) tests were carried out on the patterns, in the same way as described for the concordance test in sub-section B of 2.4.2 above. The null hypotheses were that

(i) x_i values for the i intra-fruit sub-regions within a given fruit did not differ from each other, or from that estimated for the whole fruit; and similarly

(ii) for the p_i values amongst themselves.

The research hypotheses were that differences did exist due to the pattern of pollen tube penetrations and the other intra-fruit differences postulated to affect abortion rates enumerated in the sub-section of C above.

E. In sections 2.5.1.4 and 2.5.2.4 for autumn and summer sets respectively, t difference in the competition factor x_i (defined in D above) between adjacent carpellary margin and placental sub-regions is tested. The test used was the t-test for paired differences, applied to the four pairs (A - a, B - b, C - c, D - d) for each fruit. The $X^2 = \left[\Sigma - 2 \ln p\right]$, (described in sub-section C abov on the probability values (p) for the series of fruit t-tests was also applied to the series as a whole.

The adjacent carpellary margin and placental edge sub-regions were approxi mately equidistant from the point where the pollen tubes entered the ovary.

Nevertheless, as found in 1.3.1.3, differences existed with regard to the exten of pollen tube penetrations of ovules of the various sub-regions. The research hypothesis, therefore, was that differences would exist in the competition factor x_i (i.e. extent or intensity of early seed development) between even adjacent carpellary versus placental edge sub-regions. Differences in x_i were also postulated or predicted on the basis of differences in the maturity of ovu at anthesis (1.3.1.2), and also on the differences in the mean distance of the ovule vascular connections to the main vascular bundle. (This is the ventral bundle running just under the surface through the middle of the carpellary marg regions, Figs. 1 and 2.) The null hypothesis, of course, was that any differen in x_i would not be significant within any given fruit, and therefore not signi-ficant for the fruit sets as individual whole series as well.

The validity of the t-test probability values (p) of course are subject to uncertainty because of the, as yet, unknown correlation between the index x_i an quantitatively measurable physiological differences postulated, as pointed out in the preceding sub-section D above. Consequently, the $\chi^2 = \left[\Sigma - 2 \ln p\right]$ pro-bability value for a whole series is also uncertain. The results in these sections (2.5.1.4 and 2.5.2.4) are therefore meant to be taken provisionally.

F. In sections 2.5.1.5 and 2.5.2.5, one group each from autumn and summer set respectively are tested for differences in abortion rates within (i) carpellary margin sub-regions only, and (ii) placental edge sub-regions only. (This was done to control the effects of differences between carpellary margin and placen edge sub-regions.) In the tests in (i) and (ii) above, the abortion rates p_i are also tested in relation to the competition factor x_i described in a previou sub-section (D).

By way of introduction to the statistical method used to test the above relationship, it may be useful to recall a chi-square test used in sub-section viz. a chi square for "differences" between the p_i of two regions. Where more than two regions (or "classes") are involved, a chi square is available to test whether significant differences exist among such classes (or, here, sub-regions Such a chi-square test, although valid, lacks sensitivity when the several "samples" (sub-regions) possess an intrinsic ordering. Fleiss (1973) describes a chi-square method of analysis for where such ordering is quantitative, i.e. for where "a measurement x_i is naturally associated with the i^{th} sample". He then describes a chi-square analysis (which, in terms of the variables of this sub-section, tests the (usual) "total" χ^2 for the presence of differences in th proportion, p_i , over several sub-regions, then provides chi-square statistics test (i) whether the association between x_i and p_i is linear; viz. "χ^2 linear

and (ii) the significance of the slope of a line representing such a linear relationship, viz. "X^2 slope". These tests are applied to the autumn and summe set groups referred to at the beginning of this sub-section.

In a third group, viz. from data of the sample at the sixth week in the 1971 autumn set, (a study on early autumn-set seed development), a similar type of test was applied on two relationships. For the first, it was postulated tha early seed abortion (estimated as the proportion of pollinated seeds without normal endosperm) was linearly related to a competition factor estimated by the mean size of sampled ovules/seeds, i.e. by a measure of the intensity of early seed development. In the second relationship x_i was estimated by the percentag of ovules in a given sub-region penetrated by pollen tubes by the sixth week.

The null hypotheses in all the tests of this sub-section (F) was that (i) no differences existed in p_i within the carpellary margin sub-region or within the placental edge sub-regions; and alternatively, (ii) if there were a differences these were not linearly related to the various x_i's postulated.

Again, it should be pointed out that, with the exception of the test in which x_i measured the mean size of ovules and seeds, the above tests are subjec to some uncertainty due to the doubt surrounding the level of measurement involved in the x_i's used.

G. In sections 2.5.1.6 and 2.5.2.6 for autumn and summer sets respectively, t ordered differences in abortion rates (p_i) within the carpellary margin or the placental edge sub-regions were not postulated to be necessarily quantitatively related to the competition factor x_i. A more general hypothesis was postulated that abortion rate (p_i) differences existed along the longitudinal axis of the carpellary margin (and also that of the placental edge) sub-regions. In this simplified form, it was postulated that there was initially probably greater competition (unmeasured) at the apex end of the fruit (than at the base) becaus of the earlier development of the top. It was also postulated that the basal part of the fruit, being closer to the supply of metabolites, and other substrates from the rest of the plant, would have an advantage in this respect as well.

Fleiss (1973) describes a chi-square analysis due to Bartholomew (1959a, 1959b) to test the hypothesis that m proportions are arranged in a prespecifie order. It can be used where it is suspected beforehand that a gradient in proportions exists because of different levels of some associated factor, but for which no numerical values can be naturally assigned to (i.e. Fleiss is presumably taking into account the question of "levels of measurement" discusse in Siegel, 1956).

Bartholomew's method, to paraphrase from Fleiss (1973), even allows for slight departures from an hypothesized order. "Suppose the hypothesis predicts that the ordering (in proportions) $p_1 > p_2 > \ldots > p_m$ should obtain, but that departures from this ordering are observed. For example ... if the ordering $p_1 > p_2 > p_3 > p_4$ was predicted, but instead we obtained $p_1 < p_2$, and then, as predicted, $p_2 > p_3 > p_4$, ... then weighted averages of those adjacent proportions that are out of order are taken until, when the averages replace the original proportions, the hypothesized ordering is observed. The revised proportions are denoted p' ." (The effect of this weighting of adjacent proportions is to lower the chi square then obtained, but leaving the hypothesized ordering intact.) This particular ("qualitative") chi square is calculated as

$$\bar{\chi}^2 = \frac{1}{pq} \sum_{i=1}^{m} n_i (p_i' - \bar{p})^2$$

where $q = (1 - p)$ and $\bar{p}$ is the weighted mean of the proportions, p_i , or p_i and p_i' . Special tables for testing this chi square are provided in Fleiss (1973). In the case where the number of proportions, m , is equal to four (such as they were in the tests for these sub-sections, viz. 2.5.1.6 and 2.5.2.6) C_1 and C_2 , (two values used in looking up the $\bar{\chi}^2$ tables), are calculated as follows:-

$$C_1 = \sqrt{\frac{n_1 \cdot n_3}{(n_1 + n_2)(n_2 + n_3)}}$$

and

$$C_2 = \sqrt{\frac{n_2 \cdot n_4}{(n_2 + n_3)(n_3 + n_4)}}$$

where n_1 , n_2 , n_3 and n_4 are the total number (or weighting factor) on which the proportions p_1 , p_2 , p_3 and p_4 are based.

To sum up then, the hypothesized ordering for the p_i of the carpellary margin sub-regions was $A > B > C > D$, and for the placental edge sub-regions, it was that $a > b > c > d$. The tests of this sub-section are basically about the same things as those of sub-section F, viz. in 2.5.1.5 and 2.5.2.5, but without the uncertainty of the level of measurement of x_i .

H. In sub-section 2.5.1.7 for two autumn set groups, and sub-section 2.5.2.7 for a group set in summer, the differences in the rates of abortion, p_i , within the longitudinal axis of the carpellary margin sub-regions alone, and also within those of the placental edge sub-regions alone, are tested. The differ-

between the tests in this sub-section and those of G above is that whereas in sub-section G a definite gradient of differences along the fruit base-apex axis was postulated, this sub-section only postulated differences between various groupings of sub-regions. It was assumed that there were at least discrete morphological differences between the top and bottom halves of a papaya fruit, (e.g. the vascular supply pattern appears non-identical between the top and bottom halves in cleared ovaries and young fruits). There could, quite likely, be other intrinsic differences in the fruit tissues, and it was postulated that such assumed differences would affect the susceptibility of certain placental areas to seed abortion.

Fleiss (1973) describes a chi-square analysis to test for differences betw sub-groups within a larger group of samples when the general χ^2 test has shown the larger group as having significant differences within it. "Having found th proportions to differ significantly, one would next proceed to identify the samples or groups of samples that contributed to the significant difference ... Suppose that the m samples (or groups or sub-regions) are partitioned into two groups, the first containing m_1 samples (or sub-regions) and the second m_2, where $m_1 + m_2 = m$. Define

$$n_{(1)} = \sum_{i=1}^{m_1} n_i$$

to be the total number of subjects in the first group of samples" [or, in the author's application to seed abortion rates, $n_{(1)}$ = the total number of ovules/seeds (on which the abortion rate is based, i.e. the weighting factor) in the first group of intra-fruit sub-regions] "and

$$n_{(2)} = \sum_{i=m+1}^{m} n_i$$

to be the total number of subjects in the second group. Let the proportion in the first group be denoted $\bar{p}_1$, where

$$\bar{p}_1 = \frac{\sum_{i=1}^{m_1} n_i p_i}{n_{(1)}} \quad ;$$

and in the second group be denoted $\bar{p}_2$ (worked out with its appropriate $n_{(2)}$). Then

$$\chi^2 \text{ diff} = \frac{1}{\bar{p}\bar{q}} \times \frac{n_{(1)} n_{(2)} (\bar{p}_1 - \bar{p}_2)^2}{n} \quad ,$$

with one degree of freedom, may be used to test for the significance of the difference between $\bar{p}_1$ and $\bar{p}_2$, ($\bar{q} = 1 - p$; and $n = n_{(1)} + n_{(2)}$) . The statis

$$X^2 \text{ group}_1 = \frac{1}{\bar{p}\bar{q}} \sum_{i=1}^{m_1} n_i(p_i - \bar{p}_1)^2 \ ,$$

with $m_1 - 1$ degrees of freedom, may in turn be used to test the significance of the differences among the m_1 proportions in the first group, and the statistic

$$X^2 \text{ group}_2 = \frac{1}{\bar{p}\bar{q}} \sum_{i=m_1+1}^{m} n_i(p_i - \bar{p}_2)^2 \ ,$$

with $m_2 - 1$ degrees of freedom, that among the second group." However, if the partitioning of the samples into groups is suggested by the data instead of being planned beforehand, "... each of the X^2 values should be referred to the critical value of chi square with $m - 1$ degrees of freedom, (i.e. the largest degrees of freedom number) and not to the critical values of chi square with 1 , $m_1 - 1$ and $m_2 - 1$ degrees of freedom respectively." (The effect of using t larger number of degrees of freedom is of course to render the test more conservative, i.e. larger chi-square values are required for significance.)

The above X^2 analysis and its related note on the permissible number of degrees of freedom was applied to the sets of data of sub-sections 2.5.1.7 and 2.5.2.7. The purpose of these tests was to statistically identify specific int fruit sub-regions in which abortion was more prevalent. One of the longer-term purposes of the tests of this sub-section was to identify specific sub-regions of the fruit which could, in the future, be subjected to a more intensive comparative study.

The differences between the carpellary margin and placental edge sub-regio suggested itself even before examining the data; and these were tested against the one degree of freedom chi-square value. Other groupings were tested agains the more conservative chi-square values. Finally, a total X^2 over the whole series of similar tests (i.e. for a whole set of fruit for any given specific intra-fruit sub-regional comparison) were applied to test for consistency of th differences over a whole set.

I. In sub-sections 2.5.1.8, 2.5.1.9 and 2.5.1.10 for an autumn set, a multipl regression analysis is presented to test the separated simultaneous effects of competition factor x_i (extent or intensity of early seed development) and a positional effect (viz. either that a sub-region occurred along the carpellary margin or else along the placental edge) on the intra-fruit abortion rate. Th

regression model used, which is presented in Appendix 15 as well, was

$$p = b_0 + b_1x_1 + b_2x_2 + b_3x_3$$

where p = regression function for the proportion of aborted seeds, in the trans formed mode of angular degrees. The reason the abortion proportions were trans formed to angular degrees was because it was intended to test the significance of the regression co-efficients, b_1 , b_2 and b_3 ; and t-tests on the latter ar only valid on data which, on the null hypothesis, have an underlying normal dis tribution (Siegel, 1956; Rayner, 1969).

In the above model: b_0 , b_1 , b_2 and b_3 are regression constants for a given fruit - (that is, regression equations were fitted for each fruit in an autumn set); x_1 = a "dummy" verisble = 0 for the A, B, C, D (carpellary margin fruit sub-regions, and x_1 = 1 for the a, b, c, d (placental edge) sub-regions; $x_2 = x_i$, a competition factor (extent or intensity of early seed development introduced in sub-section D); and $x_3 = (x_i)^2$. The use of a "dummy" variable (the concept and application of which is explained in Draper and Smith, 1966), was made in order to separate out the effects due to the carpellary margin vers placental edge position within the fruit.

Being a multiple linear regression model, the residuals, e_i (formed when the regression was applied to the data) were examined. For tests of significan on the regression co-efficients b_1 , b_2 and b_3 to be valid, the $e_i = (p_i - \hat{p}_i)$ should be randomly distributed (Draper & Smith, 1966). An $e_i = (p_i - \hat{p}_i)$ = a residual value when an estimated $\hat{p}_i$ is subtracted from a given observed p_i in the transformed mode. A $\hat{p}_i$ is estimated by the regression function "p" of a given fruit for a particular (i^{th}) fruit sub-region when appropriate regressio constants and the observed corresponding x_i (and x_1 = 0 or 1) values are sub- stituted into the regression function, p . To illustrate: if the computed regression function for a fruit is $p = 50,0 + 15,0\ (x_1) - 1,5\ (x_2) + 0,01\ (x_3)$ then when x_1 = 1 (e.g. from the b intra-fruit sub-region), x_2 = 30,0 and x_3 = 900 (i.e. $x_3 = x_2^2 = 30^2$) ; $\hat{p}_i$ for the above substitutions is then

$$\hat{p}_i = 50,0 + 15,0\ (1) - 1,5\ (30,0) + 0,01\ (900)$$

$$= 29 \text{ angular degrees.}$$

If the observed abortion rate in the transformed angular mode for that particular (i^{th}) sub-region for that fruit was p_i = 37 , then $e_i = p_i - \hat{p}_i = 37 - 29 = 8$. If the e_i for the eight (A, a ... D, d) intra- fruit sub-regions are randomly distributed in a narrow parallel band about zer for the range of x_i values substituted, then the linear model is appropriate t the data, and tests of significance on the regression co-efficients will be

valid (Draper & Smith, 1966). If the residuals fan out, or follow an arc, or deviate in some other noticeable pattern, then the model needs to be altered. Thus, a band of residuals in an arc form suggests that perhaps a quadratic term is required. The model actually presented for the data analysed in Appendix 15 and sub-sections 2.5.1.8 to 2.5.1.10 actually needed the quadratic term $x_3 = (x_i)^2$.

The e_i residuals should be random. In terms of the format of the data use viz. that p_i and x_i values were actually drawn from either A/a , B/b , C/c or D/d sub-regions, the residuals had to be traced back to their sub-regional sources to see if any non-random patterns persisted. One way of doing this was to rank the e_i for any given fruit in terms of their magnitude. A concordance (W) test was applied to such rankings for all the fruit of the autumn set in question. A significant (W) or X^2 test would imply that the largest to smalles deviations from the fitted regression line tended to concentrate in some persistent, i.e. non-random pattern, thus invalidating the regression model used, and casting doubt on the regression co-efficients and their tests.

Two-tailed t-tests were carried out on the regression co-efficients of eac fruit, and the chi-square test, $X^2 = \left[\Sigma - 2 \ln p\right]$, was applied to the probabil values associated with these t-tests, thus giving an overall chi-square analysi for the whole set of fruit.

This concludes the overview of the rationale and statistical methodology that is applied to the data presented in 2.5.1 and 2.5.2. Once the results and separate implications of each sub-section has been presented, it will remain to draw them all together into an overall assessment and conclusion, and relate this to the anatomical and morphological survey presented in 2.3.

2.5 RESULTS AND DISCUSSION: INTRA-FRUIT DISTRIBUTION OF ABORTION

2.5.1 Autumn sets

Table 12 presents the distribution of normal and aborted ovule/s types as found in 14 ripe fruit set in autumn, 1970. This set had been hand-pollinated. The various ovule/seed types are those referred to in Plate 2b. In Table 12 the two typologies are set side by side to show their equivalencies

From Table 12 it can be seen that, of the sum of all ovules plus seeds, (mean 1635 per fruit), approximately 30 per cent were 'unfertilized', (U); approximately 35 per cent were slightly developed, (S); very few 'partially' developed (P); and approximately 35 per cent reached full development, (F).

TABLE 12 Distribution of normal and aborted seeds and ovules from 14 ripe whole papaya fruits set in autumn, 1970 (hand-pollinated)

Seed/ovule type designation	Total no.	Mean no. per fruit	%	Seed/ovule type designation	Mean no. per fruit	%
dB	219	15	1,0	F	572	34,9
dG	7 782	556	34,0			
cDL	73	5	0,3	P	7	0,5
cWL	32	2	0,1			
cWa	631	45	2,8	S	569	34,8
b	7 332	524	32,0			
a	6 825	487	29,8	U	487	29,8
TOTAL:	22 894	1 635	100	TOTAL:	1 635	100

Most of the latter were 'grey' (dG) seeds. Of the slightly developed seeds (S) the great majority were small, flattened (b) seeds.

Table 13 represents data of Table 12 when divided into the four fruit quarters - Aa , Bb , Cc , Dd . As a preliminary remark it may be noted that th total number of ovules and seeds in the top quarter, Aa , viz. 4 175 , is noticeably less than that of the other quarters, even that of the bottom quarter Dd. It could be expected that Aa and Dd , with similar shapes (Plate 2a), relative to that of the Bb , Cc sub-regions, would have had similar numbers. The difference is due to a larger proportion of the ovules in the Dd quarter not having been fertilized, so that for a similar placental (surface) area, the latter had many more ovules. There were differences between the thickness of the fruit wa beneath the placental surface, as may be seen in Plate 2a. This difference in thickness seemed to be related to (i) the difference in morphological position in the fruit; and (ii) the proportion of ovules for the same placental surface area which had become fully developed seeds.

With regard to the comparative distribution of each ovule/seed type, the highest percentage of fully developed seeds (F) occurred in the second quarter Bb , followed by Cc , Aa and Dd . The range was from approximately 40 to 28 pe cent. With regard to the partially-developed seeds, the highest percentage wa in Cc , followed by Bb , Dd and finally, Aa , but the actual proportions were

TABLE 13 Distribution of seed/ovule types within fruit-quarters of 14 ripe whole papaya fruit of 1970 autumn-set (hand-pollinated)

FRUIT SUB-REGION		SEED/OVULE TYPE				Total
		F	P	S	U	
Aa	No.	1 265	15	2 195	679	4 175
	%	30,8	0,38	52,6	16,3	100
	Rank	3	4	1	4	
Bb	No.	2 430	29	2 553	1 023	6 035
	%	40,3	0,48	42,3	17,0	100
	Rank	1	2	2	3	
Cc	No.	2 539	32	1 940	2 027	6 538
	%	38,8	0,49	29,7	31,0	100
	Rank	2	1	3	2	
Dd	No.	1 747	28	1 275	3 096	6 146
	%	28,4	0,46	20,7	50,4	100
	Rank	4	3	4	1	
Total no.		8 001	105	7 963	6 825	22 894
Mean no. per fruit		572	7	569	487	1 635
Overall %		34,9	0,5	34,8	29,8	100

Rank refers to the % score in a given column, i.e. for a particuler seed/ovule type down the fruit sub-regions.

rather low, ranging from 0,49 to 0,38 per cent. (The ranking order then, was not important.)

For the slightly developed seeds (S), however, the range in percentage was quite marked, (approximately 53 to 21 per cent), and the order was straight dow the fruit quarters, viz. Aa , Bb , Cc , Dd . Similarly, for the unfertilized ovules (U), the percentage range was from approximately 16 to 50 per cent, but with the highest proportion being at the bottom of the fruit (Dd), the order be the reverse of that for "S" seeds, viz. Dd , Cc , Bb , Aa . This order of "U" ovules reflects the pattern of sub-regions with least to most penetration by pollen tubes.

On the other hand, since there were very few partially-developed seeds (P) and most of the slightly-developed seeds (S) were the flattened "b" type (Table 12), the order for "S" seems to reflect that of one peak abortion with most of it having occurred at the top of the fruit and least at the bottom. The order of the fully-developed seeds (F) seems to be the resultant of the two opposite trends in "S" and "U" ovules/seeds, the most advantageous sub-regions being in the middle of the fruit.

Table 14 sets out the same kind of data as in Table 13, but for the non-hand-pollinated autumn set of 1973. Although the mean number of the estimated sum of all ovules plus seeds per fruit (1579) was similar to that of the hand-pollinated set of 1970 (1633) the percentage of all ovules fertilized was considerably lower. This can be inferred from the finding that approximately 69 per cent of all ovules remained unfertilized in the non-hand-pollinated set (compared with the approximate 30 per cent of the hand-pollinated set).

Continuing the comparison, in the non-hand-pollinated set there were relatively more partially-developed seeds (P), almost the same amount as that of the slightly-developed seeds (S), i.e. approximately eight per cent each. There were relatively more fully-developed seeds (F) than "P" and "S" types, although compared to the hand-pollinated set, only about 15 per cent as against 35 per cent respectively. However, when, compared against "P" and "S" seeds added together, the relative proportion of "F" seeds to these was approximately the same for both sets, viz. about one to one.

There was a difference in the ranking of sub-regions for fully-developed seeds, although the Bb sub-region, again, had the largest proportion of these; the top quarter (Aa) was the second highest as against third highest in the hand-pollinated set. This was in spite of the ranking of "S" and "U" seeds/ovules being the same for both sets. The greatest proportion of partially-developed seeds (P) also occurred in Aa.

In comparing Tables 13 and 14, it appears that there was probably no peak in abortion for the non-hand-pollinated set, the abortion types being apparently more evenly distributed. This may have been because of a much lower percentage of ovules being fertilized (due to presumably lower quantity of applied pollen) with a subsequent lower inter-seed competition.

Table 15 is the data of Table 14 broken down further into the eight fruit sub-regions: (A , a , B , b , C , c , D , d). From the ranking of the "U" (unfertilized) ovules, it appears that the pattern of pollen tube penetration was A , B , a , b , C , c , D , d sub-regions. The ranking of "S" seed types was a , A , b , c , B , d , C and D . For the partially-developed seeds (P)

TABLE 14 Distribution of seed/ovule types within fruit-quarters from two to four longi- (1/5th) -portions of 15 papaya fruits of 1973 autumn set (non-hand-pollinated)

FRUIT SUB-REGION		SEED/OVULE TYPE				Total
		F	P	S	U	
Aa	No.	413	341	383	1 104	2 241
	%	18,43	15,22	17,09	49,26	100
	Rank	2	1	1	4	
Bb	No.	840	393	383	2 481	4 097
	%	20,50	9,59	9,35	60,56	100
	Rank	1	2	2	3	
Cc	No.	513	257	242	3 230	4 242
	%	12,09	6,06	5,70	76,14	100
	Rank	3	3	3	2	
Dd	No.	233	132	106	2 553	3 024
	%	7,71	4,37	3,51	84,42	100
	Rank	4	4	4	1	
Total No. ...		1 999	1 123	1 114	9 368	13 604
Estimated no. per whole fruit		232	130	129	1 088	1 579
Overall % ..		14,69	8,25	8,19	68,86	100

Rank refers to the % score in a given column, i.e. for a particular seed/ovule type down the fruit sub-regions.

TABLE 15 Distribution of seed/ovule types within the 8 sub-regions from two to four longi- (1/5th) -portions of 15 papaya fruits of 1973 autumn set (non-hand-pollinated)

FRUIT SUB-REGION		SEED/OVULE TYPE				Total
		F	P	S	U	
A	No.	238	141	118	356	853
	%	27,90	16,53	13,83	41,74	100
	Rank	2	1	2	8	
a	No.	175	200	265	748	1 388
	%	12,61	14,41	19,09	53,89	100
	Rank	6	2	1	6	
B	No.	510	193	109	850	1 662
	%	30,69	11,61	6,56	51,14	100
	Rank	1	3	5	7	
b	No.	330	200	274	1 631	2 435
	%	13,55	8,21	11,25	66,98	100
	Rank	4	4	3	5	
C	No.	336	127	71	1 273	1 807
	%	18,59	7,03	3,93	70,45	100
	Rank	3	5	7	4	
c	No.	177	130	171	1 957	2 435
	%	7,27	5,34	7,02	80,37	100
	Rank	7	6	4	3	
D	No.	167	56	29	1 061	1 313
	%	12,72	4,27	2,21	80,81	100
	Rank	5	8	8	2	
d	No.	66	76	77	1 492	1 711
	%	3,86	4,44	4,50	87,20	100
	Rank	8	7	6	1	
Total No.		1 999	1 123	1 114	9 368	13 604
Overall %		14,69	8,25	8,19	68,86	100

Rank refers to the % score in a given column, i.e. for a particular seed/ovule type down the fruit sub-regions.

it was A , a , B , b , C , c , d , D . It seems as if the order of abortion increased the closer a sub-region was to the stigma-end, or the earlier a sub-region received pollen tube penetrations. From the ranking of fully-developed seeds (F), viz. B , A , C , b , D , a , c , d , the carpellary margin sub-regions also appeared to be more favourable for a higher proportion of "F" seed With such a high percentage of total ovules not being fertilized, both the ranking of sub-regions with fully-developed seeds, and that of abortive types was approximately the same (i.e. these rankings were not mutually exclusive).

If one discounts the "U" ovules as being a component part of seed abortion one is left with the proportion of (P + S) seeds relative to (F + P + S) seeds as being the estimator of seed abortion. Table 16 presents this rate for the non-hand-pollinated autumn set as a whole. The ranking of sub-regions relative to this seed abortion rate was a , d , c , b , A , B , C , D . Conversely, of just those ovules which (most likely) received a pollen tube, the order of sub-regions to have developed the most normal (F) seeds was D , C , B , A , b , c , d , a . That is, the greatest frequency of abortion occurred along the placental edge as opposed to the carpellary margin; and within either of these two major sub-regions, the top quarter of the fruit had the most abortions.

The above tables presented data for whole sets of fruits. The sets were not necessarily homogeneous, especially that of the non-hand-pollinated autumn set of 1973. The data has therefore been broken down into that of individual fruits and various statistical tests have been applied to this body of data.

2.5.1.1 Concordance test on the distribution of ovule and seed types. Appendix 3 provides the results of concordance tests on the ranks of the intra-fruit proportions of different ovule/seed types for the hand-pollinated set of autumn, 1970. From Appendix 3, Table 3.1, it can be seen that the overall ranking (for the whole set) of the proportion of "a" ovules to all ovules and seeds was significant ($p \leq 0,01$). The ranking in terms of the highest to lowest proportions of "a" unfertilized ovules was Dd , Cc , Bb , Aa . This conforms the impression formed from Table 13 (ranking of "U" ovules).

The pattern of "b", flattened, slightly-developed seeds, relative to the total number of ovules/seeds was also significant ($p \leq 0,01$). The overall ranking for the whole set was Aa , Bb , Cc , Dd , i.e. the more of these the closer the sub-region was to the stigma end (Appendix 3, Table 3.2). The patterns for "cWs", "cWL" and "cDL" seeds, however, were not significant (Appendix 3, Tables 3.3, 3.4 and 3.5 respectively). It has already been pointed out that the greatest proportion of "aborted seeds" for this set was amongst the "b" seeds, with only a relatively small contribution from the other types - (Table 12). The

TABLE 16 Distribution of seed types and seed abortion rates within 8 sub-regions from two to four longi- (1/5th) -portions of 15 papaya fruits of 1973 autumn set (non-hand-pollinated)

FRUIT SUB-REGION		SEED TYPE			"Seeds" $\sum$	Seed abortion rate $\frac{(P + S)}{(F + P + S)}$ %
		F	P	S		
A	No.	238	141	118	497	
	%	47,89	28,37	23,74	100	52,11
	Rank	4	3	5		5
a	No.	175	200	265	640	
	%	27,34	31,25	41,41	100	72,66
	Rank	6	2	1		1
B	No.	510	193	109	812	
	%	62,81	23,77	13,42	100	37,19
	Rank	3	7	6		6
b	No.	330	200	274	804	
	%	41,04	24,88	34,08	100	58,96
	Rank	5	5	4		4
C	No.	336	127	71	534	
	%	62,92	23,78	13,30	100	37,08
	Rank	2	6	7		7
c	No.	177	130	171	478	
	%	37,03	27,20	35,77	100	62,97
	Rank	6	4	2		3
D	No.	167	56	29	252	
	%	66,27	22,22	11,51	100	33,73
	Rank	1	8	8		8
d	No.	66	76	77	219	
	%	30,14	34,70	35,16	100	69,86
	Rank	7	1	3		2
Total no.		1 999	1 123	1 114	4 236	
Overall %		47,19	26,51	26,30	100	52,81

Rank refers to % score in a given column, i.e. for a particular seed type down the fruit sub-regions.

non-significant results for the "c(Ws , WL , DL)" seeds was thus not surprising.

The pattern of fully-developed, grey seeds was significant ($p \leq 0,01$; Appendix 3, Table 3.6). The highest relative frequency was in the Bb sub-regio followed in order by Cc , Dd , Aa . The lowest ranking for the top quarter, Aa , ties in with that of the reversed (highest) ranking for the "peak" abortio type, "b" . The overall ranking for the black, "fully-developed" seeds, dB , was not significant (Appendix 3, Table 3.7). It has already been seen from Table 12 that there were relatively very few such seeds, so this result is not surprising.

Appendix 5 presents a similar concordance test on the rankings of ovule/seed types from the non-hand-pollinated autumn set. This was done on the "F - P - S - U" typology of ovule/seed types.

From Appendix 5, Table 5.1, it is clear that the overall ranking of sub-regions for the proportion of "U" ovules relative to the sum of all ovules plus seeds was significant ($p < 0,001$). The overall ranking, in terms of highest to lowest frequency per sub-region was d , D , c , C , b , B , a , A . This probably reflects the effect of the pattern of pollen tube penetration.

The overall ranking of the pattern of "S" seeds per total ovules and seeds was also significant ($p < 0,001$). The order from highest to lowest was a , A , b , c , B , d , C , D . Relative to the total of ovules plus seeds, the overall ranking of "P" seeds was also significant ($p < 0,001$; Appendix 5, Table 5.3). The order for highest to lowest frequency was A , a , B , b , C , d , c , D . The top half of the fruit thus was more susceptible to having this type of seed

Fully-developed (F) seeds were also significantly ranked for the whole set ($p < 0,001$; Appendix 5, Table 5.4). The overall ranking was B , A , C , D , b , a , c , d . The greatest proportion of fully-developed seeds tended to be concentrated along the carpellary margin, from the top of the fruit to the bott (except that the B sub-region was higher than that of the A sub-region). The pattern seems to reflect that of the most likely pollen tube penetration.

When the contribution of "U" ovules was discounted, so that the rankings o the remaining types was relative to only that of the seeds which showed signs o development, the distribution of "S" seeds was still significant ($p < 0,001$; Appendix 5, Table 5.5). The order then was a , c , b , d , A , D , C , B . Again, this overall ranking suggests that abortions of this seed type were more prevalent along the placental edge, and more at the fruit apex. The overall ranking of "P" seeds to total (F + P + S) seeds was <u>not</u> significant (Appendix 5

Table 5.6); but that of the "f" seeds was significant ($p < 0,001$; Appendix 5, Table 5.7). The overall ranking of "f" to nil seeds was D , C , B , A , c , d , b , a . That is, the greatest proportion of fully-developed seeds were alo the carpellary margin, from the base of the fruit up to the apex or top quarter The same trend, from base to apex, existed for the placental edge sub-regions, except for an interchange in order between c and d sub-regions.

The concordance tests of Appendices 3 and 5 were largely confirmatory with respect to the distribution of undeveloped ovules "U" or "a", and of fully-developed seeds "f". A difference between the hand- versus non-hand-pollinated sets was in the significance of the "P" seed type (cWL plus cDL). The failure to find significance for this type in the hand-pollinated set was probably due to its generally low proportion in this set. However, when "P" seeds were compared against the total number of seeds (i.e. excluding ovules), their distribution showed non-significance in the non-hand-pollinated set as well.

2.5.1.2 χ^2 tests on the difference in abortion rates between carpellary margin and placental edge regions. Appendix 4 provides the basic data from which further tests were applied to the non-hand-pollinated autumn set of 1973. Appendix 6, Table 6.1 presents "Total χ^2" on the abortion rates (p_i) for all sub-regions of each fruit of this set. The additive Total χ^2 of the individual fruit Total χ^2 was highly significant; as was the Heterogeneity χ^2, so that the Pooled χ^2 value was somewhat meaningless. However, the chi-square value ($\chi^2 = \left[\Sigma - 2 \ln p\right]$) gave another check on the whole set, and whilst this chi-square value (with a greater number of degrees of freedom, and hence more stringent test) was lower than that of the Pooled χ^2, it was still highly significant. The implication, then, was that there were significant differences among fruit sub-regions with regard to the abortion rate p_i (Appendix 4), and that these differences also occurred throughout the set as a whole.

Following on from that result, Appendix 6, Table 6.2 presents "χ^2 differen tests on the abortion rates p_i between carpellary margin (A , B , C , D) and placental edge (a , b , c , d) fruit sub-regions. The additive Total χ^2 value for the individual fruits' "χ^2 differences" values was highly significant. The was, again, a highly significant Heterogeneity χ^2, implying that the extent of "differences" varied from one fruit to the next. Thus the Pooled χ^2 value for the whole set is misleading. However, the alternative χ^2 value = $\left[\Sigma - 2 \ln p\right]$ was still highly significant. This implies that although the fruits of this s varied appreciably in regard to the "differences" in abortion rates between carpellary margin and placental edge sub-regions, these "differences" were

nevertheless large enough throughout the whole set when considering one fruit after the other.

To test this in another way (Appendix 7), a concordance test on the ranks of the abortion rates p_i , tests the consistency of the order of p_i rates from one fruit to the next. The result was highly significant, and the overall ranking of abortion rates per fruit sub-region was a , b , d , c , A , B , C , D . That is, abortion rates were consistently higher in the placental edge regions, and consistently higher towards the upper part of the fruit for both placental edge and carpellary margin sub-regions (with the exception that in th placental edge sub-regions, the basal d region tended to have a higher rate tha that of the adjacent c region).

2.5.1.3 Concordance test on the distribution of a competition factor. Appendix 8 provides a concordance test on the rankings of a competition factor x_i of Appendix 4, viz. the intensity or extent of early seed development per fruit sub-region. The test was highly significant, implying that there was a consistent pattern between fruits of the 1973 autumn set. The overall ranking was (in order of highest to lowest degree of early seed development) A , a , B b , C , c , D , d . This was as expected, given the findings of 1.3.1 on early seed development in the 1971 autumn set, particularly that of the pattern of pollen tube penetrations (1.3.1.3, Fig. 6), viz. a pattern virtually the same a the above.

2.5.1.4 X^2 and t-tests on the difference in the competition factor intens between carpellary margin and placental edge regions. Taking t test of Appendix 8 still further, Appendix 9 shows the overall $X^2 = \left[\Sigma - 2 \ln p\right.$ on a series of paired t-tests. The t-tests evaluated the associated probabilities of getting the mean difference in the competition factor (extent or intens of early seed development) between adjacent four pairs of carpellary margin versus placental edge sub-regions for the given individual fruits. The author interprets these test results to imply that although about half the individual t-tests, (with only three degrees of freedom each), proved inconclusive, the overall pattern as judged by the overall $X^2 = \left[\Sigma - 2 \ln p\right]$ was significant. That is, even the mean value of the four pairs of differences (A - a , B - b , C - c , D - d) was likely to be significant in a given fruit.

2.5.1.5 Quantitative χ^2 tests on the relation between the competition factor and abortion rates. Given the previous results indicating differences in the extent or intensity of early seed development within a fruit, Appendix 10 shows the quantitative relationship between this competition factor and the abortion rates within the fruit. Appendix 10, Table 10.1 shows χ^2 tests for the carpellary margin (A , B , C , D) sub-regions whereas Appendix 10, Table 10.2 shows these for the placental edge (a , b , c , d) sub-regions.

Taking Appendix 10, Table 10.1 only, the additive Total χ^2 on the individual Total χ^2's was highly significant. However, the Heterogeneity χ^2 was also significant, implying differences between fruits with regard to the differences in abortion rates within fruits. Disregarding the Pooled χ^2 for this "Total χ^2" then, the alternative $\chi^2 = \left[\Sigma - 2 \ln p\right]$ was still highly significant. That is, differences in abortion rates within the carpellary margin sub-regions existed for the set of fruit as a whole.

Testing thereafter, the relationship between the competition factor and abortion rates, the additive Total χ^2 on individual "χ^2 slope" was highly significant. The Heterogeneity χ^2 for the same series was just significant at the five per cent level, so disregarding the significant Pooled χ^2, the alternative $\chi^2 = \left[\Sigma - 2 \ln p\right]$ was still highly significant. Although not presented here, the regression relationship between the competition factor and the abortion rates tended to be positive. This trend can be picked up by comparing the pair of x_i and p_i values of Appendix 4. The implication here was that although nearly half of the individual tests on the regression co-efficient, as judged by "χ^2 slope", did not reach significance, the overall trend was significant. That is, generally, greater abortion rates tended to be positively associated with greater degrees of early seed development within any given fruit.

The additive Total χ^2 test on the individual "χ^2 linearity" values were highly significant, suggesting that the relationship between the competition factor and abortion rates was not linear. The Pooled χ^2 for the series of "χ^2 linearity" suggest that there was no significance, thus suggesting that the differences among fruits with regard to the degree of linearity cancelled each other out when data was pooled. However, the Heterogeneity χ^2 for this series was significant. In addition, the 'significant' alternative $\chi^2 = \left[\Sigma - 2 \ln p\right]$ test also suggested that the relationship was not well represented by a straight line. To put it in another way, the abortion rates within the fruits, although tending to be positively associated with the extent of early seed development, was nevertheless not well represented by a single termed linear relationship.

Appendix 10, Table 10.2 presents the same analysis for the placental edge sub-regions on their own. The results are the same as those for the carpellary

margin sub-regions, the difference being that the X^2 values for just about every test were higher for the placental edge sub-regions.

The above Appendix 10 related abortion rates found within ripe fruits with the estimated intensity of early seed development for the same fruits. Appendix 11 represents a similar analysis on the effect of early seed development or early seed abortion as observed at the sixth week after anthesis in the 1971 hand-pollinated autumn set. In Appendix 11, Table 11.1, the estimator for early seed development was the mean cross-sectional area of the median longitudinal plane between inner integuments for a given fruit sub-region. The measure for early seed abortion was the proportion of pollinated seeds lacking normal endosperm. A second estimator of early seed development was used, as shown in Appendix 11, Table 11.2, viz. the percentage of pollen tube penetrations. The latter approximates the measure of early seed development used on samples from ripe fruits, already presented in previous appendices, viz. the percentage of total ovules plus seeds that were fertilized,

$$\left[\frac{F + P + S}{F + P + S + U}\right]_i \quad ,$$

for each fruit sub-region.

Appendix 11, Table 11.1 provides the basic data for this sample under n_i , x_i and p_i . The rest of this table provides details of the regression and X^2 types of analyses (only part of which has been presented in previous appendices). Considering now only the X^2 analysis, and taking the analysis represented at the bottom of the table first, the "X^2 total" for the sub-regions A , a , ... D , d was highly significant. The "X^2 slope" was also highly significant, and negative in slope. The X^2 linearity was also significant at the five per cent level, implying that the tested relationship was not linear.

Considering now only the carpellary margin sub-regions, A , ... D , the "X^2 total" was just significant at the five per cent level. "X^2 slope" was significant at the one per cent level, and the slope was negative. "X^2 linearity" was not significant, implying that the relationship between x_i and p_i (i.e. between the estimator of intensity of early seed development and the measure of the abortion rate) <u>was</u> linear.

With regard to the placental edge sub-regions on their own, i.e. a , ... d the "X^2 total" was highly significant; "X^2 slope" was significant at the five per cent level, and the slope negative; whilst the "X^2 linearity" was significant at the one per cent level, implying that the relationship was <u>not</u> linear.

The X^2 analysis of Appendix 11, Table 11.2 follows very closely that of Appendix 11, Table 11.1, suggesting that the percentage of pollen tube penetrations was an accurate index for the methodologically more appropriate (parametric) measure of x_i in Appendix 11, Table 11.1. Perhaps then the index, x_i, used in the samples from ripe fruits, viz.

$$\left[\frac{(P + S)}{(F + P + S)}\right]_i ,$$

was a good measure of the degree or intensity of early seed development.

Comparing the results of Appendices 10 and 11 respectively, one marked difference was that whereas:

(i) the effect of a greater degree of early seed development in the hand-pollinated autumn set of 1971 at the sixth week was associated with lower proportions of early seed abortion; and

(ii) in the case of the non-hand-pollinated autumn set of 1973 at fruit ripening, the effect on later and final seed abortions was positive, (i.e. larger degrees of early seed development associated with higher abortion rates).

In comparing x_i and p_i data of the hand-pollinated set of Appendix 11, Table 11.2 (at the sixth week after anthesis) with that of the non-hand-pollinated set of Appendix 4 (at fruit ripening), it is interesting to note that the percentage of pollen tube penetrations (x_i) was much higher for the hand-pollinate set at the sixth week, whereas the abortion rates of the same hand-pollinated set were much lower than those of the non-hand-pollinated set seen at fruit ripening. It has already been suggested in 2.3.2 that the bulk of early seed abortion occure after the sixth week. This seems to be supported by the evidence of low levels of apparent seed abortion at the sixth week, and the apparent opposite effect of the intensity of early seed development on seed abortion The seed abortion up to the sixth week may have been related more to the lateness in arrival of pollen tubes. This lateness in arrival would likely have be negatively correlated with the percentage of pollen tube penetrations.

2.5.1.6 Qualitative $\bar{X}^2$ tests on an ordered distribution of abortion along the fruit stem-apex axis. Appendix 12, Table 12.1 presents the result of a qualitative chi-square ($\bar{X}^2$) test on an ordered distribution of seed abortions in the carpellary margin sub-regions. This hypothesized order was $A > B > C > D$. This order was confirmed in half the fruit ($p \leq 0,05$), and

about two-thirds had associated $\overline{X}^2$ probability levels less than 10 per cent. (The author knows of no overall chi-square test applicable to a series of these $\overline{X}^2$ tests.)

The results of this test on the abortion rates of the placental edge sub-regions was similar to that of the carpellary margin sub-regions. From these tests it is apparent that the majority of fruits sampled from the autumn set of 1973 had a gradient of seed abortion, increasing from the base to the stigma en of the fruit.

2.5.1.7 X^2 tests on the distribution of abortion within the fruit stem-apex axis. Appendix 13 presents a series of X^2 tests on the differences in abortion rates between selected sub-regions within either the carpellary margin or the placental edge for fruits set in autumn, 1973. An additive total X^2 was applied to each of these comparisons. The results were a follows:-

Within the carpellary margin sub-regions

(i) there was no significant differences between ABC versus D sub-regions (Appendix 13, Table 13.1);

(ii) highly significant differences between A versus BC sub-regions (Appendix 13, Table 13.2); and

(iii) no significant differences between BC versus D sub-regions (Appendix 13, Table 13.3).

With regard to the placental edge sub-regions:-

(i) there were significant differences at the five per cent level for abc versus d sub-regions (Appendix 13, Table 13,4);

(ii) there were highly significant differences between a versus bc sub-regions (Appendix 13, Table 13.5); and

(iii) there was no significant differences between bc versus d sub-regions (Appendix 13, Table 13.6).

Since the result of Appendix 13, Table 13.6 was not significant, the signi ficance between abc versus d sub-regions was really due to the abortion rates of sub-region a. Thus the results of Appendix 13 indicate that there were two significant sub-regions along the fruit stem-apex, viz. at A and a .

When "X^2 differences" tests were applied to the data of early seed abortio of the autumn set of 1971, at the sixth week, the results were as follows (Appendix 14):-

(i) There was a significant difference (five per cent) between the carpellar margin fruit sub-regions (A , B , C , D) versus the placental edge sub-regions (a , b , c , d);

(ii) there was almost a significant difference between carpellary margin A, B versus C, D sub-regions (i.e. top half versus bottom half of the fruit);

(iii) there was no significant difference between the corresponding a, b versu c, d placental edge sub-regions; and

(iv) there was a highly significant difference between the bottom quarter of the fruit (D, d) and the top three-quarters (A, a, B, b, C, c).

Thus even at the sixth week after anthesis, differences existed between th carpellary margin and the placental edge regions. The difference at the lowest quarter would appear to be due to the lateness in arrival of the pollen tubes into this sub-region. Again, the component of abortion that appears to have taken place as early as the sixth week probably only formed a small part of the final abortion rates.

2.5.1.8 Multiple regression equations on intra-fruit abortion rates. Multiple linear regression equations were fitted to data of Appendix 4, and the model used is outlined in Appendix 15. A dummy variable was used to represent the location of a sub-region as being along the carpellary margin ($x_1 = 0$) or along the placental edge ($x_1 = 1$). It was assumed that a sub-region being alon the placental edge would have been more subject to seed abortion, and thus this region was assigned the dummy variable of one; as opposed to that of zero assigned to the carpellary margin. The other independent variable was the deg of early seed development, x_i of Appendix 4. When regression equations were fitted using just these two independent variables, and even after using the angular degree transformation of abortion proportions, the residual (e_i) still remained patterned in an arc. The square of x_i , viz. $(x_i)^2$ was then introduc as an additional term, and the residuals tended to be more randomly spread aro the regression lines. (This latter trend is dealt with again in 2.5.1.10.)

Appendix 15, Table 15.1 presents the regression constants of weighted equations of each of eleven fruits of the autumn set of 1973. The reason for

them being weighted was because on the null hypothesis the abortion rate or proportion was taken to be the same throughout all the fruit sub-regions in a given fruit. Any deviations from the fruit's seed abortion rate, (or 2/5th or 4/5th portion depending on the amount used), was assumed to be due to "error". However, since the total number of seeds (F + P + S), on which the abortion rates were based, varied from sub-region to sub-region, those sub-regions with the greater number of these (e.g. B/b to C/c sub-regions) could be thought of as providing a more accurate estimate of the whole fruit abortion rate than tho of the naturally smaller sub-regions (A/a , D/d). Thus, on the null hypothesis the regression equations were weighted, i.e. each set of $\left[p_i , (x_1 , x_2 , x_3)_i\right]$ were weighted by the factor w_i of Appendix 4. (Weighted regression equations to estimate proportions were also used in 2.5.1.5 after the computational metho of Fleiss, 1973.)

Appendix 15, Table 15.1 presents the equations together with their multipl correlation co-efficients. (These weighted regression equations also provided slightly better fits, with slightly higher multiple correlation co-efficients than unweighted equations.) The multiple correlation co-efficients ranged from 0,718 to 0,945. The co-efficient of multiple determination which is the square of the correlation co-efficient, (Ezekiel & Fox, 1959), thus ranged from 51 to 89 per cent. That is, these regression equations accounted for 51 to 89 per cent of the variation in the data.

Concerning the regression constants themselves, only b_1 (the dummy variabl had a consistent sign, viz. it was positive for all fruits. The b_2 and b_3 , which indicated the amount of effect on the abortion rate caused by the intensi of early seed development as a competition factor, changed signs relative to ea other; i.e. one was always positive and the other negative, (with the exceptio of fruit No. 15, where both were positive). The two (b_2 and b_3) were really a division of this total "seed competition" effect into linear and quadratic com- ponents. For some fruit the best combination to fit the data was a negative linear together with a positive quadratic; in others the best combination was positive linear together with a negative quadratic. The b_0 value also varied in sign from fruit to fruit, depending on the data and the other 'fitted' re- gression constants.

The meaning of these regression co-efficients were as follows, using fruit No. 1 as an illustration. In a given intra-fruit sub-region, one positive unit change in x_1 was calculated to be accompanied by plus 15,09 units of p , the proportion of aborted seeds, whose unit was angular degrees. One positive unit change in x_1 was equivalent to shifting from the carpellary margin to the placental edge sub-regions. The calculated effect on abortion in a given

intra-fruit sub-region due to changes in x_i of Appendix 4, i.e. due to changes in the index of seed competition, had a more complex expression. A positive unit change in this factor was calculated to be accompanied by a negative component (x_2) of 1,044 angular degrees, and a positive component (x_3 of 0,0172 times "the square of the change in the competition index", also as angular degrees of seed abortion.

Thus for a change of "x_i" = +1,0 per cent, the nett effect on abortion would have been a decrease of 1,027 angular degrees. A maximum decrease in abortion would have been reached for a positive change in "x_i" close to +30 per cent change, i.e. close to -15,84 angular degrees. With greater increases in change in "x_i" the abortion rate would have started to increase so that with a positive change of "x_i" = 61 per cent, the nett change in abortion would have be +0,317 angular degrees. The b_0 co-efficient = 47,99 means that irrespective of changes in either x_1 or "x_i" (x_2 , x_3) , a basal value of +47,99 angular degrees would have had to have been allowed for.

And so on for all the other fruits. What would have been the effect of just changing "x_i" , the competition factor? The estimates differ for each fruit, an for different amounts of change in this factor. But when considered from zero up to those changes required to increase "x_i" to 80 per cent for each sub-region, the nett effect averaged over all those fruits remained close to zero. The possibility of this result was suspected on just examining the b_2 and b_3 values for the whole series (Appendix Table 15.1).

2.5.1.9 χ^2 and t-tests on regression co-efficients. Appendix 15, Table 15 provides the probability values of t-tests carried out on the b_1, b_2 and b_3 regression co-efficients for each of the eleven fruits. A $\chi^2 = \left[\Sigma - 2 \ln p\right]$ tes was carried out on these t-test (p) values for each of these regression co-efficients to determine their significance for the whole set of fruits. This latter overall test was highly significant for the b_1 co-efficient, but not sign ficant for the b_2 and b_3 co-efficients. That is, although the regression equati (Appendix Table 15.1) gave reasonably close fits to the data, and the b_1 co-effi cient was consistently and accurately estimated, not much store can be given to the values of the b_2 and b_3 co-efficients. Their real values may have actually been close to zero. It seems that the "intensity of early seed development" (as measured here) was not a major factor in seed abortion.

2.5.1.10 Concordance check tests on the distribution of the regression equation residuals. Appendix 15, Table 15.3 presents a concordance test on the ranks of the residuals (e_i) formed when the observed set o x_1 , x_2 and x_3 values of a particular fruit were substituted into the computed regression equation of such a fruit (Appendix 15, Table 15.1) and the resultant $\hat{p}_i$ compared with the observed p_i . Repeating this substitution for each of the i fruit sub-regions provided a set of e_i residuals, and these were ranked accor ing to magnitude, with the largest positive residual in the first rank and the largest negative residual in the eighth rank. This ranking was carried out for each of the fruit, with ranks identified to the particular (i^{th}) sub-region from which the $(x_1 , x_2 , x_3)_i$ arose. The concordance test on the whole set of fruit was W = 0,126 or X^2 = 9,727 , with an associated probability of p = 0,204 This implies that the set of regression equations did not have a significant pattern of residuals (at the five per cent level). The latter finding would ha invalidated the regression model used. When the quadratic term (x_3) was not used, this test was significant.

Nevertheless, this p value of 0,2046 is not too far off significance. Interestingly enough, the overall ranking (which would not normally be useful t present with a nonsignificant concordance test) shows that the largest residual tended to occur at the A/a fruit sub-regions.

Thus the regression model and measurements used gave fairly close 'fits' to the data, but failed to provide either consistent or accurate measures of th "intensity of seed development" competition effect. Furthermore, it left unexplained an almost significant deviation of the data from the fitted regress lines in the region of the top quarter of the fruit.

2.5.2 Summer sets

Table 17 presents the distribution of normal and aborted ovule/ seed types found in 24 ripe fruit set in summer, 1970. It can be compared with that of the 1970 autumn set (2.5.1 and Table 12). Both were hand-pollinated. The mean number of total ovules plus seeds was 2 016 (versus 1 635 of the autum set). Approximately twelve per cent were unfertilized (U), (30 per cent in autumn set); about seven per cent (versus 35) were slightly developed (S); eight-and-a-half per cent reached partial development (P); and nearly seventy- three per cent reached full development (F). Of the latter nearly nine per cen were of the dB ('black') type. In comparison, very few autumn set seeds were o the partially-developed type (P); and 35 per cent (nearly all dG, "grey") reached full development.

TABLE 17 Distribution of normal and aborted seeds and ovules from 24 ripe whole papaya fruits set in summer, 1970 (hand-pollinated)

Seed/ovule type designation	Total no.	Mean no. per fruit	%	Seed/ovule type designation	Mean no. per fruit	%
dB	4 107	171	8,5	F	1 462	72,5
dG	30 988	1 291	64,0			
cDL	2 024	84	4,2	P	172	8,5
cWL	2 103	88	4,4			
cWs	2 715	113	5,6	S	133	6,6
b	472	20	1,0			
a	5 978	249	12,4	U	249	12,4
TOTAL	48 387	2 016	100	TOTAL	2 016	100

In comparing the subdivisions of the slightly-developed (S) category, only a small proportion were of the 'b' (flattened) type, the rest being the unflatte ed, slightly larger 'cWs' type. In the autumn set (Table 12), nearly all seeds of (S) type were of the 'b' sub-category. In the partially-developed (P) categ the summer-set seeds were evenly divided between 'cWL' and 'cDL' types.

So, there was a more even spread of seed types among the sub-categories of the summer set than in the autumn set. Seed abortion would appear, then, to have been more evenly 'spread out' in time of occurrence. There were, of cours many more seeds reaching full development in the summer set, and correspondingl fewer ovules remaining unfertilized.

No table corresponding to that of Table 13 for the autumn set, giving a breakdown of the ovule/seed type categories according to fruit sub-regions, is available. At the time of making the ovule/seed counts, the summer-set fruits had been cut longitudinally into 1/5th portions, but not further subdivided. From the data gathered there, it was seen that the variation from one (fifth) portion to another, in a fruit, was seldom great, thus allowing for the use of two- to four-fifth portions to estimate whole fruit patterns in subsequent stud

Table 18 sets out the data for ovule/seed type relative to fruit sub-regio found in 21 fruits of the non-hand-pollinated summer set of 1972/73. (This is also comparable with that of the 1973 autumn-set data set out in Table 14.) As

TABLE 18 Distribution of seed/ovule types within fruit quarters from 2/5th longi-portions of 21 papaya fruits of 1972/73 summer set (non-hand-pollinated)

FRUIT SUB-REGION		SEED/OVULE TYPE				Total
		F	P	S	U	
Aa	No.	1 583	154	60	428	2 225
	%	71,2	6,9	2,70	19,2	100
	Rank	1	1	1	4	
Bb	No.	3 095	274	119	984	4 472
	%	69,2	6,1	2,66	22,0	100
	Rank	2	2	2	3	
Cc	No.	2 702	215	73	1 673	4 663
	%	58,0	4,6	1,57	35,9	100
	Rank	3	3	3	2	
Dd	No.	1 612	147	53	2 180	3 992
	%	40,4	3,7	1,33	54,6	100
	Rank	4	4	4	1	
Total no.		8 992	790	305	5 265	15 352
Estimated no. per whole fruit		1 124	99	38	658	1 919
Overall %		58,6	5,2	2,0	34,3	100

Rank refers to the % score in a given column, i.e. for a particular seed/ovule type down the fruit sub-regions.

was found with the two comparable autumn sets, the estimated mean number of tota ovules plus seeds for hand-pollinated versus non-hand-pollinated fruits was very nearly the same, viz. 2016 versus 1919 respectively (and 1633 versus 1579 in the respective autumn sets). And again, many more ovules remained unfertilized in the non-hand-pollinated summer set (34 versus 12 per cent). There were, of course, many more unfertilized ovules in the two autumn sets (69 and 30 per cen for non- versus hand-pollinated sets respectively).

Table 19 is the data of Table 18 broken down further into the eight fruit sub-regions, just as Table 15 is the more detailed version of Table 14 (2.5.1) for the comparable autumn set. From the rankings of the "U" (unfertilized) ovules the likely pattern of early pollen tube penetration of ovules would have been the reverse of this, viz. B, A, a, C, b, c, D, d (A, B, a, b, C, c, D, d for the autumn set, Table 15). Apart from reversals in the first and second, and fourth and fifth rankings respectively, the summer- and autumn-sets orderin are identical.

The rankings for the "S" seed type, viz. a, b, d, C, B, c, A, D compares w that of a, A, b, c, B, d, C, D of the autumn set. Both sets had the same sub-regions for the first, fifth and last ranks, and in both of the first four rank ings: three were from the placental-edge sub-regions. In both of these non-hand-pollinated sets, the overall level of abortion was low. The question of significance of the ordering the "S" types in the summer set is dealt with in 2.5.2.1.

The order for the partially-developed seeds, (P), in the summer set was a, b, A, B, C, c, d, D as against A, a, B, b, C, c, d, D of the autumn set (Table 15). These were identical for the bottom half of the fruit. The only difference in the top half was that in the summer set, the placental edge regio were apparently more susceptible to abortions of the "P" type than the carpella margin sub-regions. Otherwise the orderings were the same for both seasons. T top quarter was more susceptible than the second quarter. All in all, it seems that the patterns of seed abortion in summer and autumn sets share many similar ties, differing mostly in the degree of abortion and the more detailed distri-bution within sub-categories.

The rankings for the fully-developed "F" seeds in the summer set was B, A, C, a, b, c, D, d as against that of B, A, C, b, D, a, c, d of the autumn set (Table 15). The ordering was identical for the first three, and last, places. For the remaining (fourth to seventh) places, viz. a, b, c, D for summer and b, D, a, c for autumn, the order was more regular down the placental edges in summer. In the autumn set, where relatively greater levels of abortions occurr

TABLE 19 Distribution of seed/ovule types within the 8 sub-regions from 2/5th longi-portions of 21 papaya fruits of 1972/73 summer set (non-hand-pollinated)

FRUIT SUB-REGION		SEED/OVULE TYPE				Total
		F	P	S	U	
A	No.	675	57	12	122	866
	%	77,9	6,6	1,39	14,1	100
	Rank	2	3	7	7	
a	No.	908	97	48	306	1 359
	%	66,8	7,1	3,53	22,5	100
	Rank	4	1	1	6	
B	No.	1 515	104	29	247	1 895
	%	80,0	5,5	1,53	13,0	100
	Rank	1	4	5	8	
b	No.	1 580	170	90	737	2 577
	%	61,3	6,6	3,49	28,6	100
	Rank	5	2	2	4	
C	No.	1 418	99	33	479	2 029
	%	69,9	4,9	1,63	23,6	100
	Rank	3	5	4	5	
c	No.	1 284	116	40	1 194	2 634
	%	48,8	4,4	1,52	45,3	100
	Rank	6	6	6	3	
D	No.	817	59	15	818	1 709
	%	47,8	3,5	0,88	47,9	100
	Rank	7	8	8	2	
d	No.	795	68	38	1 362	2 283
	%	34,8	3,9	1,66	59,7	100
	Rank	8	7	3	1	
Total no.		8 992	790	305	5 265	15 352
Overall %		58,6	5,2	2,0	34,3	100

Rank refers to the % score in a given column, i.e. for a particular seed/ovule type down the fruit sub-regions.

in the top quarter placental edge sub-region (a), and also earlier pollen tube penetrations into D (relative to the nearby placental edge regions), there was a slight displacement in the ordering relative to that of the summer set.

Table 20 presents the seed abortion rate [estimated by $(\frac{P + S}{F + P + S})$] for the 1972/73 non-hand-pollinated summer set as a whole. The rank order of abortion was b, a, d, c, A, C, D, B as compared to a, d, c, b, A, B, C, D of the autumn set (Table 16). [In both, abortion was greatest in the placental edge sub-region. The overall level (10,86 per cent) in the summer set was much lower than that in the autumn set (52,81 per cent).] So, although there were some changes within the order of both placental edge and carpellary margin sub-regions respectively the seed abortion rates within these groups were so close that perhaps the only striking feature was that the a/A quarter again had the highest rates.

Considering the "S" component of total seed abortion for the non-hand-pollinated summer set (Table 20), the rank ordering was b, a, d, c, C, B, D, A compared to a, c, d, b, A, B, C, D of the corresponding autumn set. But, the overall seed abortion rate for this component ("S") was so low (3,02 per cent compared to 26,30 per cent for the autumn set) that, again, the only relevant feature is the greater susceptibility of the placental edge sub-regions.

For the "P" component the summer set rank ordering was d, b, a, c, A, D, C, B compared to d, a, A, c, b, C, B, D in the corresponding autumn set. The overall abortion rate for this component was 7,8 per cent for the summer set compared to 26,5 per cent for the autumn set. Again, given the low abortion rate and relatively narrow range, about the most that can be said is that the placental edge was, again, more susceptible to abortion.

The rank ordering of the percentage of fully-developed seeds ("F") relative to all seeds (excluding "unfertilized ovules") was B, D, C, A, c, d, a, b for the summer set (Table 20). The comparative ranking for the autumn set was D, C, B, A, b, c, d, a. The overall percentage of "F" seeds was 89,1 per cent, ranging from about 86 to 92 per cent (overall 47,2 per cent, range about 27 to 66 per cent in the autumn set). The striking features, then, were the relatively high overall percentage, plus the narrow range of the summer set, and that the carpellary margin sub-regions had more developed "F" seeds than the placental sub-regions.

The previous tables represented the pooled data of the summer sets. As was done with the data of the autumn sets, series of statistical tests were also applied to individual fruits and whole sets (where applicable). The results of these follow.

TABLE 20 Distribution of seed types and seed abortion rates within 8 sub-regions from 2/5th longi-portions of 21 papaya fruits of 1972/73 summer set (non-hand-pollinated)

FRUIT SUB-REGION		SEED TYPES			"Seeds" $\sum$	Seed abortion rate $\frac{(P + S)}{(F + P + S)}$ %
		F	P	S		
A	No.	675	57	12	744	
	%	90,73	7,66	1,61	100	9,27
	Rank	4	5	8		5
a	No.	908	97	48	1 053	
	%	86,23	9,21	4,56	100	13,77
	Rank	7	3	2		2
B	No.	1 515	104	29	1 648	
	%	91,93	6,31	1,76	100	8,07
	Rank	1	8	6		8
b	No.	1 580	170	90	1 840	
	%	85,87	9,24	4,89	100	14,13
	Rank	8	2	1		1
C	No.	1 418	99	33	1 550	
	%	91,48	6,39	2,13	100	8,52
	Rank	3	7	5		6
c	No.	1 284	116	40	1 440	
	%	89,17	8,06	2,78	100	10,83
	Rank	5	4	4		4
D	No.	817	59	15	891	
	%	91,69	6,62	1,68	100	8,31
	Rank	2	6	7		7
d	No.	795	88	38	921	
	%	86,32	9,55	4,13	100	13,68
	Rank	6	1	3		3
Total no.		8 992	790	305	10 087	
Overall %		89,14	7,83	3,02		10,86

Rank refers to the % score in a given column, i.e. for a particular seed type down the fruit sub-regions.

2.5.2.1 Concordance tests on the distribution of ovule and seed types. Appendix 17 presents the results of concordance tests applied to the data derived from Appendix 16. These Appendix tables correspond to those of Appendices 5 and 3, respectively, of an autumn set.

From Appendix 17, Table 17.1, it is clear that the overall ranking of sub-regions with regard to the proportion of unfertilized ovules ("U") to total ovules and seeds was significant ($p < 0{,}001$). This ranking order was d, D, c, b, C, a, A, B. That of the corresponding autumn set was d, D, c, C, b, B, a, A. That of the bottom quarter (the furthest from the stigma end) was the same for both sets, but the remaining rankings differed just a little, there being some minor displacements.

From Appendix 17, Table 17.2 ranking of slightly-developed seeds ("S") to total ovules plus seeds was significant at five per cent level (cf. $p < 0{,}001$ for the autumn set, Appendix 5, Table 5.2). The overall ranking was a, b, C, B and c, d, A, D (cf. a, A, b, c, B, d, C, D of the autumn set, Appendix 5, Table 5.2). There was even a slight variation between the overall ranking of Appendix 17, Table 17.2 and that of the pooled data in Table 19, but the aborti rates were so low and close to each other that these variations are not importa

The concordance test on the ranking of the proportion of partially-develop seeds ("P") to total ovules plus seeds was not significant (Appendix 17, Table 17.3). The corresponding test on the autumn set had been highly significant (Appendix 5, Table 5.3). This non-significance finding for the "P" seeds was i spite of the fact that there were about twice as many "P" seeds as "S" seeds (whose rank ordering was just significant).

The rank ordering of the proportion of fully-developed seeds ("F") to tota ovules plus seeds of the summer set was significant (Appendix 17, Table 17.4); the overall ranking having been B, A, C, a, b, c, D, d (cf. B, A, C, D, b, a, c, d of the autumn set, Appendix 5, Table 5.4). The major difference between the two sets was that the bottom quarter carpellary margin sub-region (D) came a good deal further down the ranking in the summer set. This possibly implies that the pollen tubes entered and promoted normal development earlier and more fully in the upper placental sub-regions in the summer set period.

When the unfertilized ovules ("U") were excluded from the calculations and "F", "P" and "S" seeds were considered on their own, relative to the total numb of seeds, then both "S" and "P" seeds had non-significant rank orderings (Appendix 17, Tables 17.5 and 17.6). In contrast, the ranking of the "S" seeds of the autumn set had been significant. The non-significance of the "S" and

"P" seeds was partially due to the rather low frequencies of these two in the summer set.

The ranking of the "F" seed proportions to total seeds still remained significant in the summer set (Appendix 17, Table 17.7). The overall ranking was B, A, D, C, c, d, a, b (cf. D, C, B, A, c, d, b, a in autumn set, Appendix 5, Table 5.7). In both sets there was an apparently greater proportion of fully-developed seeds in the carpellary margin sub-regions. The ranking of the top quarter sub-region (A), i.e. second, appears to have reflected a greater capacity for sustained development of "F" seeds in this sub-region when compared with that in the autumn set, i.e. fourth. And, of course, the proportion of seeds reaching full, normal development was much higher in the summer set.

2.5.2.2 χ^2 tests on the difference in abortion rates between carpellary margin and placental edge regions. Appendix 18 presents χ^2 tests on the above differences in abortion rates for a sub-set of five of the summer-set fruit. Only these five had a sufficient number of aborted seeds in all sub-regions to allow for χ^2 tests to be applied. Appendix 18, Table 18.1 presents a "total χ^2" or the abortion rates for all the intra-fruit sub-regions. This table follows the format of that of Appendix 6, Table 6.1 for the autumn set and the results were all significant, as they were for the autumn set (2.5.1.2). That is, there were differences among the eight sub-regions with regard to the abortion rates.

Appendix 18, Table 18.2 presents the results of a "χ^2 differences" test between the carpellary margin (A, B, C, D) and placental edge (a, b, c, d) sub-regions, for the summer set. The Total Additive χ^2 on the individual total χ^2 was highly significant, whilst the Heterogeneity χ^2 was not significant, implying that the Pooled χ^2 for these five fruit (which was highly significant) was a valid measure for this sub-set. The alternative Overall $\chi^2 = \left[\Sigma - 2 \ln p\right]$ was also highly significant. For this sub-set, then, just as for the autumn set as a whole, differences existed in the abortion rate between the A, B, C, D versus a, b, c, d sub-regions.

Appendix 19, Table 19.1 presents a concordance and χ^2 test on the ranks of the eight intra-fruit sub-regions with regard to seed abortion rates for each of the twenty summer-set fruits. The χ^2 test was significant for this whole set, (as had been the case, at a greater level of significance, with the autumn set, Appendix 7, Table 7). The overall ranking was b, a, d, c, D, C, A, B (cf. a, b, d, c, A, B, C, D for the autumn set, Appendix 7, Table 7). Appendix 19, Table 19.2 presents the same analysis on the sub-set of five fruits introduced in Appendix 18, Table 18. Even although there were only five fruits,

the rankings were still consistent enough to reach significance. However, the overall ranking was: a, A, b, B, d, c, D, C - somewhat different from that of the larger set. The fruit of this sub-set seem to have been more susceptible to seed abortion in the top half of the fruit rather than primarily along the placental edge.

2.5.2.3 Concordance test on the distribution of a competition factor. Appendix 20, Table 20.1 presents this test on the distribution of a competition factor (x_i of Appendix 16 - "intensity of early seed development"). The ranking of the magnitude of this "factor" was highly significant, implying a regular pattern from fruit to fruit. The ranking order was B, A, a, C, b, c, D, d. Appendix 20, Table 20.2 presents the same analysis for the subset of five, which was again significant, with the overall ranking having been B, A, a, C, b, c, D, d - identical to that of the larger common set. In comparison to the two above summer sets, the autumn set's rank ordering was a straight A, a, B, b, C, c, D, d (Appendix 8). In the summer set there was a displacement between A and B, (and therefore 'a' as well); and between b and C. The general tendency was the still for greater early development in sub-regions closer to the stigma end.

2.5.2.4 X^2 and t-tests on the difference in the competition factor intensity between carpellary margin and placental edge regions. Appendix Table 21.1 further shows that there were significant differences even between adjacent pairs of sub-regions along the fruit stem-apex-axis. An overall $X^2 = \left[\Sigma - \ln p\right]$ on the probability values of a series of t-tests on paired differences was highly significant. These tests were of the same type as those presented in Appendix 9 for the autumn set (also highly significant). Appendix 21, Table 21.2 presents the same analysis on the subset of five fruit of the summer set. The overall $X^2 = \left[\Sigma - 2 \ln p\right]$ was just significant at the five per cent level. That is, there were also significant differences in the extent or intensity of early seed development between adjacent carpellary margin and placental edge sub-regions along the whole fruit stem-apex-axis for this sub-set.

2.5.2.5 Quantitative X^2 tests on the relation between the competition factor and abortion rates. Following on from the establishment of differences in the competition factor between carpellary margin and placental edge sub-regions, and of differences between these regions in regard to abortion rates as well, quantitative X^2 were tried on the relation between the competition factor and abortion rates within each of these longitudinally placed sub-regions on their own.

Appendix 22, Table 22.1 presents χ^2 total, χ^2 slope and χ^2 linearity analyses of the sub-set of five summer-set fruit for the carpellary margin sub-region. These are the same kind of analyses as those of Appendix 10 for the autumn set (2.5.1.5). For these five fruit, the additive Total χ^2 for individu total χ^2 was significant at the five per cent level. The heterogeneity χ^2 for this same χ^2 was almost significant, suggesting that these five were perhaps no homogeneous enough to be pooled together for one common set. (If one accepts them as being homogeneous, then the pooled χ^2 was very nearly significant at the five per cent level.) Although only one of the fruit showed a significant total χ^2, the alternative overall $\chi^2 = \left[\Sigma - 2 \ln p\right]$ suggests that the trend was significant; i.e. the data as a whole, together with the four overall chi squares, pointed towards there being differences in the abortion rates within the carpellary margin sub-regions. The χ^2 slope, on the other hand, was not significant. That is, the null hypothesis that the slope was zero was not negated. The series of overall chi squares on the linearity was significant, suggesting that whatever differences there were within the carpellary margin sub-regions, these could not be represented by a linear line relating the abortion rate to differences in the competition factor, x_i .

Appendix 22, Table 22.2 presents a similar χ^2 analysis of the relation between the competition factor and seed abortion rates within the placental edg sub-regions on their own. There were far more significant indications of differences within these sub-regions (χ^2 total analysis). There were also sign ficant results in the χ^2 slope analysis, and the slope was interpreted to be positive, i.e. higher values of the competition factor were related to higher values of the abortion rate. The χ^2 linearity analysis was not quite significant, suggesting that a linear line gave a satisfactory description of the relationship between the competition factor (intensity or extent of early seed development) and the seed abortion rate.

Thus, to sum up, whereas in the autumn set a positive, non-linear relation ship appeared to have existed between the intensity of early seed development and seed abortion rates for both the carpellary margin and placental edge sub-regions, this was not the case in the summer set. In the latter, a significant (linear) relationship only seemed to exist in the placental edge sub-regions.

2.5.2.6 Qualitative $\bar{\chi}^2$ tests on an ordered distribution of abortion along the fruit stem-apex axis. Chi-square tests of the same kind as were applied to a postulated ordering of abortion within carpellary margin and placental edge regions, respectively, for an autumn set (Appendix 12; 2.5.1.6) were also applied to the subset of fruit of the 1972/73 non-hand-pollinated

summer set. In Appendix 23, Table 23.1, two out of the five fruit showed $\overline{\chi}^2$ probability values less than ten per cent on the postulated ordering of A > B > C > D for seed abortion rates (cf. seven out of eleven fruit of the autumn set). In the placental edge sub-regions, however, four out of five frui had $\overline{\chi}^2$ probability values less than ten per cent on the postulated abortion rat ordering of a > b > c > d (cf. seven out of eleven fruit in the corresponding autumn set, Appendix 12; 2.5.1.6). Thus in the subset of the summer set, at least the placental edge sub-regions showed a susceptibility to seed abortion increasing in extent from the base of the fruit towards the apex.

2.5.2.7 χ^2 tests on the distribution of abortion within the fruit stem-apex axis. Appendix 24 presents the results of chi-square analyses on the distribution of seed abortion within the fruit stem-apex axis of the 1972/73 summer set, viz. between A versus BC (Appendix 24, Table 24.1); BC versus D (Appendix 24, Table 24.2); within the carpellary margin region; a between a versus bc (Appendix 24, Table 24.3) and bc versus d (Appendix 24, Table 24.4) regions of the placental edge. Of all these tests, only that of a versus bc sub-regions was significant (Appendix 24, Table 24.3). The autumn set, in comparison, showed significant tests for A versus BC; abc versus d and a versus bc respectively, the last mentioned being the greatest. So, for a least both the autumn and summer sets, significant differences in seed abortion rates were detected between the top quarter and middle half of the fruit along the placental edge sub-regions.

2.6 GENERAL DISCUSSION

Taken as a whole, the results presented in 2.5 point towards the general finding that differences existed in the seed abortion rates between the placental edge and carpellary margin sub-regions. This was so as early as the sixth week after anthesis in the autumn-set fruit. Another general finding was that in fruits examined at fruit ripening, a difference existed in the seed abortion rates between the top (apical) quarter of the fruit when compared with that of the rest of the fruit. In contrast to that, the bottom (basal) quarter of fruits at the sixth week after anthesis in an autumn set had significantly more seed abortion than in the remainder of the fruit. At that stage, however, abortion rates were still relatively low, suggesting that the major phase(s) of abortion occurred after that period. Turning again to the abortion rates found at fruit ripening, the differences were in the same direction but much more marked in the fruits set in autumn as compared to those set in summer.

Differences also existed between the sub-regions of the carpellary margin versus those of the placental edge in regard to the postulated competition fact viz. the extent or intensity of early seed development. This was so even betwe adjacent (latitudinal) pairs. These differences existed in fruits set in autum and in summer.

That this postulated competition factor was actually a contributory factor to the abortion rates remains less clear. The deviations from linearity in the models used to quantitatively relate the competition factor and abortion rates casts doubts on some of the results which suggested such a relationship. A more parametric set of measurements may finally clear this issue.

Again, whether the apparent gradient in abortion rates along the fruit stem-apex axis was due to differences in the distance of ovules/seeds from the stalk of the fruit or else to a coincidentally greater susceptibility of the top quarter of the fruit remains to be cleared.

Another set of findings was that higher levels of ovule fertilization occurred when fruits were hand-pollinated, in both autumn and summer sets. In the autumn sets the levels of overall fertilization $\left[\frac{F + P + S}{F + P + S + U}\right]$ were 70,2 per cent for the hand-pollinated set (from Table 12) and 31,1 per cent for the non-hand-pollinated set (from Table 16). In the summer sets the respective contrasting levels were 87,6 and 65,7 per cent (from Tables 17 and 20).

In the autumn sets the higher ovule fertilization levels had no apparent effect on the overall level of seed abortion rate as measured by $\left[\frac{P + S}{F + P + S}\right]$. For example, in the hand-pollinated set this abortion rate was 50,2 per cent (from Table 12) and the contrasting level in the non-hand-pollinated set was 52,8 (Table 16).

In the summer sets the levels of seed abortion were 17,3 and 10,9 per cent for the hand-pollinated versus non-hand-pollinated sets respectively. Neverthe less, this apparent difference does not appear important by virtue of the general low levels of abortion in summer-set fruits.

The above results thus create a further reservation in the mind of the author with regard to the postulate that higher levels of early seed developmer are a major factor in seed abortion. It seems instead that if there was a competitive effect leading to seed abortion this was only a secondary factor. Again, as regards the earliest signs of seed abortion (sixth week in autumn), high levels of early seed development did not appear to increase seed abortion.

Turning to the types of seed abortion or their time of occurrence, the mos concentrated and distinctly patterned distribution was that for the slightly-

occurred over the coldest months of the year for Pietermaritzburg (June to August). Another possible contributory factor to this peak in abortion may have been a general lack of assimilates. Extensive leaf abscission often occurs over this period at the Ukulinga Research Station. This possible relationship could be looked into in the future. The relationship between seed growth and fruit growth will be examined further in Chapter III.

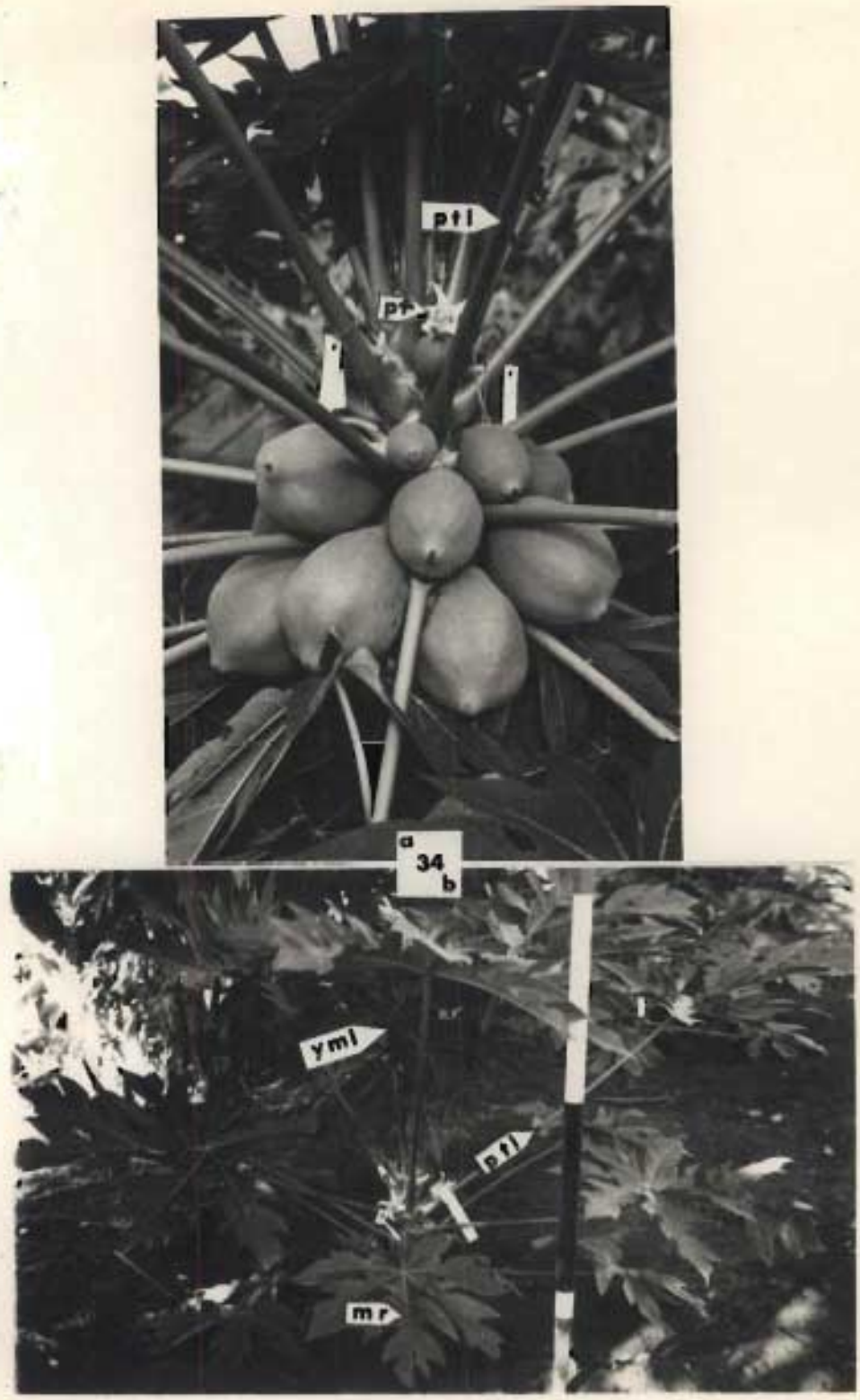

PLATE 34 (a) Summer set papaya fruit at the bottom, and autumn set fruits and flowers at the top, clone 'Honey Gold'.

(b) Leaf canopy in summer of young plant grown from a cutting.

See Abbreviations.

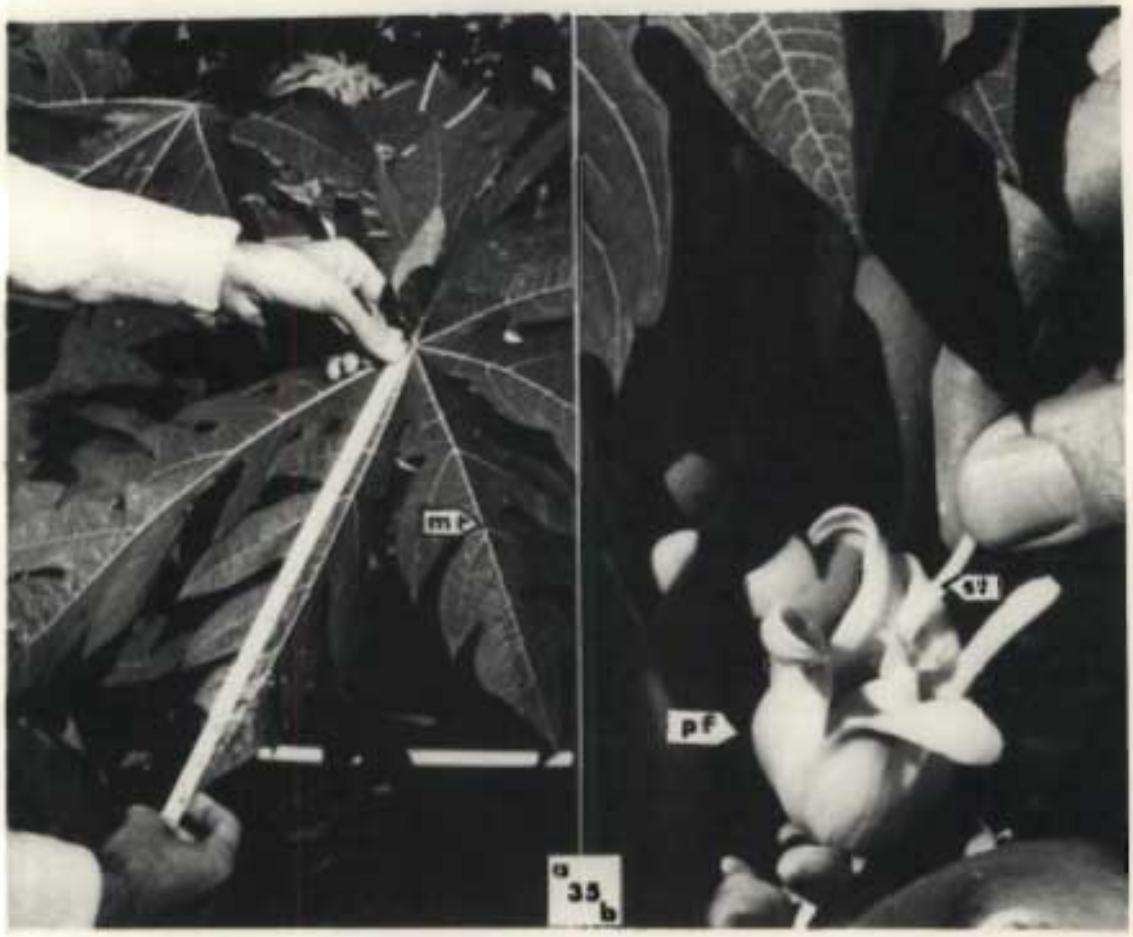

PLATE 35 (a) Measuring main leaf vein lengths as index of leaf area.

(b) Hand-pollination of pistillate flower with pollen of a staminate flower.

See Abbreviations.

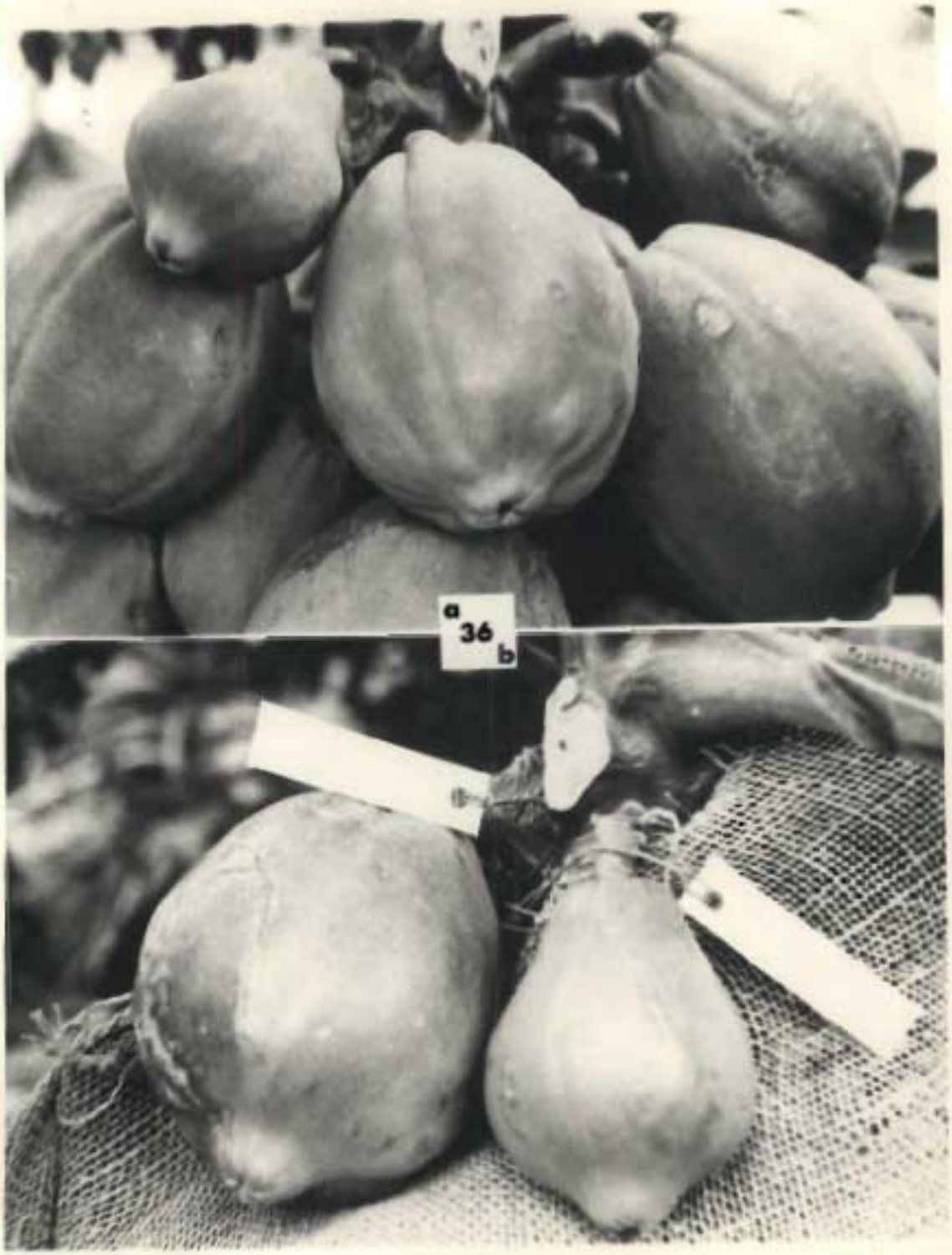

PLATE 36 (a) Stem with fruit set at different times in autumn.

(b) Fruit set on the same day in autumn, with larger one having contained more fertilized and developed seeds.

PLATE 37 Apical end of week-1 summer fruit after hand-pollination. Thread-like mass on placental surface above and between ovules are pollen tubes stained with aniline blue (magnification approximately x 400).

CHAPTER III

CORRELATION AND REGRESSION STUDIES ON SEED AND FRUIT GROWTH

3.1 LITERATURE REVIEW

Crane (1964) and Nitsch (1965) have provided surveys on the extensive research on the effect of seeds on fruit size and shape. Allan (1969), in the course of reporting on studies of the effect of seeds on fruit mass in Carica papaya noted a number of observations on the findings and conclusions from the above reviews and further literature. The following short review is meant merely to recap and illustrate some of these and other findings in order to set the stage for the studies that follow.

In pome fruits Schander (1955) found a significant correlation between (a) the number of seeds per fruit and fruit mass; and (b) between seed mass and fruit mass. Nitsch (1952) had previously concluded that the ultimate size of a fruit is proportional to the number of well developed ovules and not to the total number of seed-like structures. Kobel (1954), however, concluded that "empty" seeds influenced fruit mass to virtually the same extent as seeds with normal embryos because in his view seeds have their strongest influence on fruit mass in the early stages of development before the embryos abort. Denne's (1963) finding that a better correlation existed between apple fruit mass and seed number when aborted seeds were included appears to support Kobel's (1954) conclusion. Again, in regard to apple fruits, Abbott (1959) found that their growth was only dependent on the presence of seeds in the early stages of growth. In Allan's (1969) work on papaya, it appears that the inclusion of the number of aborted seeds with that of the number of normal seeds would improve the fit of the regression of fruit mass on seed number. In contrast to the above findings Nitsch (1950) showed that in the strawberry the removal of achenes even a short time before maturity stopped further growth of the receptacle.

Nitsch (1950) also showed that the shape of the strawberry receptacle could be markedly influenced by the removal of some of the achenes. The effect of the distribution of seeds on fruit shape (and hence localized intra-fruit growth) can also be seen in the pear. If this fruit has seeds on only one side, that side of the fruit develops preferentially, resulting in a distorted asymmetrical fruit (Luckwill, 1959).

In all the above cases the relation between seed and fruit mass is con-

curve, such as in the peach, the period of suspended fruit flesh growth is the same as that for maximum growth of the seed (Tukey, 1933). From such cases it appears that there may be a competitive interaction between seed and fruit growth. This possibility was also implicit in some of the literature reviewed in Chapter II. Generally then, in those fruits in which a strong correlation exists between seeds and fruit mass (not all fruits have this), the "seeds" appear to provide an influence ranging from the strongly promotive to the inhibitory, depending upon the stage of fruit growth measured (Leopold & Kriedemann, 1975). This of course can have some bearing on how important ovule fertilization is, and on whether seed abortion is a deleterious, neutral or desirable event for the size and shape of the fruit, depending on when it occurs and on the fruit in question.

A number of plant hormones have been correlated with the growth of certain fruits. In some cases a particular hormone has been correlated with a fruit's growth at a given stage but not at other stages; in other fruits the regulatio may be the result of the interactions of multiple hormones (Leopold & Kriedeman 1975). In some fruits the hormones have been found to be produced in one or other tissue of the fruit itself, in others the richest source has been found to be in ovule or seed tissues. Then again in fruits which have shown their richest source in the seeds, parthenocarpic or seedless varieties of some of these species seem to compensate for the missing seeds by synthesising the hormones in fruit tissues instead (Leopold & Kriedemann, 1975).

The basis then for the oft reported correlations between seeds and fruits is generally thought to be due to the complementary production of hormones in the fruits' ovules or seeds (Crane, 1965; Jackson, 1968). Allan (1969) has speculated that underdeveloped (or aborted seeds) also influence fruit growth by producing hormones in certain tissues.

As the studies in this chapter focus on the seed/fruit correlations of a clone in Carica papaya, the rest of this review likewise focuses on studies and reports on this fruit. Firstly, Agnew (1948) stated that the mass and size of these fruits was roughly proportional to the number of seeds set, varying with seasonal conditions at the time of flowering, and the individuality of the tree (seedlings). Some trees may even bear seedless or nearly seedless fruits, with the ovules being shrivelled and shrunken even in the bud stage of the flower. He considered this to be a heritable character.

Since papaya fruits can contain up to 2 000 seeds per fruit, as opposed to the few found in pome fruits and grapes, Allan (1969) considered this fruit would provide a good example on which to carry out a more detailed study on

the seed/fruit correlation. He also wished to check the effect of season of maturity on the correlation to see whether greater competition between fruits at certain periods affected results. This was done in the belief that average mass of fruits decreases the larger the crop that is borne by a tree. Potter (1927) for example, had found a high negative correlation between mass of fruit per tree and mean fruit mass in apples.

Accordingly Allan (1969) picked all the fruits from a first crop of female seedling trees according to three periods:

(a) from late October to late December ('spring' fruits);
(b) during peak production in February ('summer' fruits); and
(c) from March to early June ('autumn' fruits).

The above groups of fruits were judged to have set (after open pollination) during (a) mid- to late summer; (b) late summer to early autumn; and (c) mid- to late autumn respectively, in the preceding nine to eleven months. From the above one may surmise that individual fruits varied with respect to their associated climatic conditions not only 'between seasons' but also 'within seasons' as well. The significance of the extent of this 'within season' variation is unknown to the author.

Allan (1969) found that the correlations between seed number, and seed mass, with that of fruit mass were highly significant for each of the above periods of maturity or setting. The correlations varied from +0,643 to +0,867, much larger than many correlations reported in other fruits up to that time. The correlation between seed mass and fruit mass was higher than that between seed number (of fully developed seeds) and fruit mass for all periods tested. In the fruits set in autumn, a proportion of fruits had many underdeveloped (aborted) seeds, and the correlations between the number and mass of well developed seeds with that of fruit mass from these fruits were lower than that found in fruits with relatively few underdeveloped seeds. (Correlations that included fully- plus underdeveloped seeds were not calculated.) The correlations between seed and fruit mass in the autumn set fruits (which were also smaller sized) were higher than those of the summer set. This seemed to support Denne (1963) who had previously quoted other workers who found a better correlation with the smaller fruits on a tree.

The regression coefficients for fruit mass on seed number or seed mass were significantly higher for fruits maturing in spring (seed number only) and autumn than for fruits maturing in summer when the peak crop was harvested. Thus a smaller mass of fruit was 'produced' per unit number or mass of fully developed seeds in the summer-ripening fruits which had had to compete with

large numbers of other fruits over their entire period of development. The spring- and autumn ripening fruits on the other hand experienced shorter periods of intense competition and produced a greater mass of fruit per unit of seeds. As previously quoted, Allan (1969) also found that the inclusion of the number of aborted seeds with that of the number of normal seeds appeared to improve the fit of the regression of fruit mass on seed number.

Taking all these findings together, Allan (1969) suggested that hormones influencing fruit growth may be produced in the integuments and nucellus, as well as the endosperm and embryo, and that seeds affect fruit growth in the papaya fruits not only in their early stages but throughout their whole period of development. He also stated (Allan, 1958) that from observation the influence of the seeds "... is greatest on the adjacent fruit tissue, causing thicker flesh and better fruit development in that region...."

With regard to the effect of crop load on the number of seeds set, Allan (1958) reports a trial in which "... an average 4,5 fruits per stem were removed from 13 trees or side branches of ... 'stripped' trees in March (early autumn) while on nine 'control' trees or side branches, from which no fruits were removed, an average of four fruits were left per stem. After this an average of five new fruits per stem set on both the 'control' and 'stripped' trees. The average number of fully developed seeds per new fruit was 628 on the 'stripped' trees compared with only 371 on the 'control' trees". A conclusion from this and other trials (Allan, 1967 b) was that by removing fruits that set before March (up to early autumn) allows the fruits that set later to be subject to less competition, resulting in greater ovule fertilization and fruit development and ultimate size. However, from the peculiarly economic or marketing point of view, one drawback in increasing fruit size by this method is that those fruits that set after the stripping (of competing fruits) mature somewhat more rapidly. This tends to defeat the objective of producing a later crop in the out-of-season period (Allan, 1967 b, 1976).

Allan (1958) also made a preliminary comparison of the effects of hand versus open pollination on the number of seeds set and the size of fruits. He used an average of about five (comparative) pairs per period sampled, the range being from eleven (during peak flowering in January) to two pairs in June - July (winter) respectively. Fruits that were pollinated from mid-December to mid-January (start of flowering season) had significantly more seeds and were of greater mass than corresponding naturally pollinated fruits. There was a comparatively large number of empty testas in these early fruits (there being relatively more of these in the open pollinated fruits than in

those hand-pollinated with stored pollen). Allan (1958) suggested that this pointed to embryo abortion brought about by fruit competition (of the previous crop not yet harvested). The ovaries of the early set fruits were also small with perhaps fewer well-developed ovules.

Subsequently, in those fruits set in mid-summer, the hand-pollinated ones had even more seeds and larger fruits than naturally pollinated fruits, and the seed numbers and fruit sizes were greater than those of the early summer set. There were also far fewer 'testas' (aborted seeds) in both.

However, from March until May (autumn), hand-pollination appeared to have no beneficial effect on fruit mass or (normal) seed number. But there were more empty testas in the hand-pollinated fruits, from which Allan (1958) surmised that competition from fruits that had already set prevented more than a certain number of seeds from developing.

However, with the last few pistillate flowers formed in early winter, hand-pollinated ones in June and July had a greater seed number than naturally pollinated ones, although very few seeds were formed in both. Allan (1958) considered that the difference was due to reduced insect activity brought about by the colder weather. The fruits were also much smaller. The small number of seeds per fruit in both natural and hand-pollinations was ascribed to (a) competition between fruits already set; (b) poor pollen viability and pollen tube growth; and (c) small ovaries and possibly poorly developed ovules.

Free (1975) has reported that (in the 'winter' months) in Jamaica, hand pollination does not increase fruit set in pistillate flowers of papaya. He did, however, refer to literature which indicated that unfertilized flowers can produce fruits when these are borne on vigorous trees in a favourable season. In Free's study 65 per cent of all pistillate flowers labelled three weeks previously (at anthesis) had 'set', there being little difference between hand-pollinated, insect-pollinated and bagged flowers.

Although it is fairly well known that mature papaya plants are fairly drought resistant, a few weeks of dry weather can cause blossom drop. Under Florida (U.S.A.) conditions it is often possible to double production by irrigation, and in South Africa both larger and better crops, and better leaf cover which reduces the incidence of sunburn, are obtained with irrigation (Allan, 1974). Similarly, in Queensland (Australia) irrigation during dry spring months can induce flowering in early summer. In Hawaii too, plants in high irrigation plots grow more rapidly during summer and autumn than those in low irrigation plots. The driest months in Pietermaritzburg are from June to August/September (winter to early spring) with wide and rapid fluctuations

between absolute maximums and minimums in August and September (Allan, 1958). Hot 'Berg winds are also characteristic for this latter period. Although not noted in the literature by the present author, it is conceivable that prolonged dry weather, 'Berg winds and rapid wide fluctuations in temperatures could stress papaya plants sufficiently to affect seed development and abortion as well.

3.2 RATIONALE, METHODS AND MATERIALS

3.2.1 Inter-fruit studies

The studies under this section were undertaken in order to test further the seed mass/fruit mass correlation in papayas when certain conditions and co-variables were allowed for. Thus in Allan's work (1958, 1969) seedlings were used, whereas these studies were based on fruits growing on rooted cutting of the clone Honey Gold . These comprised 102 stems from six rows of a block at the University of Natal research farm, Ukulinga.

As it was of interest to have an indication of the leaf area and fruit competition at different times of the year, occasional records were taken of the number of leaves and fruit per plant stem (Plate 34a, b) during autumn, spring and summer over the period May 1969 to April 1971. Estimates of the mean leaf area of these 102 plant stems were also determined. This was done by sampling ten leaves from each row, ranging from the oldest, lowest-most leaf to the top of the second tier or tuft or whorl of leaves. The latter is about the youngest expanded leaf (Plate 34b) and subtends a flower close to its time of anthesis.

Since the papaya leaf does not present a simple pattern nor uniformly thick tissue for determining leaf area, the petiole and mid-ribs (Plate 34b) were cut out, and the leaf area was determined on the remaining leaf blade tissue. For each leaf, the mass of the remaining leaf blade was determined (A), then the mass (B) of representative sections of the former of determined area (C). The latter was found by using a dot-grid method (Benjamin, Freeman & Brown, 1968) which on these papaya leaves gave an estimate to within three per cent. The latter compares favourably with a method using an air-suction device which only estimated leaf area means to within ten per cent, because air was sucked through the leaf tissue with that method (particularly on older leaves).

In April 1971 the lengths of all the leaf veins of 31 leaves were measured and the leaf areas determined as before. Correlations and regressions were

measured, and the leaf areas determined as before. Correlations and regression were calculated between these leaf vein lengths and the leaf areas. Looking down on the upper surface of the leaf, with the petiole end away from one, as in the lower leaf of Plate 34b and the leaf in Plate 35a, the leaf veins were numbered clockwise, the shortest veins being number one and ten or eleven, and the longest being numbers five, six and seven. Of the individual veins, the central number six turned out to be the longest and also had the best correlation, viz. +0,878. Measuring in cm (X), the regression of

$$Y \text{ (leaf area, cm}^2\text{)} = -2\,079 + 114{,}2X \ .$$

Summing up vein lengths numbers five, six and seven provided an even better correlation, as will be reported later. So in April 1971 the total summed length of these three veins for all the leaves from the oldest to the top-most leaf of the second tier for each plant stem having a labelled fruit was determined. A rapid way of doing this was to extend string from a roll along vein number five, pass it on, extend a further section of string along vein number six, pass that on, then onto vein number seven, then vein number five of the next leaf, etc., until all the expanded leaves of that plant stem had been dealt with. The accumulated string was then measured in cm, and this recorded as an index of total expanded leaf area for that plant stem at that time.

In 1969 a record was also kept of the abscission of fruit of a set of 48 fruits hand-pollinated in the autumn (April) of that year. Measurements of fruit diameter were also carried out on these fruits, as depicted in Figure 26 and already reported on in Chapter I.

As pointed out in the literature review, Allan (1958, 1969) used ripe fruit that had set over extended periods. Since it is highly likely that both seed mass and fruit mass are both correlated with temperatures during growth, fruits and seeds growing together over a warmer period could be larger than those growing over a cooler section of time, even if set over the same season. A correlation based on the combined set of such fruit could be 'inflated' by the effect of the different temperature regimes experienced by individual fruits, assuming these regimes were significantly different from each other.

An attempt was made to control for this effect in the late summer/early autumn study (March 1971). Fruits were set in four successive weekly batches over that month of March. Half the fruit of each batch was harvested exactly three months after setting (i.e. over the four weeks of June), whilst the other half was harvested exactly seven months after fruit set (i.e. over four weeks in September/October). Each of the pistillate flowers were hand-pollinat by brushing on the pollen of three stamens (Plate 35b) picked at the male

Daily temperature data for the periods preceding anthesis and the periods of fruit growth were available from a thermograph instrument situated in an adjacent block. An objective of the above procedure was to check for the effect of temperature differences over the four temperature regimes that were expected to result (corresponding to the four succeeding weeks of fruit set).

The objective of splitting the batches into the three and seven month periods was to check firstly the correlation at the onset of the coldest period i.e. after three months, over June (and about the time the first major seed abortions would occur). This would also have been the period leading up to or including the onset of endosperm cellularization. Secondly, to check the correlation at seven months, in spring, after most of the seed abortions would have occurred, and seed growth would have started to slow down, and at a time of increasing temperatures. To have delayed the harvest further could have led to a greater confounding of effects, since the last batches which initially grew through assumably the colder periods end up growing through warmer final periods.

A way of accounting for the heat effect was somewhat problematic. The author wished to use a heat unit measure, but it was not clear what the minimum temperature for seed or fruit growth in papaya is. According to Kuhne and Allan (1970) temperatures below 19°C adversely affect cell division in the fruits during the first few months of growth, but subsequently growth of fruits by cell enlargement continues even between 11° and 19°C. Examination of Kuhne and Allan's figures, however, show that the rate of fruit volume growth was still positive during the coldest month of June when the mean was between 13° and 14°C. Young papaya <u>seedling</u> growth has been measured to just occur between 4° and 12°C (Lange, 1961). Allan (1958) also observed that the minimum temperature for papaya flower growth was about 12°C. Thus a base of 12°C was chosen for this study, although the true base was unknown.

The formulas used to measure the heat effect were as follows. In the cases where the minimum temperature (w°C) for a 24-hour period was above the base temperature (t = 12°C), then the degree-day for that period was calculated as

$$(w - t) + \frac{(h - w)}{2} ,$$

where h was the maximum temperature for that period. Where the minimum dropped below 12°C, the formula used was

$$\frac{(h - t)^2}{2(h - w)} .$$

For a given period of growth then, the measure of 'effective heat' was the summation of degree-days (base 12°C).

Fruit diameters of all labelled fruit were taken at the time of hand-pollination. The length of leaf veins numbers five, six and seven for each of the subtending leaves of these labelled fruit were also measured with a ruler at this time (Plate 35a). Finally, at harvesting (after three and seven months) the seed mass and fruit flesh mass (i.e. excluding seeds) for each fruit was determined. /In Allan's work (1969) the correlations were between seed mass and fruit plus seed mass. Since that entailed an inflated correlatio seed and fruit flesh mass were separated for this study./

The variables then for the three and seven month growth studies were:-

(i) The sum of degree-days (above 12°C) for the 40 days preceding anthesis (i.e. over the major portion of flower bud growth);

(ii) sum of degree-days (above 12°C) for the three days prior to anthesis, a possibly critical period for the relation between mean temperatures then and the subsequent germination of fresh pollen, and their tube growth, as indicated by studies of Allan (1963);

(iii) sum of degree-days (above 12°C) for the period from anthesis until the 12th week of growth, i.e. June, for the three month study, and until the 15th week, in July, for the seven month study;

(iv) fruit diameter at anthesis (mm);

(v) the leaf area index of the subtending leaf (cm);

(vi) the total available leaf area index for April, calculated as the sum of the lengths of veins number five, six and seven of all expanded leaves on a plant stem divided by the number of fruit on that stem at the end of April (cm per fruit);

(vii) seed mass after three or seven months growth (g); and

(viii) fruit flesh mass after three or seven months growths (g).

Sums of degree-days after 15 weeks, from the end of July and onwards, were not considered for the seven month growth study because temperatures were on the increase then, with the later set batches always being just slightly warmer Also, since Kuhne and Allan (1970) had shown in a seasonal trial that when their pair of clones were set in March in Pietermaritzburg, it was the initial 12 to 16 weeks respectively of growth that was crucial to the ultimate size of

their fruits. The comparative time to maturity of the clone 'Honey Gold' used in the present studies falls between those of the clones reported on by Kuhne and Allan (1970). Thus it was considered that the temperature data up to the 15th week in July would give a reasonable measure of the initial 'temperature' effect.

Total or simple correlations were calculated between fruit flesh mass and each of the other variables within each of the three and seven month growth studies respectively. A stepwise regression procedure described by Draper and Smith (1966) was then applied to the data, examining the partial correlations, the residuals and the effect of the variables incorporated into the model at each stage of the procedure.

3.2.2 Intra-fruit studies

In the summer of 1973, 21 fruits which had set during the previous summer of 1972/73 and were just beginning to ripen were picked and set aside for an intra-fruit seed/fruit correlation study. Similarly, in the autumn of 1974, 17 fruits which had set in late autumn of the previous year (1973) were also set aside for similar reasons. These two batches of fruit had been left to open pollination, not hand-pollinated. In both batches, the top (stigma) end of the fruits just to the plane where the interior (seed) cavity begins was cut off. A similar parallel cut was made at the base of the fruit so that what was left was the fruit flesh immediately adjacent to the seeds of the Aa to Dd intra-fruit seed subregions (see Figure 3 for these subregions). The discarded portions averaged 15 per cent of the original total fruit flesh mass (excluding seeds). A longitudinal cut from the apex to base along one dorsal bundle and its opposite ventral bundle (Figures 1 and 2) was made. This ensured that the blade of the knife passed between the seed areas of two adjacent placental regions, but the opposite placental region was cut, dislodgi some of these seeds. This placental region was discarded, leaving four-fifths of the fruit entact. Such four-fifth longitudinal sections were used in the autumn set study, but in the (earlier) summer set, only two-fifth portions were used. The longitudinal portions were further cut into quarters to provide Aa, Bb, Cc and Dd subregions (Figure 3). The corresponding seed mass and fruit flesh mass (excluding seeds) for each subregion for each fruit was determined.

In five of the autumn set fruits, the fruit was further subdivided into the four 1/5th longitudinal sections, and from each of these four longitudinal sections, the total mass of all seeds (fully to slightly developed) was determined for each of the eight intra-fruit subregions (A, a, ..., D, d; Fig. 3) respectively. In one other fruit three 1/5th longitudinal fruit

sections were used, and in two others three 1/5th longitudinal sections.

For each of the above intra-fruit subregions, length and breadth measurements of a sample of ten unfertilized ovules were made using a graticule placed in the eyepiece of a microscope. The product of these two measurements was used as an index of the ovule volumes. The mean index of unfertilized ovule volume formed one variable. The other variable, a measure of the relative concentration of seed mass, was arrived at by dividing the summed mass of F + P + S seeds by the total number of seeds and ovules (F + P + S + U). The correlation between these two variables was determined.

The purpose of all the determinations in this section was to test for whether the correlations between seed mass and fruit mass reported in inter-fruit studies also held at more localized regions, i.e. within the fruit. It was also intended to test formally Allan's (1958) assertion that in papaya, seeds influence the growth of immediately adjacent fruit flesh.

3.2.3 Further seed growth, abortion and fruit size studies

These studies in this section focus on the correlations between seed numbers (corresponding to the types of seeds of Chapter II), seed mass, fruit mass (inclusive and exclusive of seed mass) and seed abortion rates. The data was drawn from the following fruit sets:-

(a) Eighteen fruit set in April 1969 (autumn), maturing in February 1970;

(b) fourteen fruit set late in April 1970 (autumn), maturing early March 1971; and

(c) twenty-four fruit set in early February 1970 (summer), maturing late November 1970.

All the above had been hand-pollinated. In addition comperative data was available from twenty-one fruits set over the summer of 1972/73 and seventeen fruit set over the autumn of 1973, already described in 3.2.2. The latter two sets were open pollinated (not hand-pollinated).

In the cases of (b) and (c), whole fruits with their total complements of seeds were used. For the case of the open pollinated sets (3.2.2), comparative whole fruit mean values were derived by multiplying the measured values by 5/4 or 5/2 etc., depending on whether 4/5th or 2/5th etc. longitudinal portions had been used. In addition, the fruit flesh mass was further multiplied by a factor of 1,15 to compensate for the fruit flesh previously cut away and discarded (3.2.2).

The data from (a), the autumn 1969 set presented a peculiar problem. These eighteen fruits were part of a larger set (48 fruits) whose diameters and lengths were recorded at frequent intervals throughout their growth.

Some of these fruits abscissed (3.2.1). Some were harvested and sold before the author 'saved' the balance of eighteen. The mass of these fruits (including their seeds) were determined at the time of harvest. Seed masses were not determined. As a preliminary survey, the author had also made seed counts on the 1/5th longitudinal portion that seemed to have the most typical amount and distribution of seeds for the whole fruit in question. Where a fruit appeared to vary more widely than usual between 1/5th longitudinal portions, the whole fruit's seeds were counted. Overall then, estimates were derived for total fruit seed counts. On the basis of this survey, the author decided to carry out more detailed seed count studies (Chapter II). It was then not his intention to include in addition the seed counts of the 1969 study. However, in the light of the analysis of other results, and even in the course of having this thesis typed, it suddenly dawned on the author that the (correlationally) unanalysed data of the 1969 set could, in fact, supply extra information.

Fortunately when the author had done the seed counts on the 1970 summer set (24 fruits) he had cut the fruits into five 1/5th longitudinal portions as before, identified again what appeared to be the most typical 1/5th portion, and then counted all seeds for each of the five 1/5th portions separately. An examination of that data has since revealed that the identified 'typical' 1/5th estimated the whole fruit's fully developed (F) seed count to within 14 per cent, and the fully plus partially plus slightly developed seed counts (F + P + S) to a similar degree. Being summer set fruits, i.e. with relatively few (P) and (S) seeds, the (P + S) seed counts on their own were only estimated to within 23 per cent. The estimates for the total seed plus ovule counts (F + P + S + U) ranged between five and fifteen per cent of those of whole fruit counts.

Now the correlations between the estimated (F) seed count (and also that of the (F + P + S) counts), and that of fruit flesh mass was less than ten per cent different from that of the correlation based on the total fruit's seed counts. In the case of the (P + S) seeds alone the difference was greater, nearly 20 per cent. But this was understandable in terms of the relatively few (P + S) seeds and because of that, the very low correlation the (P + S) seed count alone had with fruit flesh mass. In the light of the otherwise reasonably close correlations, and also because in the autumn sets

there was a far greater proportion of (P + S) seeds, it was decided to analyse the estimates derived from the 1969 autumn set. Naturally the results and conclusions from that study must be made with due regard for margins of error.

The reason for wanting to use the above data was that for each of those 18 fruits with their estimated seed-type counts there was a record of their diameter and length growth from anthesis to maturity. It became a point of interest then to correlate the different seed-type counts (and their combinations) with fruit volume throughout fruit development, thereby possibly isolating the periods during which seeds affect fruit growth.

3.2.4 Supplementary survey on pollen tube growth

In the autumn (April) and winter (June) of 1971 and the summer (February) of 1972, sets of unopened pistillate flowers were bagged. At anthesis these were debagged and hand-pollinated with the stamens of three male flowers or with stored pollen (winter). Starting from the second or third day after pollination, and then every two days thereafter, two to three flowers were picked per sampling period to measure pollen tube growth. The flowers/fruits were cut longitudinally and a few drops of aniline blue were poured into the ovarian cavity. Then after a minute the stain was gently washed out. The stained pollen tubes (Plate 37) were then measured, from their entrance into the ovarian cavity (As intra-fruit subregion) to the tips of the furthermost pollen tubes. The length of the ovarian cavities were also measured. Maximum and minimum temperatures (within the row of plants used above) were also recorded.

In the May of 1972 maximum and minimum temperatures were kept within a plastic cover structure placed over some papaya plants. Temperatures were also recorded in uncovered plants in the same row.

The purpose of this survey was to see how pollen tube growth is affected by prevailing temperatures in the different seasons of fruit set, and to see to what extent plastic or polythene cover structures influence ambient temperatures.

3.3 RESULTS

3.3.1 Inter-fruit correlations and regressions

Two of the factors expected to influence the fruit/seed correlation were leaf area and the number of competing fruit. Both of these varied over the seasons as fruit and leaf abscissions, fruit harvest, and the emergenc

Figure 33 gives the rate of fruit abscission for the fruit set in autumn, 1969. The highest recorded interim rate (0,17) occurred early in ~~July~~ June, eight weeks after anthesis. The second largest rate, (0,06) was in early ~~June~~ May, a month before. No fruit abscissions occurred after October (late spring, six months after anthesis). Thus the fruit abscissions were more or less confined to the cold spells of mid-winter and the dry ('Berg wind) conditions of spring. The accumulated proportion of fruit abscissed was approximately a third of that originally set. In comparison Free (1975) found an abscission of 35 per cent three weeks after anthesis in winter in Jamaica, whereas in these studies only ten per cent had abscissed in that initial period. The period during which the major proportion of fruits abscissed in the autumn set fruits corresponded quite well with the period over which most of the seed abortions occurred. The latter can be illustrated in Figures 28 and 29 where the earliest recorded aborted-seed measurements and the cessation in growth of the largest aborted seeds covers the same period, i.e. mostly between June and October.

Table 21 provides estimates of mean leaf areas and number of fruit on the 102 fruit stems sampled from during a two-year period. The largest mean individual leaf areas were recorded during the autumns, at the end of the growing season and before the major rates of fruit and leaf abscissions occurred.

TABLE 21 Estimated leaf areas and number of fruit of 102 papaya stems at different times during a two-year period

Season	Mean leaf area (cm^2)	Mean number of leaves per stem	Mean number of fruit per stem	Mean total stem leaf area per fruit (cm^2)
May '69 autumn	3 538	25,2	25,4	3 518
Oct. '69 spring	1 650	-	-	-
May '70 autumn	3 291	19,8	25,2	2 600
Oct. '70 spring	828	10,1	23,6	356
Feb. '71 summer	2 873	13,6	6,5	6 011
April '71 autumn	3 173	23,5	14,7	5 072

Leaf abscissions appeared to occur throughout the year, but were more pronounced during winter and early spring. (Unfortunately no leaf area measurements were made during the winter months.)

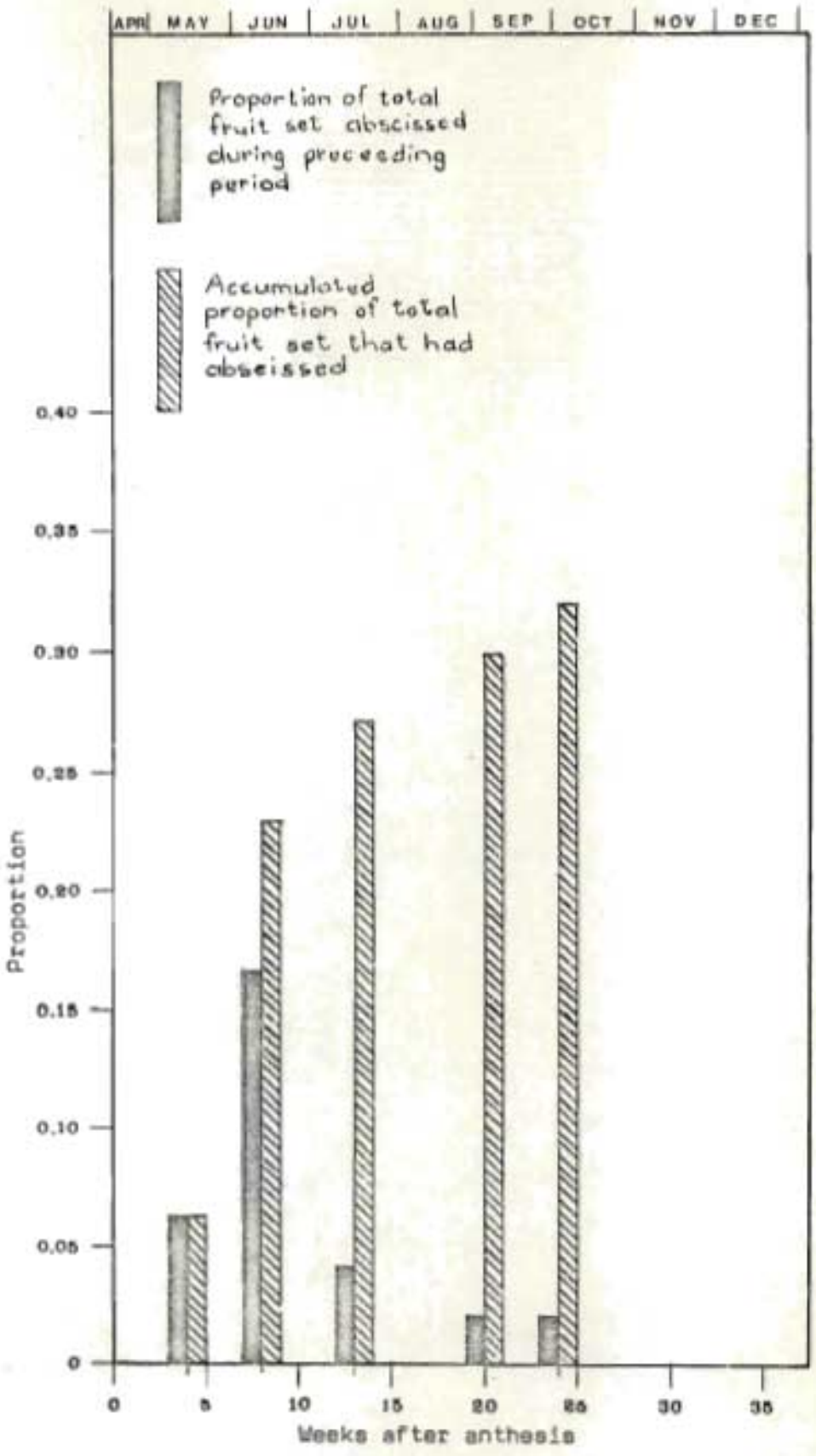

FIGURE 33 Proportion of papaya fruits abscissed during fruit growth in fruits set in autumn, 1969, with hand-pollination. (Based on 48 fruits.)

There appeared to be a decline in the mean leaf areas of autumn over this period. This may have been due to a decline in vigour of the older plants (four of the six rows), although two rows were just coming into full production The above trend can also be seen in the mean number of leaves per stem over this period. It was highest in autumn 1969 (25,2), fell to 19,8 in 1970, and then increased again in 1971 (23,5) when the younger plants were becoming larger.

The spring mean individual leaf areas were the smallest. This was after many of the oldest and largest leaves had abscissed, often leaving only a tuft of smaller leaves at the top. This is illustrated by the small number of leaves (10,1) for spring 1970. The only recorded summer figures shows that the mean individual leaf areas and number of leaves per stem lay between those of spring 1970 and autumn 1971 figures, in the middle of the active growth period.

The mean number of fruit per stem for the autumns of 1969 and 1970, and also the spring of 1970, were very much the same (23,6 to 25,4). The peak crop was rather early in the summer of 1970/71, and when the 1971 summer counts were made there were only an average 6,5 fruit per stem. Flowering and fruit set after that was not as high as usually recorded, and only an average 14,7 fruits had set by April, 1971 (about the time of the correlational and regressional growth studies that follow).

The last column of Table 21 shows what the estimated total stem leaf area was per fruit. It is quite apparent that it was the number of leaves to number of fruit ratio that largely corresponded with this figure. It can be seen that in the spring of 1970, when there were very few leaves but most of the crop was still on the stems, each fruit on average could only draw on the assimilates produced by 356 cm^2 of leaf tissue. Again, although the mean individual leaf area of the autumn 1969 was larger than that in autumn of 1971, because of the much smaller crop in 1971, there was a greater available leaf area per fruit per stem in April 1971 (5 072 cm^2) than in May 1969 (3 518 cm^2).

What was rather peculiar to 1971 was that the available total leaf area per fruit in early February 1971 (6 011 cm^2) was greater than that in April 1971 (5 072 cm^2). Quite often there has still been a late crop on the trees in early February such that summer set fruits usually start off competing with a large load of other fruit (as described by Allan, 1969).

At the time the correlational and regressional studies were undertaken in March 1971, leaf area was correlated with and regressed on the summed length of the three longest leaf veins (Appendix Table 25). Since this correlation of 0,909 was highly significant and gave a coefficient of determination of

82,7 per cent, it was decided to use the leaf vein length measurements as an index of leaf area in those studies. Hence two of the conditions thought to be of importance in fruit growth and seed/fruit correlations, viz. leaf area and relative leaf to fruit competition, were measured using this leaf area index. (It should be pointed out that the regression equation based on that data could only be used there and not again with different years, different trees, etc. Different studies require their own regressions if leaf areas per se are needed.)

3.3.1.1 Three month growth study. Appendix Table 26 provides multiple correlation and regression information on the fruit grown for three months after setting over the month of March, 1971. Of the variables enumerated in 3.2.1, the stepwise regression procedure selected (i) seed mass; (ii) the index for available leaf area per fruit; and (iii) the sum of degree-days above 12°C for the three days preceding anthesis. The partial regression coefficients a_1 , a_2 and a_3 corresponding to (i), (ii) and (iii) above were

a_1 = 6,75 (very highly significant);
a_2 = 0,258 (significant); and
a_3 = 1,47 (nearly significant at the five per cent level).

The coefficient of multiple correlation R = 94,4 per cent was very highly significant.

Of the individual variables themselves, the mean of the index of available leaf area per fruit of 183,2 cm was equivalent to 5 701 cm^2 per fruit, using the regression of Appendix Table 25. The mean of the third variable, sum of degree-day for the three days preceding anthesis, 27,7 , corresponded to the mean temperature of 21,2°C. The range in values corresponded to the daily mean range of 17°C to 25°C. But note that this variable took on only four values. The regression coefficients are all therefore limited by the fact that this last variable effectively took on only four values. (It is however a 'continuous' type of variable.)

With regard to the total correlation coefficients, note the very high correlation of 0,926 between seed mass and fruit flesh mass after 12 weeks growth Of the other total correlations, the heat variable for the period preceding anthesis was correlated with both fruit flesh mass (0,541) and seed mass (0,467).

Two selected partial correlations are given. That for $r_{1y,23}$, viz. the correlation between seed mass and fruit flesh mass after first allowing for the apparent associations of both the available leaf area per fruit (X_2) and the

sum of degree days above 12°C for the three days preceeding anthesis (X_3) with both the seed and fruit flesh masses (X_1 and Y) was 0,9199, highly significant. That for $r_{2y,13}$ was 0,3898 , significant at the five per cent level. That is, after first allowing for the apparent effects of seed mass (X_1) and the temperature variable (X_3) , available leaf area per fruit was still found to have a significant positive association with fruit flesh mass.

Another way of expressing some of the apparent relationships in the data is in the form of Figure A of Appendix 26. Observed fruit flesh masses have been plotted against their respective seed masses, and a regression equation $y = 66,96 + 7,083\ X_1$, represented by the black line, has been fitted to this data. This last mentioned equation was for all the data, irrespective of variations in X_2 and X_3 . The simple or total correlation $r_{1y} = 0,9257$ (or 0,93) "corresponds" to this regression.

The coloured lines (blue, green and red) again represent simple linear regressions of fruit flesh mass (Y) on seed mass (X_1) but this time taking separate levels of X_2 , the available leaf area per fruit variable, into account. Thus the blue line represents only those fruits (with their respective seed masses) which had values of X_2 greater than 190. The respective regressions and their corresponding simple or total correlations can be found on the figure. Finally, the geometric symbols around each associated fruit flesh mass (Y) and seed mass (X_1) point represent the various levels of X_3 , the temperature variable used.

From this figure it is apparent that the regression of Y on X_1 was steeper for higher levels of X_2 . More particularly, at the lowest level of X_2 there was an apparently diminished effectiveness of seed mass on fruit flesh mass. That is, the apparent influence of seed mass on fruit flesh mass over the first three months of growth was limited by the relative amount of available leaf area per fruit. Another apparent pair of relationships was that between X_3 , the temperature variable, positive with both X_1 (seed mass) and Y (fruit flesh mass).

For the record, the variables not accepted into the regression equation were (a) the sum of degree-days for the 40 days prior to anthesis (hardly any differences between sub-sets); (b) fruit diameter at anthesis (range 14 to 20 mm); (c) the index of the leaf area of the subtending leaf (range 106 to 148 cm, mean 133,4 cm, the latter equivalent to 3322 cm^2 leaf tissue); and (d) the sum of degree-days for the period from anthesis to harvesting at 12 weeks (the range for which, in terms of mean daily temperatures was equivalent to 16,2°C to 18,3°C).

3.3.1.2 Seven month growth study. Appendix Table 27 provides the first choice multiple linear regression equation when following strictly the stepwise procedure of Draper and Smith (1966). The first variable accepted was that of seed mass. Then in order to correct for a non-random trend in the error residuals the second variable was derived from the first, viz. its square. (That is, 'seed mass' was expressed by two terms in the linear equation.) This had not been necessary in the three month study.

The third variable accepted by the procedure was the sum of degree-days above 12°C for the forty-day period preceding anthesis. The author feels this was a somewhat 'spurious' choice as this variable, when converted to mean temperatures for that period, had only the range of 20,4°C to 20,7°C. (It also took on only four values.) In terms of the procedure for fitting variables, after some of the variation in fruit flesh mass had been accounted for by the seed mass variables, that which remained unaccounted for was best fitted with the above temperature variable, i.e. better fitted than by the variations in the other remaining variables. Whether this sequence of fitting would occur in a separate study remains open to testing. An alternative regression model will be presented after this one, using a different temperature variable.

The fourth variable accepted into this present model was the index of total available leaf area per fruit during April. The range was 112 cm to 370 cm with a mean of 192 cm (equivalent to about 6000 cm^2 leaf tissue per fruit), slightly higher than that for the three month growth batch (5700 cm^2) during April.

The mean for fruit flesh mass after seven months growth was 779 grams. If these March-set fruits had been allowed to grow to maturity (at about ten months), their mean fruit flesh mass would have been about 1100 grams. This would have been between the means of the hand-pollinated summer (February) and autumn (April/May) sets of 1970, as would be expected.

The variables not accepted by the procedure were (i) the diameter of the fruit at anthesis (range 14 to 20 mm); (ii) sum of degree-days above 12°C from anthesis until the 15th week (which was used in the alternative regression to follow); and (iii) the index of the subtending leaf's area (range 98 to 157 cm, mean 133,5 cm, the latter equivalent to about 3400 cm^2).

In terms of the simple or total correlations with fruit flesh mass, the highest was with seed mass, 0,777 , again highly significant. This was apparently less than that for the three month study (0,926). On transforming these into z values, the 'u value' of their difference (Kendall, 1948) was 2,184 , significant at the five per cent level. This result could be interpreted as a chance result,

with a very small probability that the high correlation of the three month study would be repeated again. Other hypotheses are also possible. It could be that the period of seed influence on fruit flesh mass for fruits set in March in this locality lasts for less than seven months, and that certain amounts of seed and fruit flesh mass growth outside of the effective period is less or uncorrelated. Hence a lowered total correlation. These hypotheses need to be tested, though.

The partial correlation between seed and fruit flesh masses after first allowing for the apparent effects of the temperature and 'leaf area' variables, viz. $r_{1y,34} = 0,8235$ was actually higher than the simple correlation. The partial correlation between the index of available leaf per fruit during April and fruit flesh mass (after first allowing for the apparent associations with seed mass and the temperature variable), viz. $r_{4y,13} = 0,3249$ was only significant at the ten per cent level. If a more extended measurement of the leaf area variable had been undertaken throughout the course of growth, the unmeasured effects of leaf abscission may have been accounted for and a leaf area variable could well be more important. That much was apparent in the discussion of the Appendix 26 Figure A. That leaf area variable was most likely more adequately representative in the three month growth study.

In an alternative regression model (Appendix 28), the sum of degree-days from anthesis until the 15th week was substituted as the third variable in place of the degree-days before anthesis (Appendix 27). The averaged mean daily temperatures corresponding to these degree-days values ranged from 15,9°C to 17,6°C with an overall mean of 16,8°C, slightly lower than that for the three month period's range of 16,2°C to 18,3°C (presumably because of cooler conditions in July). The range was again very restricted, and of course there were only four values. If a wider range and a greater number of values were represented, the author feels a more significant regression co-efficient would be obtained. Simple comparisons between the data of autumn and summer sets in this thesis, and the studies of Kuhne and Allan (1970) suggest temperature related conditions are important for both seed and fruit growth.

In comparison to the model of Appendix 27, this one had only a very slightly lower multiple correlation co-efficient (0,8813 versus 0,8867). The variables chosen, however, were in reality probably more important. The partial correlation $r_{1y,34} = 0,8258$ was even slightly higher here than in Appendix Table 27. That of $r_{4y,13} = 0,3208$ was again only significant at the ten per cent level, with the same qualifying comments made in the discussion of Appendix 27.

As the simple correlation between seed mass and available leaf area per fruit was -0,2205 , and seed mass was significantly correlated with the

temperature variable (r_{13} = 0,5286), the partial correlation $r_{14,3}$, i.e. between seed mass and the leaf area variable after first allowing for the associations with the temperature variations, was checked (-0,2408). This was not significant.

As was done in 3.3.1.1 for the three month study, the relation between seed mass and fruit flesh mass given associated measurements of the leaf area and temperature variables is shown graphically in one way in Figure A of Appendix 28. A number of features will be briefly pointed out.

Firstly the pattern of the data points around the simple regression line (solid black) was the reason for introducing the quadratic term (X_2) which effectively broke up this pattern in the residuals (not shown here). Secondly the regression line most similar to those of the three month study (3.3.1.1) was that for those fruits with the highest level of available leaf area per fruit (blue). Without accurate information on leaf abscission it is hazardous to make any inferences on this. It can be suggested of course that the relation of seed and fruit flesh mass is dependent on the amount of available leaf area. This also fits in with expectations. The actual relationships however, need more rigorous testing. Thirdly, twelve of the fifteen largest seed masses were associated with temperatures in the upper half of their (admittedly restricted) range. (This was the case for only eight of the fifteen largest fruits.) The fifteen smallest fruits seem to have been more sensitive to lack of seed mass than to the other variables. It seems to the author that these smaller fruits may have suffered from a greater lack of viable pollen (possibly too immature when hand-picked) with presumably lower proportions of fertilized ovules.

In summary then, the results of this section (3.3.1) seem to be that (i) seed mass was an important variable, even when allowance was made for the other covariables, given the limitations of their measurement; (ii) fruit competition for available leaf area (and presumably assimilates) as measured by the index of available leaf area per fruit may have restricted the size of fruits even when there was adequate seed mass; and (iii) lack of viable pollen for fertilizing ovules may have led to the restricted size of the smallest fruits. The pervasive effect of temperature on seed mass, fruit mass and leaf area (and abscission) was not adequately measured in these studies and needs further attention.

3.3.2 Intra-fruit correlations

3.3.2.1 Intra-fruit seed/fruit correlations. Appendix Table 29 refers to open pollinated fruits set in the autumn of 1973. The rows across the table refer to individual fruits, with the final column providing summed totals for seed and fruit flesh mass respectively for the four intra-fruit subregions. (The fruit flesh mass excluded the apical and basal bits previously cut off, as explained in 3.2.2. The seed and truncated fruit flesh masses were estimated from 4/5th longitudinal portions.) Each of the columns provides means and seed/fruit correlations for the particular intra-fruit subregion(s) across the 17 fruits.

The four seed mass means for the intra-fruit subregions Aa to Dd were 5,49 , 8,93 , 5,83 and 2,14 grams respectively. In terms of surface (placental) area the Bb and Cc regions, being rectangular, were approximately equal in size and larger than the more triangular Aa and Dd subregions. That the Bb subregion had a larger mean seed mass than that of the Cc subregion expressed a difference due to a greater proportion of ovules being fertilized in the Bb subregion in the autumn set (Chapter II). The much smaller mean seed mass for the Dd subregion also illustrates the low intensity of pollen tube penetration into that subregion in autumn.

The corresponding four fruit flesh mass means were 107,60 , 120,21 , 93,19 and 57,95 grams respectively. The Bb subregion was again greater than that of Cc, due to a thicker mesocarp. Even the placentally smaller Aa subregion had a larger mean fruit flesh mass than that of the Cc subregion, due again to its greater thickness.

The four corresponding seed mass/fruit flesh mass correlations were 0,591 , 0,617 , 0,635 and 0,658 respectively. The first (for Aa) was significant at the five per cent level, the remaining all being significant at the one per cent level. That for the four subregions summed together ('whole fruit'), viz. 0,623 was also significant at the one per cent level.

The overall ratio of the fruit flesh mass to seed mass for this set of fruit was considerably greater at the apical and basal ends, even after the end bits had been cut off. This may reflect an inherent characteristic of the papaya fruit, i.e. that its flesh thickens at the ends irrespective of the further effec of seeds. It was because it was suspected that the fruits have such an inherent intra-fruit morphological difference that these correlations were within Aa's, Bb's, etc. rather than within, say, mixtures of Aa's and Bb's, etc.

The appendix figures of Appendix 29 (viz. Figures A to E) illustrate the simple regressions corresponding to the data of the five 'column' sets of the correlation table of Appendix 29. The regression equation of fruit flesh mass on seed mass (Y on X) appears in each figure, together with standard errors of: the estimate of Y on X (Sy. x); of the regression coefficient of X (S_1); and of the intercept on the Y axis (S_0). The corresponding correlation coefficients (r) are also provided.

If the standard errors are taken into account, there was much overlapping between the same coefficients for all four subregions, with the exception of the intercept for Figure D. Greater replication would be needed to test whether there were differences. Using the present data, as a matter of interest, it can be shown by simple arithmetic that the regression coefficient of Y on X for the 'whole' fruit (Fig. E) was nearly equal to the average of the same coefficient for the four intra-fruit subregions, and similarly for the standard errors of this coefficient. This was also the case for the correlation coefficients.

On the other hand, the intercept on the Y axis for the regression of the whole fruit (Fig. E) was nearly equal to the sum of the values of the same intercept on the four subregions. All the above results were closer if weighted according to the average relative sizes of the four subregions. Whether these relationships do exist will only be found with further replication. Assuming they did seems to suggest that the 'effect' of the seeds on fruit flesh mass was both localized (and thus also dependent on the amount of seed mass in each subregion) and yet fairly similar on a per seed gram basis for all subregions. The 'effect' over the whole fruit could be an average of all the localized effect

The intercept values on the Y axis could be interpreted as the resultant of other factors, part of which could be inherent morphological factors, other facto could be the condition of the trees etc. The relative contributions of factors is a more complex matter, as hinted at in 3.3.1. But in order to reach maximum fruit sizes, given the other conditions during fruit set and growth, it would still be desirable to ensure a high degree of ovule fertilization and seed growth

Similarly Appendix 30 refers to an open pollinated set of fruit set in the summer of 1972/73. But in this case the estimates were from randomly chosen 2/5th truncated longitudinal fruit portions (3.2.2).

An inspection of this Appendix shows that the seed and fruit mass means were considerably larger than those of the autumn set. The ratio between the highest subregion (Bb) and the lowest (Dd) was also much narrower, reflecting a more even and higher level of ovule fertilization.

With regard to the correlations, apart from the Dd subregion these were lower than those in the autumn set. This may in part have been due to the use of only 2/5th longitudinal portions. Thus the disregarded 3/5th portions (used only for the seed count studies in Chapter II) may have exerted some influence on neighbouring regions, 'distorting' the correlation and probably lowering it relative to a study using all five longitudinal portions.

Again the highest calculated correlations were for the lower half of the fruit, where there was less seed mass. And again the apical and basal portions, Aa and Dd, had a greater fruit flesh mass to seed mass ratio relative to the central portions. But the ratios were generally lower than that of the autumn set, with the overall 'whole' fruit ratio (excluding cut portions) being 7,53 as opposed to 16,95 in the autumn set. When seed masses were included with the fruit flesh masses (as in Allan, 1969) then the respective ratios were 8,53 and 17,95 for the summer and autumn truncated fruits respectively. These were of the same order as Allan's (1969) ratios of 11,4 , and between 17,4 and 22,1 , for untruncated summer and autumn set fruits respectively. More is said of such ratios in 3.3.3.4.

The regressions of fruit flesh mass on seed mass for the summer set of 1972/73 have not been illustrated here. Generally the intercept on the Y axis is much higher and the regression coefficients for Y on X were lower. For the 'whole' fruit the regression was $Y = 611{,}25 \pm 133{,}63 + \left[2{,}649 \pm 1{,}032\right]X$. More accurate estimates would probably have been found if all five longitudinal portions of each fruit had been used. But these estimates illustrate again that the regression coefficient of fruit mass on seed mass for summer set fruits may be lower than that of autumn set fruits, as it also appeared in Allan's (1969) data. In other respects the regressions in this section (3.3.2.1) are not comparable to either Allan's (1969) or those of 3.3.1 because we have been dealing here with parts of fruits only.

3.3.2.2 Intra-fruit seed/non-fertilized ovule size correlations. In the reports and discussion on ovule and early seed growth in Chapter I, it was noted that there was a pattern of growth initially related to the location of the ovules and their proximity to the apical end of the flower/fruit. Note was also made that unfertilized ovules in close proximity to a concentration of developing seeds were larger than similar ovules in less developing subregions (1.3.1.9).

Appendix Table 31 associates relative concentrations of seed mass (covariable x) for each of the eight intra-fruit subregions with the mean size of unfertilized ovules (covariable y) for these subregions, all measured at fruit maturity. In the body of this table every pair of figures in a given column corresponds to the covariables x and y associated with a specific subregion (rows). Each column in turn refers to a given 1/5th longitudinal portion. The averages in the 'MEAN' column refer to the mean values for x and y for a specific intra-fruit subregion for the whole set of 1/5th longitudinal portions. The 'RANK' column refers to the ordering of the above x and y mean values respectively.

From these rankings it can be seen that with regard to the x variable (concentration of seed mass), on the average the 'A' subregion had the highest concentration, the 'd' subregion the lowest. Similarly, with regard to the y variable (volume index) the largest unfertilized ovules were in the 'B' subregion, the smallest in 'd'. Overall the ordering for x was A, B, C, a, D, b, c, d and for y it was B, A, C, a, b, D, c, d i.e. a rather similar ordering.

Appendix Table 32 tests the above apparent association. To illustrate, the x/y pairs of a given column in Appendix Table 31 (corresponding there to a given fruit 1/5th longitudinal portion) have been correlated, the results for all such columns appearing in the rows of the column under r_{xy} in Appendix Table 32. Each of these correlations have been transformed (Z column) in order to carry out the test of homogeniety. This X^2 (with 26 degrees of freedom) of 1,333 was not significant, implying that a common, average correlation coefficient could be presented. Its detransformed value was r = 0,753 , a close association. Even when using only a conservative six degrees of freedom (based on N = 8 for each fruit subregion, that is disregarding a possible larger contribution to degrees of freedom from the 27 portions) this correlation was still significant at the five per cent level.

Thus the influence of developing seeds on neighbouring unfertilized ovules already measurable between the second and fourth week after anthesis (1.3.1.9) was still apparent at fruit maturity. If one recalls that unfertilized ovules

are genetically maternal tissue, i.e. genetically identical to the fruit (but not the fertilized seeds), then these results are another way of illustrating the 'seed'/'fruit' correlation in papaya at the intra-fruit level.

3.3.3 Further seed growth, abortion and fruit size correlations

3.3.3.1 Autumn 1970 fruit set study. Appendix Table 33 sets out correlations and selected partial correlations of several seed measures, fruit growt seed abortion and fruit competition. The variable x_1 , a measure of the early seed development intensity, was used in intra-fruit studies in Chapter II. It has been used here for the whole fruit, and as a check on its relation to abort rates when tested between fruits. (In Chapter II it was unclear whether aborti rates were really related to intra-fruit seed competition.) This x_1 was also included here to compare it with the variable x_4 , the sum of fully developed, partially and slightly developed seeds, which in turn can be related to Allan's (1969) correlations between seed number, seed mass and fruit mass (including seeds).

The reason for transforming x_1 (and x_2 , the abortion rate for the whole fruit) to angular degrees was again to be able to attach probability statements to correlations involving these variables. The x_3 and x_4 variables were seed count measures in contrast to the corresponding mass measures of x_5 and x_6 respectively. Allan (1969) used principally the x_3 , x_5 and x_6 measures. The variable y , fruit mass, excluded seed mass in order to avoid the effect of self-correlation. The variable x_7 was intended to provide some index of fruit competition during the early part of fruit growth. The variable x_8 was intende as another index of the relative competitive advantage/disadvantage of a given fruit in terms of the ratio of leaves per fruit on the stem during autumn.

Total Correlation Coefficients

The variables x_1 and x_4 were highly correlated (0,868) as could be expecte from the way they were derived. Each of their respective correlations with the other variables were also similar, with the x_4 being generally better correlate especially with y , fruit flesh mass (0,727 versus 0,560). Neither of them was significantly correlated with seed abortion (0,022 and 0,019 respectively). [The reason x_1 (and not x_4) had been used in the intra-fruit studies of Chapter was because the subregions A, a, ... D, d differed markedly with respect to placental area and the derivation x_1 sought to allow for this there. This was not considered to have the same relevance between whole fruits.]

The fact of non-correlation with the seed abortion rate supports the tentative conclusion of Chapter II studies that the extent of early seed development was not related to seed abortion (2.5.1.8). A conclusion now is that boosting the proportion of ovules that are fertilized by means of hand-pollination does not by itself induce seed abortion. In the Chapter II study with open pollination, the average proportion of ovules fertilized was about 31 per cent (Table 14). In the present hand-pollinated study, the proportion of total ovules fertilized varied from 38 to 86 per cent, with a mean of 70 per cent, yet there was no correlation with seed abortion. The seed abortion rate was also not significantly correlated with fruit competition as measured either by x_7 , number of competing fruit (-0,069) or x_8 , leaf to fruit ratio (-0,272). Nevertheless the correlation measured between seed abortion and the leaf area per fruit (r_{28}), i.e. 'fruit competition', was higher than that between seed abortion and seed competition (r_{24}).

Seed abortion was correlated with x_3 , the sum of fully developed seeds (-0,584), with x_5 , mass of fully developed seed (-0,605) and x_6 , mass of all seeds (-0,590), all significant at the five per cent level. This was because, given the relatively high proportion of ovules originally fertilized in this fruit set, the higher the abortion rate, the fewer the likely number of fully developed seeds (and hence seed mass). The abortion rate <u>per se</u> however, was not correlated with fruit flesh mass (0,038). A possible explanation for that is presented later in this discussion of results.

In regard to the x_3/x_5 comparison (F seed count and mass respectively), th fact that their correlation was not unity pointed to some variation in the average seed mass of individual F seeds between fruits. It should also be obvious that the correlation between x_1 and x_3 (r_{13} = 0,676) would have been greater than that between x_1 and x_5 (r_{15} = 0,623) because x_1 and x_3 are both 'count' measures whilst x_5 was a 'mass' measure. Similarly for r_{34} versus r_{45} and r_{56} versus r_{36} .

However, with regard to y (fruit flesh mass), x_5 (F seed mass) had a higher correlation (0,661) than x_3 , F seed count, (0,520), the latter being non-significant. Allan (1969) also found a higher correlation for F seed mass than for F seed count. This probably has to do with the importance of mean individual seed mass in different fruits, not accounted for in F seed counts. With regard to the fruit competition variables x_7 and x_8 , x_5 (F seed mass) again had a higher correlation (-0,208 and 0,491 versus -0,162 and 0,441 respectively) than x_3 (F seed count), although none of these were significant. Allan (1969) had found that stripping off fruits (lowering fruit competition)

appeared to increase the number of well developed seeds. These present findings are in the same direction, with the ratio of leaves to fruit being more importan than merely the number of fruits.

The variables x_4 (sum of F, P and S seeds) and x_6 (mass of all seeds) provided interesting information. In relation to seed abortion, x_6 (mass of all seeds) was significantly correlated (-0,590) by virtue of the component of F seed mass which was affected by seed abortions. In contrast x_4 was not correlated (0,019). But with regard to y , fruit flesh mass, x_4 (F + P + S count) had a greater correlation (0,727) than x_6 , mass of all seeds, (0,670). Both were significant. One possible reason for this was that before the (P + S) seeds aborted, all (F + P + S) were affecting fruit flesh mass growth, but after abortion, the continued growth of F seeds was not much correlated with further fruit growth. Another way to state this is to say that if the mass of (F + P + seeds were taken nearer to the time of seed abortions, then x_6 (seed mass) would more likely have been more correlated. That is what appears to have been the case in the three and seven month studies in 3.3.1. This aspect is examine again in further analysis of this and other fruit sets that are to follow.

Because of the similarity between x_5 (mass of F seeds alone) and x_6 (mass of all seeds), r_{5y} (0,661) and r_{6y} (0,670) were very similar. As found by Allan (1969), the inclusion of the mass of the smaller (P + S) seeds increased the correlation. In contrast, with the seed count measures x_4 and x_3 (which were more different than x_6 and x_5 were from each other), r_{4y} (0,727) was marke higher than r_{3y} (0,520). Again it points to the (P + S) seeds having contribut to the seed/fruit flesh interaction. And hence a possible reason why abortion rates were not correlated with fruit mass.

Finally, with regard to the fruit competition variables x_7 and x_8 , although none were significant, x_8 (leaf to fruit ratio) was more correlated to the seed variables x_1 to x_6 than x_7 (number of competing fruit). But with regard to fruit flesh mass, x_7 had a higher correlation (-0,425 versus 0,360). It may be that seeds were more sensitive to leaf area than were the fruits. Interestingly the correlations between x_8 and the seed variables were higher (and positive) in this study than that of the comparable available leaf area index of the three and seven month studies of 3.3.1. In those studies the apparently (slight) negative effect of leaf area on seed growth was rather puzzling. This aspect needs further clarification.

In summary, the conclusions from the analysis of the total correlation matrix were as follows:-

(i) The extent of seed fertilization per se did not affect seed abortion rates.

(ii) There was some tendency (not significant) for an on-stem competitive factor involving leaf area to fruit-load to increase seed abortion rates and lower seed mass (through a lowering of the number of fully developed seeds).

(iii) There was also a tendency (not significant) for on-stem fruit competition to lower fruit flesh mass.

(iv) Seed abortion lowered seed mass (by reducing the number of F seeds) but had no significant effect itself on fruit flesh mass, because aborted seeds themselves apparently contributed to the latter.

Selected First Order Partial Correlations

A number of these were also calculated in order to further assess some of the seed/fruit correlations once the effects of seed abortion and fruit competition had been accounted for.

The partial correlations between seed abortion (x_2) and x_4, the number of (F + P + S) seeds ($r_{24,7}$ or $r_{24,8}$), although greater than their corresponding simple correlations, remained non-significant when the effects of fruit competition (x_7 or x_8) were accounted for. The parallel correlations $r_{21,7}$ and $r_{21,8}$ were also not significantly affected. The correlation $r_{28,4} = -0,302$ implied that when possible intra-fruit seed competition was accounted for, on-stem leaf/fruit competition factors showed a slightly stronger association with seed abortion, but this was not significant; similarly for $r_{28,1}$.

The correlation between the sum of F seeds and fruit flesh mass ($r_{3y} = 0,520$) increased when the effects of seed abortion on both were eliminated ($r_{3y,2} = 0,668$), being significant at the five per cent level. By contrast, eliminating the effects of x_8 depressed the r_{3y} ($r_{3y,8} = 0,431$), pointing to the possible importance of x_8 to both x_3 and y.

Unlike the effect on x_3 (number of F seeds alone), eliminating the effect of seed abortion rate on r_{4y} had no effect ($r_{4y,2} = 0,727$). But in the case of x_5 (mass of F seeds) and x_6 (mass of all seeds), eliminating the effects of abortion increased r_{5y} and r_{6y} from 0,661 and 0,670 to 0,860 and 0,858 respectively. The effect was undoubtedly through x_3 (number of F seeds). The apparent relation between F seeds and fruit flesh mass (as measured by the total correlations) was represented in a distorted way if (P + S) seeds were also affecting fruit growth - hence eliminating this source (as in $r_{3y,2}$, $r_{5y,2}$ and $r_{6y,2}$) increased the strength of these associations with fruit flesh mass.

Thus one can conclude that seed abortion 'masks' or 'hides' the full extent to which F seed is associated with fruit flesh mass. Hence Allan's (1969) findings that in fruits with relatively more under-developed seeds, the correlation between fully developed seeds and fruit mass was lower.

With regard to eliminating the effects of x_7 and x_8 , the latter had the greater (depressive) effect on all three (r_{4y} , r_{5y} and r_{6y}). Since x_8 was better correlated with fruit flesh mass and the seed measures, eliminating this common co-variable brought down seed/fruit correlations. In fact, only the partial correlation between the number of (F + P + S) seeds and fruit flesh mass remained significant. This puts the seed-leaf area-fruit competition complex into some perspective. A tentative formulation from this study is that the total available leaf area per fruit on a stem is important to both fruit and seed growth, nevertheless the early part of seed growth (up to seed abortion) itself has a sufficiently determining effect on final fruit size.

Appendix 34 is a closer analysis of the seed count correlations of the 1970 autumn set (Appendix 33). Specifically, one can ask about what happens correlationally when each category of seed is added to a previous more developed type or types. For convenience, the seed type distributions examined in Chapter II for this set have been recorded here. Over the whole set F seeds comprised 0,349 of all seeds and ovules; P seeds (comprising cTL and cWL - see glossary) only 0,005 ; S seeds 0,348 of which cWs was 0,028 and the smallest slightly developed seeds, b, 0,320 ; and unfertilized ovules the remaining 0,298 .

The correlation between sum of F seeds and fruit flesh mass was 0,520 (not significant) - already discussed for 'x_3' in Appendix 33. The correlation of the sum of (F + P) seeds was slightly less, at 0,516 . But that of $\left[F + P + (cWs)\right]$ seeds was 0,611 , significant at five per cent. It appears that even though the cWs portion only averaged 0,03 , it was an important enough component to increase the correlation. Finally, when the more numerous b seeds in this set were added (x_4) , the correlation was 0,727 , significant at the one per cent level. Adding the unfertilized ovules, although of about the same number as b seeds, reduced the correlation to 0,506.

Thus from the study of these distributions, it is clear that for a contribution to have been important it had to represent not only a sizeable 'count' proportion, but that it at least represented a phase or phases of seed development. To relate this to a possible physiological base, if the major influence of seeds on papaya fruit growth is indeed hormonal, then the likely quantitative measures could be the amount(s) of the effective hormone(s) produced. At the critical period(s) of effectiveness, fully developing seeds (F), being larger,

may well be producing a greater quantity per seed than abortive types, and perhaps for a longer period. Nevertheless a sizeable proportion of less developed seeds could still conceivably produce effective quantities, thus influencing correlations based purely on seed counts. Unfertilized ovules would appear to provide little effect, limited as they are in the amount of relevant tissues, whichever these are.

One final note on this set. The overall ratio of fruit flesh mass to seed mass was 14,61. When seed mass was included, as in Allan's (1969) studies this ratio increased by unity to 15,61. Allan's autumn set fruits' ratios averaged between 17 and 22 grams. The sets are thus quite comparable.

3.3.3.2 Summer 1970 fruit set study. As a comparison Appendix Table 35 sets out only the simple (total) correlations of certain seed count combination with fruit flesh mass and seed abortion in the 1970 summer set. In this set the overall ratio of fruit flesh mass to seed mass was 9,38 , and 10,38 when seed mass was included with fruit mass. The latter compares closely to Allan's (1969) summer set fruit (11,4 grams). Again these summer set ratios are considerably smaller than the corresponding autumn set ratios.

The overall seed type ratios for this summer set were: F seed 0,725 (far more than in the autumn set); P seed 0,086 (again more than in the autumn set); S seed 0,065 (made up of cWs 0,056 and b 0,009), much less than in the autumn set; and 0,124 for the U ovules.

The simple (total) correlations with fruit flesh mass were 0,509 (significant at five per cent) for the number of F seed; 0,557 for (F + P) seeds, 0,538 for $\left[F + P + (cWs)\right]$ seeds, and 0,523 for (F + P + all S) seeds, the latter all significant at the one per cent level. The total number of seeds and ovules were not significantly correlated (0,321) with fruit flesh mass, as was also the case with the 1970 autumn set. Total seed mass was significantly correlated with fruit flesh mass at the one per cent level (0,552).

From the above it is apparent that with the greater relative proportion of P seeds (cf. autumn set, Appendix 34), the (F + P) seed count correlation became the largest. The (F + P + S) correlation, by contrast, was less, indicative of the smaller contribution the fewer, smaller aborted seeds made towards fruit flesh growth. Since all types were summed together without differentiating for size perhaps a distortion in the correlation occurred. Or to put it in another way, the effect of seeds probably covered a period beyond the abortion times of the fewer and smaller aborted seeds, so that these received an inflate relative weight in the correlation. The seed mass to fruit flesh mass

correlation on the other hand was very close to the (F + P) correlation because the seed mass was just about made up by that component in this set.

Abortion rates were negatively related with fruit flesh mass, but the correlation (-0,248) was not significant, as was also found in the 1970 autumn set. And again, the level of ovule fertilization (intra-fruit 'seed competitio x_4 , which was quite high in the summer set (mean of 87,6 per cent) was not correlated with levels of abortion (-0,125). In fact the mean overall abortion rate was only 0,158. This adds weight to the accumulative evidence of this thesis that intra-fruit seed competition as measured purely by seed number was not a factor in seed abortion.

3.3.3.3 Autumn 1969 fruit set study. A group of fruit set in the autumn of 1969 as described in 3.2.3 provided further information on seed count correlations. These fruit were set on three different classes of plant stem. Type (a), the smallest and youngest, and generally a side stem, bore only fruit that had set that autumn (Appendix Table 36). Type (b) also bore fruit that had set a few months previously in summer (Plate 36a), and type (c) stems in addition were still bearing some ripening fruits from the previous late autumn set. The latter stems bore the most fruit (25,39) , but this was not due to a large number of ripening previous autumn set fruit but because they were the main stems of the plants. They were more vigorous, and they also had the most leaves (25,24).

In terms of mean individual leaf areas, the order of magnitude was c > b > a stems, viz. 3 538 , 1 882 and 1 434 cm^2 in May respectively and 1 650 , 1 155 and 1 063 cm^2 in October. The same order of ranking occurred with regard to the number of leaves per stem and the number of fruit per stem at the time of fruit set. However, from observation during the course of winter the relative mean leaf area ratios appear to have become closer when the oldest, largest leaves abscissed. This narrowing of the ratios was reflected in the resulting relative ratios of the October measurements.

In May 1969 the mean total stem leaf area per fruit was much greater for a - stems (5 241 cm^2 per fruit), whilst there was little difference between b- and c-stems (3 658 and 3 518 cm^2 per fruit) respectively. However, the apparent greater advantage of a-stems was probably nullified by them being the 'weakest' stems, and the c-stems probably had the greatest apical dominance.

Appendix 37 sets out the correlational analyses of this set, using basically the same set of variables as in Appendix Tables 34 and 35. The differences were that there was no variable for seed mass (not directly measured) and

fruit mass included that of the seeds. In addition an index of fruit volume, based on the volume formula for a prolate spheroid, ($4/3\pi l b^2$, where l and b were the lengths and diameters of the fruit respectively) was calculated for each of the 18 fruit throughout growth. The initial and final fruit volume indices are included in this appendix.

Appendix Table 37.1 sets out the data, the means for the fruit of a-, b- and c-stems (described in Appendix Table 36) and overall means for the 18 fruits. From mere inspection there appeared to be little difference between fruits of the different stems in all the variables except perhaps x_4, x_6, y and z (sum of seeds and ovules, fruit volume at anthesis, and final fruit volume and mass respectively). There was virtually no difference in abortion rates (x_5) between stems. Nevertheless t-tests were carried out and these are reported on after the following paragraph.

The mean ratios of seed types for the whole set were 0,371 for F seeds, 0,182 for P seeds, 0,066 for S seeds and 0,381 for unfertilized ovules respectively. The major differences between these and the autumn set of 1970 (Appendix 34) was that there was a greater proportion of P seeds relative to S seeds in this 1969 autumn set (0,182 versus 0,005) and that the combined (P + S) seed proportion was less in 1969 than in 1970 (0,248 versus 0,353). There were also more unfertilized ovules (0,381) in autumn 1969 than in autumn 1970 (0,298).

Appendix Table 37.2 sets out t-tests on the differences between fruit stem types for the various variables. The only significant differences occurre in x_4 (total number of seeds and ovules per fruit) and x_6 (fruit volume at anthesis).

Of the t-tests for the x_4 variable the largest difference was that between a- and c-stems, and between a- and b- versus c-stems for the x_6 variable.

The similarity in these two could be expected in that larger flowers at anthesis would tend to have a larger number of total ovules. What is interesti is that these differences in size of flower between stems did not persist in the fruits. Obviously the extent of the variation in ovule fertilization and seed development after pollination nullified the differences between stems so that these were no longer significant.

Nevertheless the fruits from the more vigorous stems were on the average larger. Also, because of the relatively few number of fruits in each stem class, just one poorly fertilized fruit in the c-type effectively reduced the mean size of that whole subset. These would otherwise have probably been

significantly greater. Thus one can conclude by saying that

(i) vigour of stem probably was important; and

(ii) the effect of that could nevertheless be nullified by the extent of ovule fertilization, itself dependent on pollination, conditions for pollen germination and pollen tube growth.

Since it was known from correlation studies on other fruit sets that the x_4 and x_6 variables were not strongly correlated with final fruit mass (and therefore volume), it was decided to pool the subsets together and calculate correlation coefficients based on all 18 fruits.

Appendix Table 37.3 sets out the matrix of total (simple) correlations between the variables, plus a few selected first order partial correlations. The sum of F seed (x_1) was obviously highly correlated with x_2 and x_3 (0,848 and 0,821) because they shared common elements. Interestingly x_1 was not significantly correlated with x_4, the total number of ovules and seeds (0,242). This was because there was on the whole a sizeable proportion of ovules not fertilized in spite of using hand-pollination. (Of course the level of fertilization was higher than in the open pollination of the 1973 autumn set.) Thus the potential implied in flowers having a large number of ovules remains dependent on adequate pollination and fertilization and seed development.

The number of fully developed F seeds (x_1) was correlated with the rate of seed abortion (-0,454) at the ten per cent level. In other words abortion tended to affect the distribution of the number of fully developed seeds per fruit in the set.

The correlation of 0,289 between x_1 and x_6, fruit volume at anthesis was not significant. Just as in the case of x_4, the potential implied in larger flowers is dependent on adequate pollination and subsequent fertilization. The number of fully developed seeds (x_1) was highly correlated with both y (fruit volume at fruit ripening, 0,748) and z (fruit mass, including seeds, 0,765). (Plate 36b shows two labelled fruits of this set: the difference in fruit size was paralleled by their difference in quantity of developed seed.) The two variables y and z were highly correlated (0,989), showing the usefulness of the formula used. Pereira (1968) had previously shown that fruit diameter in this clone was a good if not perfect estimator of fruit volume throughout growth, but this formula had an even higher correlation (0,989 versus 0,958). The closer correlation between x_1 and fruit mass z (as compared to x_1 and y) was partially because of the inclusion of seed mass in z. The relation of x_1 and z is illustrated in Figure A of this Appendix.

With regard to the x_2 variable (F + P seed count), the high correlation with x_3 was again obvious - a high proportion of shared elements. The low

x_2/x_5 correlation (0,046) was because seed abortion levels affected F and P seed counts in relatively balanced opposite directions in this set. With regard to y and z , x_2 and these were more highly correlated (0,794 and 0,831 respectively) than in the case of x_1 (F seeds alone). This was the case again for x_3 (F + P + S seeds) and y (0,793), although the latter did not increase over that of x_2 . The correlation r_{3z} also did not increase over that of r_{2z} . In this set, in contrast to the 1970 autumn set, there was a greater differential between x_2 and x_1 than between x_3 and x_2 . In other words, the P :: S ratio was greater in the 1969 autumn set. Hence the relatively greater influence of P seeds on the correlations in the latter set. In the 1970 set, the influence of S seeds, particularly the more numerous b seeds, were more important. (The relation of x_3 and z is shown in Figure 8 of this Appendix.)

The volume of fruits at anthesis (x_6) was correlated (0,514) with x_4 , the total number of ovules and seeds, at the five per cent level. Obviously larger flowers had more ovules.

Considering the selected first order partial correlations, all of these were improved by the elimination of the effect of seed abortion rates. Of these seed count variables, x_1 (sum of F seeds) was the most improved relative to its total correlation with z (and obviously y). This was because x_1 was the most influenced by abortion rates and because aborted seeds themselves were probably influencing fruit growth. That is the abortive seeds masked or hid the greater degree of association between the number of fully developing seeds and fruit growth, as suggested in the discussion on the 1970 autumn set. This influence of abortive seeds in this 1969 set is dealt with more directly in 3.3.3.4.

The partial correlations presented here (0,830 to 0,845) were all highly significant. Both fully developed seeds, and these plus aborted seeds, had an apparently large influence on fruit growth. Their influence as measured by these correlations may have been overestimated by virtue of using the particular 1/5th longitudinal portion estimates (3.2.3). But the total correlation between F seed count and fruit (plus seeds) mass of 0,765 lay between the correlations of 0,867 and 0,643 found by Allan (1969) for the same measure and season of set. Examining the column of figures for x_{1A} (whose frequency distribution appears 'normal') shows an average spread of about 42 per fruit. Since the 1/5th longitudinal portions used can be expected to have estimated the whole fruit F seed counts to within 15 per cent (3.2.3), and since 0,15 of the mean of x_1 (558) is about 84, the order or rank of these fruits, in terms of the number of F seeds, could have been displaced by up to two positions, up or down, for each fruit. The author has randomly changed the x_1 values by

0,15, up and down, so as to maintain the same mean, and then correlated the new series with the original z values. From ten such sets the lowest correlation was 0,61 (significant at one per cent) and the mean was 0,71. This variation in the estimates of the F seed count correlation was of the same order as that for the 1970 summer set (3.2.3). The (P + S) seed count in this autumn set was of course higher than that of the 1970 summer set, and so the autumn set correlation estimates for (P + S) seeds can be expected to be much closer than those of the summer set. The results thus appear reliable, and they also approximated the results of previous independent studies already discussed.

3.3.3.4 Comparative and concluding correlation studies. Appendix 38 provides comparative data and results drawn or extracted from Appendices 34, 35 and 37. These refer to the hand-pollinated autumn sets of 1969 and 1970, and the 1970 summer set. The new extracted values are for the number of P seed alone, and (P + S) on their own. The purpose of this was to test their significance when separated from the sum of F seeds.

Fruit flesh mass (y) and fruit flesh plus seed mass (z) were both used because in the autumn set of 1969 the former (y) was not available, and Allan (1969) also worked with (z).

Appendix Table 38.1 sets out the mean values of selected variables for the three sets. The two autumn sets had similar F seed counts (x_1) whereas that of the summer set was about two and a half times larger (1 462). The latter summer set's fruit plus seed mass (1 550 grams) was about two times greater than that of the autumn sets.

Although the ratio between the summer and the autumn sets with regard to the F seed count (x_1) was about $2\frac{1}{2}$, that for seed mass (x_5) for the 1970 sets was three. It was the additional, relatively large P seeds of the summer set, together with the larger individual F seeds in summer (Figure 28, Chapter I) that accounted for the increased ratio for x_5 relative to x_1 between these two sets.

Considering just the total correlations with fruit flesh mass (y, Appendix Table 38.2), for the summer and autumn sets of 1970, then it can be seen that the F seed correlations, r_{1y}, were quite similar (0,509 and 0,520 respectively). But the correlation with (P + S) seeds alone (x_3) was a good deal higher for the autumn set (0,557 versus -0,154). This was probably because the complement (P + S) relative to x_1 was higher in the autumn (Appendix Table 38.1); similarly for the r_{4y} correlations. With regard to total seed mass to fruit flesh mass correlation, the higher autumn set correlation (0,670 versus 0,552) was again evident. But because of the higher abortion rates in the autumn set,

the r_{4y} correlation was actually higher than the seed mass correlation.

Appendix Table 38.3, using fruit mass that included the seeds, enables one to compare three sets. Comparing Appendix Tables 38.3 to 38.2, the effect of including the seed mass in that of the fruit mass was to increase all the correlations except one (r_{3z} for autumn 1970). Otherwise the pattern between the summer and autumn sets of 1970 for r_y were virtually repeated with r_z .

In comparing the two autumn sets, the (P + S) seed count (x_3) was less in 1969 (373 versus 576), as was the r_{3z} (0,478 versus 0,526). But in 1969 there was on average a sizeable P seed count (273) so that r_{2z} reached 0,320 , even if not significant.

Examining the first order partial correlations with y , fruit flesh mass, in Appendix Table 38.4 relative to Appendix Table 38.2 shows that for the 1970 summer set the largest positive change in r_{1y} was when the effects of x_2 (the sum of P seeds alone) were eliminated. The correlation went up from 0,509 to 0,545 , increasing in its level of significance. Similarly, r_{2y} was also most affected when the effects of x_1 (sum of F seeds alone) was eliminated, the correlation between P seed count and fruit flesh mass increasing from -0,143 to 0,266 . This points to the importance of the P seed complement in the 1970 summer set.

In the case of the 1970 autumn set there were very few P seeds so that this correlation was not even considered. But note the increase of r_{1y} from 0,520 to 0,566 , another level of significance, with the elimination of the effects of x_3 (P + S seeds).

The same pattern of Appendix Table 38.4 is repeated in Appendix Table 38.5 for the 1970 autumn and summer sets, except that the correlations were higher because of the inclusion of seed mass in fruit mass. In the case of the 1969 autumn set, the most marked changes involved x_2 (sum of P seeds). Thus r_{1z} increased from 0,573 (Appendix Table 38.3) to 0,818 ($r_{1z,2}$) when x_2 was eliminated, and r_{2z} increased from 0,320 to 0,533 ($r_{2z,1}$) when the effec of x_1 were eliminated. The mean sum of P seeds (x_2 = 273) was of course quite high in relation to the mean sum of F seeds (x_1 = 558) in this set.

One perhaps obvious conclusion from the above findings is that the relativ contribution of the F, P and S seeds to fruit growth depends on their relative ratios to the sum of F + P + S seeds. What about the individual sizes of these seeds? In the 1970 autumn set there were approximately 500 (P + S) seeds per fruit, mostly S seeds. Eliminating the effects of (P + S) seeds increased r_{1z} by about eight per cent. In the 1969 autumn set, eliminating the effects of just P seeds (average of about 270 per fruit) increased r_{1z} by about seven

per cent. In the 1970 summer set, eliminating the effect of about 170 P seeds increased r_{1z} by about five per cent. Another way of putting this is that by eliminating

(i) S seeds of 1970 autumn set increased r_{1z} by 0,016 per cent per S seed;
(ii) P seeds of 1969 autumn set increased r_{1z} by 0,025 per cent per P seed;
(iii) P seeds of 1970 summer set increased r_{1z} by 0,029 per cent per P seed.

That is, the larger the aborted seed, the greater was its effect on the seed/fruit correlations.

Figure 34 provides a graphic illustration of how the various seed count correlations in the 1969 autumn set varied over time. Three sets of seed counts for each of 18 fruits, viz.

(i) the sum of F seeds alone;
(ii) the sum of (P + S) seeds alone; and
(iii) the sum of (F + P + S) seeds together

were correlated with their corresponding fruit volume (indices) throughout the course of fruit development. In addition the fruit volumes of each of the fruits at any given sampling (measuring) period were correlated with the fruit volumes of these same fruits at the time of fruit ripening, when the seeds were counted. Of course at the latter time, forty to forty-three weeks after anthesis, these volumes coincided so that the correlation was unity. In contrast to this, Figure 34 shows for example correlations between the sum of aborted seeds (P + S) with fruit volumes at two weeks after anthesis before these seeds had actually aborted. One could view them as potentially abortive seeds at that stage. Because (F), (P + S) and (F + P + S) seeds in this autumn set on average formed relatively large and relatively balanced components (558, 373 and 931 respectively), one could expect them to have had noticeable effects on fruit growth, and this should have been reflected in changes in their respective correlations over time.

All the correlations started off at relatively low levels. Of these, that between fruit volume at anthesis and that at fruit ripening was the highest, 0,418. In the course of growth the subsequent fruit volumes became more and more correlated with their final volumes. This increase was rapid over the first six weeks of growth (May, June), followed by a less rapid phase of increase up to the 18th week (September) and then a final more gradual phase up to unity at fruit ripening, week 43 (March).

The correlation between the number of fully developed seeds (F) alone and fruit volume at a given period developed in two main phases. The first phase

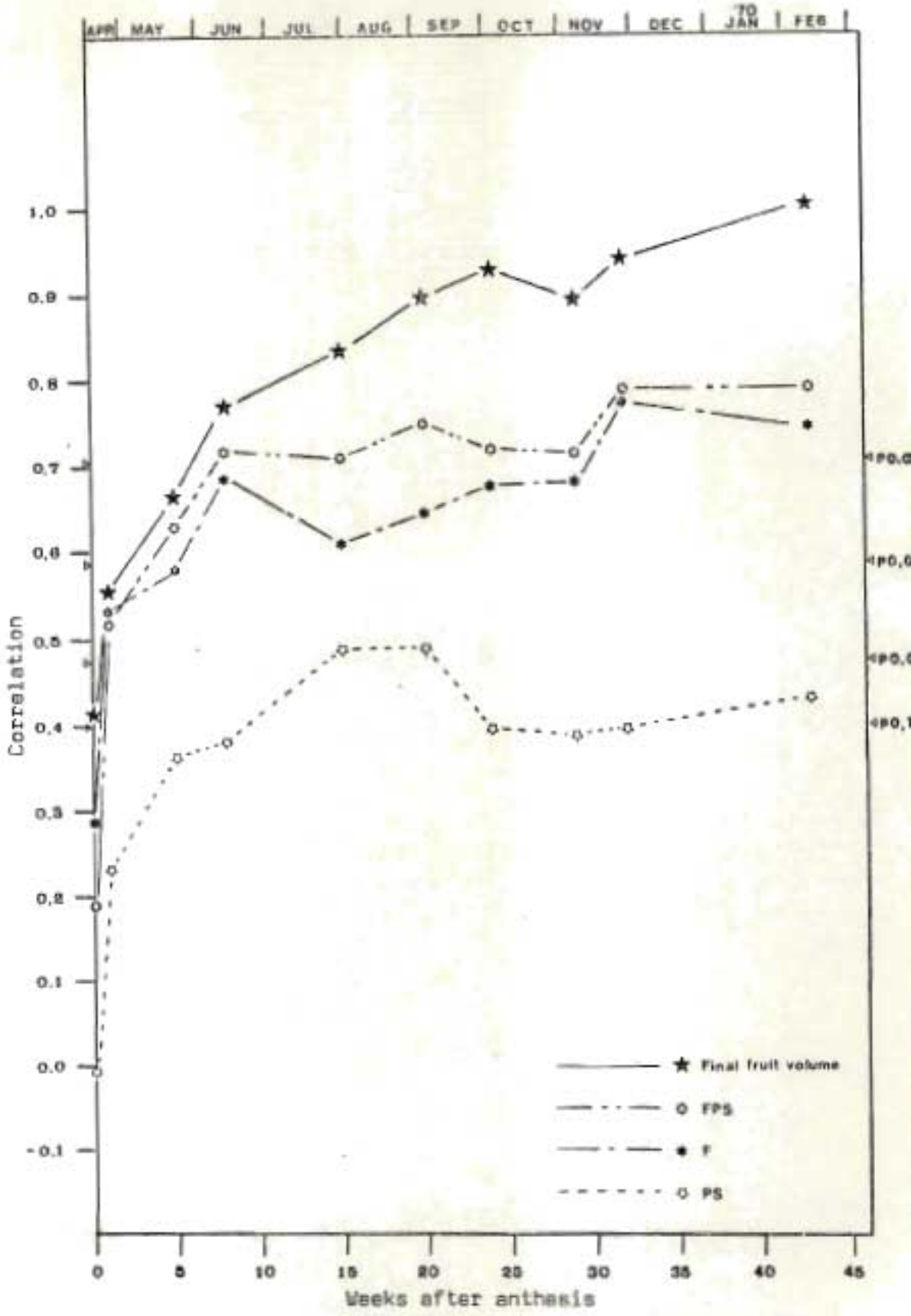

FIGURE 34 Correlations of final fruit volume; and of the estimated number of fully developed seeds (F), aborted seeds (PS) and all fertilized seeds (FPS): with fruit volume during growth in 18 fruits set in autumn, 1969.

◁ indicate significant probability levels.

until just before fruit ripening (0,748). An apparent decline at about the 15th week (August) could have been merely due to inaccurate measuring or recording of fruit dimensions at that time.

Correlation between the sum of aborted seeds alone (P + S) developed in three phases. The first phase appeared to last about five weeks (May, June), possibly before the abortions actually set in. This was followed by a slower increase to about 0,49 at the 15th week (August, when S seeds would have already aborted and the more numerous P seeds were beginning to) and this level was apparently maintained until about the 20th week (September, by which time most of these P seeds would also have aborted). Thereafter there was a slight drop in this correlation (to 0,40).

The correlation for the sum of fully developed, partially and slightly developed seeds (F + P + S) also had three phases. It was higher than the (F) or (P + S) correlations, and appeared to reflect a resultant of the two latter curves, ending finally at about 0,79.

Looking at Figure 34 as a whole, it can be seen that the correlation curve for fruit volume during fruit growth increased and diverged away from that of the three seed count correlations, particularly from August onwards. This would seem to imply that factors other than seeds were influencing the individual fruits in the later stages.

Figure 35 shows the three seed count correlations over time with the increments in fruit volume growth. The "curves" are much sharper than those of Figure 34. The F seed curve seems to have risen more sharply than that of the (P + S) curve. Perhaps (P + S) seeds, i.e. the ones that finally aborted, were seeds that started to develop more slowly, or later (due to delayed fertilization) or because of less potent pollen tubes. The (P + S) curve also seems to have peaked after that of the (F) seeds' (August versus June/July). It would appear that the (P + S) seeds contributed to increments of fruit volume until about the 15th week (August), but with abortions having set in (approximately eighth to 15th week, July/August) there was a rapid decline in their effectiveness after this. The growth of aborted seeds themselves had also ceased from that time (Chapter II).

The (F) seeds seem to have contributed positively and significantly, (even if at a declining rate after the first eight weeks) until about the time the endosperm of all seeds had cellularized and the embryos had entered the rapid phase of growth. This was by the 27th week in November of the 1969 set (1.3.5). This was also the most likely time according to the F seed data on Figure 35 that the F curve went lower than the 0,46 correlation level, the five per cent

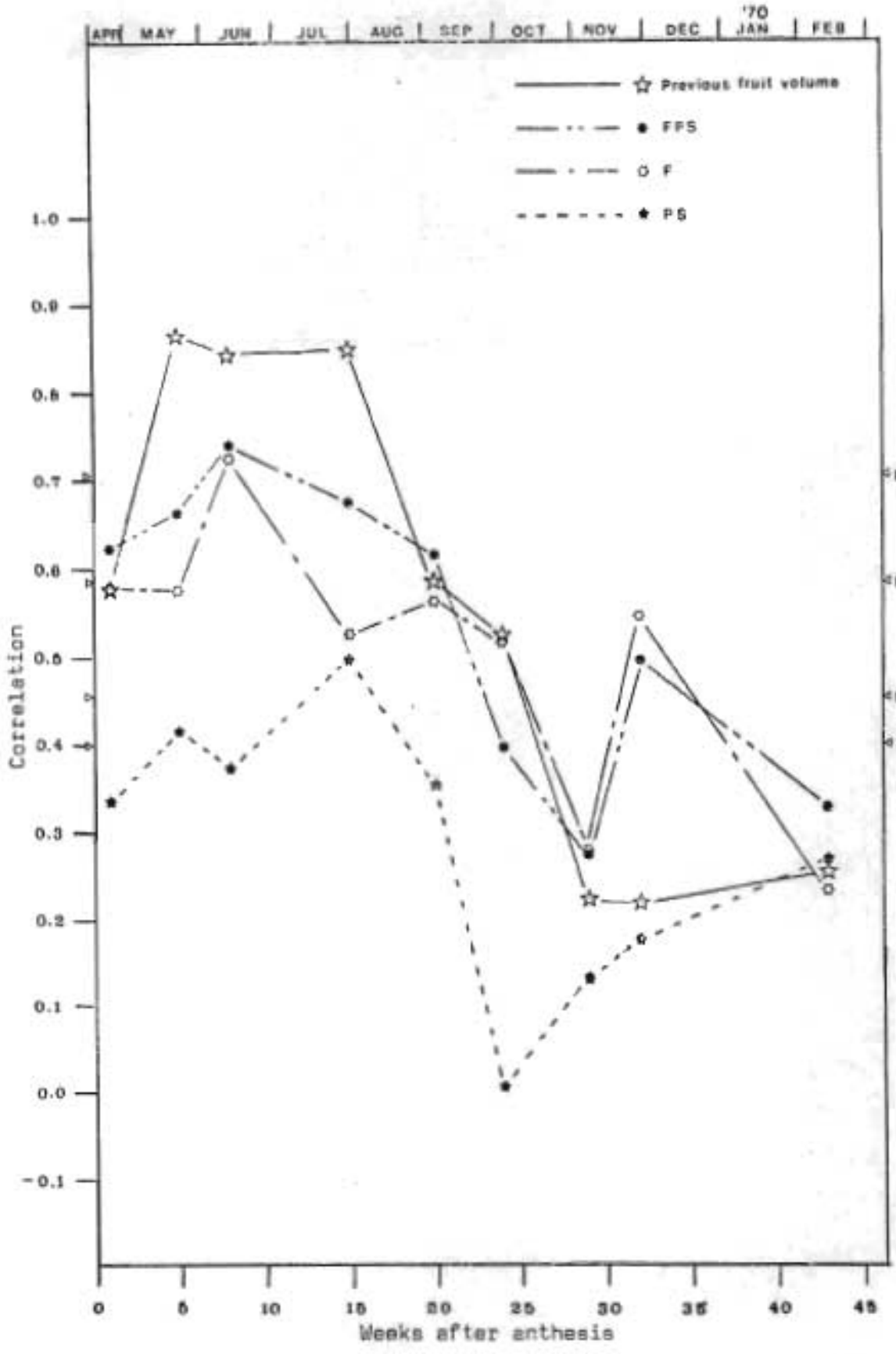

FIGURE 35 Correlations of the previously attained total fruit volume; and of the estimated number of fully-developed seeds (F), aborted seeds (PS) and all-fertilized seeds (FPS): with increments in fruit volume growth in 18 fruits set in autumn, 1969.
◁ indicate significant probability levels.

level of significance. The later rise in the graph at week 32 is puzzling. Was it due to measuring, recording or random errors, or was there actually a late seed influence on increments of fruit growth associated with the late testal developments of F seed prior to final thickening of these tissues? The author is inclined to believe it was a spurious effect, but these results really need further checking, and of course using more accurate whole fruit seed counts

The correlation curve for the (F + P + S) seed counts again generally reflect a resultant of the subsets (F) and (P + S), as in Figure 34. All seed effects were negligible in the later third to half of fruit development. Why then, were the correlation curves at a high level over this period in Figure 34? Partially because the accumulative effects on increments of fruit growth for the first half ensured a high total correlation at that stage. At that stage (week 20) the fruit volumes were to be highly correlated with their final fruit volumes (0,90 , Figure 34). Since the cell division phase of fruit growth (which determines the number of cells available for further enlargement) occurs in the first third to half of growth, according to season of fruit set (Kuhne & Allan, 1970) the strong correlation was understandable. These results also indicate though that the seeds had little or no effect on the process of cell enlargement in the last half of fruit growth.

What was surprising was that the later <u>increments</u> in growth were poorly correlated with the fruits' previously achieved volume (Figure 35). This again seems to point to other unmeasured on-tree or site factors influencing the later cell enlargement phase. Such possible factors could have been soil moisture, and leaf to fruit ratios, during the spring and summer months (September onwards).

One final point about Figures 34 and 35. They were based on the median 1/5th longitudinal fruit portion estimates, and the correlations at fruit ripening may have been overestimated by ten per cent or so. But the general character of the curves themselves (rather than the actual height or level of correlation) has been the point of this presentation. In the author's opinion the curve types, and the approximate times during development at which the seed type/fruit mass associations increased or diminished were probably reliable representations. Assuming their reliability suggests an explanation for observed differences in correlations of the other studies in this thesis and in Allan's studies (1958, 1969). That is that both fully developing and abortive seeds influence fruit growth positively. Fully developing seeds do so to a greater individual extent and for a longer period. The positive effect of abortive seeds is limited by their individual size and to the time before their abortion. This explains why in the comparison between autumn and summer set

correlations, both here and in Allan's work, allowance needs to be made for the presence of aborted seeds in autumn sets (especially). It also offers an explanation as to why the seed mass/fruit mass correlations appeared higher after 12 weeks than after 28 weeks in the studies in 3.3.1. Further growth in seed and fruit flesh masses after the onset of the cellularization of endosperm and rapid growth of embryos could have been uncorrelated, thus leading to a lowering of the correlation in the later sampled fruits. Similarl the more protracted early phases of seed development in autumn sets (about 22 weeks) provided a greater opportunity for influencing final fruit size than in summer sets with 12 weeks to endosperm cellularization. Hence the higher autumn correlations.

Finally, Table 22 provides a comparative display of several seed/fruit measures from five of the fruit sets looked at in this thesis. In order to render these more comparable, fruit mass here includes seed mass, and the estimated fruit mass of the apical and basal fruit portions cut off in the 1972/73 summer and 1973 autumn sets have also been included.

TABLE 22 Ratios of types of seeds and of fruit plus seed mass to seed mass and counts in several sets of papaya fruits

	SEASON OF FRUIT SET				
	Summer 1970	Autumn 1969	Autumn 1970	Summer 1972/73	Autumn 1973
Type of pollination	Hand	Hand	Hand	Open	Open
Number of fruit	24	18	14	21	17
Mean ratio of F : P : S seeds	83 : 10 : 7	60 : 29 : 11	50 : 1 : 49	89 : 8 : 3	47 : 26 : 26
Mean sum of all F, P and S seeds	1 767	931	1 148	1 261	491
Mean seed mass (g)	149,4	-	46,4	125,2	22,4
Mean fruit plus seed mass (g)	1 550	713	725	1 240	470
Ratio of fruit plus seed mass to seed mass	10,4	-	15,6	9,9	21,0
Ratio of fruit plus seed mass to sum of F, P and S seeds	0,88	0,77	0,63	0,98	0,96

With regard to the mean F : P : S seed count ratios, the two summer sets (one hand-pollinated, the other open) had similar ratios (83 : 10 : 7 and 89 : 8 : 3 respectively). The three autumn sets differed. The one hand-pollinated autumn set (1969) had a similar ratio relation as that of the summer sets, viz. that F > P > S . Otherwise this autumn set had a relatively smaller F seed proportion: 60 per cent as against the 80 per cent plus of the summer sets. The other hand-pollinated autumn set (1970) had nearly all its aborted seeds in the form of S , and the proportion between F and S seeds was nearly equal. The open-pollinated autumn set (1973) also had an approximate even proportion between fully developed and aborted seeds, but in this case the aborted seeds were evenly distributed between P and S seeds.

The relative seed type ratios was one thing. The mean total sum of F, P and S seeds together was something else. The hand-pollinated summer set (1970) had the largest mean number (1 767), followed at a good deal lower level by the open-pollinated 1972/73 summer set (1 261). This was followed closely by the hand-pollinated autumn set of 1970 (1 148) and then by the other hand-pollinated autumn set of 1969 (931). Much lower down was the open-pollinated 1973 autumn set (only 491). Three of the interesting points here were that firstly hand-pollination to the extent used greatly increased the total number of fertilized ovules in the autumn sets, almost to the level of the open-pollinated summer set. This was, however, still far below that of the hand-pollinated summer set. Secondly, that although the relative ratios of the two summer sets' seed types were similar, hand-pollination had increased the total number of ovules fertilized. This was also apparent in the figures for Allan's (1958) summer and late autumn sets. Thirdly, temperature (during season of set and early development) was a crucial factor influencing both the total number of ovules fertilized and also the relative ratio of fully developed seeds. Thus hand-pollinated fruits set in summer had the greatest number of ovules fertilized and also the greatest number of fully developed seeds.

The highest measured mean seed masses per fruit were in the summer sets, with the hand-pollinated 1970 set being the highest (149 versus 125 grams respectively). The relative difference between the two was not as great as for the sum of F, P and S seeds. This was in part due to the slightly higher ratio of fully developed seeds in the open pollinated 1972/73 summer set. The autumn sets on the other hand had much lower mean seed masses, with the hand-pollinated 1970 set in turn having approximately twice the mean seed mass of the 1973 set (46 versus 22 grams respectively). The large difference between the open-pollinated 1972/73 summer set and the hand-pollinated 1970 autumn set, even though they had similar mean total (F + P + S) seed counts was due to

(i) the higher F seed ratio in the summer set; and (ii) the larger size of individual F seeds found in summer sets (e.g. Figure 28).

The rank of the mean fruit masses (including seeds) was firstly the hand-pollinated summer set (1 550 grams), followed by the open-pollinated summer set (1 240 grams), then the two hand-pollinated autumn sets (724 and 713 grams) and lastly, the open-pollinated autumn set (470 grams). In terms of the ratio of fruit plus seed mass to seed mass, the two summer sets were similar (10,4 and 9,9). The two autumn sets measured averaged higher ratios (15,6 and 21,0), with the latter open-pollinated set's being nearly twice as great as the summer sets'. In Allan's (1969) data the autumn set fruits also averaged a higher ratio than the summer set fruit. This might appear to indicate the presence of some general competition between seeds and fruit tissue for substrates, resulting in a diminishing ratio as the total seed mass increases.

However, when the ratio involving fruit plus seed mass was expressed relative to the number of (F + P + S) seeds, the resultant ratios were much closer. The open-pollinated summer and autumn sets had the highest estimated ratios (0,98 and 0,96 respectively). This was followed by the hand-pollinated summer set (0,88) and then the two hand-pollinated autumn sets (0,77 and 0,63). The difference in the two latter autumn sets seems to lie in their different relative proportions of S seeds, the 1970 autumn set with the more numerous S seeds having the lowest fruit mass to seed count ratio.

The latter results seem to suggest that even if seeds did compete to some extent with fruit flesh for available substrates, the larger P seeds nevertheless contributed more to fruit flesh growth than S seeds. P seeds that aborted at the time of endosperm cellularization (Chapter II) could have contributed for as long as F seeds, even if not to the same individual quantitative extent.

3.3.4 Supplementary survey on pollen tube growth

Table 23 shows that pollen tube growth at different seasons of fruit set was quite markedly influenced by prevailing temperatures. In the time (seven days) that it took pollen tubes to first reach the mid-point of flowers pollinated in autumn (April 1971), their counterparts in summer had nearly reached the basal-most ovules. In the latter season, pollen tubes had already reached the mid-point of the flowers after four days. The mean temperatures for the autumn-set batch was 17 to 17,5°C, whereas that of the summer set was 22°C.

On the other hand in the time it took pollen tubes to reach the base of flowers in the above autumn set, their counterparts in flowers pollinated in winter (June) had only reached the [illegible]

TABLE 23 Times taken for pollen tubes to reach mid-point and base of papaya fruits when pollinated in April (autumn), June (winter) and February (summer)

Date of hand-pollination	Number of days to first reach Cc subregion	Number of days to first reach basal ovules of Dd subregion	Mean temperature during growth (°C)
17 April, 1971	7	14	17,0
23 April, 1971	7	13	17,5
1 June, 1971	12	Not reached after 24 days	13,1
27 June, 1971	16	Not reached after 28 days	14,3
8 February, 1972	4	9	22,0

flowers the pollen tubes never reached the base. Prevailing mean temperatures there were between 13,1 and 14,3°C.

The above findings corroborate with those of the pollen tube growth and ovule fertilization studies in Chapter I (1.3.1.3). Together they indicate the importance of prevailing temperature for the speed and extent of ovule fertilization. Together with the type of fertilization (hand- versus open-pollination and source of pollen), it appears to determine to a large extent the quantity and quality of further seed development, which in turn has been shown to be well correlated with fruit growth.

Table 24 gives some indication of how much prevailing temperatures can be influenced by using a plastic or polythene cover structure. In a rather warm

TABLE 24 Mean temperatures in uncovered papaya trees versus trees under a plastic structure over a twelve-day period in May 1972 (autumn)

	MEAN TEMPERATURES: °C		
	Maximum	Overall mean	Minimum
Covered trees	34,9	23,0	11,1
Uncovered trees	27,0	19,6	12,3

period in May, 1972 (autumn) the prevailing mean temperature in a row of papaya trees for a 12-day period was 19,6°C. In trees of the same row covered with the structure the mean temperature for the same period was 23,0°C. The latter temperature compares with the summer (February, 1972) mean of 22°C in Table 23. The possibility thus exists for raising prevailing temperatures in marginal climatic areas to ensure a more rapid and more extensive fertilization of ovules. However, it should be noted that the minimum temperatures were hardly affected (in fact recorded lower) under the plastic structure. If low temperatures in some way promote growth inhibitive factors then such plastic structures (e.g. cloches) may not be a sufficient means for improving ovule fertilization, seed and fruit development. This apsect needs further study.

GENERAL DISCUSSION AND CONCLUSIONS

The anatomical studies of the first chapter have provided a basis for comparing the development of seeds in the clone Honey Gold with that of papaya seeds reported in the literature. No striking differences were seen. The development of nucleated cytoplasmic nodules in the endosperm reported by Singh (1961) to occur in plants from cold regions was not seen. But Singh's (1960) contention that the bottom layer of the 'sarcotesta' at the base of the testal furrows was derived from the endotesta and not from the outer epidermis has been supported in these studies. The outer epidermis of the inner testa (integument) in this clone looked more like longitudinally elongated fibres (Winton & Winton, 1935) than stone cells (Foster, 1943; Singh, 1960). But this interpretation may depend on the orientation of examination, as discussed in 1.3.3.5 (a). The vascular supply was not seen to enter the inner integument, which supports Singh's (1960) finding over against the apparent implication that it does (Foster, 1943).

The measurement of growth of all seed tissues, which had not been reported in the literature before, together with the description of their 'correlative' developments formed a useful basis for comparing seeds of fruits set in summer and autumn. The above was also useful for estimating the developmental periods at which seed abortions occurred.

Seed development in fruits hand-pollinated in February (late summer), during peak flowering in Pietermaritzburg, can be placed into five phases (see also SUMMARY and ∇ in ABBREVIATIONS). The first phase lasted about ten weeks, from anthesis and pollination in February (late summer) to mid-April (mid-autumn). This was a period characterized by rapid increase in free nuclear endosperm but very little embryo development. Seed size during this period was well correlated with the number of free nuclear endosperm nuclei. There was also a rapid increase in the amount of nucellus tissue, even though some of it was being consumed by the endosperm. The latter was inferred from the anatomical appearance of the nucellus close to the endosperm and from the fact that seeds which had just started to abort at the end of this phase had less endosperm but more nucellus than normally developing seeds, whereas both of these types had far more endosperm and nucellus than seeds which had aborted earlier on (2.3.1).

The second phase covered roughly the next ten weeks, from mid-April to mid-June (mid-autumn to mid-winter respectively). It was characterized in the beginning by the transition of endosperm from the free nuclear to the cellular

state. It was a period during which the embryo began to develop rapidly, with the final shape (but not size) being attained by the end of this phase. Calcium oxylate crystals began to form in the inner epidermis of the outer testa, and for a short period in this phase this epidermis virtually ceased to grow. The adjacent outer epidermis of the inner testa virtually ceased growing throughout this phase. The adjacent inter-epidermal tissues of the inner testa reached their final sizes during this phase. During this phase too, the cell walls of the endotestal ridges took on a buckled appearance, which lasted through to the fourth phase and provided one of the tell-tales for estimating abortion times. Thus in this phase crucial developmental changes in the state of the endosperm and the embryo were correlated with abrupt slowing down in growth or changes in the testal tissues. Nucellus tissue stopped dividing and began to slow down in expansion, all the while being consumed by the endosperm.

The third phase lasted about eight weeks, from mid-June to mid-August (mid- to late winter). Throughout this phase the innermost band of the endotesta virtually ceased to grow, but the previously quiescent outer epidermis of the adjacent inner testa quickened much in growth. The outer testal tissues beyond the quiescent band of the endotesta also reached maximal rates of cell expansion, although cell divisions had ceased at the beginning of this phase. At approximately similar times the embryo and cellular endosperm stopped dividing and then reached maximal rates of cell expansion, in the middle of this phase (July).

The fourth phase of development lasted about a month, between mid-August and mid-September (late winter to early spring). It was characterized by a quickening of growth of the inner band of the endotesta, consumption of the innermost surface of the cellular endosperm by the embryo, then a general slowing down of cell expansions in all tissues still growing. Testal tissues were thickening considerably, with wall pittings becoming evident in the inner band of the endotesta and testal tissues within this band. With the thickening of testal walls in general, the buckled appearance of the endotestal ridge cell walls disappeared.

The fifth and final phase of seed development began in mid-September (early spring) and was characterized by a general maturation of tissues and the tailing off of growth. At first numerous vacuoles formed in the endosperm and embryo, followed by general amorphous cytoplasmic depositions. In normal seeds reserve materials were deposited in the form of aleurone grains. The thickening of the testal tissues together with cytoplasmic depositions in the sarcotesta contributed to the darkening and colouring of normal seeds during this phase. Adjacent fruit tissue also began to colour up in this phase.

When seed development in the summer set was compared to that of fruit development, it was found that the seeds reached the stage of endosperm transition (phase two) and maximal rate of whole seed (volume) growth in the period that fruits reached their maximum rate of growth. Both of these occurred within three months of fruit set, in the period late summer to mid-autumn. Most of the other major seed developments (and maximal rates of seed cell enlargements) occurred only after this stage, in the remaining six to seven months growth during winter and spring. This was also the period of later, continuing cell enlargement of fruit (mesocarp) tissue. Although cell division in several seed tissues carried on beyond the inflexion point of the whole seed growth curve, the maximal rates of cell division in the endotesta, and the fastest expansion of the embryo sac occurred near the inflexion point, hence the position of this inflexion.

The seeds of autumn set fruits went through similar tissue and phase correlated stages of development. But the inflexion point of both the seed and fruit growth curves occurred only about half way through the total developmental period. Thus the first phase of seed development (free nuclear endosperm development) and the cell division stage in the fruit growth was dragged out over nearly five months, from April/May to mid-September, October (late autumn, winter and spring). The remaining four phases of seed development and continuing cell enlargement in fruit tissue was compressed into the remaining five months (spring, summer, early autumn).

From the above account it is evident that the cell division stage in fruit tissue growth, whether the fruits set in summer or autumn, covers approximately the period of rapid increase in free nuclear endosperm nuclei and the most rapid stages of cell division in the nucellus and testal tissues of normally developing seeds. The cell division stage in the (fruit) mesocarp is important for laying one limit to the potential of the fruits' size, as later growth can only be by further enlargement of the existing cells. The latter process is less affected by cold weather than the cell division process (Kuhne & Allan, 1970), hence the larger summer set fruits, even though both sets receive similar amounts of total heat units. By getting the mesocarp cell division stage over before the winter sets in, the summer set fruits produce a larger number of cells in a shorter time than their autumn set counterparts. Similarly the seeds of the summer set fruits had both a larger number of cells and bigger individual cells at the inflexion point of the growth curves compared to their autumn counterparts. As will be discussed later, the fruits set in summer had in addition a larger number of normally developing seeds throughout this crucial first stage.

The differences in the time taken for endosperm to begin cellularizing in these studies, and in comparison to Foster's (1943) studies, are no doubt related to differences in climatic conditions, particularly temperatures. But apart from that, what triggers the transition? Why does it occur when it does? This could be an interesting developmental question to pursue.

Using a recently formulated clearing fluid enabled the author to make a detailed survey of the positional pattern of ovule development at the time of anthesis, of the pattern of pollen tube penetrations and fertilizations, and the subsequent early seed growth in relation to position within the fruit. To the author's knowledge this has not been done in this detail with papaya before. A brief sketch of the results of these and more conventional anatomic and dissection studies can be found in the SUMMARY. One of the main features there was the more rapid and more extensive development in the fruits set in summer versus those set in autumn. Another main feature in both autumn and summer sets was the tendency for pollen tubes to enter only mature ovules. One can surmise from these studies ~~was~~ that the last seeds to start developing did so either because as ovules they were late to mature, or else they only received the late to arrive or slow to grow pollen tubes, or both sets of reasons applied. These could be the most likely seeds to abort.

The anatomical studies on aborted seeds revealed that the approximate peri at which a seed aborted could be judged by comparing the developmental phase that the various seed tissues had reached relative to the developmental sequence of normal seeds. The measurements of cell sizes and whole aborted seeds corroborated such estimates. The studies on the contents of dissected seeds al helped to indicate the general extent of intra-testal development. The studies on the relative frequency of each of the seed abortant types provided further information for inferring when the bulk of the abortions occurred in various seasons of set. The following general picture emerged.

Those ovules that were not fertilized hardly grew larger than fertilized seeds at the second week after anthesis in summer or the fourth week after anthesis in autumn. Within this period their amount of nucellus had increased. The further differentiation of the integuments into testal tissues seemed to have required fertilization and subsequent endosperm/embryo development. In only a few cases of those examined were there testal developments without signs of previous endosperm. But even in those cases it may have happened that the last traces of endosperm had been consumed in the course of testal development. However, there is also the further possibility that in some cases development in adjacent seeds may have stimulated testal development. The branches in the

vascular connections of adjacent ovule and seed funicula or stalks can be quite close, as seen through the clearing fluid.

Referring now just to seed abortions in fruits set in summer, the little abortion that did occur (average of ten per cent of fertilized ovules) only began to do so in March (early autumn), about five weeks after anthesis. These were mostly of the cWs type, with a few of the earlier and smaller b type also occurring. The last abortions in summer fruits occurred about 30 weeks after anthesis (end of August, late winter). The 'frequency distribution' in terms of time to abort was fairly evenly spread between early autumn and late winter.

The seeds of the top (apical) quarter of the fruit were more prone to abortion than those of the lower three-quarters. Comparing the frequencies along a different spatial location, seeds closer to the placentary edges were also more prone to abort than those closer to the carpellary margins.

Examination of the contents and development of aborted seeds of the autumn sets revealed that most of these occurred before the transition phase of endosperm development (before phase two). The major period of abortion was from the end of May until the end of July, the coldest period in Pietermaritzburg. Most of the remainder aborted between August and October (late winter to mid-spring). Even though in one year (1969) the seed abortant types were more equally represented, the majority of abortions still occurred before the endosperm began to cellularize.

The very earliest signs of abortion (in May) were more concentrated in the basal (stalk) end of the fruit, implying perhaps that such seeds and/or the pollen tubes were too old or degenerating at the time of fertilization. But in fruits looked at after harvesting the greatest proportions were again in the apical quarter, and also generally greater nearer the placentary edges, as in summer set fruits. Even the earliest signs of abortion in May were more prevalent near the placentary edges. Seed abortion rates were much higher in autumn set fruits (50 per cent of ovules that were fertilized, whether by hand- or open pollination).

What were the most likely reasons for seed abortion? How would these explain the times at which abortion occurred and the positional patterns within the fruits? In Chapter II it was argued that although the positional patterns of concentration of early seed growth in open pollinated fruits were like that of the patterns for concentration of seed abortions, it was doubtful whether there was a causal link between the two. If there was, then one could expect that in comparing fruits set and grown at the same time, fruits with overall

higher proportions of early seed development should also have had overall higher abortion rates. When this was examined in Chapter III, it was found not to be the case. Seed competition therefore is not considered to have been a cause of seed abortion. The two patterns were merely coincidental. It was in fact more likely that fruit competition affected seed abortion rates (3.3.3.1). Allan's (1958) data had also suggested that fruit competition may increase seed abortion levels. However, this trend in the present studies did not reach statistical significance.

Another postulated cause of seed abortion had been that adverse climatic conditions in spring, in the form of rapid and steep fluctuations in available moisture would have brought on abortions. Furthermore, the seeds at the apical end, and those nearer the placentary edges along the whole longitudinal axis, being presumably at a positional disadvantage in the vascular network, should have been subject to the greatest stress. There may well have been moisture and nutritional stresses during the spring months, but these did not result in the predicted positional pattern of abortions in the seeds that abort during that period (2.5.1.1). The pattern at that time was random. In additio relatively little abortion occurred in this period in both summer and autumn set fruits. Since the bulk of the abortions occurred earlier, during late autumn and winter months, a more likely factor was low temperatures. How could this then have affected the striking positional patterns?

The postulated explanation is as follows. At anthesis the ovules nearer the carpellary margins are more mature than those nearer the placentary edges. The first and most vigorously growing pollen tubes (Allan, 1963) are drawn chemotropically in the present author's opinion by the more mature ovules, entering such ovules nearer the stigma end first, but continuing on towards the 'D' subregion. The lower quarter, 'Dd' , but particularly the placentary edge 'd' subregion received the last of the longer growing pollen tubes. In the autumn sets this was occurring even four weeks after pollination. Thus the first abortions tended to occur there in the autumn sets but not the summer set Pollen tubes reached the base of fruits by the second week in the latter sets.

Between the second and fourth weeks in the autumn sets pollen tubes were still entering the ovules along the whole length of the placentary edges. This pattern of later entrances into these subregions also occurred in the summer set fruits, but these were still much earlier than in the autumn sets. Thus the postulate is that it was the late to start seeds that were the most likely to abort. Sizes of seeds in the earlier part of phase one were correlated with the number of free nuclear endosperm nuclei, and the earlier developing seeds were also larger. When older seeds (twelve weeks after pollination in autumn)

were teased open and examined in the clearing fluid, the smaller, abortive seeds had far less endospermic nuclei and the endospermic strands were flimsier in comparison with those of larger, normal seeds.

The above explanation seems to account for the pattern of abortion between the placentary and carpellary margins in both summer and autumn sets, and for the pattern at the base of the fruits in autumn sets. But what about the upper quarter? An explanation could be that the pollen which was slowest to germinat and made the slowest growth (as correlated by Allan, 1963) could only penetrate as far as the top quarter. Presumably, ovules fertilized from such a source develop for a limited period only. This needs further study.

The above explanations could account for the patterns of the bulk of abortions. On this basis the differences between autumn and summer sets are due to differences in temperatures at the time of pollination and fertilization Low temperatures not only reduce the number of mature ovules, but reduce germination and pollen tube growth, leading to reduced fertilizations and greater abortion. It can even happen then that hand-pollination does not increase fruit size, as found in one batch by Allan (1958).

One motivating reason for these studies on normal and abortive seed develo ment derived from Allan's (1969) report of high correlations between seed number/mass and fruit mass. If these correlations still held when other concomitant factors were allowed for, then the importance of pollination, seed development and seed abortion for fruit growth warranted further assessment. Using vegetatively propagated material, setting some fruits together so as to have similar conditions of growth, measuring initial sizes as well as leaf area and fruit competition - the resulting analyses still showed that seeds were highly correlated with fruit growth. The effect could even be measured in the fruit tissue beneath the seeds for all subregions along the fruits' longitudina axis.

Temperature was important not only for leaf abscission and seed abortion. It was important too, for seed and fruit growth, as could be inferred from the growth graphs for individual seeds and fruits set in autumn and summer, and as also shown for fruit growth by Kuhne and Allan, (1970). Fruits and seeds that started their growth in summer achieved a greater size than those starting in autumn.

In the studies on fruit set over March (early autumn) in 3.3.1.2, it was felt that the temperature range used was too limited to make a proper assessmen between temperature, seed and fruit mass. In the study on 32 fruits grown for 28 weeks the simple correlations between

(i) seed mass;
(ii) sum of degree-days during flower bud development before anthesis; and
(iii) sum of degree-days for the 15 weeks after anthesis with that of fruit flesh mass were

(i) 0,777 ; (ii) -0,2083 . and (iii) 0,208 respectively.

Only that between seed mass and fruit flesh mass was significant. The partial correlations involving just those four variables taken together (not given in 3.3.1.2) were (a) 0,809 ; (b) 0,185 ; and (c) -0,2195 between

(a) seed mass;
(b) the 'temperatures' before anthesis; and
(c) 'temperatures' after anthesis with fruit flesh mass respectively.

Again only the seed mass partial correlation was significant. The partial correlation between the temperature variable after anthesis and seed mass (0,3317) was nearly significant.

But the author also has further data not presented here on fruits set later in April and May of that same year. These were set in a separate papaya block, about 50 metres from the one used in the studies reported in 3.3.1.2. No leaf area measurement or initial fruit sizes and fruit competition data had been taken on these and on some of them various strengths of a boric acid solution had been applied to the stigma before hand-pollination. Therefore the data from this had not been included with that of 3.3.1.2. However, in the light of the limited temperature range used in the March settings, and the suspected importance of temperature, all the data has since been pooled together (54 fruits as against 32 in 3.3.1.2) and the following comparative correlations were obtained.

After 28 weeks growth the simple correlations for

(i) seed mass;
(ii) sum of degree-days during flower bud development before anthesis; and
(iii) sum of degree-days for 15 weeks after anthesis [as (i) - (iii) above] with that of fruit flesh mass were

(i) 0,919 ; (ii) 0,829 ; and (iii) 0,785 respectively; all highly significant. These figures show that when seed and fruit mass correlations were calculated from fruits set at different times within one season (early to late autumn) the correlations increased because of the correlations with temperatures, as previously suspected. This can also be seen from partial correlations involving just these four variables, viz. (a) 0,725 ; (b) 0,412 ; and (c) -0,186 for (a) seedmass; (b) 'temperatures' before anthesis; and (c) 'temperatures' after anthesis with fruit flesh mass respectively.

The first two were (highly) significant; but the partial correlation between the third, 'temperatures' after anthesis and seed mass (0,550) was also highly significant. That for the temperatures before anthesis and seed mass was not significant.

The above results appear to support the results reported in 3.3.1.2. That is, that when temperatures were taken into account, the correlation between seed mass and fruit flesh mass, although dropping, was still highly significant. Nevertheless the temperature variables were still less extensively sampled than the seed variable, and the low "temperature after anthesis" to "fruit mass" correlation may have been due to this. Since seed mass seems to have been an important variable in its own right, and also quite sensitive to temperatures after anthesis, and because of the nature of the sampling used, some of the apparent seed-effect could still have been a temperature effect disguised (by the partial correlation and regression procedures) in the seed-fruit mass asscci ations. On the other hand, the apparent effect of temperature conditions after anthesis on fruit growth could come in (at least) two forms: one directly on physiological processes in the fruit flesh itself, and another through seed mediated or localized processes affecting fruit growth which could themselves be temperature sensitive.

Kuhne and Allan (1970) have found that fruits set in summer make relatively rapid growth, reaching the inflexion point in the sigmoid growth curve about a third of the way through development and before the cold winter conditions set in. In such fruits cell enlargement during the coldest months is not adversely affected. Fruits set in autumn, however, have to go through winter and half way through development, before they complete the earlier phase encompassing cell division. The cell division period is adversely affected during the coldest months.

From the above discussions it could be that part of the critical temperatu effect on the fruits' cell divisions could be through the temperature effect on ovule fertilization, early seed growth and physiological processes localized in these seeds.

The correlation analyses of 3.3.3 also suggested that the seed effect on fruit growth could be limited to the period up to the inflexion point, i.e. the period of fruit cell divisions. This appeared to be supported by the comparisc between seed/fruit mass correlations after 12 and 28 weeks growth (3.3.1). This however needs further testing. Seeds that aborted also appeared to influence fruit growth, their postulated positive influence being limited by the time of their abortion and their relative size. The apparently better correlat

between the number of fully developed seeds and fruit mass in autumn compared to summer set fruits, and the higher fruit per seed mass regressions could be due to the postulated more prolonged effect of seeds in autumn sets, and sometimes to the unaccounted effects of aborted seeds (where the numbers of fully developed and aborted seeds are positively correlated).

It is not clear whether seeds affect the relatively little fruit cell enlargement that occurs before the inflexion point. The specific effects of seeds on fruit cell divisions and cell enlargement could be partially tested by anatomically comparing fruits with many and few seeds at the inflexion point and again at maturity. (Even better would be appropriate physiological investigations.)

Kuhne (1967) made a preliminary limited trial on the effects of 2,4,5-T , GA, NAA, Kinetin and IAA on papaya fruit growth. Of these 2,4,5-T appeared to have slightly increased fruit volume and mass throughout growth for fruits set in summer, autumn and spring. The other substances, except for IAA, for an initial period on fruits set in winter had no effects, although only one level of each of the substances was used. The greater effectiveness of the 2,4,5-T sprays may have been due to a greater and quicker absorption of the chemical. There appeared to be no effect on cell number, (although the number of replicates used was low) so that the effect of 2,4,5-T appears to have been on cell enlargement and not cell division. These substances had toxic and distorting effects on the leaves.

The possible basis, then, for the effect of seeds on fruit growth during the first stage of fruit growth remains unclear. Assay for growth substances, particularly during specific phases of seed growth could prove quite useful. It would be of interest to test abortive seeds (generally the smaller seeds after three to four weeks growth) as well. The anatomy sections of this thesis should prove useful as a guide with regard to the times to test testal and intra-testal tissues. It would also be useful to assay the fruit flesh itself.

Apart from the possibility of finding some particular substances, or a sequence of substances promotive of fruit growth at different times during development, what else can be said about boosting fruit size in fruits maturing out of season? What can be done with the inferences made from these studies? There is little doubt that hand-pollination increases the proportion of ovules that are eventually fertilized. The data presented has suggested that flower buds developing in warmer (summer-like) conditions not only have more ovules, but that a greater number of these are mature at the time of pollination and soon after. Large proportions of such early maturing ovules could be

fertilized if good pollen were used and conditions for pollen tube growth over the first two to three weeks were more summer-like. [Lack of temperature would appear to have led to little response from hand-pollination trials (e.g. Allan, 1958).] The above would insure a more extensive, even and rapid development of those ovules that were fertilized. If warmer conditions were maintained during the winter months (June to August) as well, the greater proportion of fully developing seeds could be more effective and for a longer period than abortive seeds. This could result in a larger number of fruit cells which could be available for enlargement even once the seeds presumably ceased to have further effect.

Adequate irrigation and soil fertility could also help in the later stages, as could better leaf cover. The two would go together. Allan and De Jager (19[illegible] have found that under conditions of water stress(wilting) the assimilation of CO_2 ceases, and measureable photosynthesis only begins about three days after irrigation. In that study Allan also found that net photosynthesis decreased rapidly at flux densities below about 300 Wm^{-2}. It could be advantageous, then, to ensure firstly that papaya plants do not wilt; and secondly, that leaf cover be increased to the point where average flux densities did not go below 300 Wm^{-2}. The clone Honey Gold in fact is inclined to lose much of its leaf cover over winter, a characteristic apparently inherited through Hortus Gold. The latter is the chief genetic source of papayas in South Africa hence this problem could be quite general in South Africa (Allan, 1979).

Until the first crops are harvested in spring (October onwards in Pietermaritzburg) the plants are carrying peak crop loads with minimal leaf cover. This is a critical period for fruit growth when seeds are apparently losing their effect on fruit growth. The regressions of 3.3.1 also suggested that lack of leaf cover could be a limiting factor.

There is a need therefore for finding a way of retaining leaves by some chemical means (such as cytokinins) or for breeding for leaf retention. Better leaf cover at maturity also ensures sweeter, better flavoured fruits (Allan, 1977).

To what extent could these various measures increase the size of fruits se in late autumn in cool sub-tropical conditions such as at Pietermaritzburg? Some idea can be estimated from making the following comparisons. Allan (1958) quoted long term mean temperatures in Pietermaritzburg, for example February (21,4°C); March (20,2°C); April (19,0°C); May (17,2°C); June (14,1°C); July (14,7°C); August (15,8°C); September (16,8°C); and October (18,8°C). Since plastic or polythene cover structures (e.g. cloches) might increase the

mean temperatures about 15 per cent (3.3.4), the mean temperatures could become April (21,9°C); May (19,8°C); June (16,2°C); July (16,9°C); August (18,2°C); September (19,3°C); and October (21,6°C). The mean temperatures for the first critical four months of uncovered fruits set in February (late summer) would be about 19,5°C. That for fruits set in March (uncovered), 17,6°C. That for fruits set in cloches in May could be about 17,8°C, i.e. comparable to fruits set without covering in March. However, the effect of low minimum temperatures still attained under cloches still needs to be tested.

Now the fruits set over the month of March (3.3.1.2) would probably have averaged 1 180 g to 1 240 g (including seed mass) if allowed to grow to maturity ($9\frac{1}{2}$ to 10 months respectively) the next February. So although Allan (1976 a) felt that the use of 'tunnels' may only be of practical use in areas with warmer winters than Pietermaritzburg, he was referring specifically to flower and fruit set through winter, not the growth of fruits set in late autumn.

Thus using hand-pollination in April/May and cloches for the period late March (for flower, bud and ovule development) to August, could well result in a mean fruit mass of about 1 200 g in February/March during the out-of-season period the following year. Better leaf retention, and reduced fruit competition (by stripping some of the recently set summer fruits to ensure better flower production for autumn fruit setting and also to increase the total leaf area per fruit ratio) could increase this still further. Limiting the time under covers to the coldest period could help to limit the hastening of fruit maturity brought about by warmer temperatures. It could also limit the occasion for deleterious effects of high temperatures on photosynthesis. Allan and De Jager (1978) have found that from 31°C to 41°C the net rate of photosynthesis drops to half its maximum rate.

An average of 1 200 g for fruits ripening in February/March in Pietermaritzburg is considerably larger than that of fruits left to open pollination and no covering. The latter average between 400 g to 500 g. In fact, fruits set in summer with open pollination only average about 1 200 g to 1 300 g themselves.

Allan's (1958) data suggest that fruits set in early spring in Pietermaritzburg have significant rates of seed abortion. The same may apply to the Transvaal lowveld areas. Thus in these areas, the use of pollen from a good source which has been stored in a refrigerator over winter (Allan, 1963), together with cloches during flower bud development over winter and in the first month or two in spring, may also lead to increased fruit sizes in fruits also destined to mature during the out-of-season period. However, care would have to be taken that temperatures did not rise too high during these later

months, as it is the maximum temperatures that are induced to rise the most, and not the minimum temperatures (Allan, 1976 a).

These studies, together with Allan's (1958, 1963, 1969) on pollen, seeds and fruits; and Kuhne and Allan's (1970) on temperature and fruit growth, have helped to crystallize the major probable sources of the small fruit problem mentioned in the introduction. The problems seem to revolve around low temperatures leading to limited pollen and ovule quality and development; slow and low rates of ovule fertilization and early seed development; increased leaf abscission; and slow rates of fruit development during the cell division stage of the latter.

The means for overcoming these deficiencies in cool regions or seasons could be by using sufficient and timely applications of good pollen (i.e. from one to three staminate buds at the balloon stage, per pistillate flower at anthesis); and providing that temperatures during the pre-anthesis to fruit cell division stage of development were increased sufficiently. Given sufficien leaf cover, this is predicted to result in a greater number of larger, normally developing seeds and larger fruits.

These ideas warrant testing, including an economic assessment of the worth of such practices. Included here could be an assessment of the best height for plants and the cost of cloches for these. (Plastic growth tunnels would probabl be too expensive.) Prospects could be good in the cooler sub-tropical areas (if the minimum temperatures do not prove problematic), particularly over the first few years if vegetatively propagated plants are used. These bear their first crop low down on the stem. Thought would also need to be given for the best time for starting such cuttings.

To put parts of this thesis into a nutshell then, it has supported the finding ~~idea~~ that there exist significant positive correlations between seed number (and mass) and fruit flesh mass in Carica papaya. It has been suggested that increasing the proportion of ovules fertilized does not increase the rate of seed abortion (with the possible exception of the case of using inferior pollen) whereas such a practice could increase fruit size. Due to the significant seed number (and mass) - fruit flesh mass correlations, seed abortion can be considered to be deleterious to the extent that abortion curtails the duration of time, and the quantitative intensity, of the apparent effect of seeds on fruit growth. Low temperatures during early seed growth has been considered to be one of the main factors retarding pollen tube growth, ovule fertilization and increasing seed abortion. The relative ratio of total leaf area to fruit crop

load, and prevailing temperatures, have also been considered to be important factors affecting seed and fruit growth. The thesis has also drawn attention to a number of possible research topics, one of which could 'practically' solve the (out-of-season) small-fruit problem.

SUMMARY

In cool subtropical areas the fruits of Carica papaya L. that set in autumn mature in the out-of-season period the following late summer and autumn. These, however, are usually much smaller than those set in summer and matured during peak production. The following is a summary of studies on the relation of ovule and seed development to fruit growth, with the out-of-season small fruit problem in mind. These studies were conducted in Pietermaritzburg on clonal material of a recently named cultivar, Honey Gold, developed from the variety Hortus Gold.

A special clearing fluid enabled an extensive whole mount examination of ovule and early seed development. At anthesis the ovules nearer the carpellary margins had more advanced megagametophytes, larger integuments and a more extensive vascular system than those nearer the placentary edges.

After hand-pollination in autumn the initial pattern of pollen tube penetration was into the closest mature ovules, predominantly those nearer the carpellary margins. Up to the second week pollen tubes appeared to enter only ovules with mature megagametophytes. At this time all but the basal quarter of the fruit had received appreciable numbers of penetrations. Between the second and fourth weeks more ovules were penetrated, particularly those closer to the placentary edges. It was evident that by the fourth week some pollen tube penetrations had not stimulated further embryo sac developments. After the fourth week only the ovules in the basal quarter received significant additional penetrations.

Following fertilization cell divisions occurred throughout the nucellus but after eight weeks this was confined to the periphery. Over the first six weeks it was evident that the earlier a seed was fertilized, the greater were its amounts of nucellus and endosperm. Four weeks after pollination in autumn more than 80 per cent of those ovules that were fertilized appeared to have normally developing endosperm, but by the sixth week this dropped to 50 per cent in seeds at the base of the fruit, particularly those nearer the placental edges. In these initial weeks embryo development was very slow in comparison to that of the free nuclear endosperm.

Tannin was deposited into a region above the hypostase between the second and fourth weeks in autumn pollinated fruits; the process occurring first in ovules and seeds closer to the carpellary margins. Over the first eight weeks the outer integument had increased in size through cell division and enlargement and had differentiated into six cell types, which included sarcotestal an

endotestal tissues. The apparent innermost tissue of the sarcotesta at the bottom of the furrows between endotestal ridges was actually derived from the endotesta.

In this initial period the number of layers between the epidermises of the inner integument increased to six, the final number. Tannin was being deposited into the innermost epidermis.

The size of unfertilized but mature ovules also increased over the first six weeks after anthesis in autumn. These also had increasing amounts of nucellus, having as much nucellus as seeds with defective endosperm, but were smaller, with less nucellus, than seeds with normally developing endosperm. The largest unfertilized but mature ovules came from intra-fruit subregions with the greatest amounts of seed development.

A brief comparative study on early seed development in a summer set was also made using the clearing technique. The proportion of mature ovules at anthesis was higher than that in autumn, with a similar, but less pronounced, difference between carpellary margin and placental edge ovules. The initial rate of development was also faster in summer; the sizes and development reached after eight weeks in autumn set fruits being reached in three to four weeks in summer fruits. There were more layers in the endotesta of summer fruit seed at this stage.

Correlations ranging from 0,62 to 0,84 were found between the number of free nuclear endosperm nuclei and seed size within a given intra-fruit subregion two weeks after pollination.

Normal seed development beyond the fourth week in summer set fruits was studied with standard sectioning and staining techniques. Seed development could for convenience be grouped into five major phases. The first lasted two to three months, from the time of anthesis in late summer until mid-autumn. It was characterized by rapid increases in the amount of free nuclear endosperm and nucellus, and by cell divisions in the integumentary tissues.

The second phase lasted about two months, from mid-autumn until mid-winter. It began with the transition of free nuclear endosperm into the cellular form, and by the end nearly all of the central vacuole had been replaced with cellular endosperm. During this phase the previously slow growing embryo underwent rapid changes, reaching its final shape but not size. Some testal tissues virtually stopped growing.

The third phase lasted about two months, from mid- to late winter. Cell divisions ceased in the endotesta, embryo and endosperm, followed by maximal

rates of cell enlargements in these and other testal tissues. Slowing down or increasing rates of growth occurred in some testal tissues.

The fourth phase lasted four to six weeks, from late winter to early sprin Final spurts of growth occurred in some testal tissues, and the process of cell wall thickening became prominent.

The final phase, from early spring until fruit ripening lasted another four to six weeks. During this phase final testal cell wall thickenings occurr and general maturation of the endosperm and embryo took place.

In terms of specific tissues, the key features were as follows. From the beginning, nucellus tissue was broken down and utilized by both the embryo and even more extensively the endosperm. Cell divisions in the nucellus stopped early in phase two, followed soon after by maximum cross-sectional areas and then rapid consumption by the endosperm.

Four specialized subregions of the nucellus at the chalazal end, as described by previous workers, were also found in this material. Tannin deposi tion was along cell walls (although occasionally into the centre of cells) in one of these subregions. The cell walls of the hypostase tissue thickened in the final phase.

The formation of cellular endosperm in the second phase progressed inwards from the periphery. Cell expansion followed a sigmoid pattern, the inflexion occurring in phase three. Aleurone grains were deposited in the final phase. Some endosperm breakdown occurred at the embryo interface during the final phas

At the onset of endosperm cellularization (phase two) the embryo was still small and globular, then became heart-shaped and finally torpedo or cotyledonar shaped (but not full sized) at the end of this phase. Rate of length growth wa slow during phase one, then speeded up and reached a maximum at the end of phase two. All divisions ceased early in phase three, followed shortly by maximum rate of cell expansion. Cell expansion virtually stopped during the final phase.

With regard to the testal tissues derived from the outer integument, the outer epidermal cells above the endotestal ridges reached maximum rates of cell expansion in phase three, just after that of the ridge cells. The outer epi- dermal cells between the ridges reached maximum rates of cell expansion in phase two, before the ridge cells. The sub-epidermal cells of the sarcotesta in the testal furrows reached maximum rates of cell expansion at the end of phase three. The colour of seeds in ripe fruit was partly due to the cellular depositions into this tissue during the final phase, and partly due to the general thickening of cell walls of the testal tissues during the final two

In the large-celled tissue of the endotesta, which forms the ridges, periclinal divisions ceased early in phase three, resulting in about 28 layers in summer fruit seeds. Maximum rates of cell expansion occurred at about the same time, finally ceasing during the fifth phase. Cell walls took on a buckled appearance at the beginning of phase two, and the buckling disappeared with the onset of cell wall thickening at the beginning of phase four. Wall thickening began in the corners. The process began first in tissue adjacent to the inner band of endotesta, and lastly at the crest of the ridges.

Periclinal divisions in the small-celled, inner band tissue of the endotesta ceased early in phase three, resulting in about 29 layers in the seeds of summer fruits. Cell expansion in this tissue followed a double sigmoid form. Apparent cessation in cell expansion lasted for virtually the whole of the third phase. The second growth period was limited to the fourth phase. Cell walls began thickening and forming pits during their second growth period.

The inner epidermis of the outer testa also had a double sigmoid form of cell expansion. Its period of quiescence was shorter, occurring in the middle of phase two, that is ahead of that of the adjacent inner band of the endotesta. Calcium oxylate crystals began to appear at the beginning of phase two, were conspicuous by the end of this phase, and a crystal filled each of the cells of this epidermis at maturity. The inner walls began thickening at the end of phase three.

With regard to the testal tissues derived from the inner integument, the depth of the outer epidermis, adjacent to the outer testa, also underwent a double sigmoid pattern of growth. The period of quiescence lasted the second phase of seed development. This was the first and innermost of the testal tissues with this pattern to enter quiescence. The order of entrance into quiescence was from the innermost to the outermost of these three juxtaposed tissues. Virtually 70 per cent of growth in depth in this epidermis occurred during its second period of growth. These longitudinally elongated fibres became thick-walled and pitted, and were the main mechanical layer of the seed coat. They resembled stone cells near the micropyle.

The inter-epidermal tissue of the inner testa reached a final number of four to six layers in phase one and final cross-sectional areas were reached by the middle of phase two. Cell walls began thickening only in the middle of phase three, finally becoming pitted.

The inner epidermis of the inner testa reached final cross-sectional cell size early in phase three. Tannin deposition, usually into the centre but sometimes along cell walls, followed a variety of shapes. The tannin appeared quite pliable.

The vascular supply into the seeds appeared confined to the chalaza, not entering into the inner integument. Normal development of seeds in fruits set in autumn was not followed to the same detailed extent after the cellularization of endosperm (phase two). Cursory examinations indicated that the coordination of tissue developments in the final three phases were similar to that of the summer seeds. Differences lay mainly in the time to reach major phases. Whilst it took two to three months for seeds in summer set fruit to begin endosperm cellularization, the seeds in autumn fruits took four to six months. The approximate timings of the last three phases was not ascertained.

The number of layers in the ridge and inner band of the endotesta were about 23 each, that is, less than in the summer seeds. Mean individual cell cross-sectional areas in all tissues were about 80 per cent of those in summer seeds.

When whole seed and fruit volumes were measured, peak fruit growth rates were reached at the time the endosperm became cellular in the most advanced seeds, those along the carpellary margins. In autumn set fruits this occurred after about 18 weeks, whereas in summer set fruits it took only about 10 weeks. Individual seed volume growth patterns virtually paralleled that of fruit volume growth, both being sigmoid. Seeds nearer the carpellary margins always remained larger than those nearer the placentary edges, the latter attaining about 90 per cent the volume of the former. At fruit ripening, normal individual seeds in autumn set fruits were about 70 per cent the size of those in summer set fruit. Rate of growth of summer seeds was not affected by winter conditions, but seeds in autumn set fruits only accelerated in growth after the coldest months in mid-winter. Seeds and fruits set in summer took nine-and-a-half to ten months to develop to maturity, whilst their counterparts in autumn sets took ten to eleven months.

Testal development of unfertilized ovules did not proceed beyond that of fertilized seeds at the fourth or eighth week after pollination in summer or autumn respectively. Such ovules also lost most of their nucellus, inner integumentary and part of their outer integumentary tissues in the course of fruit growth.

The small, 'empty', slightly developed white 'cWs' seeds had a relatively more rigid endotesta than the similar or slightly smaller, flattened 'b' seeds. Six months after anthesis in summer the testal development of empty 'cWs' seeds was similar to that of normal seeds at the beginning of endosperm cellularization, phase two, three months after anthesis. The size, however, of such 'cWs' seeds after six months was smaller than that of normal seeds at three months.

Some 'b' and 'cWs' seeds had received no pollen, although most had. A few unfertilized ovules reached the testal development, but not size, of normal seeds at the beginning of phase two. Endosperm and embryo tissue, when still present in 'b' and 'cWs' seeds at fruit ripening, was rather distorted and disorganized.

There was a range of developments in the 'filled cWs' to the darkened, partially developed 'filled cDL' seeds. In general there was a closer association between the degree of endosperm and embryo tissue development with that of cell development of the inner testal tissues than with the cell development of the endotestal tissues. The size of the endotestal tissues, however, was associated with the quantity of endosperm. The difference between the smaller slightly developed S seeds (b and cWs) and the larger, partially developed P seeds (cWL and cDL) lay largely in the differences in quantity of endosperm. Growth in size, but not necessarily cell development or degeneration, generally ceased at the time of abortion.

At the beginning of phase two, with the transition of the form of the endosperm, P seeds actually had more nucellus than normally or fully developing F seeds. The latter had more endosperm which was consuming more nucellus. At this time, too, F seeds had larger amounts of endotesta than P seeds. Both F and P seeds had greater amounts of endosperm, nucellus and endotesta than S seeds at this time.

The endosperm and embryo tissue found in P seeds at fruit ripening had less content than that of F seeds. Cytoplasmic deposition in the final phase was in the form of phytin globoids and crystaloids and not aleurone grains. The embryos were small, often distorted and had often failed to complete all the normal changes in shape.

In in the apparently normally developed F seeds, some of the black seeds in this clone were defective with regard to endosperm and embryo development. All the as yet grey seeds appeared normal, although some embryos were small.

Most of the abortions in one autumn set occurred before the cellularization of the endosperm (phase two), the major period of abortion being from the end of May until the end of July, the coldest two months of the year. Most of the remainder to abort did so between August and October (spring). In another autumn set there was a more even spread in abortion period, but the peak time and major proportion was again before phase two. In a summer set most abortions occurred at a later stage in development than in the autumn sets, and the spread in the time to abort was more evenly represented. However, summer fruits had set earlier, so that nearly all abortions had occurred before the end of winter (August).

With regard to the positional pattern of abortion, in autumn set fruits, this was already more evident nearer the placental edges in general, and the basal quarter of the fruits, six weeks after anthesis. In ripe fruits, however, the greatest proportions occurred nearer the apical end, in both hand- and open-pollinated fruits. Abortions were still more frequent nearer the placental edges than nearer the carpellary margins.

A greater proportion (0,7) of ovules were fertilized with hand-pollination in autumn than with open-pollination (0,3). Of those fertilized, about 50 per cent aborted, in both hand- and open-pollinated fruits.

The pattern for the concentration of early seed development followed that of early pollen tube penetration. It appeared from patterns in ripe fruits (but not six-week-old fruits) that there had been a positive association between the concentration of early seed development and abortion rates for intra-fruit subregions in a given fruit. This relationship was not consistent. A closer examination of the data against the statistical models used, suggested that it was doubtful that seed competition caused abortion.

Examination of fruits set in summer showed that these had a greater total number of ovules than autumn set fruits (2 000 versus 1 600). In a hand-pollinated set nearly 90 per cent of summer ovules were fertilized, as against 65 per cent in an open-pollinated summer set. Abortion rates in summer fruits were much lower than in autumn fruits (10 per cent versus 50 per cent). Positional patterns within the fruits, however, were similar. Although there were higher levels of early seed development in summer fruits, the positional patterns were again similar. In spite of higher concentrations of early seed development, abortion rates along the carpellary margins were not related to the postulated seed competition. As in autumn, hand- versus open-pollination in summer when using basically the same pollen source had no apparent effect on abortion rates.

A third of the leaves that subtended fruits set in autumn abscissed over winter and spring, peak abscission occurring over mid-winter. This corresponded with the periods of seed abortion. Largest mean leaf areas were recorded in autumn, at the end of fruit setting. Smallest mean leaf areas were recorded in spring. Leaf area available to the fruits also depended on the number of fruits. This ratio was smallest in spring before the first harvests and before new leaves had grown out. Leaf area was highly correlated (0,9) with the length of the three longest leaf veins. The latter was used as an index of leaf area.

Multiple regressional and correlational analyses were carried out between fruit flesh mass and seven other covariables for fruit set at weekly intervals over March (early autumn) and picked either three or [illegible]

a low and restricted range of initial growth temperatures for the four batches, the three most important covariables as measured for the three-month growth were

(i) seed mass;
(ii) available leaf area per fruit; and
(iii) sum of effective heat units in the three days preceding anthesis.

After seven months growth the most important covariables had been

(i) seed mass;
(ii) available leaf area per fruit; and
(iii) sum of effective heat units from anthesis until the 15th week.

Covariables not finally included in the models were

(i) diameter of fruit at anthesis;
(ii) area of the leaf subtending the labelled fruit; and
(iii) a restricted range of effective heat units over the period of flower bud development.

Later evidence suggested that this last covariable could in fact be important. Total and partial correlational coefficients for seed and fruit flesh masses were highly significant after three and seven months growth. There was, however a significant drop in these correlations from the third to the seventh months. Seed mass was correlated with temperatures for at least the first 15 weeks after pollination.

The seed mass/fruit mass correlation held at the intra-fruit level in both autumn and summer set fruits. The size of unfertilized ovules from intra-fruit subregions in ripe fruits was also correlated with the relative amount of seed from the same subregions. Similar results had been found after only two and four weeks growth.

In a further inter-fruit correlation study on fruits set with hand-pollination in autumn, the extent of ovule fertilization and early seed development was not correlated with seed abortion rates. There was some tendency (but not significant) for an on-stem competition factor involving leaf area to fruit-load to increase seed abortion rates. There was also a tendency (not significant) fo on-stem fruit competition to lower fruit flesh mass. The sum of fully developed and aborted seeds was more highly correlated with fruit flesh mass (0,727) than the mass of all (F + P + S + U) seeds (0,670). Seed abortion lowered seed mass by reducing the number of fully developed seeds but had no significant effect on fruit flesh mass because aborted seeds contributed to the latter to some extent.

A basically similar set of results was found for fruit set with hand-pollination in summer. The seed/fruit correlations were lower (but still significant) when compared with those set in autumn. The extent of early seed development and presumably seed competition was again not correlated with seed abortion rates.

In yet another hand-pollinated autumn set (1969) there was virtually no difference in abortion rates in fruits from stems of different vigour. An inde of fruit volume was highly correlated with fruit mass (0,99). Ovary volume at anthesis was correlated with the total number of ovules (0,51). The number of all fertilized seeds was again more highly correlated with fruit mass than just the number of fully developed seeds (0,83 versus 0,77). Seed abortion masked and lowered the actual correlation between the number of fully developed seeds and fruit mass in autumn sets.

Comparison of results for various fruit sets indicated that the larger and more advanced an aborted seed was the more it had influenced fruit growth. An examination was made of the correlations between the estimated numbers of various combinations of seeds and the increments in fruit volume growth from anthesis until maturity in one autumn set. Tentative conclusions were as follows. All seed influence was negligible in the latter third to half of grow of fruits set in autumn. Fully developing seeds had a positive influence on fruit growth from fertilization until the phase of endosperm cellularization (October), but in subsequent phases of seed development their influence diminished to zero. Their peak influence in autumn fruits was over the first eight weeks. Abortive seeds had a slower and smaller positive influence, lasting about 15 weeks (until August), but when most abortions had set in by then, thei influence ceased.

The apparent influence of seeds coincided approximately with phase one of seed development and the cell division phase of fruit growth, but not with the following phase comprising only fruit cell enlargement. It seems that other factors affected increments in fruit growth in the later stages. The higher seed/fruit correlations of autumn versus summer sets was probably due to the proportionately more protracted phase one of seed development and fruit cell divisions in autumn sets (22 out of 42 weeks), in comparison to summer sets (12 out of 38 weeks).

Further comparisons between fruits of different seasons of setting showed that hand-pollination increased the proportion of total ovules fertilized in comparison to open pollination. The warmer the season of fruit set and initial growth the greater the total number of ovules fertilized and also the greater the proportion of seeds that reached full development.

Supplementary surveys on pollen tube growth within fruits during summer, autumn and winter indicated that such growth was markedly influenced by prevailing temperatures. Placing a plastic tunnel over plants in autumn raised the mean temperature to that found in uncovered plants in late summer.

An overall inference was that low temperatures in the winter months was a major cause of seed abortion in fruits set in summer and autumn. Seeds in autumn sets, particularly late starters, having made less growth and development before the onset of winter, were thought to have been more susceptible. Poor development and lower potency of some pollen was thought to be a contributory factor. The latter, slow to germinate and grow, was thought to contribute to the abortions that occurred in the upper quarter of the fruit.

It was suggested that further trials be undertaken in which cloches be placed over young cuttings from a period extending from one month before actual anthesis in late autumn until the end of winter, in order to increase temperatures during this period. It was further suggested that if the flowers opening in late autumn under such cloches are hand-pollinated with good pollen, and that if the developing fruits have an adequate leaf cover, and also if minimum temperatures attained are not inhibitive, then it was predicted that the resulting mean size of such out-of-season fruits would be the same as that of open pollinated uncovered fruits set during the summer period. The latter, however, are harvested during peak production. Using closer spacing and genetically superior plants propagated from cuttings, which bear their first crop lower down the stem, may minimize the relative costs associated with using cloches and hand-pollination. Removing some of the fruits that might set in summer may ensure both a larger set of fruits in late autumn and a better leaf to fruit ratio.

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APPENDIX 1

CORRELATION BETWEEN NUMBER OF ENDOSPERM NUCLEI AND SIZE OF DEVELOPING SEED

TABLE 1.1 Correlation between number of free nuclear endosperm nuclei and the intra-integumentary cross-sectional area along the radius plane of seeds two weeks after anthesis, in fruit set in summer, 1970

FRUIT SUB-REGIONS									
A				B				C	
No. of nuclei	"Seed size" $mm^2 \times 10^{-3}$	No. of nuclei	"Seed size" $mm^2 \times 10^{-3}$	No. of nuclei	"Seed size" $mm^2 \times 10^{-3}$	No. of nuclei	"Seed size" $mm^2 \times 10^{-3}$	No. of nuclei	"Seed size" $mm^2 \times 10^{-3}$
62	455	118	454	52	277	34	228	17	277
84	552	104	437	33	258	78	405	44	329
52	447	100	441	57	291	101	418	13	258
29	296	70	405	111	360	85	453	21	371
67	349	41	422	28	198	81	451	54	428
60	451	68	433	61	343	51	353	44	381
66	433	72	393	93	416	54	349	6	296
31	309	43	399	68	360	17	284	33	346
32	399	10	338	84	378	9	196	30	334
66	403	87	467	112	383	17	282	14	198
42	356	19	319	21	200	51	268	42	346
33	306	80	392	105	478	77	405	46	335
83	493	33	371	53	343	79	405		
24	349	51	390	94	411	104	405		
47	469	17	390	80	383	73	412		
44	379	32	341	94	439	99	376		
47	470	38	376	59	351	73	412		
50	346	32	420	44	239	37	314		
70	360	47	354						
47	354	70	439						
83	460	52	376						
70	362	62	497						
90	478								
Mean no. of nuclei		56,11		65,81				30,33	
Mean "seed size" $mm^2 \times 10^{-3}$		403,11		347,89				324,92	
Correlation co-efficient Y		+0,5167		+0,8444				+0,7438	
No. of observations		45		36				12	
Probability p		$p < 0,0005$		$p < 0,0005$				$0,0025 < p < 0,005$	

APPENDIX 2

INTRA-FRUIT DIFFERENCES IN PROPORTION OF OVULES WITH MATURE MEGAGAMETOPHYTES AND YOUNG SEEDS WITH NORMAL ENDOSPERM

TABLE 2.1 X^2 tests on proportion of ovules with mature megagametophytes at anthesis, autumn fruit-set, 1971

i	Fruit/flower sub-region	n_i	P_i
1	A	50	0,92
2	a	50	0,42
3	B	50	0,96
4	b	50	0,28
5	C	50	0,94
6	c	50	0,40
7	D	50	0,86
8	d	50	0,44
Sub-regions	Total X^2	Degrees of freedom	Probability
A, B, C, D only	3,804	3	NS
a, b, c, d only	3,273	3	NS
A, a, ..., D, d	130,886	7	< 0,00001

i = i^{th} sub-region, corresponding with fruit sub-regions.

n_i = number of ovules examined in i^{th} sub-region.

P_i = proportion of n_i with mature megagametophytes.

APPENDIX 2 (contd.)

TABLE 2.2 X^2 tests on proportion of ovules/seeds with normal secondary endosperm four weeks after anthesis, autumn-set, 1971

i	Fruit sub-region	n_i	P_i
1	A	50	0,86
2	a	50	0,82
3	B	50	0,78
4	b	50	0,64
5	C	50	0,66
6	c	50	0,44
7	D	50	0,32
8	d	50	0,20

Sub-regions	Total X^2	Degrees of freedom	Probability
A, B, C, D	37,593	3	< 0,00001
a, b, c, d	42,727	3	< 0,00001
A, a, ..., D, d	86,151	7	< 0,00001
A, a, B, b	7,885	7	NS
C, c, D, d	23,965	7	0,001

$i = i^{th}$ sub-region, corresponding with fruit sub-regions.

n_i = number of ovules/seeds examined in i^{th} sub-region.

P_i = proportion of n_i with apparently normally developing secondary endosperm.

APPENDIX 2 (contd.)

TABLE 2.3 χ^2 tests on proportion of ovules with mature megagametophytes at anthesis, summer fruit-set, 1970

i	Fruit/flower sub-region	n_i	P_i
1	A	50	0,84
2	a	50	0,56
3	B	50	0,82
4	b	50	0,58
5	C	50	0,88
6	c	50	0,64
7	D	50	0,86
8	d	50	0,56

Sub-regions	Total χ^2	Degrees of freedom	Probability
A, B, C, D only	0,784	3	NS
a, b, c, d only	0,886	3	NS
A, a, ..., D, d	36,200	7	< 0,00001

i = i^{th} sub-region, corrresponding with fruit sub-regions.

n_i = number of ovules examined in i^{th} sub-region.

P_i = proportion of n_i with mature megagametophytes.

APPENDIX 3

DATA AND CONCORDANCE (W) TESTS ON RANKS OF THE INTRA-FRUIT PROPORTION OF DIFFERENT OVULE/SEED TYPES FOR FRUIT HAND-POLLINATED AND SET IN AUTUMN, 1970

NOTATION

i = i^{th} sub-region being ranked.

j = j^{th} fruit providing the rankings.

P = proportion of ovule/seed type being tested relative to total number of ovules/seeds in the i^{th} sub-region of the j^{th} fruit.

R = rank of i for the j^{th} fruit.

R_j = sum of the ranks assigned to the i^{th} sub-region by the k fruits.

Kendall's co-efficient of concordance: W .

$$W = \frac{s}{\frac{1}{12}k^2(n^3 - n) - k\sum_T T}$$

$$s = \sum \left(R_j - \frac{\Sigma R_j}{n} \right)^2$$

k = number of sets of rankings, viz. number of fruits providing the rankings.

n = number of sub-regions ranked, viz. for Appendix 3 $n = 4$.

$T = \frac{\Sigma(t^3 - t)}{12}$ = correction factor for tied ranks.

t = number of observations in a group tied for a given rank Σ here directs one to sum over all groups of ties within any one of the k rankings.

$\sum_T$ directs one to sum the values of T for all the k rankings.

For ovule/seed types a, b, cWs, cWL, cDL, dG and dB, see Plate 2(b).

APPENDIX 3 (contd.)

TABLE 3.1 Test on "a" ovules in proportion to total ovules/seeds per fruit sub-region

FRUIT		SUB-REGION								Proportion of "a" for whole fruit
		Aa		Bb		Cc		Od		
No.	i / j	1		2		3		4		
		P	R	P	R	P	R	P	R	
14	1	0,108	4	0,165	3	0,375	2	0,640	1	0,355
37	2	0,099	4	0,102	3	0,127	2	0,266	1	0,146
2	3	0,098	4	0,114	3	0,183	2	0,354	1	0,188
28	4	0,276	3	0,176	4	0,361	2	0,535	1	0,339
16	5	0,102	4	0,102	3	0,199	2	0,377	1	0,189
26	6	0,139	4	0,173	3	0,495	2	0,896	1	0,557
27	7	0,152	4	0,229	3	0,397	2	0,448	1	0,318
54	8	0,091	4	0,186	3	0,267	1	0,218	2	0,198
55	9	0,119	4	0,149	3	0,199	2	0,303	1	0,197
94	10	0,251	3	0,196	4	0,323	2	0,557	1	0,338
65	11	0,140	4	0,183	3	0,348	2	0,439	1	0,305
40	12	0,526	3	0,419	4	0,561	2	0,883	1	0,624
58	13	0,167	4	0,181	3	0,377	2	0,606	1	0,345
13	14	0,125	3	0,076	4	0,154	2	0,216	1	0,142
	R_j		52		46		27		15	
Overall rank			4		3		2		1	

$W = 0,892$.

$s = 874,16$ $(p \leq 0,01)$.

APPENDIX 3 (contd.)

TABLE 3.2 Test on "b" ovule/seeds in proportion to total ovules/seeds per fruit sub-region

FRUIT		SUB-REGION								Proportion of "b" for whole fruit
		Aa		Bb		Cc		Dd		
No.	i / j	1		2		3		4		
		P	R	P	R	P	R	P	R	
14	1	0,464	1	0,384	2	0,192	3	0,122	4	0,265
37	2	0,442	1	0,384	2	0,355	3	0,282	4	0,366
2	3	0,397	1	0,290	2	0,196	3	0,141	4	0,248
28	4	0,591	2	0,602	1	0,289	3	0,275	4	0,440
16	5	0,577	1	0,466	2	0,352	3	0,204	4	0,406
26	6	0,344	1	0,214	2	0,152	3	0,018	4	0,129
27	7	0,444	1	0,338	2	0,145	4	0,207	3	0,269
54	8	0,588	1	0,401	2	0,333	3	0,313	4	0,396
55	9	0,490	1	0,436	2	0,309	3	0,296	4	0,374
94	10	0,319	1	0,279	2	0,255	3	0,199	4	0,258
65	11	0,673	1	0,555	2	0,463	3	0,338	4	0,480
40	12	0,188	2	0,205	1	0,120	3	0,013	4	0,117
58	13	0,631	1	0,417	2	0,220	3	0,130	4	0,318
13	14	0,612	1	0,496	2	0,334	3	0,246	4	0,405
	R_j		16		26		43		55	
Overall rank			1		2		3		4	

$W = 0,924$.

$s = 906,00 \quad (p \leq 0,01)$.

APPENDIX 3 (contd.)

TABLE 3.3 Test on "cWs" seeds in proportion to total ovules/seeds per fruit sub-region

FRUIT		SUB-REGION								Proportion of "cWs" for whole fruit
		Aa		Bb		Cc		Dd		
No.	i / j	1		2		3		4		
		P	R	P	R	P	R	P	R	
14	1	0,130	1	0,062	3	0,103	2	0,016	4	0,072
37	2	0,019	4	0,026	2	0,038	1	0,020	3	0,026
2	3	0,012	2	0,004	4	0,019	1	0,007	3	0,011
28	4	0,042	3	0,066	2	0,079	1	0,037	4	0,055
16	5	0,058	1	0,043	2	0,028	4	0,034	3	0,041
26	6	0,020	3	0,022	2	0,051	1	0,010	4	0,025
27	7	0,058	2	0,040	3	0,077	1	0,029	4	0,052
54	8	0,018	2	0,032	1	0,010	4	0,014	3	0,019
55	9	0,007	2	0,006	3	0,004	4	0,010	1	0,006
94	10	0,023	2	0,042	1	0,020	3	0,013	4	0,025
65	11	0,027	2	0,020	3	0,011	4	0,034	1	0,023
40	12	0,009	1	0,006	4	0,007	2	0,007	3	0,007
58	13	0,024	1	0,019	2	0,015	3	0,014	4	0,017
13	14	0,011	1	0,008	3	0,000	4	0,010	2	0,007
	R_j		27		35		35		43	

W = 0,131 .

s = 128,00 (NS).

APPENDIX 3 (contd.)

TABLE 3.4 Test on "cWL" seeds in proportion to total ovules/seeds per fruit sub-region

FRUIT		SUB-REGION								Proportion of "cWL" for whole fruit
		Aa		Bb		Cc		Dd		
No.	i / j	1		2		3		4		
		P	R	P	R	P	R	P	R	
14	1	0,000	3,5	0,002	2	0,000	3,5	0,004	1	0,002
37	-	-	-	-	-	-	-	-	-	0,000
2	-	-	-	-	-	-	-	-	-	0,000
28	2	0,000	3,5	0,002	2	0,000	3,5	0,003	1	0,001
16	-	-	-	-	-	-	-	-	-	0,000
26	3	0,000	4	0,009	1	0,009	2	0,002	3	0,005
27	-	-	-	-	-	-	-	-	-	0,000
54	-	-	-	-	-	-	-	-	-	0,000
55	-	-	-	-	-	-	-	-	-	0,000
94	4	0,003	4	0,005	3	0,012	1	0,009	2	0,008
65	5	0,004	2	0,000	3,5	0,000	3,5	0,009	1	0,003
40	6	0,000	3	0,000	3	0,002	1	0,000	3	0,001
58	-	-	-	-	-	-	-	-	-	0,000
13	-	-	-	-	-	-	-	-	-	0,000
	R_j		20		14,5		14,5		11	

W = 0,231 .

s = 35,95 (NS).

APPENDIX 3 (contd.)

TABLE 3.5 Test on "cDL" seeds in proportion to total ovules/seeds per fruit sub-region

FRUIT		SUB-REGION								Proportion of "cDL" for whole fruit
		Aa		Bb		Cc		Dd		
No.	i / j	1		2		3		4		
		P	R	P	R	P	R	P	R	
14	1	0,000	3,5	0,002	2	0,014	1	0,000	3,5	0,005
37	–	–	–	–	–	–	–	–	–	0,000
2	2	0,000	3	0,000	3	0,002	1	0,000	3	0,001
28	3	0,000	3	0,000	3	0,003	1	0,000	3	0,001
16	–	–	–	–	–	–	–	–	–	0,000
26	4	0,007	3	0,035	1	0,014	2	0,002	4	0,012
27	–	–	–	–	–	–	–	–	–	0,000
54	5	0,000	3	0,002	1	0,000	3	0,000	3	0,001
55	–	–	–	–	–	–	–	–	–	0,000
94	6	0,040	1	0,020	3	0,008	4	0,031	2	0,023
65	7	0,000	3	0,000	3	0,000	3	0,002	1	0,001
40	8	0,000	3	0,000	3	0,002	1	0,000	3	0,001
58	9	0,004	1	0,000	3,5	0,002	2	0,000	3,5	0,001
13	–	–	–	–	–	–	–	–	–	0,000
	R_j		23,5		22,5		18		26	

W = 0,083 .

s = 25,31 (NS).

APPENDIX 3 (contd.)

TABLE 3.6 Test on "dG" seeds in proportion to total ovules/seeds per fruit sub-region

FRUIT No.	i / j	SUB-REGION Aa 1 P	Aa 1 R	Bb 2 P	Bb 2 R	Cc 3 P	Cc 3 R	Dd 4 P	Dd 4 R	Proportion of "dG" for whole fruit
14	1	0,289	3	0,370	1	0,311	2	0,215	4	0,293
37	2	0,426	3	0,469	1	0,467	2	0,413	4	0,445
2	3	0,489	4	0,590	2	0,599	1	0,494	3	0,550
28	4	0,091	4	0,154	2	0,269	1	0,151	3	0,164
16	5	0,242	4	0,368	3	0,416	1	0,386	2	0,352
26	6	0,457	2	0,538	1	0,247	3	0,070	4	0,256
27	7	0,340	3	0,387	1	0,379	2	0,312	4	0,357
54	8	0,300	4	0,379	3	0,388	2	0,455	1	0,385
55	9	0,384	4	0,408	2	0,488	1	0,391	3	0,423
94	10	0,326	3	0,415	1	0,333	2	0,157	4	0,307
65	11	0,140	4	0,241	1	0,166	3	0,172	2	0,180
40	12	0,274	3	0,361	1	0,306	2	0,097	4	0,248
58	13	0,171	4	0,369	1	0,365	2	0,226	3	0,301
13	14	0,246	4	0,420	3	0,510	2	0,528	1	0,445
	R_j		49		23		26		42	
Overall rank			4		1		2		3	

W = 0,480 .

s = 470,00 ($p \leq 0,01$).

APPENDIX 3 (contd.)

TABLE 3.7 Test on "dB" seeds in proportion to total ovules/seeds per fruit sub-region

FRUIT		SUB-REGION								Proportion of "dB" for whole fruit
		Aa		Bb		Cc		Dd		
No.	i / j	1		2		3		4		
		P	R	P	R	P	R	P	R	
14	1	0,010	2	0,014	1	0,006	3	0,004	4	0,008
37	2	0,013	4	0,020	1	0,014	3	0,020	2	0,017
2	3	0,006	1	0,002	3	0,002	4	0,005	2	0,003
28	-	-	-	-	-	-	-	-	-	0,000
16	4	0,022	1	0,020	2	0,004	3	0,000	4	0,012
26	5	0,033	1	0,009	3	0,032	2	0,003	4	0,016
27	6	0,006	2	0,007	1	0,002	4	0,005	3	0,005
54	7	0,003	1	0,000	3,5	0,002	2	0,000	3,5	0,001
55	-	-	-	-	-	-	-	-	-	0,000
94	8	0,039	3	0,042	2	0,051	1	0,034	4	0,042
65	9	0,016	1	0,000	4	0,011	2	0,007	3	0,008
40	10	0,004	2	0,009	1	0,002	3	0,000	4	0,004
58	11	0,004	4	0,014	3	0,021	2	0,024	1	0,017
13	12	0,007	1	0,000	3,5	0,002	2	0,000	3,5	0,002
	R_j		23		28		31		38	

W = 0,168.

s = 118,00 (NS).

APPENDIX 4

ABORTION AND RELATED DATA OF FRUIT ORIGINALLY SET WITHOUT HAND-POLLINATION IN AUTUMN, 1973

TABLE 4.1 Data for 2/5th portion of fruit No. 1

i	Fruit sub-region	w_i	x_i	p_i
1	A	42	61,76	0,5476
2	a	42	42,86	0,6190
3	B	32	44,44	0,4063
4	b	25	27,17	0,4000
5	C	18	21,95	0,2778
6	c	15	11,72	0,7333
7	D	6	7,59	0,3333
8	d	8	9,09	0,7500

$i = i^{th}$ sub-region corresponding to fruit sub-region.

w_i = weighting factor = (F + P + S) seeds in i .

x_i = competition factor = $\left[(F+P+S)/(F+P+S+U)\right]_i$ %, index of early seed development intensity.

p_i = proportion of seeds aborted in i = $\left(\frac{P+S}{F+P+S}\right)_i$.

APPENDIX 4 (contd.)

TABLE 4.2 Data for 2/5th portion of fruit No. 2

i	Fruit sub-region	w_i	x_i	p_i
1	A	25	69,44	0,2800
2	a	38	39,58	0,8947
3	B	27	43,55	0,1852
4	b	44	36,36	0,3636
5	C	21	25,00	0,0476
6	c	30	33,71	0,2333
7	D	15	20,00	0,1333
8	d	13	17,11	0,1538

Notation as for Appendix Table 4.1

TABLE 4.3 Data for 2/5th portion of fruit No. 3

i	Fruit sub-region	w_i	x_i	p_i
1	A	23	62,16	0,3043
2	a	34	58,62	0,7647
3	B	46	57,50	0,3478
4	b	37	43,53	0,5135
5	C	28	29,17	0,2500
6	c	27	18,75	0,4815
7	D	14	17,95	0,4286
8	d	5	5,81	0,6000

Notation as for Appendix Table 4.1

APPENDIX 4 (contd.)

TABLE 4.4 Data for 2/5th portion of fruit No. 5

i	Fruit sub-region	w_i	x_i	p_i
1	A	45	69,23	0,9556
2	a	62	64,58	1,0000
3	B	47	55,29	0,7447
4	b	76	67,86	1,0000
5	C	51	57,95	0,5490
6	c	76	52,78	0,9868
7	D	19	48,72	0,5263
8	d	39	43,82	0,9487

Notation as for Appendix Table 4.1

TABLE 4.5 Data for 2/5th portion of fruit No. 7

i	Fruit sub-region	w_i	x_i	p_i
1	A	29	76,32	0,5862
2	a	37	74,00	0,8919
3	B	43	84,31	0,1628
4	b	52	55,91	0,7308
5	C	45	54,22	0,1333
6	c	34	25,95	0,5000
7	D	20	35,71	0,0500
8	d	8	9,41	0,2500

Notation as for Appendix Table 4.1

APPENDIX 4 (contd.)

TABLE 4.6 Data for 3/5th portion of fruit No. 9

i	Fruit sub-region	w_i	x_i	P_i
1	A	23	57,50	0,5652
2	a	40	38,83	0,7250
3	B	42	36,84	0,3333
4	b	29	19,46	0,6897
5	C	22	17,74	0,3636
6	c	17	12,23	0,5294
7	D	10	18,52	0,4000
8	d	15	23,81	0,6667

Notation as for Appendix Table 4.1

TABLE 4.7 Data for 4/5th portion of fruit No. 10

i	Fruit sub-region	w_i	x_i	P_i
1	A	52	81,25	0,3846
2	a	67	54,03	0,4328
3	B	98	67,12	0,2653
4	b	86	32,70	0,3372
5	C	81	49,69	0,1975
6	c	61	22,18	0,3279
7	D	52	34,44	0,2308
8	d	40	14,23	0,5000

Notation as for Appendix Table 4.1

APPENDIX 4 (contd.)

TABLE 4.8 Data for 4/5th portion of fruit No. 12

i	Fruit sub-region	w_i	x_i	p_i
1	A	34	48,57	0,6471
2	a	37	29,60	0,9459
3	B	65	41,67	0,6000
4	b	50	20,16	0,6600
5	C	63	35,20	0,5714
6	c	36	16,36	0,6944
7	D	25	21,93	0,5600
8	d	23	20,00	0,9130

Notation as for Appendix Table 4.1

TABLE 4.9 Data for 4/5th portion of fruit No. 13

i	Fruit sub-region	w_i	x_i	p_i
1	A	22	59,46	0,6818
2	a	23	45,10	0,8261
3	B	23	26,74	0,6957
4	b	44	39,29	0,8636
5	C	15	18,52	0,8667
6	c	28	28,87	0,8571
7	D	7	14,00	0,7143
8	d	11	22,00	1,0000

Notation as for Appendix Table 4.1

APPENDIX 4 (contd.)

TABLE 4.10 Data for 4/5th portion of fruit No. 14

i	Fruit sub-region	w_i	x_i	p_i
1	A	29	45,31	0,8621
2	a	38	33,63	0,9737
3	B	19	13,29	0,4737
4	b	61	27,60	0,9836
5	C	10	6,37	0,5000
6	c	28	12,79	0,9286
7	D	5	5,38	0,2000
8	d	15	14,85	0,6667

Notation as for Appendix Table 4.1

TABLE 4.11 Data for 4/5th portion of fruit No. 15

i	Fruit sub-region	w_i	x_i	p_i
1	A	63	80,77	0,8413
2	a	96	64,00	0,9167
3	B	131	75,72	0,6870
4	b	126	54,55	0,7937
5	C	93	46,50	0,6022
6	c	79	37,09	0,6962
7	D	43	38,74	0,4651
8	d	32	25,81	0,7500

Notation as for Appendix Table 4.1

APPENDIX 5

CONCORDANCE (W) AND X^2 TESTS ON THE RANKS OF THE INTRA-FRUIT PROPORTION OF DIFFERENT OVULE/SEED TYPES FOR FRUIT SET WITHOUT HAND-POLLINATION IN AUTUMN, 1973

NTATION: As for Appendix 3, except that n = 8 . X^2 tests each with df = 7 .
For ovule/seed types F, P, S and U, see Plate 2(b).

TABLE 5.1 Test on "U" ovules in proportion to total ovules/seeds per fruit sub-region

FRUIT		S U B - R E G I O N																W: 0,760
		A		a		B		b		C		c		D		d		p < 0,001
o.	i	1		2		3		4		5		6		7		8		X^2 : 58,485
	J	P	R	P	R	P	R	P	R	P	R	P	R	P	R	P	R	Overall P
1	1	0,382	8	0,571	6	0,556	7	0,728	5	0,780	4	0,883	3	0,924	1	0,909	2	0,734
2	2	0,306	8	0,604	6	0,565	7	0,636	5	0,750	3	0,663	4	0,800	2	0,829	1	0,667
3	3	0,378	8	0,414	7	0,425	6	0,565	5	0,708	4	0,813	3	0,821	2	0,942	1	0,678
5	4	0,308	8	0,354	6	0,447	4	0,321	7	0,421	5	0,472	3	0,513	2	0,562	1	0,422
7	5	0,237	7	0,260	6	0,157	8	0,441	5	0,458	4	0,741	2	0,643	3	0,906	1	0,543
9	6	0,425	8	0,612	7	0,632	6	0,805	4	0,823	2	0,878	1	0,815	3	0,762	5	0,748
0	7	0,188	8	0,460	6	0,329	7	0,673	3	0,503	5	0,778	2	0,656	4	0,858	1	0,634
2	8	0,514	8	0,704	5	0,583	7	0,798	3	0,648	6	0,836	1	0,781	4	0,800	2	0,729
3	9	0,405	8	0,549	7	0,733	4	0,607	6	0,815	2	0,711	5	0,860	1	0,780	3	0,693
4	10	0,547	8	0,664	7	0,867	4	0,724	6	0,936	2	0,872	3	0,946	1	0,851	5	0,815
5	11	0,192	8	0,360	6	0,243	7	0,455	5	0,535	4	0,629	2	0,613	3	0,742	1	0,482
	R_j		87		69		67		54		41		29		26		23	
verall rank			8		7		6		5		4		3		2		1	

TABLE 5.2 Test on "S" seeds in proportion to total ovules/seeds per fruit sub-region

FRUIT		SUB-REGION																W: 0,545
		A		a		B		b		C		c		D		d		p < 0,001
o.	i	1		2		3		4		5		6		7		8		X^2: 41,970
	j	P	R	P	R	P	R	P	R	P	R	P	R	P	R	P	R	Overall P
1	1	0,118	2	0,133	1	0,097	3	0,054	5	0,024	7	0,055	4	0,000	8	0,034	6	0,064
2	2	0,056	1	0,042	3	0,000	7	0,041	4	0,000	7	0,045	2	0,013	5	0,000	7	0,025
3	3	0,027	2	0,103	1	0,025	3	0,000	8	0,021	5	0,007	7	0,013	6	0,023	4	0,023
5	4	0,354	4	0,406	2	0,153	8	0,500	1	0,216	6	0,382	3	0,154	7	0,281	5	0,329
7	5	0,211	3	0,380	1	0,039	5	0,247	2	0,036	6	0,069	4	0,018	7	0,000	8	0,111
9	6	0,125	2	0,194	1	0,061	4	0,054	5	0,032	6	0,022	7	0,019	8	0,079	3	0,067
0	7	0,016	8	0,021	1	0,007	4	0,004	7	0,006	6	0,007	4	0,007	4	0,011	2	0,009
2	8	0,143	2	0,224	1	0,103	3	0,069	6	0,073	5	0,055	7	0,044	8	0,096	4	0,091
3	9	0,243	2	0,275	1	0,081	6	0,232	3	0,037	8	0,206	4	0,080	7	0,100	5	0,156
4	10	0,219	2	0,292	1	0,000	7	0,199	3	0,000	7	0,059	4	0,000	7	0,040	5	0,097
5	11	0,385	2	0,467	1	0,289	4	0,320	3	0,105	7	0,188	5	0,081	8	0,145	6	0,244
	R_j		30		14		54		47		70		51		75		55	
verall rank			2		1		5		3		7		4		8		6	

APPENDIX 5 (contd.)

TABLE 5.3 Test on "P" seeds in proportion to total ovules/seeds per fruit sub-region

FRUIT		SUB-REGION																W: 0,571
		A		a		B		b		C		c		D		d		p < 0,001
No.	i	1		2		3		4		5		6		7		8		X^2: 43,939
	j	P	R	P	R	P	R	P	R	P	R	P	R	P	R	P	R	Overall P
1	1	0,221	1	0,133	2	0,083	3	0,054	4	0,037	5	0,031	7	0,025	8	0,034	6	0,072
2	2	0,139	2	0,313	1	0,081	4	0,091	3	0,012	8	0,034	5	0,013	7	0,026	6	0,091
3	3	0,162	4	0,345	1	0,175	3	0,224	2	0,052	7	0,083	5	0,064	6	0,012	8	0,124
5	4	0,308	1	0,240	3	0,259	2	0,179	4	0,102	8	0,139	5	0,103	7	0,135	6	0,181
7	5	0,237	2	0,280	1	0,098	4	0,161	3	0,036	6	0,061	5	0,000	8	0,024	7	0,095
9	6	0,200	1	0,087	2	0,061	5	0,081	3	0,032	8	0,043	7	0,056	6	0,079	4	0,069
10	7	0,297	1	0,210	2	0,171	3	0,106	4	0,092	5	0,065	7	0,073	6	0,060	8	0,108
12	8	0,171	1	0,056	8	0,147	2	0,065	6	0,106	3	0,059	7	0,079	5	0,087	4	0,089
13	9	0,162	1	0,098	6	0,105	5	0,107	4	0,123	2	0,041	7	0,020	8	0,120	3	0,094
14	10	0,172	1	0,035	6	0,063	3	0,072	2	0,032	7	0,059	5	0,011	8	0,059	4	0,059
15	11	0,295	1	0,120	4	0,231	2	0,113	5	0,175	3	0,070	7	0,099	6	0,048	8	0,136
	R_j		16		36		36		40		62		67		75		64	
Overall rank			1		2,5		2,5		4		5		7		8		6	

TABLE 5.4 Test on "F" seeds in proportion to total ovules/seeds per fruit sub-region

FRUIT		SUB-REGION																W: 0,612
		A		a		B		b		C		c		D		d		p < 0,001
.	i	1		2		3		4		5		6		7		8		X^2: 47,114
	j	P	R	P	R	P	R	P	R	P	R	P	R	P	R	P	R	Overall P
1	1	0,279	1	0,163	3	0,264	2	0,163	4	0,159	5	0,031	7	0,051	6	0,023	8	0,130
2	2	0,500	1	0,042	8	0,355	2	0,231	5	0,238	4	0,258	3	0,173	6	0,145	7	0,218
3	3	0,432	1	0,138	5	0,375	2	0,212	4	0,219	3	0,097	7	0,103	6	0,023	8	0,175
5	4	0,031	4	0,000	7,5	0,141	3	0,000	7,5	0,261	1	0,007	6	0,231	2	0,023	5	0,068
7	5	0,316	4	0,080	7	0,706	1	0,151	5	0,470	2	0,130	6	0,339	3	0,071	8	0,250
9	6	0,250	1	0,107	5	0,246	2	0,060	7	0,133	3	0,058	8	0,111	4	0,079	6	0,116
0	7	0,500	1	0,306	4	0,493	2	0,217	6	0,399	3	0,149	7	0,265	5	0,071	8	0,249
2	8	0,171	2	0,016	8	0,167	3	0,069	5	0,218	1	0,050	6	0,095	4	0,017	7	0,091
5	9	0,189	1	0,078	3	0,081	2	0,054	4	0,025	7	0,041	6	0,040	5	0,000	8	0,057
4	10	0,063	2	0,009	7	0,070	1	0,005	8	0,032	4	0,009	6	0,011	5	0,050	3	0,029
6	11	0,128	4	0,053	8	0,237	1	0,113	6	0,185	3	0,113	5	0,207	2	0,065	7	0,138
	R_j		22		65,5		21		61,5		36		67		48		75	
erall rank			2		6		1		5		3		7		4		8	

TABLE 5.5 Test on "S" seeds in proportion to total (F + P + S) seeds per fruit sub-region

RUIT	SUB-REGION																W: 0,489
	A		a		B		b		C		c		D		d		p < 0,001
i \ j	1		2		3		4		5		6		7		8		X^2: 37,629
	P	R	P	R	P	R	P	R	P	R	P	R	P	R	P	R	Overall P
1	0,191	6	0,310	3	0,218	4	0,199	5	0,109	7	0,470	1	0,000	8	0,374	2	0,241
2	0,081	4	0,106	3	0,000	7	0,113	2	0,000	7	0,134	1	0,065	5	0,000	7	0,075
3	0,043	5,5	0,176	2	0,043	5,5	0,000	8	0,072	4	0,037	7	0,073	3	0,397	1	0,071
4	0,512	5	0,628	4	0,277	8	0,736	1	0,373	6	0,723	2	0,316	7	0,642	3	0,569
5	0,277	3	0,514	1	0,046	7	0,442	2	0,066	5	0,266	4	0,050	6	0,000	8	0,243
6	0,217	4	0,500	1	0,166	7	0,277	3	0,181	5	0,180	6	0,103	8	0,332	2	0,266
7	0,020	4,5	0,039	2	0,010	8	0,011	7	0,012	6	0,032	3	0,020	4,5	0,077	1	0,025
8	0,294	5	0,757	1	0,247	6	0,342	3	0,207	7	0,335	4	0,201	8	0,480	2	0,336
9	0,408	6	0,610	2	0,303	7	0,590	3	0,200	8	0,713	1	0,571	4	0,455	5	0,508
10	0,483	3	0,869	1	0,000	7	0,721	2	0,000	7	0,461	4	0,000	7	0,268	5	0,524
11	0,476	5	0,730	1	0,382	6	0,587	2	0,226	7	0,507	4	0,209	8	0,562	3	0,471
R_j		51		21		72,5		38		69		37		68,5		39	
erall ank		5		1		8		3		7		2		6		4	

TABLE 5.6 Test on "P" seeds in proportion to total (F + P + S) seeds per fruit sub-region

RUIT	S U B - R E G I O N																W: 0,119
	A		a		B		b		C		c		D		d		NS
i / j	1		2		3		4		5		6		7		8		X^2: 9,152
	P	R	P	R	P	R	P	R	P	R	P	R	P	R	P	R	Overall P
1	0,358	2	0,310	4	0,187	7	0,199	6	0,168	8	0,265	5	0,329	3	0,374	1	0,271
2	0,200	3	0,790	1	0,186	4	0,250	2	0,048	8	0,101	6	0,065	7	0,152	5	0,273
3	0,260	6	0,589	1	0,304	5	0,515	2	0,178	8	0,444	3	0,358	4	0,207	7	0,385
4	0,445	2	0,372	3	0,468	1	0,264	5	0,176	8	0,263	6	0,211	7	0,308	4	0,313
5	0,311	2	0,378	1	0,116	6	0,288	3	0,056	7	0,236	5	0,000	8	0,255	4	0,208
6	0,348	3	0,224	6	0,166	8	0,415	1	0,181	7	0,352	2	0,303	5	0,332	4	0,274
7	0,366	3	0,389	2	0,255	6	0,324	4	0,185	8	0,293	5	0,212	7	0,423	1	0,295
8	0,352	5	0,189	8	0,353	4	0,322	6	0,301	7	0,360	3	0,361	2	0,435	1	0,328
9	0,272	4	0,217	6	0,393	3	0,272	5	0,665	1	0,142	8	0,143	7	0,545	2	0,306
10	0,380	5	0,104	8	0,474	2	0,261	6	0,500	1	0,461	3	0,204	7	0,396	4	0,319
11	0,365	2	0,188	7	0,305	3	0,207	5	0,376	1	0,189	6	0,256	4	0,186	8	0,263
R_i		37		47		49		45		64		52		61		41	

TABLE 5.7 Test on "F" seeds in proportion to total (F + P + S) seeds per fruit sub-region

FRUIT		SUB-REGION																W: 0,649
		A		a		B		b		C		c		D		d		p < 0,001
	i	1		2		3		4		5		6		7		8		X^2: 49,952
•	j	P	R	P	R	P	R	P	R	P	R	P	R	P	R	P	R	Overall P
	1	0,451	5	0,380	6	0,595	4	0,599	3	0,723	1	0,265	7	0,671	2	0,253	8	0,489
	2	0,720	6	0,105	8	0,816	4	0,635	7	0,952	1	0,766	5	0,865	2	0,848	3	0,655
	3	0,695	2	0,235	8	0,652	3	0,487	6	0,750	1	0,519	5	0,575	4	0,397	7	0,547
	4	0,045	5	0,000	7,5	0,255	3	0,000	7,5	0,451	2	0,013	6	0,474	1	0,053	4	0,118
	5	0,414	6	0,108	8	0,837	3	0,270	7	0,867	2	0,502	5	0,950	1	0,755	4	0,547
	6	0,435	5	0,276	8	0,668	1	0,308	7	0,638	2	0,475	4	0,600	3	0,332	6	0,460
	7	0,616	6	0,567	7	0,735	3	0,664	5	0,803	1	0,671	4	0,770	2	0,500	8	0,680
	8	0,352	4	0,054	8	0,400	3	0,342	5	0,491	1	0,305	6	0,438	2	0,085	7	0,336
	9	0,318	1	0,173	4	0,303	2	0,137	6	0,135	7	0,142	5	0,286	3	0,000	8	0,186
	10	0,139	5	0,027	7	0,526	2	0,018	8	0,500	3	0,071	6	0,796	1	0,336	4	0,157
	11	0,158	7	0,083	8	0,313	3	0,207	6	0,398	2	0,304	4	0,535	1	0,252	5	0,266
	R_j		52		79,5		31		67,5		23		57		22		64	
erall rank			4		8		3		7		2		5		1		6	

APPENDIX 6

χ^2 TESTS ON THE DIFFERENCE IN ABORTION RATES BETWEEN CARPELLARY MARGIN AND PLACENTAL EDGE REGIONS FOR FRUIT SET IN AUTUMN, 1973

TABLE 6.1 "Total" χ^2 on p_i of Appendix 4 for fruit sub-regions A, a, B, b, C, c, D, d

Fruit No.	χ^2	df	Probability, p
1	14,293	7	0,0464
2	69,122	7	< 0,00001
3	23,197	7	0,0016
5	116,375	7	< 0,00001
7	95,006	7	< 0,00001
9	19,935	7	0,0057
10	19,830	7	0,0060
12	24,832	7	0,0008
13	9,032	7	0,2504
14	63,557	7	< 0,00001
15	48,615	7	< 0,00001
Total individual χ^2	503,794	77	< 0,00001
Pooled χ^2	299,604	7	< 0,00001
Heterogeniety χ^2	204,190	70	< 0,00001
$\chi^2 = \Sigma - 2 \ln p$	$\geq$ 171,743	22	< 0,00001

APPENDIX 6 (contd.)

TABLE 6.2 χ^2 "differences" between (A, B, C, D) vs (a, b, c, d) fruit sub-regions with regard to p_i of Appendix 4

Fruit No.	χ^2	df	Probability, p
1	4,230	1	0,0397
2	20,721	1	0,00001
3	15,473	1	0,0001
5	70,166	1	< 0,00001
7	57,393	1	< 0,00001
9	14,663	1	0,0001
10	9,500	1	0,0021
12	13,111	1	0,0003
13	5,074	1	0,0243
14	30,155	1	< 0,00001
15	16,177	1	0,0001
Total individual χ^2	256,663	11	< 0,00001
Pooled χ^2	225,250	1	< 0,00001
Heterogeniety χ^2	31,413	10	0,0005
$\chi^2 = \Sigma -2 \ln p$	$\geq$ 189,808	22	< 0,00001

APPENDIX 7

CONCORDANCE (W) AND X^2 TESTS ON THE RANKS OF ABORTION RATES p_i OF APPENDIX 4 FOR FRUIT SET IN AUTUMN, 1973

TABLE 7.1

FRUIT		RANKS							
		SUB-REGIONS							
		A	a	B	b	C	c	D	d
No.	j \ i	1	2	3	4	5	6	7	8
1	1	4	3	5	6	8	2	7	1
2	2	3	1	5	2	8	4	7	6
3	3	7	1	6	3	8	4	5	2
5	4	4	1,5	6	1,5	7	3	8	5
7	5	3	1	6	2	7	4	8	5
9	6	4	1	8	2	7	5	6	3
10	7	3	2	6	4	8	5	7	1
12	8	5	1	6	4	7	3	8	2
13	9	8	5	7	3	2	4	6	1
14	10	4	2	7	1	6	3	8	5
15	11	2	1	6	3	7	5	8	4
	R_j	47	19,5	68	31,5	75	42	78	35
Overall rank		5	1	6	2	7	4	8	3

$W = 0,650$

$X^2 = 50,023$

$df = 7$

$p < 0,00001$

APPENDIX 8

CONCORDANCE (W) AND X^2 TESTS ON THE RANKS OF A COMPETITION FACTOR (x_i OF APPENDIX 4) FOR FRUIT SET IN AUTUMN, 1973

TABLE 8.1

FRUIT		RANKS							
		SUB-REGIONS							
		A	a	B	b	C	c	D	d
No.	j \ i	1	2	3	4	5	6	7	8
1	1	1	3	2	4	5	6	8	7
2	2	1	3	2	4	6	5	7	8
3	3	1	2	3	4	5	6	7	8
5	4	1	3	5	2	4	6	7	8
7	5	2	3	1	4	5	7	6	8
9	6	1	2	3	5	7	8	6	4
10	7	1	3	2	6	4	7	5	8
12	8	1	4	2	6	3	8	5	7
13	9	1	2	5	3	7	4	8	6
14	10	1	2	5	3	7	6	8	4
15	11	1	3	2	4	5	7	6	8
	R_j	12	30	32	45	58	70	73	76
Overall rank		1	2	3	4	5	6	7	8

$W = 0,760$

$X^2 = 58,485$

$df = 7$

$p < 0,00001$

APPENDIX 9

χ^2 AND t-TESTS ON THE DIFFERENCE IN THE COMPETITION FACTOR INTENSITY (x_i OF APPENDIX 4) BETWEEN CARPELLARY MARGIN AND PLACENTAL EDGE REGIONS FOR FRUIT SET IN AUTUMN, 1973

TABLE 9.1

Fruit No.	$\bar{D}x_i$	t-Value (df = 3)	Probability, p
1	11,23	2,419	0,0960
2	7,81	0,966	0,4056
3	10,02	4,398	0,0232
5	0,54	0,123	0,9222
7	21,32	3,357	0,0461
9	9,07	1,611	0,2070
10	27,34	9,424	0,0056
12	15,31	3,401	0,0452
13	-4,14	-0,663	0,5564
14	-4,63	-0,816	0,4761
15	15,07	5,960	0,0098
$\chi^2 = \Sigma - 2 \ln p = 51,956$ with df = 22			$p < 0,0003$

$\bar{D}x_i$ = mean difference in x_i between A - a, B - b, C - c, D - d fruit sub-regions.

APPENDIX 10

QUANTITATIVE χ^2 TESTS ON THE RELATION BETWEEN A COMPETITION FACTOR AND ABORTION RATES IN FRUIT SET WITHOUT HAND-POLLINATION IN AUTUMN, 1973

TABLE 10.1 For fruit sub-regions A, B, C, D only

Fruit No.	TOTAL			SLOPE			LINEARITY		
	χ^2	df	p	χ^2	df	p	χ^2	df	p
1	4,322	3	0,2289	3,837	1	0,0502	0,485	2	0,7848
2	4,551	3	0,2079	3,820	1	0,0507	0,731	2	0,6940
3	1,558	3	0,6690	0,0001	1	0,9999	1,558	2	0,4590
5	23,255	3	0,00004	15,188	1	0,0001	8,067	2	0,0177
7	28,220	3	0,00001	6,206	1	0,0127	22,015	2	0,00002
9	3,508	3	0,3200	1,750	1	0,1860	1,758	2	0,4153
10	6,060	3	0,1088	3,981	1	0,0460	2,079	2	0,3541
12	0,660	3	0,8825	0,520	1	0,4713	0,141	2	0,9322
13	1,833	3	0,6078	0,602	1	0,4379	1,231	2	0,5405
14	13,453	3	0,0038	12,253	1	0,0005	1,200	2	0,5488
15	18,394	3	0,0004	14,222	1	0,0002	4,173	2	0,1242
Total individual χ^2	105,814	33	< 0,00001	62,379	11	< 0,00001	43,438	22	0,0043
Pooled χ^2	44,469	3	< 0,00001	43,021	1	< 0,00001	1,448	2	0,4850
Heterogeniety χ^2	61,345	30	0,0007	19,358	10	0,0360	41,990	20	0,0028
$\chi^2 = \Sigma - 2 \ln p$	84,928	22	< 0,00001	84,015	22	< 0,00001	43,057	22	0,0048

APPENDIX 10 (contd.)

TABLE 10.2 For fruit sub-regions a, b, c, d only

Fruit No.	TOTAL			SLOPE			LINEARITY		
	χ^2	df	p	χ^2	df	p	χ^2	df	p
1	5,991	3	0,1121	0,360	1	0,5498	5,632	2	0,0599
2	41,460	3	< 0,00001	17,856	1	0,00002	23,604	2	0,00001
3	6,510	3	0,0894	3,549	1	0,0597	2,961	2	0,2277
5	6,837	3	0,0773	5,597	1	0,0180	1,240	2	0,5381
7	20,323	3	0,0002	19,975	1	0,00001	0,348	2	0,8406
9	2,125	3	0,5471	1,347	1	0,2460	0,778	2	0,6779
10	4,546	3	0,2084	0,033	1	0,8562	4,513	2	0,1048
12	14,074	3	0,0028	7,905	1	0,0049	6,169	2	0,0458
13	2,060	3	0,5603	1,111	1	0,2920	0,949	2	0,6224
14	21,591	3	0,0001	7,568	1	0,0059	14,023	2	0,0009
15	14,113	3	0,0028	10,461	1	0,0012	3,651	2	0,1613
Total individual χ^2	139,630	33	< 0,00001	75,762	11	< 0,00001	63,868	22	0,00001
Pooled χ^2	33,551	3	< 0,00001	24,449	1	0,00001	9,102	2	0,0106
Heterogeniety χ^2	106,079	30	< 0,00001	51,313	10	< 0,00001	54,766	20	0,00005
$\chi^2 = \Sigma - 2 \ln p$	101,821	22	< 0,00001	99,464	22	< 0,00001	63,282	22	0,00001

APPENDIX 11

DATA AND QUANTITATIVE X^2 TESTS ON RELATION BETWEEN ESTIMATORS OF COMPETITION FACTOR AND ABORTION RATES AT THE SIXTH WEEK IN FRUIT SET WITH HAND-POLLINATION IN AUTUMN, 1971

TABLE 11.1 X^2 tests on relation of first estimator of competition factor and seed abortion rate

i	Fruit sub-region	n_i	x_i	p_i	$\hat{p}_i$	$(p_i - \hat{p}_i)$
1	A	48	978,8	0,0417	0,0778	-0,0361
2	a	45	729,2	0,1778	0,2096	-0,0318
3	B	43	903,8	0,1163	0,1174	-0,0011
4	b	39	703,7	0,1795	0,2231	-0,0436
5	C	92	868,1	0,1848	0,1362	+0,0486
6	c	49	547,9	0,1633	0,3054	-0,1421
7	D	39	683,1	0,2564	0,2340	+0,0224
8	d	29	507,9	0,3517	0,3265	+0,2252
Fruit sub-region		n	$\bar{x}$	$\bar{p}$	g	h
A, ..., D only		222	866,5	0,1532	+0,7639	-0,0007
a, ..., d only		162	628,6	0,2408	+0,7937	-0,0009
A, a, ..., D, d		384	766,1	0,1901	+0,5948	-0,0005
	Type of X^2		X^2	df	Comments	
A, ..., D only	Total		8,963	3	*	
	Slope		7,574	1	** ..... (-)	
	Linearity		1,389	2	NS, .. linear	
a, ..., d only	Total		18,724	3	***	
	Slope		5,999	1	* ..... (-)	
	Linearity		12,725	2	** non-linear	
A, a, ..., D, d	Total		34,444	7	***	
	Slope		15,750	1	*** ..... (-)	
	Linearity		18,694	6	* non-linear	

$i = i^{th}$ sub-region corresponding to A, ..., d fruit sub-regions.

n_i = number of seeds on which p_i is based.

$n = \Sigma n_i$.

x_i = competition factor: first estimator for early seed development in i , viz. mean cross-sectional area of median longitudinal plane between inner-integuments ($\mu^2 \times 10^3$) .

$\bar{x}$ = weighted mean of x_i .

p_i = estimator for early seed abortion in i ; proportion of pollinated seeds without normal endosperm.

$\bar{p}$ = weighted mean of p_i .

h = regression co-efficient.

$\hat{p}_i = \bar{p} + h(x_i - \bar{x})$; weighted estimate of p_i .

$g = \bar{p} - h\bar{x}$; constant.

Probability levels:- NS $p > 0,05$
* $p \leq 0,05$
** $p \leq 0,01$
*** $p \leq 0,001$

APPENDIX 11 (contd.)

TABLE 11.2 χ^2 tests on relation of second estimator of competition factor and seed abortion rate

i	Fruit sub-region	n_i	x_i	p_i	β_i	$(p_i - \beta_i)$
1	A	48	96,00	0,0417	0,0800	-0,0383
2	a	45	90,00	0,1778	0,1215	+0,0563
3	B	43	86,00	0,1163	0,1491	-0,0328
4	b	39	78,00	0,1795	0,2045	-0,0250
5	C	92	82,88	0,1848	0,1707	+0,0141
6	c	49	61,25	0,1633	0,3203	-0,1570
7	D	39	78,00	0,2564	0,2045	+0,0519
8	d	29	58,00	0,5517	0,3427	+0,2090

Fruit sub-region	n	$\bar{x}$	$\bar{p}$	g	h
A, ..., D only	222	85,46	0,1532	+1,1499	-0,0117
a, ..., d only	162	72,69	0,2408	+0,6429	-0,0055
A, a, ..., D, d	384	80,07	0,1901	+0,7438	-0,0069

	Type of χ^2	χ^2	df	Comments
A, ..., D only	Total	8,963	3	*
	Slope	8,523	1	** ..... (-)
	Linearity	0,439	2	NS, .. linear
a, ..., d only	Total	18,724	3	***
	Slope	4,563	1	* ..... (-)
	Linearity	14,161	2	*** non-linear
A, a, ..., D, d	Total	34,444	7	***
	Slope	15,734	1	*** ..... (-)
	Linearity	18,71	6	** non-linear

$i = i^{th}$ sub-region corresponding to A, ..., d fruit sub-regions.

n_i = number of seeds on which p_i is based.

$n = \Sigma n_i$.

x_i = competition factor: second estimator for early seed development in i ; viz. % pollen tube penetrations.

$\bar{x}$ = weighted mean of x_i .

p_i = estimator for early seed abortion in i ; proportion of pollinated seeds without normal endosperm.

$\bar{p}$ = weighted mean of p_i .

h = regression co-efficient

$\beta_i = \bar{p} + h(x_i - \bar{x})$; weighted estimate of p_i .

$g = \bar{p} - h\bar{x}$; constant.

Probability levels:- NS $p > 0,05$

* $p \leq 0,05$

** $p \leq 0,01$

*** $p \leq 0,001$

APPENDIX 12

QUALITATIVE $\bar{\chi}^2$ TESTS ON AN ORDERED DISTRIBUTION OF ABORTION ALONG THE FRUIT STEM-APEX AXIS FOR FRUIT SET IN AUTUMN, 1973

TABLE 12.1 On the qualitative ordering of fruit sub-regions with respect to the weighted p_i of Appendix 4, viz. that A > B > C > D

FRUIT	SUB-REGION								C_1	C_2	$\bar{\chi}^2$	Probability, p
	A		B		C		D					
No.	w_i	p_i	w_i	p_i	w_i	p_i	w_i	p_i				
1	42	0,5476	32	0,4063	18	0,2917'	6	0,2917'	0,45	0,40	4,265	0,05 < p < 0,10
2	25	0,2800	27	0,1852	21	0,0833'	15	0,0833'	0,46	0,48	4,097	0,05 < p < 0,10
3	23	0,3333'	46	0,3333'	28	0,3095'	14	0,3095	0,36	0,46	0,068	p > 0,10
5	45	0,9556	47	0,7447	51	0,5490	19	0,5263	0,50	0,36	23,257	p < 0,005
7	29	0,5862	43	0,1628	45	0,1333	20	0,0500	0,45	0,39	28,220	p < 0,005
9	23	0,4154'	42	0,4154'	22	0,3750'	10	0,3750'	0,35	0,45	0,146	p > 0,10
10	52	0,3846	98	0,2653	81	0,2105'	52	0,2105	0,40	0,46	5,880	0,025<p<0,050
12	34	0,6471	65	0,6000	63	0,5714	25	0,5600	0,41	0,38	0,660	p > 0,10
13	22	0,7334'	23	0,7334'	15	0,7334'	7	0,7143	0,44	0,44	0,012	p > 0,10
14	29	0,8621	19	0,4828'	10	0,4828'	5	0,2000	0,46	0,47	13,433	p < 0,005
15	63	0,8413	131	0,6870	93	0,6022	43	0,4651	0,37	0,43	18,394	p < 0,005

(') - over a p_i value denotes a revised proportion after Bartholomew's method for ordered qualitative χ^2 (Fleiss, 1973)

TABLE 12.2 On the qualitative ordering of fruit sub-regions with respect to the weighted p_i of Appendix 4, viz. that a > b > c > d

FRUIT	SUB-REGION								C_1	C_2	$\bar{\chi}^2$	Probability, p
	a		b		c		d					
No.	w_i	p_i	w_i	p_i	w_i	p_i	w_i	p_i				
1	42	0,6190	25	0,5625'	15	0,5625'	8	0,5625'	0,48	0,47	0,295	p > 0,10
2	38	0,8947	44	0,3636	30	0,2333	13	0,1538	0,43	0,42	41,459	p < 0,005
3	34	0,7647	37	0,5135	27	0,5000'	5	0,5000	0,45	0,30	6,265	0,01 < p < 0,025
5	62	1,0000	76	1,0000	76	0,9868	39	0,9487	0,47	0,41	6,837	0,025 < p < 0,01
7	37	0,8919	52	0,7308	34	0,5000	8	0,2500	0,41	0,34	20,323	p < 0,005
9	40	0,7250	29	0,6897	17	0,5938'	15	0,5938'	0,46	0,54	1,441	p > 0,10
10	67	0,4328	86	0,3690'	61	0,3690'	40	0,3690'	0,43	0,48	0,842	p > 0,10
12	37	0,9459	50	0,7247'	36	0,7247'	23	0,7247'	0,42	0,48	7,896	0,01 < p < 0,025
13	23	0,8679'	44	0,8679'	28	0,8679'	11	0,8679	0,37	0,42	0,000	p > 0,10
14	38	0,9798'	61	0,9798'	28	0,9286	15	0,6667	0,35	0,49	21,553	p < 0,005
15	96	0,9167	126	0,7937	79	0,7117'	32	0,7117'	0,41	0,42	13,699	p < 0,005

(') - see Appendix Table 12.1

APPENDIX 13

X^2 TESTS ON THE DISTRIBUTION OF ABORTION WITHIN THE FRUIT STEM-APEX AXIS FOR FRUIT SET WITHOUT HAND-POLLINATION IN AUTUMN, 1973

TABLE 13.1 X^2 tests on the differences in proportions of aborted seeds p_i (Appendix 4) for fruit sub-regions ABC vs D

Fruit No.	ABC		D		X^2 "differences"	df
	n_1	$\bar{p}_1$	n_2	$\bar{p}_2$		
1	92	0,4457	6	0,3333	0,2890	3
2	73	0,1781	15	0,1333	0,1767	3
3	97	0,3093	14	0,4286	0,7946	3
5	143	0,7413	19	0,5263	3,8134	3
7	117	0,2564	20	0,0500	4,1558	3
9	87	0,4023	10	0,4000	0,0002	3
10	231	0,2684	52	0,2308	0,3107	3
12	162	0,5988	25	0,5600	0,1352	3
13	60	0,7334	7	0,7143	0,0116	3
14	58	0,6724	5	0,2000	4,4316	3
15	287	0,6934	43	0,4651	8,7315	3
				ΣX^2	22,850 ‡	33

‡ Probability, $0,85 < p < 0,95$

APPENDIX 13 (contd.)

TABLE 13.2 χ^2 tests on the differences in proportions of aborted seeds p_i (Appendix 4) for fruit sub-regions A vs BC

Fruit No.	A		BC		χ^2 "differences"	df
	n_1	$\bar{p}_1$	n_2	$\bar{p}_2$		
1	42	0,5476	50	0,3600	3,2517	3
2	25	0,2800	48	0,1250	2,6979	3
3	23	0,3043	74	0,3108	0,0035	3
5	45	0,9556	98	0,6429	15,7225	3
7	29	0,5862	88	0,1477	21,9978	3
9	23	0,5652	64	0,3437	3,4521	3
10	52	0,3846	179	0,2346	4,6170	3
12	34	0,6471	128	0,5859	0,4188	3
13	22	0,6818	38	0,7632	0,4721	3
14	29	0,8621	29	0,4828	9,4713	3
15	63	0,8413	224	0,6518	8,3053	3
				$\Sigma\chi^2$	70,410 ‡	33

‡ Probability, $p < 0,00015$

APPENDIX 13 (contd.)

TABLE 13.3 X^2 tests on the differences in proportions of aborted seeds p_i (Appendix 4) for fruit sub-regions BC vs D

Fruit No.	BC		D		X^2 "differences"	df
	n_1	$\bar{p}_1$	n_2	$\bar{p}_2$		
1	50	0,3600	6	0,3333	0,0166	3
2	48	0,1250	15	0,1333	0,0071	3
3	74	0,3108	14	0,4286	0,7395	3
5	98	0,6429	19	0,5263	0,9222	3
7	88	0,1477	20	0,0500	1,3790	3
9	64	0,3437	10	0,4000	0,1203	3
10	179	0,2346	52	0,2308	0,0032	3
12	128	0,5859	25	0,5600	0,0577	3
13	38	0,7632	7	0,7143	0,0765	3
14	29	0,4828	5	0,2000	1,3834	3
15	224	0,6518	43	0,4651	5,3470	3
				ΣX^2	10,053 ‡	33

‡ Probability, $p > 0,95$

APPENDIX 13 (contd.)

TABLE 13.4 χ^2 tests on the differences in proportions of aborted seeds p_i (Appendix 4) for fruit sub-regions abc vs d

Fruit No.	abc		d		χ^2 "differences"	df
	n_1	$\bar{p}_1$	n_2	$\bar{p}_2$		
1	82	0,5731	8	0,7500	0,9421	3
2	112	0,5089	13	0,1538	5,8936	3
3	98	0,5918	5	0,6000	0,0013	3
5	214	0,9953	39	0,9487	6,0923	3
7	123	0,7155	8	0,2500	7,5694	3
9	86	0,6744	15	0,6667	0,0034	3
10	214	0,3645	40	0,5000	3,2040	3
12	123	0,7561	23	0,9130	2,7871	3
13	95	0,8526	11	1,000	1,8682	3
14	127	0,9685	15	0,6667	20,5780	3
15	301	0,8073	32	0,7500	0,5976	3
				$\Sigma\chi^2$	49,5370‡	33

‡ Probability, $0,01 < p < 0,05$

APPENDIX 13 (contd.)

TABLE 13.5 χ^2 tests on the differences in proportion of aborted seeds p_i (Appendix 4) for fruit sub-regions a vs bc

Fruit No.	a		bc		χ^2 "differences"	df
	n_1	$\bar{p}_1$	n_2	$\bar{p}_2$		
1	42	0,6190	40	0,5250	0,7400	3
2	38	0,8947	74	0,3108	34,2503	3
3	34	0,7647	64	0,5000	6,4407	3
5	62	1,0000	152	0,9934	0,4111	3
7	37	0,8919	86	0,6396	8,0887	3
9	40	0,7250	46	0,6305	0,8702	3
10	67	0,4328	147	0,3333	1,9670	3
12	37	0,9459	86	0,6744	10,3394	3
13	23	0,8261	72	0,8611	0,1699	3
14	38	0,9737	89	0,9663	0,0478	3
15	96	0,9167	205	0,7561	10,8423	3
				$\Sigma\chi^2$	74,167 ♯	33

♯ Probability, $p < 0,0001$

APPENDIX 13 (contd.)

TABLE 13.6 χ^2 tests on the differences in proportions of aborted seeds p_i (Appendix 4) for fruit sub-regions bc vs d

Fruit No.	bc		d		χ^2 "differences"	df
	n_1	$\bar{p}_1$	n_2	$\bar{p}_2$		
1	40	0,5250	8	0,7500	1,3714	3
2	74	0,3108	13	0,1538	1,3311	3
3	64	0,5000	5	0,6000	0,1856	3
5	152	0,9934	39	0,9487	4,0060	3
7	86	0,6396	8	0,2500	4,6546	3
9	46	0,6305	15	0,6667	0,0643	3
10	147	0,3333	40	0,5000	3,7527	3
12	86	0,6744	23	0,9130	5,1790	3
13	72	0,8611	11	1,0000	1,7369	3
14	89	0,9663	15	0,6667	16,2284	3
15	205	0,7561	32	0,7500	0,0056	3
				$\Sigma\chi^2$	38,516 ‡	33

‡ Probability, $0,20 < p < 0,25$

APPENDIX 14

χ^2 TESTS ON THE DISTRIBUTION OF ABORTION BETWEEN FRUIT SUB-REGIONS AT THE SIXTH WEEK IN FRUIT SET WITH HAND-POLLINATION IN AUTUMN, 1971

TABLE 14.1

	FRUIT SUB-REGIONS							
	A, B, C, D vs a, b, c, d		A, B vs C, D		a, b vs c, d		A, a, B, b, C, c vs D, d	
n	222	162	91	131	84	78	316	68
$\bar{p}$	0,1532	0,2408	0,0770	0,2061	0,1786	0,3077	0,1488	0,3823
$\frac{1}{\bar{p}\bar{q}}$, $(\bar{q} = 1 - \bar{p})$	6,4946		7,7096		5,4707		6,4946	
df	1		3		3		7	
χ^2 "differences"	4,668		6,900		3,688		19,815	
Probability	$0,02 < p < 0,05$		$0,05 < p < 0,10$		$0,25 < p < 0,30$		$0,001 < p < 0,005$	

APPENDIX 15

MULTIPLE REGRESSION EQUATIONS ON INTRA-FRUIT ABORTION RATES FOR FRUIT SET WITHOUT HAND-POLLINATION IN AUTUMN, 1973

NOTATION AND MODEL FOR WEIGHTED REGRESSION EQUATIONS - using (weighting factor) w_i , x_i and p_i (transformed to angular degrees) of Appendix 4.

$$\text{Model:} \qquad p = b_0 + b_1x_1 + b_2x_2 + b_3x_3$$

where . . . . . p = regression function for the proportion of aborted seeds, in the transformed mode of angular degrees;

b_0 , b_1 , b_2 , b_3 = regression constants for a given fruit;

x_1 = dummy variable = 0 for A, B, C, D fruit sub-regions and = 1 for a, b, c, d fruit sub-regions;

$x_2 = x_i$ of Appendix 4 ; and

$x_3 = (x_i)^2$.

In addition, the following derived notations are also used:-

$\hat{p}_i$ = estimated proportion of aborted seeds (in the transformed mode of angular degrees), estimated by p of a given fruit for the i^{th} fruit sub-region when appropriate regression constants and x_i values are used;

$e_i = p_i - \hat{p}_i$ = a residual value when an estimated $\hat{p}_i$ is subtracted from a given observed p_i (in transformed mode). Used as a goodness-of-fit check between observed and estimated values of abortion rates.

APPENDIX 15 (contd.)

TABLE 15.1 Regression constants of weighted equations for seed abortion with associated multiple correlation co-efficients

Fruit No.	b_0	b_1	b_2	b_3	Multiple correlation co-efficient
1	47,99	15,09	-1,044	0,0172	0,853
2	-23,22	20,68	1,905	-0,0157	0,718
3	39,88	17,35	-0,684	0,0109	0,888
5	141,93	25,64	-3,777	0,0397	0,945
7	-17,85	36,95	1,087	-0,0057	0,923
9	35,95	18,84	-0,201	0,0071	0,949
10	36,57	10,55	-0,535	0,0069	0,917
12	3,36	22,91	2,367	-0,0285	0,833
13	95,72	18,07	-2,144	0,0246	0,833
14	32,52	23,59	0,992	-0,0048	0,928
15	39,25	14,90	0,022	0,0033	0,910

TABLE 15.2 χ^2 tests (df = 22) on regression co-efficients b_1, b_2, b_3 based on series of (two-tailed) t-test probability values (p) (df = 4)

Fruit No.	b_1		b_2		b_3	
	t	p	t	p	t	p
1	3,016	0,0394	1,849	0,1385	2,206	0,0921
2	1,395	0,2355	0,802	0,4678	0,585	0,5901
3	3,776	0,0195	0,811	0,4633	1,013	0,3686
5	4,725	0,0097	0,736	0,5033	0,897	0,4206
7	4,648	0,0097	1,198	0,2972	0,683	0,5327
9	5,997	0,0039	0,372	0,7288	0,907	0,4157
10	3,610	0,0226	1,843	0,1394	2,378	0,0763
12	2,763	0,0508	1,220	0,2896	0,976	0,3849
13	2,517	0,0656	1,431	0,2260	1,264	0,2754
14	2,162	0,0968	0,533	0,6226	0,135	0,8996
15	3,852	0,0183	0,027	0,9796	0,452	0,6753
$\chi^2 = \Sigma - 2 \ln p$	78,531		21,827		23,200	
p	< 0,00001		0,4704		0,3906	

APPENDIX 15 (contd.)

TABLE 15.3 Concordance (W) and χ^2 test on the ranks of e_i derived from the regression equations

FRUIT		RANKS							
		SUB-REGIONS							
		A	a	B	b	C	c	D	d
No.	j \ i	1	2	3	4	5	6	7	8
1	1	5	4	3	8	6	1	7	2
2	2	3	1	6	7	4	8	2	5
3	3	8	2	4	5	3	7	1	6
5	4	1	4	2	6	8	3	7	5
7	5	1	2	8	7	6	3	5	4
9	6	4	6	7	2	3	8	1	5
10	7	4	2	6	7	5	8	3	1
12	8	4	3	6	8	7	5	2	1
13	9	3	6	5	2	4	7	8	1
14	10	4	6	5	3	2	1	7	8
15	11	2	1	8	6	3	7	5	4
	R_j	39	37	60	61	51	58	48	42
Overall rank		2	1	7	8	5	6	4	3

$W = 0,126$

$\chi^2 = 9,727$

$df = 7$

$p = 0,2046$

APPENDIX 16

ABORTION AND RELATED DATA OF FRUIT SET WITHOUT HAND-POLLINATION IN SUMMER, 1972/73

NOTATION

$i = i^{th}$ sub-region corresponding to fruit sub-regions indicated in the tables.

w_i = a weighting factor = (F + P + S) seeds in i .

x_i = a competition factor = $\left[(F + P + S)/(F + P + S + U)\right]_i$ % , as an index of early seed development intensity.

p_i = proportion of seeds aborted in $i = \left(\frac{P + S}{F + P + S}\right)_i$.

F, P, S, and U refer to seed/ovule types - Plate 2(b).

NOTE: Data from each fruit refers to 2/5th longitudinal portions.

TABLE 16.1 Fruit No. 1

i	Fruit sub-region	w_i	x_i	p_i
1	A	18	78,26	0,0000
2	á	27	57,45	0,0370
3	B	74	86,05	0,0676
4	b	80	64,52	0,1375
5	C	67	73,63	0,1791
6	c	63	45,00	0,0794
7	D	37	50,00	0,1351
8	d	36	33,64	0,0833

APPENDIX 16 (contd.)

TABLE 16.2 Fruit No. 2

i	Fruit sub-region	w_i	x_i	p_i
1	A	38	86,36	0,0263
2	a	45	77,59	0,1111
3	B	78	83,87	0,0513
4	b	92	75,41	0,1087
5	C	103	79,84	0,0680
6	c	74	56,92	0,1351
7	D	46	59,74	0,0652
8	d	55	43,65	0,1636

TABLE 16.3 Fruit No. 3

i	Fruit sub-region	w_i	x_i	p_i
1	A	23	88,46	0,0435
2	a	29	78,38	0,0345
3	B	82	90,11	0,0000
4	b	87	87,88	0,0345
5	C	88	93,62	0,0455
6	c	89	80,18	0,0225
7	D	48	73,85	0,0000
8	d	65	59,63	0,0769

TABLE 16.4 Fruit No. 4

i	Fruit sub-region	w_i	x_i	p_i
1	A	32	88,89	0,0313
2	a	60	85,71	0,0667
3	B	75	85,23	0,0267
4	b	87	83,65	0,1609
5	C	79	80,61	0,0127
6	c	58	58,59	0,0690
7	D	49	59,76	0,0408
8	d	43	43,43	0,0930

APPENDIX 16 (contd.)

TABLE 16.5 Fruit No. 5

i	Fruit sub-region	w_i	x_i	p_i
1	A	28	77,78	0,0714
2	a	68	86,08	0,1029
3	B	64	78,05	0,0625
4	b	103	77,44	0,2136
5	C	52	50,98	0,1346
6	c	41	33,88	0,1463
7	D	20	25,97	0,2000
8	d	12	10,71	0,0833

TABLE 16.6 Fruit No. 6

i	Fruit sub-region	w_i	x_i	p_i
1	A	26	78,79	0,0769
2	a	55	77,46	0,0909
3	B	76	93,83	0,1053
4	b	81	68,64	0,1235
5	C	53	64,63	0,0566
6	c	41	39,05	0,0976
7	D	26	29,89	0,1154
8	d	15	14,02	0,0000

TABLE 16.7 Fruit No. 7

i	Fruit sub-region	w_i	x_i	p_i
1	A	15	83,33	0,0667
2	a	13	46,43	0,1538
3	B	44	78,57	0,0682
4	b	31	24,80	0,0323
5	C	22	40,74	0,0909
6	c	28	17,18	0,0714
7	D	17	14,17	0,1176
8	d	4	3,03	0,0000

APPENDIX 16 (contd.)

TABLE 16.8 Fruit No. 9

i	Fruit sub-region	w_i	x_i	p_i
1	A	48	84,21	0,0417
2	a	64	59,26	0,1094
3	B	74	88,10	0,0541
4	b	73	76,04	0,1507
5	C	73	76,84	0,0548
6	c	66	73,33	0,1061
7	D	38	74,51	0,0263
8	d	46	51,11	0,0435

TABLE 16.9 Fruit No. 10

i	Fruit sub-region	w_i	x_i	p_i
1	A	29	82,86	0,0000
2	a	41	51,25	0,1463
3	B	53	76,81	0,0943
4	b	57	32,20	0,0175
5	C	34	45,95	0,0882
6	c	26	14,86	0,0000
7	D	20	21,98	0,1000
8	d	3	2,16	0,0000

TABLE 16.10 Fruit No. 11

i	Fruit sub-region	w_i	x_i	p_i
1	A	56	91,60	0,0179
2	a	87	89,69	0,0345
3	B	92	92,00	0,0543
4	b	107	89,92	0,0374
5	C	70	83,33	0,0286
6	c	83	72,17	0,0482
7	D	49	56,32	0,0204
8	d	45	42,06	0,1333

APPENDIX 16 (contd.)

TABLE 16.11 Fruit No. 12

i	Fruit sub-region	w_i	x_i	P_i
1	A	24	75,00	0,0417
2	a	41	69,49	0,1220
3	B	56	67,47	0,0357
4	b	67	53,17	0,2239
5	C	30	37,04	0,0667
6	c	34	18,99	0,0588
7	D	26	23,64	0,1154
8	d	7	3,85	0,1429

TABLE 16.12 Fruit No. 13

i	Fruit sub-region	w_i	x_i	P_i
1	A	26	89,66	0,0000
2	a	25	78,13	0,0000
3	B	75	89,29	0,0133
4	b	68	73,12	0,0000
5	C	74	88,10	0,0270
6	c	70	60,87	0,0000
7	D	41	51,25	0,0244
8	d	29	34,94	0,0690

TABLE 16.13 Fruit No. 14

i	Fruit sub-region	w_i	x_i	P_i
1	A	28	82,35	0,1071
2	a	54	71,05	0,2222
3	B	76	88,37	0,1053
4	b	67	61,27	0,2299
5	C	64	90,14	0,0781
6	c	58	41,43	0,0517
7	D	38	58,46	0,0526
8	d	33	42,31	0,2121

APPENDIX 16 (contd.)

TABLE 16.14 Fruit No. 15

i	Fruit sub-region	w_i	x_i	p_i
1	A	51	96,23	0,0392
2	a	57	83,82	0,0351
3	B	106	93,81	0,0094
4	b	124	96,12	0,0645
5	C	124	94,66	0,0403
6	c	107	90,68	0,0374
7	D	59	89,39	0,0169
8	d	94	91,26	0,0638

TABLE 16.15 Fruit No. 16

i	Fruit sub-region	w_i	x_i	p_i
1	A	47	88,68	0,0638
2	a	61	87,14	0,0984
3	B	107	94,69	0,0374
4	b	110	89,43	0,0909
5	C	105	87,50	0,0476
6	c	97	85,09	0,1134
7	D	64	79,01	0,0938
8	d	49	72,06	0,1224

TABLE 16.16 Fruit No. 20

i	Fruit sub-region	w_i	x_i	p_i
1	A	40	68,97	0,0500
2	a	61	88,41	0,1803
3	B	67	78,62	0,0299
4	b	70	57,38	0,1286
5	C	53	55,21	0,1509
6	c	31	27,93	0,0645
7	D	26	23,21	0,0769
8	d	19	14,18	0,0000

APPENDIX 16 (contd.)

TABLE 16.17 Fruit No. 17

i	Fruit sub-region	w_i	x_i	p_i
1	A	50	87,72	0,2400
2	a	58	76,32	0,2069
3	B	103	88,79	0,0777
4	b	111	78,17	0,1622
5	C	92	69,17	0,0652
6	c	82	72,57	0,0732
7	D	54	60,00	0,0556
8	d	59	51,30	0,1186

TABLE 16.18 Fruit No. 18

i	Fruit sub-region	w_i	x_i	p_i
1	A	66	90,41	0,0909
2	a	81	92,05	0,1728
3	B	103	94,50	0,1165
4	b	120	83,33	0,0667
5	C	91	91,00	0,0549
6	c	103	66,88	0,0194
7	D	54	84,38	0,1481
8	d	56	71,79	0,0536

TABLE 16.19 Fruit No. 19

i	Fruit sub-region	w_i	x_i	p_i
1	A	34	94,44	0,6176
2	a	44	91,67	0,5909
3	B	76	96,20	0,4868
4	b	94	90,38	0,6489
5	C	82	95,35	0,4146
6	c	89	93,68	0,5730
7	D	42	87,50	0,3810
8	d	80	89,89	0,5375

APPENDIX 16 (contd.)

TABLE 16.20 Fruit No. 21

i	Fruit sub-region	w_i	x_i	p_i
1	A	52	94,55	0,1346
2	a	64	95,52	0,2188
3	B	108	94,74	0,0741
4	b	108	92,31	0,1204
5	C	102	92,73	0,0784
6	c	98	91,59	0,1429
7	D	49	83,05	0,1224
8	d	63	78,75	0,0476

APPENDIX 17

CONCORDANCE (W) AND χ^2 TESTS ON THE RANKS OF THE INTRA-FRUIT PROPORTION OF DIFFERENT OVULE/SEED TYPES FOR FRUIT SET WITHOUT HAND-POLLINATION IN SUMMER, 1972/73

NOTATION: As for Appendix 3.
For f, P, S, and U ovule/seed types, see Plate 2(b).
χ^2 tests each with df = 7 .

TABLE 17.1 Test on "U" ovules in proportion to total ovules/seeds per fruit sub-region

FRUIT		SUB-REGION														W: 0,760
		A		a		B		b		C		c		D		d		$p < 0,001$
No.	i / j	1		2		3		4		5		6		7		8		χ^2: 106,330
		P	R	P	R	P	R	P	R	P	R	P	R	P	R	P	R	Overall P
1	1	0,217	7	0,426	4	0,140	8	0,355	5	0,264	6	0,550	2	0,500	3	0,664	1	0,419
2	2	0,136	8	0,224	5	0,161	7	0,266	4	0,202	6	0,431	2	0,403	3	0,563	1	0,318
3	3	0,115	6	0,216	3	0,099	7	0,121	5	0,064	8	0,198	4	0,262	2	0,404	1	0,151
4	4	0,111	8	0,143	7	0,148	6	0,163	5	0,194	4	0,414	2	0,402	3	0,566	1	0,286
5	5	0,222	6	0,139	8	0,220	7	0,226	5	0,490	4	0,661	3	0,748	2	0,893	1	0,477
6	6	0,212	7	0,225	6	0,062	8	0,314	5	0,354	4	0,610	3	0,701	2	0,860	1	0,455
7	7	0,167	8	0,536	6	0,214	7	0,752	4	0,593	5	0,828	3	0,858	2	0,970	1	0,750
9	8	0,158	8	0,407	2	0,119	7	0,240	5	0,232	6	0,267	3	0,255	4	0,489	1	0,282
10	9	0,171	8	0,488	5	0,232	7	0,678	4	0,541	5	0,851	2	0,780	3	0,978	1	0,687
11	10	0,082	7	0,103	5	0,080	8	0,101	6	0,167	4	0,278	3	0,437	2	0,579	1	0,235
12	11	0,250	8	0,305	7	0,325	6	0,468	5	0,630	4	0,810	2	0,764	3	0,962	1	0,566
13	12	0,103	8	0,219	5	0,107	7	0,269	4	0,119	6	0,391	3	0,486	2	0,651	1	0,320
14	13	0,177	6	0,290	5	0,116	7	0,387	4	0,099	8	0,586	1	0,415	3	0,577	2	0,367
15	14	0,038	8	0,162	1	0,062	5	0,039	7	0,053	6	0,093	3	0,106	2	0,087	4	0,076
16	15	0,113	6	0,129	4	0,053	8	0,106	7	0,125	5	0,149	3	0,210	2	0,279	1	0,138
17	16	0,123	7	0,239	5	0,112	8	0,218	6	0,309	3	0,274	4	0,400	2	0,487	1	0,277
18	17	0,096	5	0,080	7	0,055	8	0,167	3	0,090	6	0,331	1	0,156	4	0,282	2	0,168
19	18	0,056	6	0,083	4	0,038	8	0,096	3	0,047	7	0,063	5	0,125	1	0,101	2	0,075
20	19	0,310	8	0,116	8	0,212	7	0,426	5	0,448	4	0,721	3	0,768	2	0,856	1	0,534
21	20	0,055	6	0,045	8	0,053	7	0,077	4	0,073	5	0,094	3	0,170	2	0,213	1	0,092
	R_j		139		106		143		95		108		55		49		26	
Overall rank			7		5,5		8		4		5,5		3		2		1	

APPENDIX 17 (contd.)

TABLE 17.2 Test on "S" seeds in proportion to total ovules/seeds per fruit sub-regions

FRUIT		SUB-REGION																W: 0,109
		A		a		B		b		C		c		D		d		p < 0,05
No.	i / j	1		2		3		4		5		6		7		8		χ^2: 15,2
		P	R	P	R	P	R	P	R	P	R	P	R	P	R	P	R	Overall
1	1	0,000	8	0,021	6	0,023	5	0,048	2	0,055	1	0,029	3	0,027	4	0,019	7	0,032
2	2	0,0227	7	0,052	2	0,000	8	0,041	3	0,023	6	0,062	1	0,039	5	0,040	4	0,036
3	3	0,038	1	0,027	3	0,000	7,5	0,030	2	0,021	4	0,009	6	0,000	7,5	0,018	5	0,016
4	4	0,028	5	0,043	2	0,000	7	0,106	1	0,000	7	0,030	3,5	0,000	7	0,030	3,5	0,031
5	5	0,028	4	0,076	2	0,000	6,5	0,135	1	0,000	6,5	0,033	3	0,000	6,5	0,000	6,5	0,039
6	6	0,000	7	0,042	2	0,037	3	0,059	1	0,0366	4	0,010	5	0,000	7	0,000	7	0,025
7	7	0,000	5,5	0,000	5,5	0,054	1	0,000	5,5	0,019	2	0,000	5,5	0,000	5,5	0,000	5,5	0,006
9	8	0,000	7,5	0,019	4	0,012	5	0,094	1	0,021	3	0,033	2	0,000	7,5	0,011	6	0,027
10	9	0,000	6	0,025	2	0,043	1	0,006	3	0,000	6	0,000	6	0,000	6	0,000	6	0,007
11	10	0,000	6	0,000	6	0,000	6	0,008	3	0,000	6	0,0087	2	0,000	6	0,0091	1	0,004
12	11	0,031	3	0,051	2	0,0120	5	0,079	1	0,0123	4	0,000	7	0,000	7	0,000	7	0,019
13	12	0,000	5	0,000	5	0,000	5	0,000	5	0,012	1	0,000	5	0,000	5	0,000	5	0,002
14	13	0,000	7	0,053	1	0,023	4	0,021	5	0,042	2	0,000	7	0,031	3	0,000	7	0,020
15	14	0,0189	3	0,029	1	0,009	5	0,016	4	0,000	7	0,000	7	0,000	7	0,019	2	0,010
16	15	0,038	1	0,014	5	0,0177	3	0,0081	6	0,0083	7	0,0175	4	0,012	6	0,029	2	0,016
17	16	0,000	6	0,000	6	0,000	6	0,000	6	0,023	1	0,000	6	0,022	2	0,009	3	0,007
18	17	0,027	5	0,080	1	0,054	3	0,021	7	0,030	4	0,006	8	0,078	2	0,026	6	0,037
19	18	0,000	6,5	0,000	6,5	0,013	1	0,000	6,5	0,012	2	0,0105	4	0,000	6,5	0,0112	3	0,007
20	19	0,000	7	0,145	1	0,012	4	0,049	2	0,021	3	0,009	5	0,000	7	0,000	7	0,025
21	20	0,018	2	0,000	7	0,000	7	0,0085	5	0,0091	4	0,0093	3	0,000	7	0,025	1	0,009
	R_j		102,5		70		93		72		90,5		93		114,5		94,5	
Overall rank			7		1		4,5		2		3		4,5		8		6	

APPENDIX 17 (contd.)

TABLE 17.3 Test on "P" seeds in proportion to total ovules/seeds per fruit sub-region

FRUIT		SUB-REGION																W: 0,0793
		A		a		B		b		C		c		D		d		NS
No.	i / j	1		2		3		4		5		6		7		8		χ^2: 11,102
		P	R	P	R	P	R	P	R	P	R	P	R	P	R	P	R	Overall P
1	1	0,000	8	0,021	5	0,035	4	0,040	3	0,077	1	0,007	7	0,041	2	0,009	6	0,029
2	2	0,000	7,5	0,034	3	0,043	1	0,041	2	0,031	5	0,015	6	0,000	7,5	0,032	4	0,027
3	3	0,000	6	0,000	6	0,000	6	0,000	6	0,021	2	0,009	3	0,000	6	0,026	1	0,009
4	4	0,000	8	0,014	4	0,023	3	0,029	1	0,0102	5	0,0101	6,5	0,024	2	0,0101	6,5	0,016
5	5	0,028	5	0,013	7	0,049	3	0,030	4	0,069	1	0,017	6	0,052	2	0,009	8	0,032
6	6	0,061	2	0,028	5	0,052	1	0,025	6	0,000	7,5	0,029	4	0,034	3	0,000	7,5	0,026
7	7	0,056	2	0,071	1	0,000	7,5	0,008	6	0,019	3	0,012	5	0,017	4	0,000	7,5	0,013
9	8	0,035	4	0,046	1	0,036	3	0,0208	6	0,021	5	0,044	2	0,020	7	0,011	8	0,030
10	9	0,000	6,5	0,050	1	0,029	3	0,000	6,5	0,041	2	0,000	6,5	0,022	4	0,000	6,5	0,013
11	10	0,016	7	0,031	3	0,050	1	0,025	5	0,024	6	0,026	4	0,011	8	0,047	2	0,030
12	11	0,000	8	0,034	2	0,012	5	0,040	1	0,0123	4	0,011	6	0,027	3	0,005	7	0,018
13	12	0,000	6,5	0,000	6,5	0,012	3,5	0,000	6,5	0,012	3,5	0,000	6,5	0,013	2	0,024	1	0,008
14	13	0,068	4	0,105	2	0,070	5	0,120	1	0,028	6	0,021	7	0,000	8	0,090	3	0,067
15	14	0,019	5	0,000	7,5	0,000	7,5	0,047	1	0,038	3	0,034	4	0,015	6	0,039	2	0,027
16	15	0,019	7	0,071	3	0,018	8	0,073	2	0,033	6	0,079	1	0,062	4	0,059	5	0,053
17	16	0,211	1	0,158	2	0,069	4	0,127	3	0,023	7	0,053	5	0,011	8	0,052	6	0,078
18	17	0,095	2	0,080	1	0,046	4	0,035	5	0,020	6	0,006	8	0,047	3	0,013	7	0,035
19	18	0,583	2	0,542	3	0,456	6	0,587	1	0,384	7	0,526	4	0,333	8	0,472	5	0,487
20	19	0,034	2	0,014	5	0,012	6	0,025	3	0,063	1	0,009	7	0,018	4	0,000	8	0,020
21	20	0,109	3	0,209	1	0,070	6	0,103	4	0,064	7	0,122	2	0,102	5	0,013	8	0,095
	R_j		96,5		69		87,5		73		88		100,5		96,5		109	

APPENDIX 17 (contd.)

TABLE 17.4 Test on "f" seeds in proportion to total ovules/seeds per fruit sub-region

FRUIT		SUB-REGION																W: 0,6914
		A		a		B		b		C		c		D		d		p < 0,001
No.	I / J	1		2		3		4		5		6		7		8		X^2 : 96,795
		P	R	P	R	P	R	P	R	P	R	P	R	P	R	P	R	Overall P
1	1	0,783	2	0,553	5	0,802	1	0,556	4	0,604	3	0,414	7	0,432	6	0,308	8	0,520
2	2	0,841	1	0,690	4	0,796	2	0,672	5	0,744	3	0,492	7	0,558	6	0,365	8	0,619
3	3	0,846	4	0,757	6	0,901	1	0,848	3	0,894	2	0,784	5	0,738	7	0,550	8	0,783
4	4	0,861	1	0,800	3	0,830	2	0,702	5	0,796	4	0,545	7	0,573	6	0,394	8	0,667
5	5	0,722	3	0,772	1	0,732	2	0,609	4	0,441	5	0,289	6	0,208	7	0,098	8	0,451
6	6	0,727	2	0,704	3	0,840	1	0,602	5	0,610	4	0,352	6	0,254	7	0,140	8	0,494
7	7	0,778	1	0,393	3	0,732	2	0,240	5	0,370	4	0,160	6	0,125	7	0,030	8	0,231
9	8	0,807	2	0,528	7	0,833	1	0,646	6	0,726	3	0,656	5	0,726	4	0,489	8	0,662
10	9	0,829	1	0,438	3	0,696	2	0,316	5	0,419	4	0,149	7	0,198	6	0,022	8	0,293
11	10	0,902	1	0,866	3	0,870	2	0,865	4	0,810	5	0,687	6	0,552	7	0,365	8	0,731
12	11	0,719	1	0,610	3	0,651	2	0,413	4	0,346	5	0,179	7	0,209	6	0,033	8	0,298
13	12	0,897	1	0,781	4	0,881	2	0,731	5	0,857	3	0,609	6	0,500	7	0,325	8	0,670
14	13	0,735	3	0,553	5	0,791	2	0,472	6	0,831	1	0,393	7	0,554	4	0,33	8	0,546
15	14	0,925	2	0,809	8	0,929	1	0,899	4	0,908	3	0,873	6	0,879	5	0,855	7	0,887
16	15	0,830	3	0,786	5	0,912	1	0,813	4	0,833	2	0,754	6	0,716	7	0,632	8	0,794
17	16	0,667	3	0,605	6	0,819	1	0,655	4	0,647	5	0,673	2	0,567	7	0,452	8	0,638
18	17	0,822	3	0,761	5	0,835	2	0,778	4	0,860	1	0,656	8	0,719	6	0,680	7	0,761
19	18	0,361	7	0,375	6	0,494	3	0,317	8	0,558	1	0,400	5	0,542	2	0,416	4	0,431
20	19	0,655	3	0,725	2	0,765	1	0,500	4	0,469	5	0,261	6	0,214	7	0,142	8	0,421
21	20	0,818	3	0,746	7	0,877	1	0,812	4	0,855	2	0,785	5	0,729	8	0,750	6	0,605
	R_j		47		89		32		93		65		120		122		152	
Overall rank			2		4		1		5		3		6		7		8	

APPENDIX 17 (contd.)

TABLE 17.5 Test on "S" seeds in proportion to total (F + P + S) seeds per fruit sub-region

FRUIT		SUB-REGION																W: 0,09
		A		a		B		b		C		c		D		d		NS
No.	i / j	1		2		3		4		5		6		7		8		χ^2: 12,
		P	R	P	R	P	R	P	R	P	R	P	R	P	R	P	R	Overall
1	1	0,000	8	0,037	6	0,027	7	0,075	1	0,0746	2	0,063	3	0,054	5	0,056	4	0,055
2	2	0,026	7	0,067	3	0,000	8	0,054	5	0,029	6	0,108	1	0,065	4	0,091	2	0,053
3	3	0,043	1	0,034	2,5	0,000	7,5	0,034	2,5	0,023	5	0,011	6	0,000	7,5	0,031	4	0,020
4	4	0,031	5	0,050	4	0,000	7	0,126	1	0,000	7	0,052	3	0,000	7	0,070	2	0,043
5	5	0,036	4	0,088	3	0,000	6,5	0,175	1	0,000	6,5	0,098	2	0,000	6,5	0,000	6,5	0,075
6	6	0,000	7	0,055	3	0,039	4	0,086	1	0,057	2	0,024	5	0,000	7	0,000	7	0,046
7	7	0,000	5,5	0,000	5,5	0,068	1	0,000	5,5	0,045	2	0,000	5,5	0,000	5,5	0,000	5,5	0,023
9	8	0,000	7,5	0,031	3	0,014	6	0,123	1	0,027	4	0,045	2	0,000	7,5	0,022	5	0,037
10	9	0,000	6	0,049	2	0,057	1	0,018	3	0,000	6	0,000	6	0,000	6	0,000	6	0,023
11	10	0,000	6	0,000	6	0,000	6	0,009	3	0,000	6	0,012	2	0,000	6	0,022	1	0,005
12	11	0,042	3	0,073	2	0,018	5	0,149	1	0,033	4	0,000	7	0,000	7	0,000	7	0,056
13	12	0,000	5	0,000	5	0,000	5	0,000	5	0,014	1	0,000	5	0,000	5	0,000	5	0,002
14	13	0,000	7	0,074	1	0,026	5	0,034	4	0,047	3	0,000	7	0,053	2	0,000	7	0,032
15	14	0,020	3	0,035	1	0,009	5	0,015	4	0,000	7	0,000	7	0,000	7	0,021	2	0,011
16	15	0,043	1	0,0164	5	0,019	4	0,009	8	0,010	7	0,021	3	0,0156	6	0,041	2	0,010
17	16	0,000	6	0,000	6	0,000	6	0,000	6	0,033	2	0,000	6	0,037	1	0,017	3	0,010
18	17	0,030	6	0,066	2	0,068	3	0,025	7	0,033	5	0,010	8	0,093	1	0,036	4	0,045
19	18	0,000	6,5	0,000	6,5	0,0132	1	0,000	6,5	0,012	3	0,011	4	0,000	6,5	0,0125	2	0,007
20	19	0,000	7	0,164	1	0,015	5	0,066	2	0,038	3	0,032	4	0,000	7	0,000	7	0,054
21	20	0,019	2	0,000	7	0,000	7	0,009	5	0,0098	4	0,010	3	0,000	7	0,032	1	0,009
	R_j		103,5		74,5		100		72,5		85,5		89,5		111,5		83	

APPENDIX 17 (contd.)

TABLE 17.6 Test on "P" seeds in proportion to total (F + P + S) seeds per fruit sub-region

FRUIT		SUB-REGION																V_t 0,0310
		A		a		B		b		C		c		D		d		NS
No.	i / j	1		2		3		4		5		6		7		8		χ^2 = 4,340
		P	R	P	R	P	R	P	R	P	R	P	R	P	R	P	R	Overall P
1	1	0,000	7,5	0,000	7,5	0,041	4	0,063	3	0,104	1	0,016	6	0,081	2	0,028	5	0,050
2	2	0,000	7,5	0,044	4	0,051	3	0,054	2	0,039	5	0,027	6	0,000	7,5	0,073	1	0,040
3	3	0,000	6	0,000	6	0,000	6	0,000	6	0,033	2	0,011	3	0,000	6	0,046	1	0,012
4	4	0,000	8	0,0167	6	0,027	3	0,034	2	0,013	7	0,017	5	0,041	1	0,023	4	0,023
5	5	0,036	7	0,015	8	0,063	4	0,039	6	0,135	2	0,049	5	0,200	1	0,083	3	0,062
6	6	0,077	2	0,036	6	0,006	4	0,037	5	0,000	7,5	0,073	3	0,115	1	0,000	7,5	0,048
7	7	0,067	4	0,154	1	0,000	7,5	0,032	6	0,045	5	0,071	3	0,118	2	0,000	7,5	0,052
9	8	0,042	3	0,078	1	0,041	4	0,027	5,5	0,027	5,5	0,061	2	0,026	7	0,022	8	0,041
10	9	0,000	6,5	0,098	2	0,038	4	0,000	6,5	0,088	3	0,000	6,5	0,100	1	0,000	6,5	0,042
11	10	0,018	8	0,034	4	0,054	2	0,028	6	0,029	5	0,036	3	0,020	7	0,111	1	0,039
12	11	0,000	8	0,049	5	0,018	7	0,075	3	0,033	6	0,059	4	0,115	2	0,143	1	0,053
13	12	0,000	6,5	0,000	6,5	0,013	4	0,000	6,5	0,014	3	0,000	6,5	0,024	2	0,069	1	0,012
14	13	0,107	4	0,148	3	0,079	5	0,195	2	0,031	7	0,052	6	0,000	8	0,212	1	0,105
15	14	0,020	5	0,000	7,5	0,000	7,5	0,048	1	0,040	3	0,037	4	0,017	6	0,043	2	0,029
16	15	0,021	7	0,08197	2	0,019	8	0,08182	3	0,038	6	0,093	1	0,078	5	0,08163	4	0,061
17	16	0,240	1	0,207	2	0,078	5	0,162	3	0,033	7	0,073	6	0,019	8	0,102	4	0,108
18	17	0,061	2	0,086	1	0,049	4	0,042	5	0,022	6	0,010	8	0,056	3	0,018	7	0,042
19	18	0,618	2	0,591	3	0,474	6	0,649	1	0,402	7	0,362	4	0,361	6	0,525	5	0,527
20	19	0,050	3	0,016	6	0,015	7	0,043	4	0,113	1	0,032	5	0,077	2	0,000	8	0,044
21	20	0,115	4	0,219	1	0,074	6	0,111	5	0,069	7	0,133	2	0,122	3	0,016	8	0,104
	R_j		102		82,5		101		81,5		96		89		82,5		85,5	

APPENDIX 17 (contd.)

TABLE 17.7 Test on "F" seeds in proportion to total (F + P + S) seeds per fruit sub-region

FRUIT		SUB-REGION																W: 0,1474
		A		a		B		b		C		c		D		d		p < 0,01
No.	i / j	1		2		3		4		5		6		7		8		χ^2: 20,636
		P	R	P	R	P	R	P	R	P	R	P	R	P	R	P	R	Overall P
1	1	1,000	1	0,963	2	0,932	3	0,863	7	0,821	8	0,921	4	0,865	6	0,917	5	0,896
2	2	0,974	1	0,889	6	0,949	2	0,891	5	0,932	4	0,865	7	0,935	3	0,836	8	0,908
3	3	0,957	6	0,966	4,5	1,000	1,5	0,966	4,5	0,955	7	0,978	3	1,000	1,5	0,923	8	0,969
4	4	0,969	3	0,933	5	0,973	2	0,839	8	0,987	1	0,931	6	0,959	4	0,907	7	0,934
5	5	0,929	2	0,897	4	0,938	1	0,786	8	0,865	5	0,854	6	0,800	7	0,917	3	0,863
6	6	0,923	3	0,909	4	0,895	6	0,877	8	0,943	2	0,902	5	0,885	7	1,000	1	0,906
7	7	0,933	3	0,846	8	0,932	4	0,968	2	0,909	6	0,929	5	0,882	7	1,000	1	0,925
9	8	0,958	2	0,891	7	0,946	4	0,849	8	0,945	5	0,894	6	0,974	1	0,957	3	0,921
10	9	1,000	2	0,854	8	0,906	6	0,982	4	0,912	5	1,000	2	0,900	7	1,000	2	0,935
11	10	0,982	1	0,966	4	0,946	7	0,963	5	0,971	3	0,952	6	0,980	2	0,867	8	0,956
12	11	0,958	2	0,878	6	0,964	1	0,776	8	0,933	4	0,941	3	0,885	5	0,857	7	0,891
13	12	1,000	2,5	1,000	2,5	0,987	5	1,000	2,5	0,973	7	1,000	2,5	0,976	6	0,931	8	0,985
14	13	0,893	5	0,778	7	0,895	4	0,770	8	0,922	3	0,948	1	0,947	2	0,788	6	0,863
15	14	0,961	5	0,965	3	0,991	1	0,935	8	0,960	6	0,963	4	0,983	2	0,936	7	0,960
16	15	0,936	2	0,902	6	0,963	1	0,909	4	0,952	3	0,887	7	0,906	5	0,878	8	0,920
17	16	0,760	8	0,793	7	0,922	4	0,838	6	0,935	2	0,927	3	0,944	1	0,881	5	0,882
18	17	0,909	5	0,827	8	0,883	6	0,933	4	0,945	3	0,981	1	0,852	7	0,946	2	0,914
19	18	0,362	7	0,409	6	0,513	3	0,351	8	0,585	2	0,427	5	0,619	1	0,463	4	0,466
20	19	0,950	3	0,820	8	0,970	2	0,871	6	0,849	7	0,935	4	0,923	5	1,000	1	0,902
21	20	0,865	6	0,781	8	0,926	2	0,880	4	0,922	3	0,857	7	0,878	5	0,952	1	0,887
	R_j		69,5		114		65,5		110		86		87,5		84,5		95	
Overall rank			2		7		1		8		4		5		3		6	

APPENDIX 18

χ^2 TESTS ON THE DIFFERENCE IN ABORTION RATES BETWEEN CARPELLARY MARGIN AND PLACENTAL EDGE REGIONS FOR A SUB-SET OF FRUIT SET IN SUMMER, 1972/73

TABLE 18.1 "Total" χ^2 on p_i of sub-set of fruit (Appendix 16) for fruit sub-regions A, a, B, b, C, c, D, d

Fruit No.	χ^2	df	Probability
14	19,837	7	0,0060
17	21,274	7	0,0034
18	19,692	7	0,0058
19	16,392	7	0,0218
21	13,863	7	0,0538
Total individual χ^2	91,258	35	< 0,0001
Pooled χ^2	32,290	7	< 0,0001
Heterogeniety χ^2	58,968	28	0,0006
$\chi^2 = \Sigma - 2 \ln p$	45,396	10	< 0,0001

APPENDIX 18 (contd.)

TABLE 18.2 X^2 "differences" between (A, B, C, D) vs (a, b, c, d) fruit sub-regions with regard to p_i of sub-set of Appendix 16

Fruit No.	X^2	df	Probability
14	8,086	1	0,0045
17	2,539	1	0,1113
18	1,198	1	0,2737
19	8,757	1	0,0031
21	2,434	1	0,1189
Total individual X^2 differences	23,014	5	0,0003
X^2 pooled differences	17,445	1	< 0,0001
Heterogeniety X^2	5,569	4	0,3505
$X^2 = \Sigma - 2 \ln p$	33,602	10	0,0002

APPENDIX 19

CONCORDANCE (W) AND X^2 TESTS ON THE RANKS OF ABORTION RATES P_i OF APPENDIX 16 FOR FRUIT SET IN SUMMER, 1972/73

TABLE 19.1 For all the fruit of Appendix 16

FRUIT		RANKS							
		SUB-REGION							
		A	a	B	b	C	c	D	d
No.	j \ i	1	2	3	4	5	6	7	8
1	1	8	7	6	2	1	5	3	4
2	2	8	3	7	4	5	2	6	1
3	3	3	4,5	7,5	4,5	2	6	7,5	1
4	4	6	4	7	1	8	3	5	2
5	5	7	5	8	1	4	3	2	6
6	6	6	5	3	1	7	4	2	8
7	7	6	1	5	7	3	4	2	8
9	8	7	2	5	1	4	3	8	6
10	9	7	1	3	5	4	7	2	7
11	10	8	5	2	4	6	3	7	1
12	11	7	3	8	1	5	6	4	2
13	12	6,5	6,5	4	6,5	2	6,5	3	1
14	13	4	2	5	1	6	8	7	3
15	14	3	5	8	1	6	4	7	2
16	15	6	3	8	5	7	2	4	1
17	16	1	2	5	3	7	6	8	4
18	17	4	1	3	5	6	8	2	7
19	18	2	3	6	1	7	4	8	5
20	19	6	1	7	3	2	5	4	8
21	20	3	1	7	5	6	2	4	8
	R_j	108,5	65	114,5	62	98	91,5	95,5	85
Overall rank		7	2	8	1	6	4	5	3

$W = 0,147$

$X^2 = 20,608$

$df = 7$

Probability $0,001 \leq p \leq 0,01$

APPENDIX 19 (contd.)

TABLE 19.2 For a sub-set of Appendix 16

FRUIT		RANKS							
		SUB-REGION							
		A	a	B	b	C	c	D	d
No.	j \ i	1	2	3	4	5	6	7	8
14	1	4	2	5	1	6	8	7	3
17	2	1	2	5	3	7	6	8	4
18	3	4	1	3	5	6	8	2	7
19	4	2	3	6	1	7	4	8	5
21	5	3	1	7	5	6	2	4	8
	R_j	14	9	26	15	32	28	29	27
Overall rank		2	1	4	3	8	6	7	5

$W = 0,482$

$\chi^2 = 16,867$

Probability, $0,01 < p < 0,02$

APPENDIX 20

CONCORDANCE (W) AND X^2 TESTS ON THE RANKS OF A COMPETITION FACTOR (x_i OF APPENDIX 16) FOR FRUIT SET IN SUMMER, 1972/73

TABLE 20.1 For all the fruit of Appendix 16

FRUIT		RANKS							
		SUB-REGIONS							
		A	a	B	b	C	c	D	d
No.	j \ i	1	2	3	4	5	6	7	8
1	1	2	5	1	4	3	7	6	8
2	2	1	4	2	5	3	7	6	8
3	3	3,5	6	2	3.5	1	5	7	8
4	4	1	2	3	4	5	7	6	8
5	5	3	1	2	4	5	6	7	8
6	6	2	3	1	4	5	6	7	8
7	7	1	3	2	5	4	6	7	8
9	8	2	7	1	4	3	6	5	8
10	9	1	3	2	5	4	7	6	8
11	10	2	4	1	3	5	6	7	8
12	11	1	2	3	4	5	7	6	8
13	12	1	4	2	5	3	6	7	8
14	13	3	4	2	5	1	8	6	7
15	14	1	8	4	2	3	6	7	5
16	15	3	5	1	2	4	6	7	8
17	16	2	4	1	3	6	5	7	8
18	17	4	2	1	6	3	8	5	7
19	18	3	5	1	6	2	4	8	7
20	19	3	1	2	4	5	6	7	8
21	20	3	1	2	5	4	6	7	8
	R_j	42,5	74	36	83,5	74	125	131	154
Overall rank		2	3,5	1	5	3,5	6	7	8

$W = 0,759$

$X^2 = 106,071$

$df = 7$

APPENDIX 20 (contd.)

TABLE 20.2 For a sub-set of Appendix 16

FRUIT		RANKS							
		SUB-REGION							
		A	a	B	b	C	c	D	d
No.	i / j	1	2	3	4	5	6	7	8
14	1	3	4	2	5	1	8	6	7
17	2	2	4	1	3	6	5	7	8
18	3	4	2	1	6	3	8	5	7
19	4	3	5	1	6	2	4	8	7
21	5	3	1	2	5	4	6	7	8
	R_j	15	16	7	25	16	31	34	38
Overall rank		2	3,5	1	5	3,5	6	7	8

W = 0,743

X^2 = 26,000

df = 7

Probability, $p < 0,001$

APPENDIX 21

X^2 AND t-TESTS ON THE DIFFERENCE IN THE COMPETITION FACTOR INTENSITY (x_i OF APPENDIX 16) BETWEEN CARPELLARY MARGIN AND PLACENTAL EDGE REGIONS FOR FRUIT SET IN SUMMER, 1972/73

TABLE 21.1 For all the fruit of Appendix 16

Fruit No.	$\bar{D}x_i$	t-Value	Probability, p
1	21,83	8,603	0,0031
2	14,06	4,088	0,0265
3	9,99	3,648	0,0382
4	10,78	2,157	0,1201
5	6,14	1,014	0,3855
6	16,99	2,990	0,0582
7	31,34	3,429	0,0416
9	15,98	3,163	0,0508
10	31,78	6,272	0,0082
11	7,40	2,366	0,0990
12	14,41	4,531	0,0214
13	17,81	5,347	0,0135
14	25,82	3,104	0,0532
15	3,05	0,889	0,4397
16	4,04	3,222	0,0485
17	6,83	1,976	0,1428
18	11,56	2,194	0,1159
19	1,97	1,159	0,3308
20	9,58	0,921	0,4253
21	1,73	1,557	0,2177
$X^2 = \Sigma - 2 \ln p = 108,765$ with df = 40			$p < 0,00001$

$\bar{D}x_i$ = mean difference in x_i between A – a, B – b, C – c, D – d .

APPENDIX 21 (contd.)

TABLE 21.2 For a sub-set of Appendix 16

Fruit No.	$\bar{D}x_i$	t-Value	Probability, p
14	25,62	3,104	0,0532
17	6,83	1,976	0,1428
18	11,56	2,194	0,1159
19	1,97	1,159	0,3308
21	1,73	1,557	0,2177
$X^2 = \Sigma - 2 \ln p = 19,332$ with df = 10			p = 0,0363

$\bar{D}x_i$ = mean difference in x_i between A - a, B - b, C - c, D - d .

APPENDIX 22

QUANTITATIVE χ^2 TESTS ON THE RELATION BETWEEN A COMPETITION FACTOR AND ABORTION RATES FOR A SUB-SET OF FRUIT SET IN SUMMER, 1972/73

TABLE 22.1 For fruit sub-regions A, B, C, D only

Fruit No.	TOTAL			SLOPE			LINEARITY		
	χ^2	df	p	χ^2	df	p	χ^2	df	p
14	1,088	3	0,7780	0,547	1	0,4603	0,541	2	0,7692
17	14,229	3	0,0026	3,603	1	0,0577	10,626	2	0,0050
18	3,856	3	0,2776	0,369	1	0,5447	3,487	2	0,1751
19	5,350	3	0,1480	0,955	1	0,3288	4,395	2	0,1111
21	2,279	3	0,5168	0,458	1	0,4995	1,821	2	0,4024
Total individual χ^2	26,802	15	0,0306	5,932	5	0,3130	20,870	10	0,0222
Pooled χ^2	7,210	3	0,0655	0,743	1	0,3892	6,467	2	0,0395
Heterogeniety χ^2	19,592	12	0,0753	5,189	4	0,2685	14,403	8	0,0720
$\chi^2 = \Sigma - 2 \ln p$	20,111	10	0,0289	12,085	10	0,2796	20,822	10	0,0225

APPENDIX 22 (contd.)

TABLE 22.2 For fruit sub-regions a, b, c, d only

Fruit No.	TOTAL			SLOPE			LINEARITY		
	χ^2	df	P	χ^2	df	P	χ^2	df	P
14	8,777	3	0,0324	4,648	1	0,0311	4,129	2	0,1270
17	5,915	3	0,1159	0,822	1	0,3649	5,093	2	0,0785
18	16,246	3	0,0010	13,272	1	0,0003	2,974	2	0,2262
19	2,365	3	0,5003	0,042	1	0,8378	2,323	2	0,3134
21	8,345	3	0,0394	6,471	1	0,0110	1,874	2	0,3919
Total individual χ^2	41,648	15	0,0003	25,255	5	0,0001	16,393	10	0,0891
Pooled χ^2	7,772	3	0,0510	4,497	1	0,0340	3,275	2	0,1947
Heterogeniety χ^2	33,876	12	0,0007	20,758	4	0,0004	13,118	8	0,1081
$\chi^2 = \Sigma - 2 \ln p$	32,898	10	0,0003	34,554	10	0,0002	16,383	10	0,0894

APPENDIX 23

QUALITATIVE $\bar{X}^2$ TESTS ON AN ORDERED DISTRIBUTION OF ABORTION ALONG THE FRUIT STEM-APEX AXIS FOR A SUB-SET OF FRUIT SET IN SUMMER, 1972/73

TABLE 23.1 On the qualitative ordering of fruit sub-regions with respect to the weighted p_i of Appendix 16, viz. that A > B > C > D

FRUIT	SUB-REGION								C_1	C_2	$\bar{X}^2$	Probability, p
	A		B		C		D					
No.	w_i	p_i	w_i	p_i	w_i	p_i	w_i	p_i				
14	28	0,1071	76	0,1053	64	0,0781	38	0,0526	0,35	0,45	1,088	p > 0,10
17	50	0,2400	103	0,0777	92	0,0652	54	0,0556	0,39	0,44	14,229	p < 0,005
18	66	0,1065′	103	0,1065′	91	0,0895′	54	0,0896′	0,43	0,44	0,251	p > 0,10
19	34	0,6176	76	0,4868	82	0,4146	42	0,3810	0,40	0,40	5,350	0,025 < p < 0,05
21	52	0,0938′	108	0,0938′	102	0,0927′	49	0,0927′	0,40	0,41	0,001	p > 0,10

(′) - over a p_i value denotes a revised proportion after Bartholomew's method for ordered qualitative χ^2 .

(Fleiss, 1973)

APPENDIX 23 (contd.)

TABLE 23.2 On the qualitative ordering of fruit sub-regions with respect to the weighted p_i of Appendix 16, viz. that a > b > c > d

FRUIT	SUB-REGION								C_1	C_2	$\bar{\chi}^2$	Probability, p
	a		b		c		d					
No.	w_i	p_i	w_i	p_i	w_i	p_i	w_i	p_i				
14	54	0,227′	87	0,2270′	58	0,1099′	33	0,1099′	0,39	0,47	5,114	0,025 < p < 0,05
17	58	0,2069	111	0,1622	82	0,0922′	59	0,0922′	0,38	0,49	5,323	0,025 < p < 0,05
18	81	0,1728	120	0,0667	103	0,0314′	56	0,0314′	0,43	0,44	15,647	p < 0,005
19	44	0,6304′	94	0,6304′	89	0,5730	80	0,5375	0,39	0,49	1,948	p > 0,10
21	64	0,2188	108	0,1311′	98	0,1311′	63	0,0476	0,42	0,45	8,118	0,005 < p < 0,01

(′) – over a p_i value denotes a revised proportion after Bartholomew's method for ordered qualitative χ^2 .

(Fleiss, 1973)

APPENDIX 24

X^2 TESTS ON THE DISTRIBUTION OF ABORTION WITHIN THE FRUIT STEM-APEX AXIS FOR A SUB-SET OF FRUIT SET IN SUMMER, 1972/73

TABLE 24.1 X^2 tests on the differences in proportions of aborted seeds p_i (Appendix 16) for fruit sub-regions A vs BC

Fruit No.	A		BC		X^2 difference	df
	n_1	$\bar{p}_1$	n_2	$\bar{p}_2$		
14	28	0,1071	140	0,0929	0,059	3
17	50	0,2400	195	0,0718	12,853	3
18	66	0,0909	194	0,0876	0,006	3
19	34	0,6176	158	0,4493	3,189	3
21	52	0,1346	210	0,0762	1,681	3
				ΣX^2	17,788‡	15

‡ Probability, $0,20 < p < 0,30$

TABLE 24.2 X^2 tests on the differences in proportions of aborted seeds p_i (Appendix 16) for fruit sub-regions BC vs D

Fruit No.	BC		D		X^2 difference	df
	n_1	$\bar{p}_1$	n_2	$\bar{p}_2$		
14	140	0,0929	38	0,0526	0,609	3
17	195	0,0718	54	0,0556	0,127	3
18	194	0,0876	54	0,1481	1,738	3
19	158	0,4493	42	0,3810	0,623	3
21	210	0,0762	49	0,1224	1,003	3
				ΣX^2	4,099‡	15

‡ Probability, $p > 0,99$

APPENDIX 24 (contd.)

TABLE 24.3 X^2 tests on differences in proportions of aborted seeds p_i (Appendix 16) for fruit sub-regions a vs bc

Fruit No.	a		bc		X^2 difference	df
	n_1	$\bar{p}_1$	n_2	$\bar{p}_2$		
14	54	0,2222	145	0,1586	1,074	3
17	58	0,2069	193	0,1244	2,541	3
18	81	0,1728	223	0,0449	14,010	3
19	44	0,5909	183	0,6120	0,065	3
21	64	0,2188	206	0,0113	18,331	3
				ΣX^2	36,021‡	15

‡ Probability, $0,001 < 0,01$

TABLE 24.4 X^2 tests on the differences in proportions of aborted seeds p_i (Appendix 16) for fruit sub-regions bc vs d

Fruit No.	bc		d		X^2 difference	df
	n_1	$\bar{p}_1$	n_2	$\bar{p}_2$		
14	145	0,1586	33	0,2121	0,519	3
17	193	0,1244	59	0,1186	0,013	3
18	223	0,0449	56	0,0536	0,049	3
19	183	0,6120	80	0,5375	1,277	3
21	206	0,0113	63	0,0476	0,554	3
				ΣX^2	2,412‡	15

‡ Probability, $p > 0,99$

APPENDIX 25

REGRESSION AND CORRELATION OF A PAPAYA LEAF'S AREA ON THE SUMMED LENGTH OF ITS THREE LONGEST LEAF VEINS, MARCH 1971

TABLE 25.1

X (cm)	Y (cm^2)	X (cm)	Y (cm^2)	X (cm)	Y (cm^2)
141,6	3 826	131,5	3 081	133,1	3 232
124,5	2 617	128,4	3 142	124,5	2 652
137,2	3 474	103,9	2 555	116,2	2 530
112,4	2 316	132,7	3 240	126,8	2 696
149,5	4 055	117,6	2 632	134,0	3 162
131,0	3 075	130,3	3 446	122,8	3 031
140,6	3 226	147,2	4 046	132,8	2 847
154,5	5 188	139,4	3 522	128,3	3 488
140,3	3 526	122,6	2 677	119,2	2 567
143,0	3 866	123,5	2 782	97,8	1 626
		130,7	3 268		

No. of observations = 31

Mean X = 129,6 cm

Mean Y = 3 141,6 cm^2

Regression co-efficients:

a_0 = - 3 048,8

a_1 = + 47,76

Regression line is:

$y = -3\,048{,}8 + 47{,}76\,x$

Co-efficient of determination:

R^2 = 82,70%

Correlation co-efficient:

Y_{xy} = + 0,9094 ($p < 0{,}001$)

Standard error of estimate of y on x:

$S_{y.x}$ = 277,9

Standard error of a_0:

S_0 = 528,1

Standard error of a_1:

S_1 = 4,06

APPENDIX 26

MULTIPLE LINEAR REGRESSION EQUATION FOR PAPAYA FRUIT SET AT WEEKLY INTERVALS OVER MARCH 1971 AND PICKED AFTER THREE MONTHS GROWTH, OVER JUNE 1971

NOTATION

X_1 - Seed mass after 3 months : g .

X_2 - An index of the leaf area available to that fruit at the time it was set: the sum of the lengths of the three main leaf veins of each of all the expanded leaves on the main stem, divided by the number of fruit on that stem at fruit set : cm/fruit (see text, 3.2.1).

X_3 - Sum of the degree-days (above 12°C) for the three days preceding anthesis.

Y - Fruit mass (excluding seeds) after 3 months : g .

No. of multiple observations = 29 .

X_1	X_2	X_3	Y
43,71	158	25	340,32
43,03	190	25	436,00
51,45	135	25	362,80
48,10	292	25	449,18
46,40	157	25	391,43
41,68	181	38	367,76
49,03	138	38	370,62
29,63	179	38	307,19
34,99	243	38	332,37
58,80	189	38	497,77
29,85	143	38	353,50
36,57	187	38	337,12
32,22	223	28	332,09
35,64	144	28	319,07
26,15	158	28	240,45
38,05	138	28	325,76

APPENDIX 26 (contd.)

X_1	X_2	X_3	Y
37,59	112	28	332,69
27,38	151	28	255,08
27,41	190	28	223,93
25,46	242	28	218,60
39,61	189	28	342,09
25,07	136	28	229,30
24,47	203	28	235,62
23,73	310	28	270,32
27,33	181	15	240,38
24,40	197	15	235,98
23,41	189	15	226,74
16,88	170	15	179,71
14,26	187	15	145,59
Means: 33,872	183,2	27,7	306,88

Multiple correlation co-efficient: R = 94,41%***

Partial regression co-efficients:	t-values for testing regression co-efficients (df = 25)
a_1 = 6,75	11,728 ***
a_2 = 0,250	2,117 *
a_3 = 1,47	1,793 $

Constant term in regression equation: a_0 = -9,685

Total correlation co-efficients:

X_1	1,0000			
X_2	-0,1378	1,0000		
X_3	0,4672*	-0,0394	1,0000	
Y	0,9257***	0,0140	0,5405**	1,0000
	X_1	X_2	X_3	Y

APPENDIX 26 (contd.)

Selected partial correlation coefficients:

$r_{1y,23}$ 0,9199***

$r_{2y,13}$ 0,3898*

‡ $p \leq 0,10$
* $p \leq 0,05$
** $p \leq 0,01$
*** $p \leq 0,001$

APPENDIX 26 (contd.)

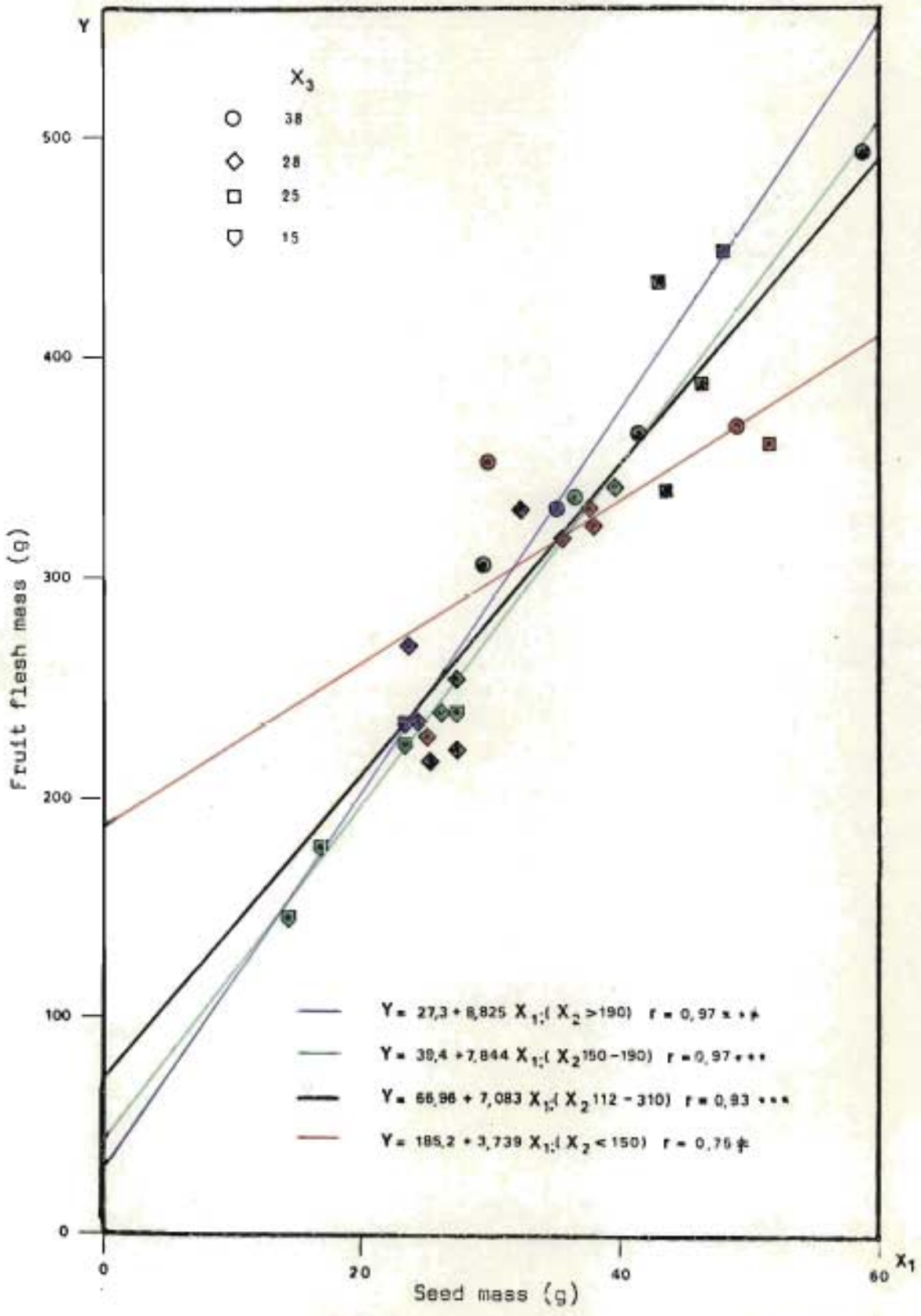

FIGURE A Regression of Y on X_1 after three months.

APPENDIX 27

MULTIPLE LINEAR REGRESSION EQUATION FOR PAPAYA FRUIT SET AT WEEKLY INTERVALS OVER MARCH 1971 AND PICKED AFTER SEVEN MONTHS GROWTH OVER OCTOBER 1971

NOTATION

X_1 - Seed mass after seven months : g .

$X_2 - \left[X_1\right]^2 \times 10^{-1}$: g^2 .

X_3 - Sum of degree-days (above 12°C) for the 40 days preceding anthesis.

X_4 - An index of the leaf area available to that fruit at the time it was set: the sum of the lengths of the three main leaf veins of each of all the expanded leaves on the main stem, divided by the number of fruit on that stem at fruit set : cm/fruit (see text, 3.2.1).

Y - Fruit mass (excluding seeds) after seven months : g .

No. of multiple observations = 32 .

X_1	X_2	X_3	X_4	Y
86,58	750	337	204	576,04
145,33	2 112	337	168	952,08
103,51	1 071	337	370	922,34
123,00	1 513	337	144	1 000,93
127,84	1 634	337	138	962,70
123,38	1 522	337	147	822,26
79,35	630	337	242	566,66
106,74	1 139	337	190	803,66
98,66	973	337	136	775,89
156,17	2 439	337	157	1 015,44
150,78	2 273	349	144	1 017,07
78,72	620	349	151	805,25
41,79	175	349	243	355,19
65,41	428	349	242	497,77
80,46	647	349	292	785,15
83,83	703	349	189	902,22

APPENDIX 27 (contd.)

X_1	X_2	X_3	X_4	Y
96,97	940	349	143	869,73
85,51	731	349	136	685,37
107,25	1 150	349	203	935,34
99,34	987	348	370	1 023,82
84,46	713	348	144	951,94
96,69	935	348	181	733,52
97,13	943	348	197	917,61
76,51	585	348	112	725,37
57,05	325	348	156	390,09
82,54	681	348	190	718,46
97,57	952	348	136	917,72
78,05	609	348	187	673,61
70,92	503	348	179	529,99
69,54	484	346	158	600,58
72,36	524	346	292	848,61
61,04	373	346	203	654,88
Means: 93,265	939,5	344,7	192,0	779,29

Multiple correlation co-efficient: R = 88,67% ***

Partial regression co-efficients:	t-values for testing regression co-efficients (df = 27)
a_1 = 19,39	5,171 ***
a_2 = -0,620	3,446 **
a_3 = 10,73	2,928 **
a_4 = 0,503	1,689 *

Constant term in regression equation: a_0 = - 4241,91

APPENDIX 27 (contd.)

Total correlation coefficients:

X_1	1,0000				
X_2	0,9862***	1,0000			
X_3	-0,5193**	-0,5059**	1,0000		
X_4	-0,2205	-0,2299	0,0118	1,0000	
Y	0,7769***	0,7149***	-0,2083	-0,0142	1,0000
	X_1	X_2	X_3	X_4	Y

Selected partial correlation coefficients:

$r_{1y,34}$ 0,8235***

$r_{4y,13}$ 0,3249‡

‡ $p \leq 0,10$
* $p \leq 0,05$
** $p \leq 0,01$
*** $p \leq 0,001$

APPENDIX 26

AN ALTERNATE LINEAR REGRESSION EQUATION FOR PAPAYA FRUIT SET AT WEEKLY INTERVALS OVER MARCH 1971 AND PICKED AFTER SEVEN MONTHS GROWTH, OVER OCTOBER 1971

NOTATION

X_1 - As in Appendix 27.

X_2 - As in Appendix 27.

X_3 - Sum of degree-days (above 12°C) for the 15-week period after anthesis (over March-June).

X_4 - As in Appendix 27.

Y - As in Appendix 27.

No. of multiple observations = 32.

		Alternate		
X_1	X_2	X_3	X_4	Y
86,58	750	584	204	576,04
etc.	etc.	584	etc.	etc.
		584		
		584		
		584		
		584		
		584		
		584		
		584		
		584		
150,78	2 273	529	144	1 017,07
etc.	etc.	529	etc.	etc.
		529		
		529		
		529		
		529		
		529		
		529		
		529		
99,34	987	438	370	1 023,62
etc.	etc.	438	etc.	etc.
		438		
		438		
		438		
		438		
		438		
		438		
		438		
		438		

APPENDIX 28 (contd.)

	X_1	X_2	Alternate X_3	X_4	Y
	69,54 etc.	484 etc.	413 413 413	158 etc.	600,58 etc.
Means:	93,265	939,5	506,9	192,0	779,29

Multiple correlation co-efficient: R = 88,13%***

Partial regression co-efficients:

	t-values for testing regression co-efficients (df = 27)
a_1 = 18,43	4,850 ***
a_2 = - 0,577	3,132 **
a_3 = - 0,797	2,660 *
a_4 = 0,487	1,792 ‡

Constant term in regression equation: a_0 = - 87,14

Total correlation co-efficients:

	X_1	X_2	X_3	X_4	Y
X_1	1,0000				
X_2	0,9862***	1,0000			
X_3	0,5286**	0,5275**	1,0000		
X_4	- 0,2205	- 0,2299	- 0,0306	1,0000	
Y	0,7769***	0,7149***	0,2078	- 0,0142	1,0000

Selected partial correlation coefficients:

$r_{1y,34}$ 0,8258***

$r_{4y,13}$ 0,3208‡

$r_{14,3}$ -0,2408 NS

‡ $p \leq 0,10$

* $p \leq 0,05$

** $p \leq 0,01$

*** $p \leq 0,001$

APPENDIX 28 (contd.)

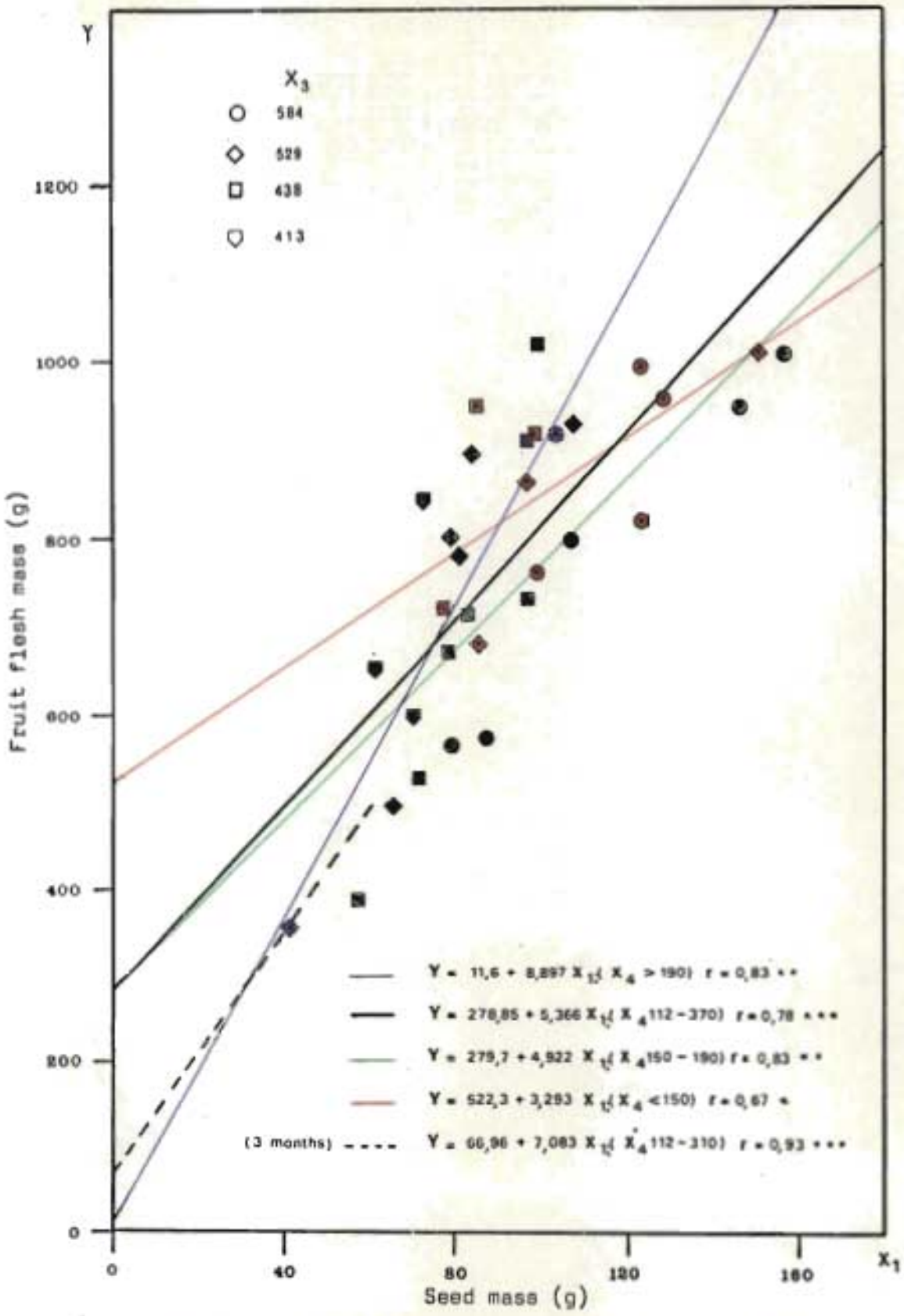

FIGURE A Regression of Y on X_1 after seven months.

APPENDIX 29

SEED MASS-FRUIT MASS CORRELATIONS FOR INTRA-FRUIT SUB-REGIONS OF PAPAYA FRUIT SET IN AUTUMN 1973 WITHOUT HAND-POLLINATION

G R A M S									
Aa		Bb		Cc		Dd		Aa + ... + Dd	
Seed	Fruit	Seed	Fruit	Seed	Fruit	Seed	Fruit	Seed	Fruit
7,10	102,95	13,05	169,70	10,71	93,05	5,83	70,78	36,69	376,48
9,06	138,63	9,76	130,15	3,61	75,11	0,56	50,10	23,00	393,99
0,98	90,11	2,79	122,55	2,80	103,54	0,94	62,28	7,50	378,48
2,00	135,68	6,34	150,28	5,60	109,64	2,73	67,61	16,66	463,20
5,40	92,34	7,24	86,21	5,21	70,33	1,48	35,61	19,33	284,49
2,56	70,43	2,45	72,94	1,61	61,45	0,20	32,28	6,83	237,09
5,58	132,63	8,34	126,70	3,76	91,45	0,70	49,33	18,38	400,10
10,54	103,13	17,43	124,96	11,36	93,20	3,45	60,85	42,78	382,14
5,74	107,49	17,28	136,79	17,68	128,96	7,86	84,31	48,55	457,45
8,19	126,75	9,55	131,16	3,29	97,84	0,31	67,31	21,35	423,06
1,65	72,05	4,10	91,05	0,66	63,63	0,05	28,03	6,46	254,75
8,15	158,80	11,94	186,80	6,44	149,10	2,41	81,38	28,94	576,08
10,28	117,18	18,01	151,70	13,28	114,71	6,00	72,60	47,56	456,39
3,26	68,39	3,05	51,59	1,18	62,94	0,80	49,09	8,29	232,00
7,95	140,18	13,76	165,24	7,88	122,49	1,24	78,23	30,83	506,13
2,00	91,78	2,48	105,28	1,13	74,33	0,40	41,03	6,00	313,40
2,61	80,71	4,16	99,56	2,75	72,49	1,35	54,21	11,08	306,98
Mean Mass: 5,49	107,60	8,93	120,21	5,83	93,19	2,14	57,95	22,36	378,95
Correlation: +0,591*		+0,617**		+0,635**		+0,658**		+0,623**	

* $p \leq 0,05$

** $p \leq 0,01$

Number of fruit = 17.

NOTE: Seed and fruit flesh masses estimated fr
4/5th longitudinal portions.
See text, 3.2.2.

Overall ratio of fruit flesh mass to seed mass:

Aa subregion: 19,60
Bb subregion: 13,46
Cc subregion: 15,98
Dd subregion: 27,08
Aa + ... + Dd subregions: 16,95

APPENDIX 29 (contd.)

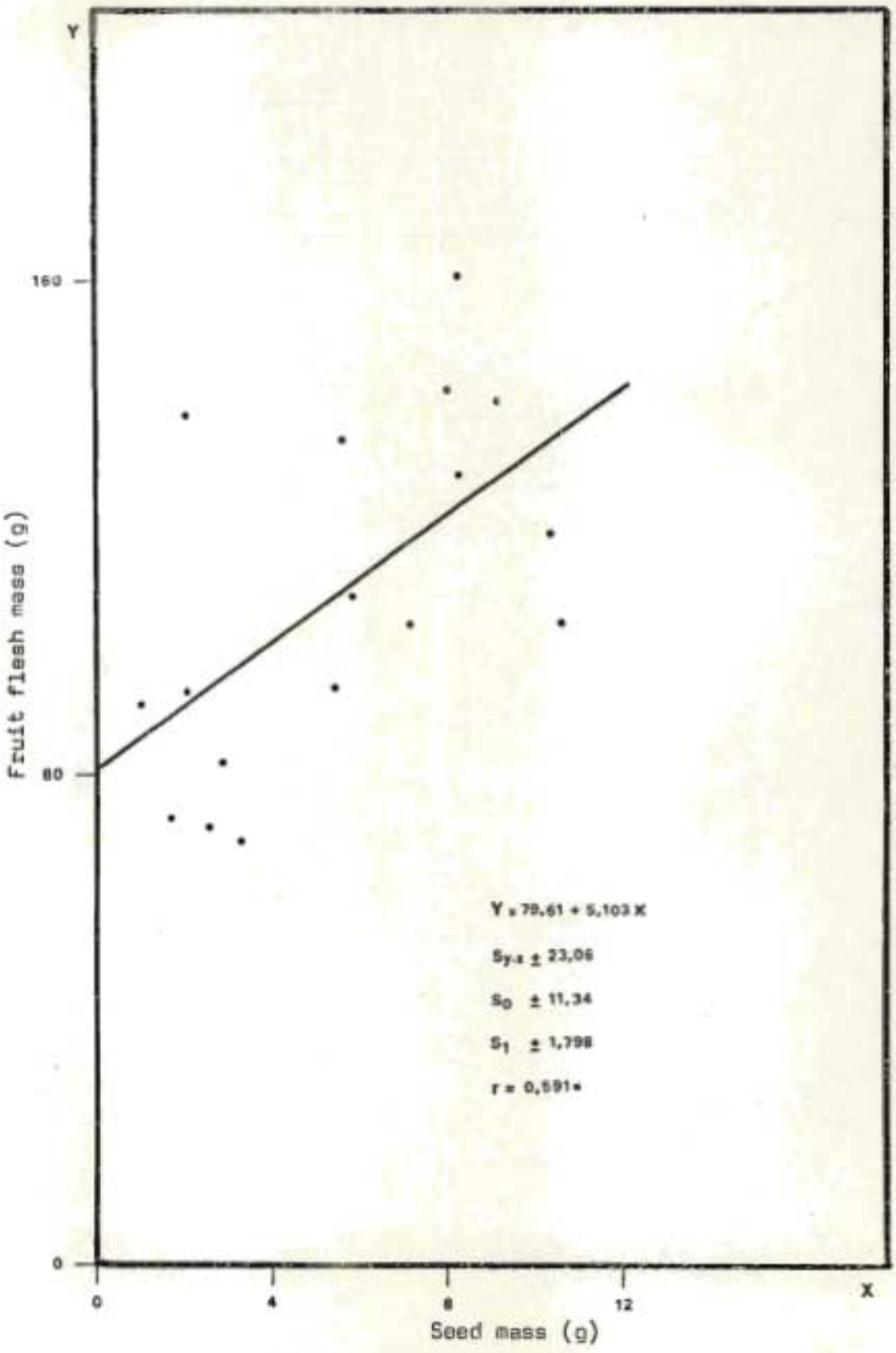

FIGURE A Regression of Y on X for Aa sub-regions.

APPENDIX 29 (contd.)

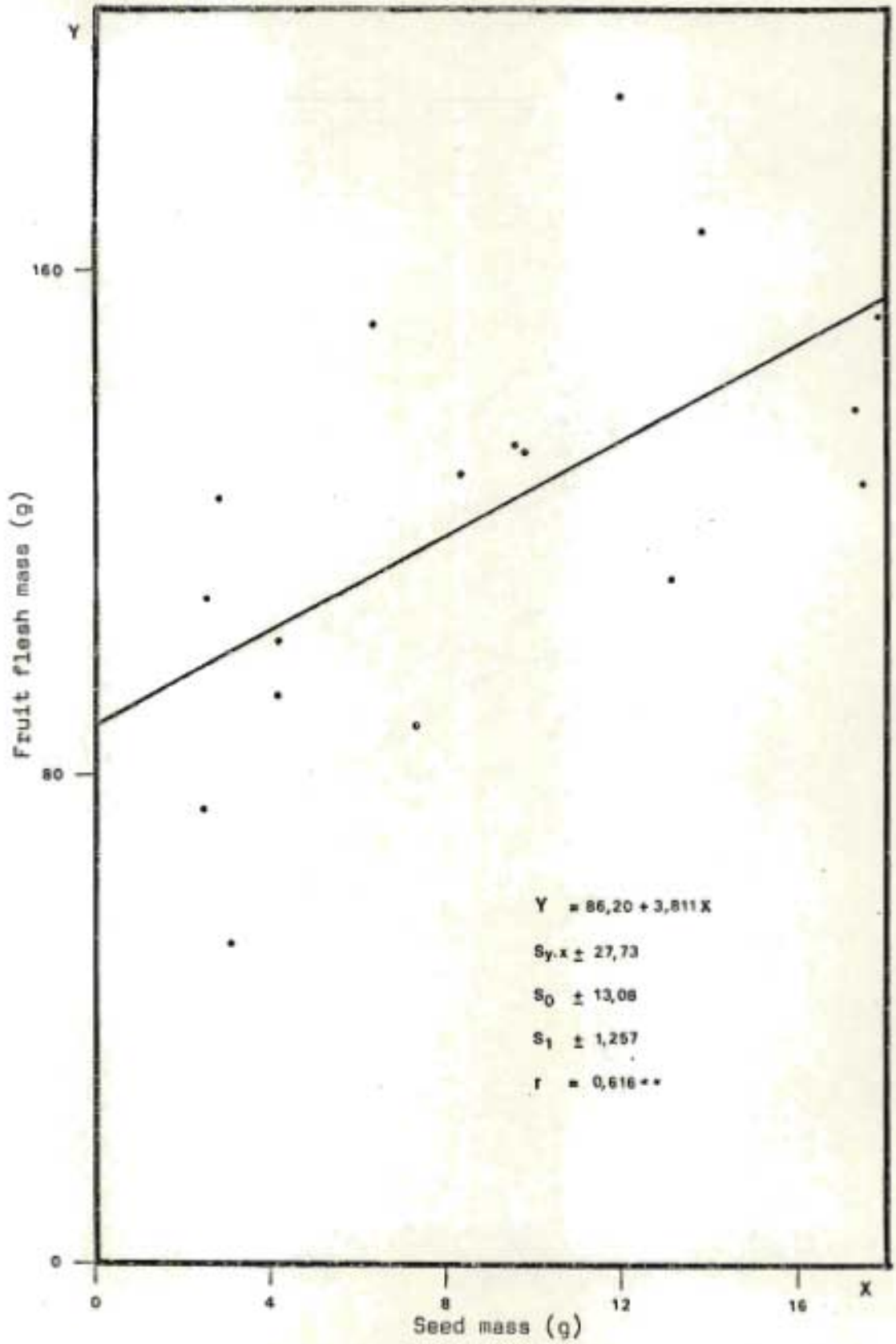

FIGURE 8 Regression of Y on X for Bb sub-regions.

APPENDIX 29 (contd.)

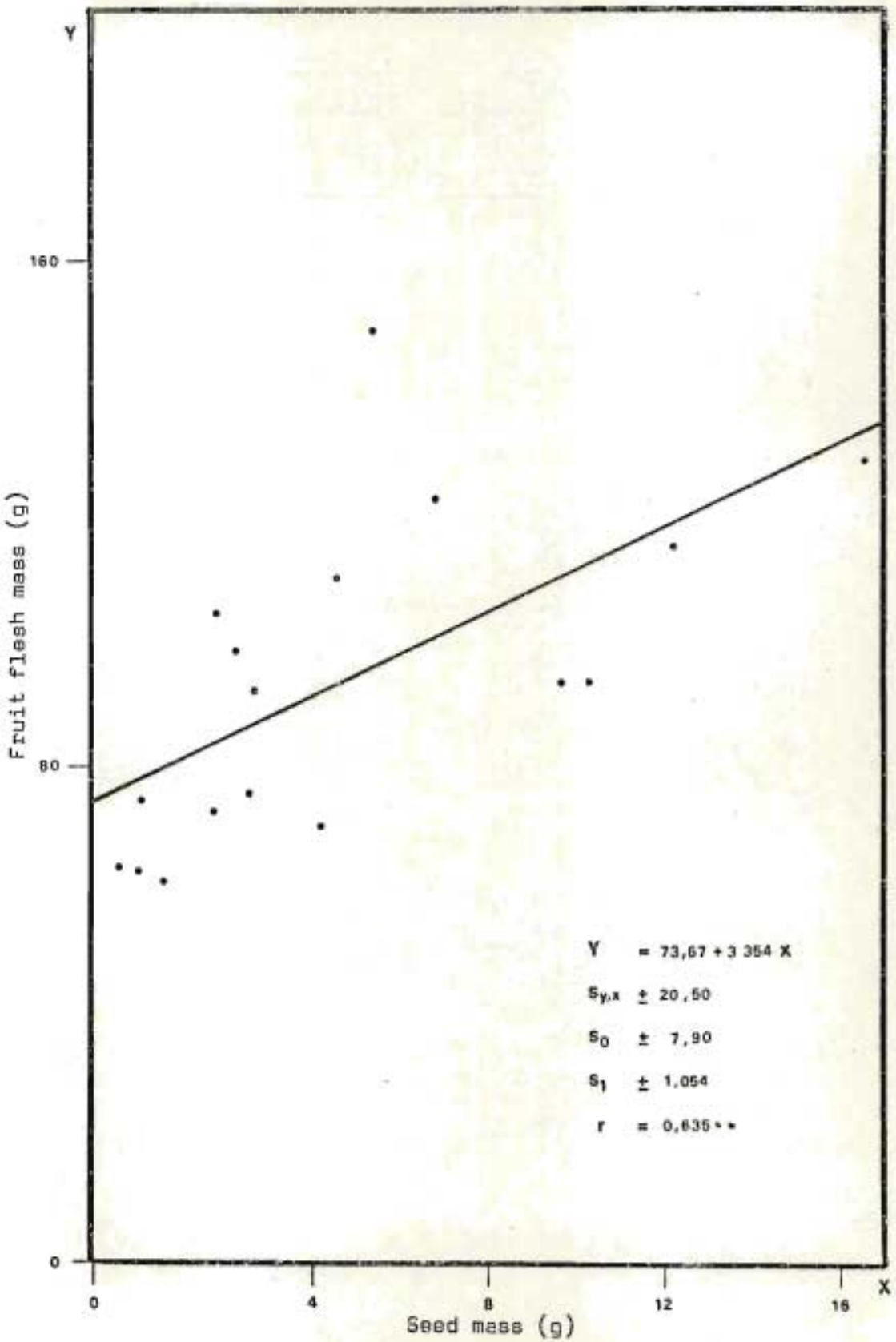

FIGURE C Regression of Y on X for Cc sub-regions.

APPENDIX 29 (contd.)

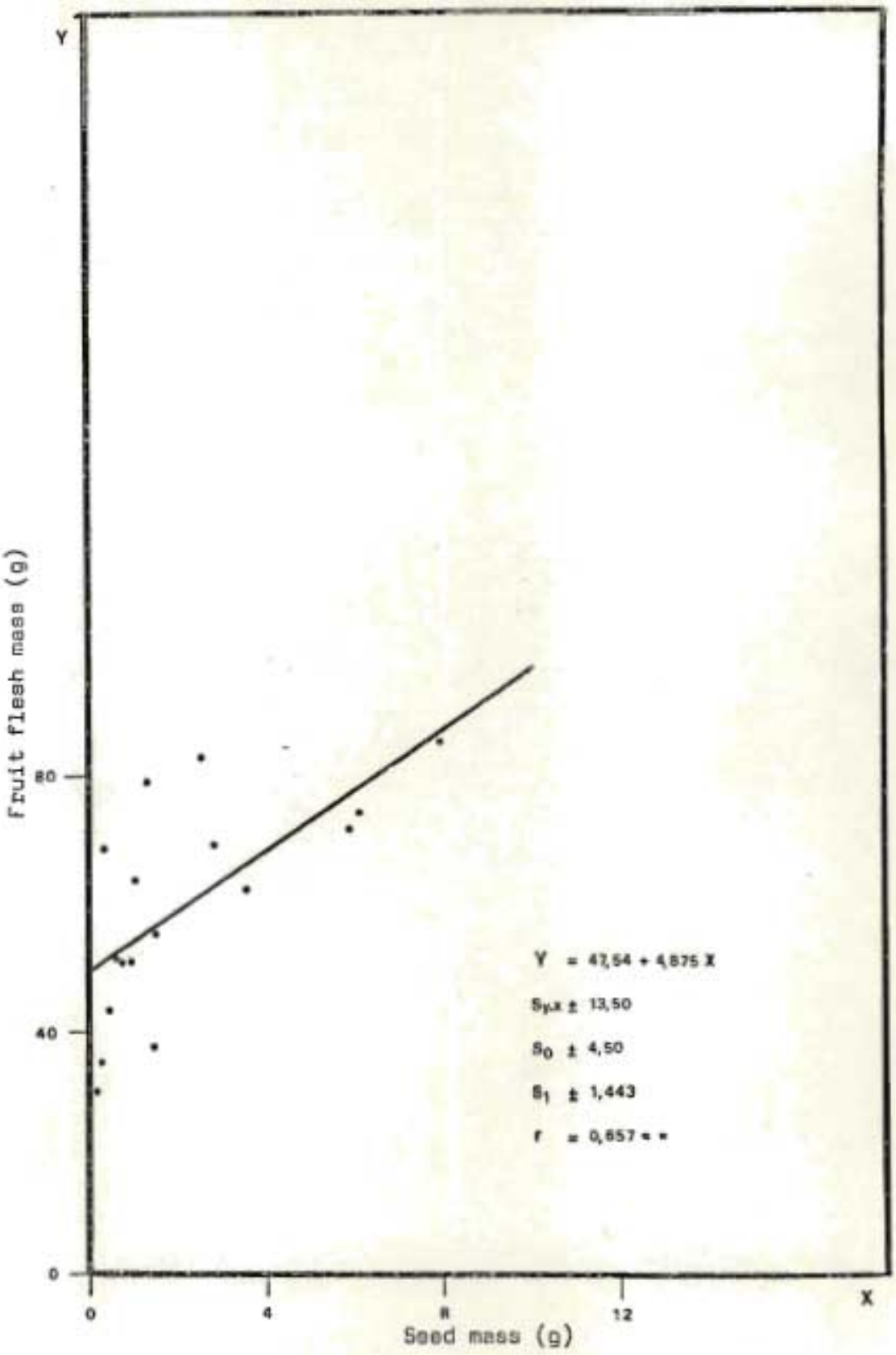

FIGURE D Regression of Y on X for Dd sub-regions.

APPENDIX 29 (contd.)

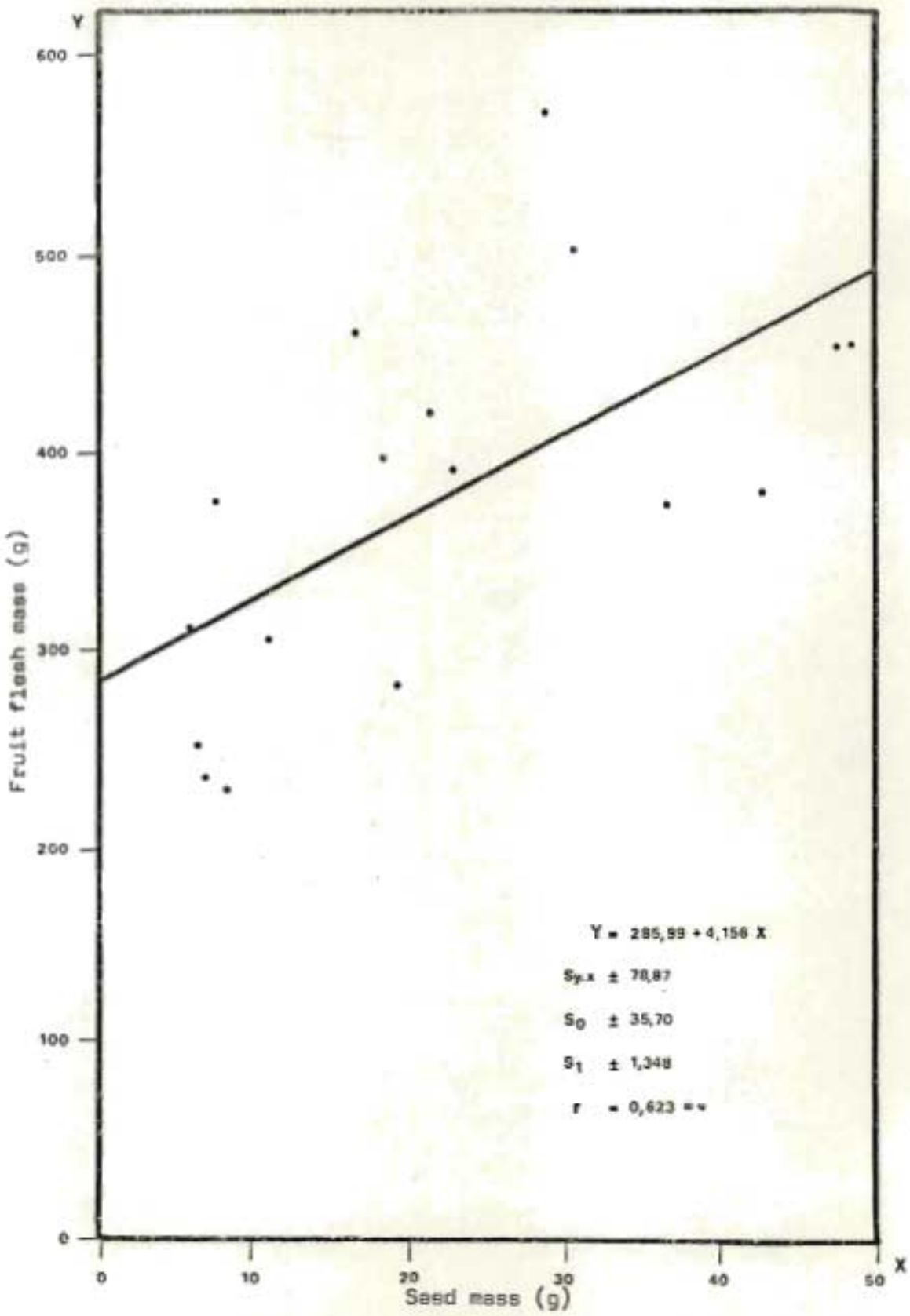

FIGURE E Regression of Y on X for Aa + ... + Dd sub-regions.

APPENDIX 30

SEED MASS-FRUIT MASS CORRELATIONS FOR INTRA-FRUIT SUB-REGIONS OF PAPAYA FRUIT SET IN SUMMER 1972/73 WITHOUT HAND-POLLINATION

G R A M S									
Aa		Bb		Cc		Dd		Aa + ... + Dd	
Seed	Fruit	Seed	Fruit	Seed	Fruit	Seed	Fruit	Seed	Fruit
8,63	177,48	38,08	339,90	37,20	365,63	17,95	253,08	101,85	1 136,08
13,18	217,13	46,95	314,80	49,35	354,28	29,30	266,70	138,78	1 152,90
28,08	295,33	49,33	303,15	55,88	397,25	32,20	266,50	165,48	1 262,23
27,13	239,93	37,20	214,98	34,63	205,23	20,15	185,30	119,30	845,43
16,98	274,43	42,33	302,05	25,80	254,98	12,23	174,75	97,33	1 006,20
28,08	252,15	40,55	295,70	26,83	264,40	10,25	171,80	105,70	984,05
14,98	195,25	33,63	231,70	19,70	159,98	11,43	98,20	79,73	685,13
18,78	288,18	60,73	390,50	53,70	312,28	38,60	260,45	171,80	1 251,40
29,45	335,80	55,78	382,70	47,35	300,83	31,83	196,85	164,40	1 216,18
22,80	257,18	32,38	223,90	23,45	226,10	9,00	146,50	87,63	853,68
27,98	234,53	47,35	239,95	41,08	230,00	21,48	178,90	138,63	883,38
16,40	232,23	28,43	212,08	14,70	167,18	6,55	134,95	66,08	746,43
13,60	196,53	48,80	229,45	35,40	216,55	14,45	146,93	112,25	789,45
21,30	241,65	38,00	286,50	38,13	264,00	24,15	211,58	121,58	1 003,73
27,68	203,13	66,73	273,95	53,63	263,43	27,25	178,48	175,48	918,98
29,78	227,23	57,20	242,38	47,08	229,30	21,40	159,05	155,45	857,95
32,05	277,93	47,45	293,00	33,90	274,50	13,70	179,75	127,10	1 025,18
36,08	225,45	62,85	237,95	57,00	215,38	27,45	157,28	183,38	836,05
15,70	190,53	40,65	229,08	32,58	191,88	18,35	161,55	107,28	773,03
24,15	262,55	34,08	230,65	24,18	194,50	11,73	148,98	94,13	836,88
24,98	186,55	39,93	204,53	30,78	171,75	20,35	173,18	116,03	736,00
Mean Mass: 22,76	238,62	45,16	270,43	37,30	250,45	19,99	183,37	125,21	942,87
Correlations: + 0,437*		+ 0,422†		+ 0,602**		+ 0,705***		+ 0,507*	

† $p \leq 0,10$
* $p \leq 0,05$
** $p \leq 0,01$
*** $p \leq 0,001$

Number of fruit = 21.

NOTE: Seed and fruit flesh masses estimated from 2/5th longitudinal portions. See text, 3.3.2.

Overall ratio of fruit flesh mass to seed mass:

Aa subregions:	10,48
Bb subregions:	5,99
Cc subregions:	6,71
Dd subregions:	9,17
Aa + ... + Dd subregions:	7,53

APPENDIX 31

CONCENTRATION OF SEED MASS AND SIZE OF UNFERTILIZED OVULES IN INTRA-FRUIT SUB-REGIONS OF RIPE PAPAYA FRUIT SET IN AUTUMN 1973

FRUIT SUB-REGION		FRUIT / 1/5th PORTION NUMBER																								MEAN	RANK	
		8		9			10				11				12				13		14				15					
		1	2	1	2	3	1	2	3	4	1	2	3	4	1	2	3	4	1	4	1	2	3	4	1	2	3	4		x	y
A	x	222	434	251	153	203	505	422	388	353	320	494	461	507	148	88	82	50	186	99	11	57	47	40	137	107	75	03	219,37	1	
	y	70	74	65	77	62	108	86	73	49	63	80	72	81	43	60	65	36	64	61	61	59	70	63	85	93	89	90	70,33		2
a	x	79	259	99	124	39	254	227	332	157	150	288	358	275	10	23	13	2	34	82	4	3	8	20	49	92	26	42	112,93	4	
	y	57	59	63	81	68	78	61	70	58	62	60	68	58	35	45	40	44	62	76	64	57	64	53	72	88	80	66	63,37		4
B	x	211	342	124	129	204	426	380	374	446	134	308	223	269	92	66	91	74	90	36	32	37	64	45	205	169	151	189	181,89	2	
	y	63	64	76	71	66	91	67	66	58	73	82	73	90	64	47	77	62	73	71	71	65	74	73	77	98	87	75	72,41		1
b	x	87	191	77	42	32	201	121	244	120	82	146	118	92	32	48	52	23	49	31	10	13	5	8	117	116	49	55	80,07	6	
	y	42	41	59	59	65	51	50	43	46	55	59	57	64	45	52	49	57	63	65	65	66	61	59	67	85	77	66	58,11		5
C	x	140	185	95	62	62	312	326	365	312	60	101	98	112	55	115	109	67	36	6	27	25	1	28	150	189	83	137	120,67	3	
	y	69	68	72	64	63	68	75	64	63	44	67	61	68	71	59	57	56	56	54	74	66	70	68	71	88	75	86	66,56		3
c	x	40	52	38	30	91	143	89	136	92	31	30	78	11	53	13	34	32	55	0	23	5	6	3	93	128	44	84	53,11	7	
	y	36	35	48	56	55	47	49	37	40	49	37	43	44	36	49	44	44	61	51	65	53	62	64	71	76	65	70	51,37		7
D	x	29	87	130	76	9	189	213	210	212	0	0	35	59	62	41	32	101	29	23	0	0	64	28	99	164	184	154	82,59	5	
	y	52	51	71	62	58	60	59	40	41	36	47	51	51	59	46	57	49	57	59	48	49	72	57	77	77	74	77	56,93		6
d	x	0	0	139	18	27	55	54	46	68	0	0	0	0	12	14	5	5	9	4	19	21	58	24	54	29	82	24	28,41	8	
	y	30	28	52	46	50	40	38	31	36	28	30	37	35	50	40	49	52	48	44	52	66	68	52	62	62	73	59	46,59		8

APPENDIX 32

AVERAGE CORRELATION BETWEEN THE CONCENTRATION OF SEED MASS AND THE SIZE OF UNFERTILIZED OVULES FROM INTRA-FRUIT SUB-REGIONS OF RIPE PAPAYA FRUIT SET IN AUTUMN 1973

NOTATION

$x = \left[\text{Summed mass of (F + P + S) seeds} \times 10^4\right] \div \left[\text{Total no. of (F, P, S, U) ovules, seeds}\right]$.

y = Index of volume of U unfertilized ovules: directly proportional to (length x diameter) of ovules.

For values of x and y correlated here, see the x and y down the columns of the body of the table in Appendix 31.

N = 8 , the number of intra-fruit sub-regions over which individual r_{xy} calculated.

r_{xy} = Correlation co-efficient between paired x and y of intra-fruit sub-regions of a given 1/5th-fruit portion (see columns of Appendix 31).

Z = Transformed value of r_{xy} .

Fruit/(1/5th) portion no.	r_{xy}	Z	Fruit and (1/5th) portion number	r_{xy}	Z
8.1	0,8300	1,188	12.1	0,1772	0,179
8.2	0,8513	1,261	12.2	0,8357	1,206
9.1	0,3167	0,328	12.3	0,7182	0,904
9.2	0,9264	1,632	12.4	0,2198	0,224
9.3	0,2889	0,297	13.1	0,5682	0,645
10.1	0,9620	1,972	13.2	0,6573	0,788
10.2	0,9499	1,831	14.1	0,6518	0,778
10.3	0,9440	1,774	14.2	0,4611	0,509
10.4	0,6621	0,796	14.3	0,7499	0,973
11.1	0,7274	0,923	14.4	0,4168	0,444
11.2	0,8359	1,207	15.1	0,4987	0,548
11.3	0,8191	1,154	15.2	0,5859	0,671
11.4	0,7573	0,990	15.3	0,1922	0,195
			15.4	0,2973	0,307

APPENDIX 32 (contd.)

Test for homogeneity of correlation co-efficients, r_{xy}'s :

$$\underset{(df = 26)}{\chi^2} = \Sigma(N - 3)Z^2 - \frac{\left[\Sigma(N - 3)Z\right]^2}{\Sigma(N - 3)} = 138,927 - \frac{(118,62)^2}{135}$$

$$= 1,333 \quad NS.$$

Thus these r_{xy}'s are homogeneous enough for computing a common, average co-efficient.

$$\text{Mean } Z = \frac{\Sigma(N - 3)Z}{\Sigma N - 3} = \frac{118,62}{135} = +0,879 .$$

$$\text{Detransformed, mean } r_{xy} = +0,7527 .$$

Using D.F. = $\underline{6}$, this is significant at p(0,05) level.

APPENDIX 33

CORRELATIONS AND SELECTED PARTIAL CORRELATIONS OF FACTORS ASSUMED RELATED TO SEED GROWTH, SEED ABORTION AND FRUIT GROWTH OF PAPAYA FRUIT SET WITH HAND-POLLINATION IN AUTUMN, 1970

NOTATION

x_1 = Early seed development intensity of the whole fruit, given by $(\Sigma F, P, S)/(\Sigma F, P, S, U)$: transformed to angular degrees.

x_2 = Seed abortion rate for whole fruit, given by $(\Sigma P, S)/(\Sigma F, P, S)$: transformed to angular degrees.

x_3 = ΣF seeds of whole fruit.

x_4 = $\Sigma F, P, S$ seeds of whole fruit.

x_5 = Mass of F seeds only : g .

x_6 = Mass of all seeds : g .

y = Mass of whole fruit (excluding seeds) : g .

x_7 = Number of fruit on stem, early May (autumn).

x_8 = (Number of leaves)/(number of fruit) of stem, early May (autumn).

(i) Number of multiple observations for $\{x_1, \ldots x_6, y\}$ = 14 , i.e. excludi x_7 and x_8 .
Degrees of freedom : total correlation = 12 ; partial correlation = 11

(ii) Number of multiple observations for $\{x_1, \ldots y, x_7, x_8\}$ = 11 .
Degrees of freedom : total correlation = 9 ; partial correlation = 8

APPENDIX 33 (contd.)

Fruit No.	x_1	x_2	x_3	x_4	x_5	x_6	y	x_7	x_8
2	65,21	34,33	1 001	1 469	69,43	71,51	744	24	0,88
13	68,14	43,80	761	1 462	64,57	67,39	836	23	1,00
14	57,55	46,89	532	1 140	45,10	47,86	791	29	0,76
16	65,34	47,93	665	1 481	47,48	49,86	819	19	0,95
26	54,33	38,47	415	677	36,52	39,84	516	43	0,65
27	56,91	43,28	611	1 153	49,70	51,76	843	29	0,69
28	56,21	60,13	234	944	19,49	21,79	690	25	0,76
37	67,97	42,65	608	1 124	47,07	48,82	705	–	–
40	42,95	35,18	364	545	28,22	29,10	398	20	0,93
54	63,90	38,23	669	1 390	55,41	59,15	837	–	–
55	64,11	43,45	728	1 382	44,26	46,06	601	34	0,79
58	56,90	45,74	514	1 058	32,63	34,60	453	40	0,62
65	57,66	58,63	300	1 108	20,47	23,08	557	28	0,70
94	56,23	43,45	599	1 136	53,80	58,75	703	–	–
Mean (14)	59,53	44,44	571,5	1 147,8	43,87	46,40	678,1	–	–
Mean (11)	58,66	45,26	556,8	1 129,0	41,62	43,90	658,9	28,5	0,794

Total correlation co-efficients:

x_1	1,000								
x_2	0,022	1,000							
x_3	0,676**	-0,584*	1,000						
x_4	0,868***	0,019	0,764**	1,000					
x_5	0,623*	-0,605*	0,931***	0,677**	1,000				
x_6	0,619*	-0,590*	0,915***	0,686**	0,998***	1,000			
y	0,560*	0,038	0,520	0,727**	0,661**	0,670**	1,000		
x_7	-0,105	-0,069	-0,162	-0,268	-0,208	-0,193	-0,425	1,000	
x_8	0,304	-0,272	0,441	0,381	0,491	0,479	0,360	-0,821**	1,00
	x_1	x_2	x_3	x_4	x_5	x_6	y	x_7	x_8

APPENDIX 33 (contd.)

Selected first order partial correlations:

$r_{24,7} = -0,001$
$r_{24,8} = 0,138$
$r_{26,4} = -0,302$

$r_{21,7} = 0,015$
$r_{21,8} = 0,114$
$r_{28,1} = -0,293$

$r_{3y,2} = 0,668*$
$r_{3y,7} = 0,505$
$r_{3y,8} = 0,431$

$r_{4y,2} = 0,727**$
$r_{4y,7} = 0,697*$
$r_{4y,8} = 0,684*$

$r_{1y,2} = 0,656*$
$r_{1y,7} = 0,679*$
$r_{1y,8} = 0,615$

$r_{5y,2} = 0,860***$
$r_{5y,7} = 0,647*$
$r_{5y,8} = 0,596$

$r_{6y,2} = 0,858***$
$r_{6y,7} = 0,662*$
$r_{6y,8} = 0,608$

$* = p \leq 0,05$
$** = p \leq 0,01$
$*** = p \leq 0,001$

APPENDIX 34

SEED-COUNTS AND -MASS CORRELATIONS WITH FRUIT-MASS IN HAND-POLLINATED AUTUMN SET, 1970

NOTATION

x_1 = Σf seeds.
x_2 = Σf and P seeds.
x_3 = Σf, P and cWs seeds (i.e. excluding b seeds).
x_4 = Σf, P and S seeds (i.e. including b seeds).
x_5 = Σf, P, S and U seeds and ovules.
x_6 = Mass of all seeds (g).
y = Mass of fruit flesh (excluding seeds) (g).

No. of multiple observations = 14 .

x_1	x_2	x_3	x_4	x_5	x_6	y
1 001	1 002	1 021	1 469	1 808	71,51	744
761	761	772	1 462	1 703	67,39	836
532	543	671	1 140	1 767	47,86	791
665	665	740	1 481	1 826	49,86	819
415	442	480	677	1 529	39,84	516
611	611	698	1 153	1 690	51,76	843
234	237	316	944	1 427	21,79	690
608	608	642	1 124	1 316	48,82	705
364	366	376	545	1 448	29,10	398
669	670	703	1 390	1 733	59,15	837
728	728	739	1 382	1 720	46,06	601
514	516	544	1 058	1 616	34,60	453
300	306	342	1 108	1 595	23,08	557
599	651	693	1 136	1 716	58,75	703
Mean: 571,5	579,0	624,1	1 147,8	1 635,3	46,40	678,1
Correlation with y: 0,520	0,516	0,611*	0,727**	0,506	0,670**	-

* $p \leq 0,05$

** $p \leq 0,01$

APPENDIX 34 (contd.)

Overall ratio of seed type to Σ F, P, S and U:

F : 0,349
P : 0,005 [cTL + cWL]

S : 0,348 { cWs : 0,028 ; b : 0,320 }

U : 0,298

Overall ratio of fruit flesh mass to:

- Seed mass : 14,61

and 15,61 when seed mass added to fruit flesh mass.

APPENDIX 35

SEED-COUNTS AND -MASS CORRELATIONS WITH FRUIT-MASS AND SEED ABORTION RATES, IN FRUIT SET WITH HAND-POLLINATION IN SUMMER, 1970

NOTATION

x_1 = ΣF seeds.
x_2 = ΣF and P seeds.
x_3 = ΣF, P and cWs seeds (i.e. excluding b seeds).
x_4 = ΣF, P and S seeds (i.e. including b seeds).
x_5 = ΣF, P, S and U seeds and ovules.
x_6 = Mass of all seeds (g).
y = Mass of fruit flesh (excluding seeds) (g).
x_7 = Seed abortion rate $\frac{\Sigma P \text{ and } S}{\Sigma F, P \text{ and } S}$, transformed to angular degrees.

Number of multiple observations = 24 .

x_1	x_2	x_3	x_4	x_5	x_6	y	x_7
1 348	1 414	1 498	1 503	1 653	133,99	864	18,73
1 811	1 904	1 952	1 966	2 167	178,88	1 643	16,31
508	553	586	601	2 306	51,29	908	23,16
1 246	1 416	1 935	1 946	2 235	132,74	1 527	36,85
1 481	1 626	1 843	1 870	1 978	150,18	1 163	27,14
1 839	1 890	1 954	1 966	2 349	178,60	1 797	14,72
764	1 228	1 492	1 600	1 906	96,94	830	46,29
1 513	1 623	1 675	1 705	1 869	147,82	1 687	19,61
1 590	1 608	1 641	1 644	1 865	152,87	1 613	10,44
1 736	1 873	1 935	1 953	2 081	173,05	866	19,47
1 915	1 997	2 109	2 129	2 273	189,94	1 792	18,48
1 840	1 918	1 998	2 096	2 249	181,03	1 627	20,08
1 805	1 924	1 984	1 992	2 031	179,22	1 801	17,84
1 365	1 592	1 715	1 732	1 874	141,81	1 359	27,41
1 017	1 036	1 047	1 052	1 679	98,29	1 256	10,51
1 651	1 706	1 807	1 824	1 967	162,37	1 510	17,94
2 108	2 159	2 203	2 209	2 341	206,57	1 362	12,35
1 761	1 870	1 922	1 928	1 983	174,56	1 552	17,12

APPENDIX 35 (contd.)

	x_1	x_2	x_3	x_4	x_5	x_6	y	x_7
	1 731	1 847	1 940	1 966	2 168	171,79	1 525	20,23
	1 508	1 649	1 727	1 731	1 784	146,59	1 272	21,03
	1 156	1 571	1 747	1 759	1 947	132,72	1 572	35,84
	381	1 329	1 547	1 554	1 817	89,71	1 385	60,32
	1 365	1 676	1 781	1 789	1 865	147,68	1 343	29,13
	1 656	1 813	1 899	1 904	2 000	167,37	1 375	21,16
Mean:	1 462	1 634	1 747	1 767	2 016	149,42	1 401	23,42‡
Correlation with y:	0,509*	0,557**	0,538**	0,523**	0,321	0,552**	-	-0,248
Correlation with x_7:				-0,125				

‡ When detransformed, mean x_7 = 0,158.

* $p \leq 0,05$

** $p \leq 0,01$

Overall ratio of seed type to ΣF, P, S and U:

F : 0,725

P : 0,086

S : 0,065 { cWs : 0,056; b : 0,009 }

U : 0,124

Overall ratio of fruit flesh mass to:

- Seed mass : 9,38

and 10,38 when seed mass added to fruit flesh mass.

APPENDIX 36

ESTIMATED LEAF AREA AND OTHER RELATED DATA OF PAPAYA FRUIT-BEARING STEMS USED FOR THE 1969 AUTUMN FRUIT SET

NOTATION

a = stem bearing only 1969 autumn set fruit;

b = stem bearing 1968/1969 summer plus 1969 autumn set fruits;

c = stem bearing ripening 1968 autumn set fruit, 1968/69 summer and 1969 autumn set fruits.

Type of Stem	MAY 1969				OCTOBER 1969
	Mean leaf area (cm^2)	Mean no. leaves per stem	Mean no. fruit per stem	Mean total stem leaf area per fruit (cm^2)	Mean leaf area (cm^2)
a	1 434	11,22	3,07	5 241	1 063
b	1 882	13,78	7,09	3 658	1 155
c	3 538	25,24	25,39	3 518	1 650

APPENDIX 37

SEED COUNTS, SEED ABORTION, FRUIT DIAMETER AND FRUIT MASS CORRELATIONS FOR PAPAYA FRUIT SET WITH HAND-POLLINATION IN AUTUMN, 1969

NOTATION

x_1 = ΣF seeds.

x_2 = ΣF and P seeds.

x_3 = ΣF, P and S seeds.

x_4 = ΣF, P, S and U seeds and ovules.

x_5 = Seed abortion rate: $\left[\frac{P + S}{F + P + S}\right]$, transformed to angular degrees.

x_6 = Index of Fruit Volume at anthesis: formula of prolate spheroid.

y = Index of Fruit Volume at fruit ripening: formula of prolate spheroid.

z = Fruit mass (including seeds): (g).

r = Correlation co-efficient.

‡ $p \leq 0,10$

* $p \leq 0,05$

** $p \leq 0,01$

*** $p \leq 0,001$

Number of fruits from a-stems: 8 .

Number of fruits from b-stems: 5 .

Number of fruits from c-stems: 5 .

Total number of fruits and multiple observations: 18 .

TABLE 37.1 Data and means

Type of stem	x_1	x_2	x_3	x_4	x_5	x_6	y	z
a	836	1 150	1 299	1 511	36.66	6.1	699	660
a	306	569	590	1 121	43,93	3,4	476	443
a	429	896	1 040	1 375	50,04	5,7	822	759
a	480	807	824	1 083	40,25	6,5	919	816
a	391	773	811	1 265	46,02	5,5	820	704
a	531	956	1 015	1 622	43,67	5,4	820	708
a	637	684	726	1 172	20,50	5,0	779	684
a	638	829	905	1 117	32,90	5,2	826	729
b	768	1 023	1 061	1 859	31,70	5,5	897	799
b	471	959	1 112	1 494	49,40	3,9	873	780
b	454	679	908	1 273	45,00	3,0	710	615
b	412	616	654	1 444	37,47	4,1	575	470
b	857	1 040	1 142	1 622	29,97	5,5	966	862
c	794	947	1 100	1 834	31,83	9,9	1 097	921

APPENDIX 37 (contd.)

Type of stem	x_1	x_2	x_3	x_4	x_5	x_6	y	z
c	832	1 146	1 367	1 685	38,73	6,5	1 145	1 063
c	552	832	938	1 893	39,90	4,7	835	740
c	106	157	157	1 830	34,75	7,1	380	327
Mean for a	531,0	833,0	901,3	1 283,3	39,25	5,4	770,1	687,9
Mean for b	592,4	863,4	975,4	1 538,4	38,71	4,4	804,2	705,2
Mean for c	568,0	798,0	934,0	1 822,8	38,02	7,4	865,6	762,4
Overall mean:	558,3	831,7	930,9	1 504,0	38,76	5,6	806,1	713,4

Overall ratio of seed type to ΣF, P, S and U ovules and seeds:

F : 0,371
P : 0,182
S : 0,066
U : 0,381

TABLE 37.2 t-values and tests for differences between fruits of stem types a, b and c for variables x_1 ... to ... z

VARIABLE	t - V A L U E S				
	a vs b	a vs c	b vs c	a vs [b & c]	[a & b] vs c
x_1	-0,590	-0,295	0,154	-	-
x_2	-0,288	0,230	0,343	-	-
x_3	-0,614	0,175	0,184	-	-
x_4	-2,159‡	-5,653***	-2,727*	-4,000**	-4,011**
x_5	0,105	0,268	0,157	-	-
x_6	1,690	-2,502*	-2,917*	-0,642	-3,333**
y	-0,417	-0,791	-0,401	-0,703	-0,810
z	-0,233	-0,694	-0,400	-0,547	-0,734

APPENDIX 37 (contd.)

TABLE 37.3 Total correlation co-efficients for 18 fruits

	x_1	x_2	x_3	x_4	x_5	x_6	y	z
x_1	1,000							
x_2	0,848***	1,000						
x_3	0,821***	0,975***	1,000					
x_4	0,248	0,196	0,233	1,000				
x_5	-0,454‡	0,046	0,119	0,076	1,000			
x_6	0,289	0,182	0,194	0,514*	-0,215	1,000		
y	0,748***	0,794***	0,793***	0,272	-0,065	0,418	1,000	
z	0,765***	0,831***	0,831***	0,210	-0,060	0,379	0,989***	1,000

Selected First Order Partial Correlations:

$$r_{1z,5} = 0,830***$$

$$r_{2z,5} = 0,836***$$

$$r_{3z,5} = 0,845***$$

APPENDIX 37 (contd.)

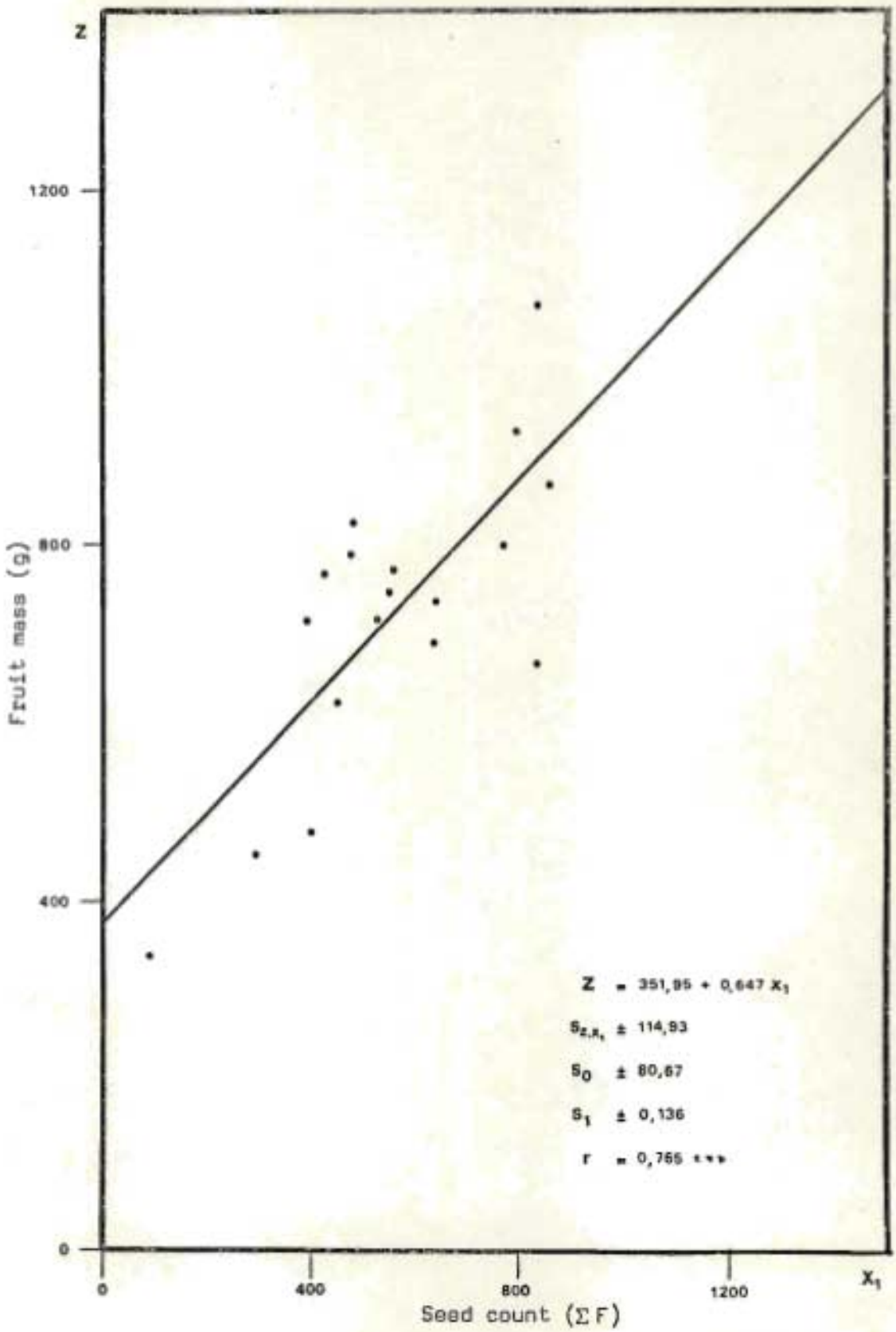

FIGURE A Regression of Z on X_1 .

APPENDIX 37 (contd.)

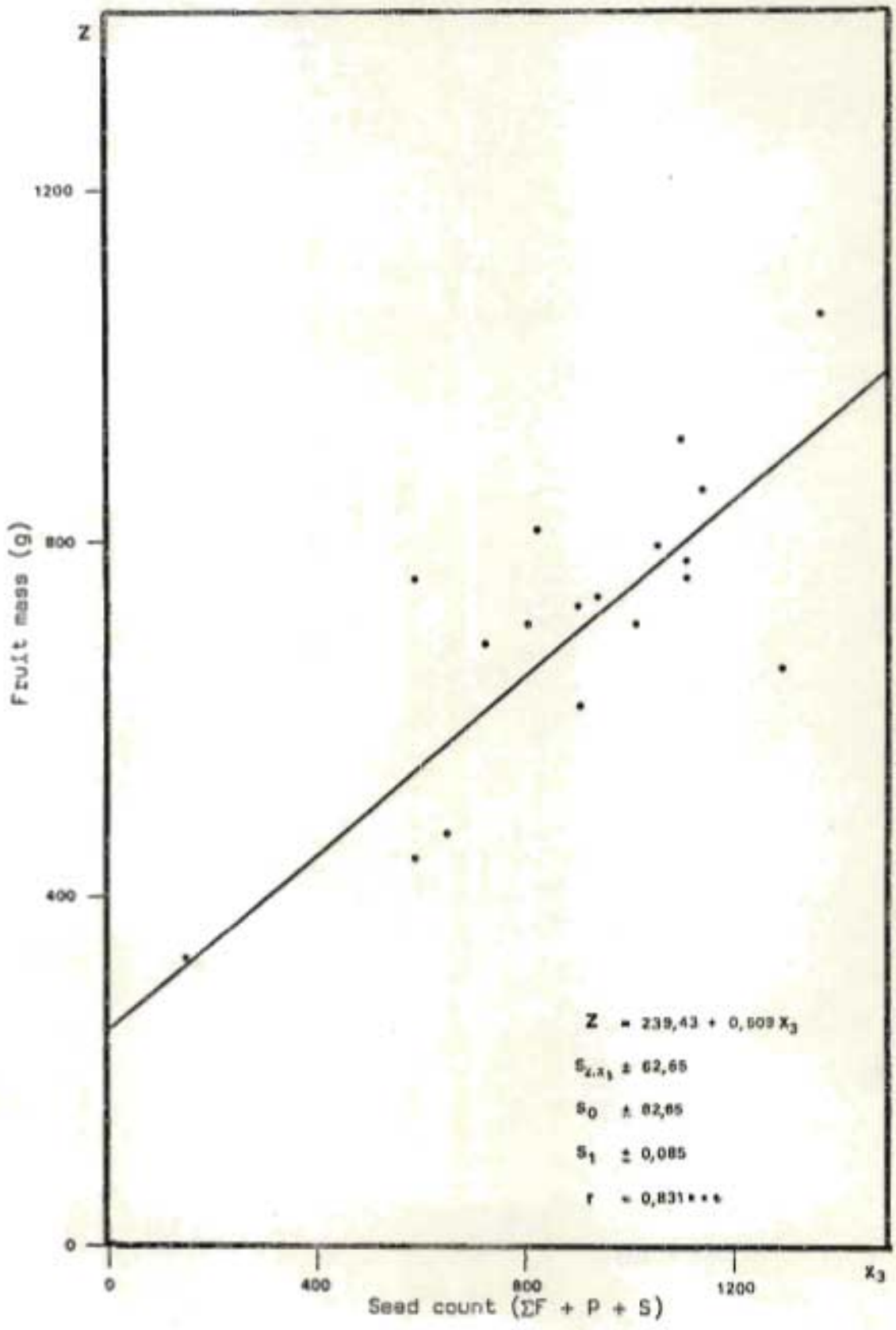

FIGURE 8 Regression of Z on X_3 .

APPENDIX 38

COMPARATIVE MEAN VALUES, TOTAL AND PARTIAL CORRELATIONS OF SELECTED SEED COUNT, SEED MASS AND FRUIT MASS VARIABLES FROM ONE SUMMER'S AND TWO AUTUMNS' HAND-POLLINATED PAPAYA FRUIT SETS

NOTATION

x_1 = Σ f seeds.
x_2 = Σ P seeds.
x_3 = Σ P and S seeds.
x_4 = Σ f, P and S seeds.
x_5 = Mass of all seeds (g).
y = Fruit flesh mass (g).
z = Fruit flesh plus seed mass (g).

S70 = Summer Set, 1970: from Appendix 35.
A69 = Autumn Set, 1969: from Appendix 37.
A70 = Autumn Set, 1970: from Appendix 34.

‡ $p \leq 0,10$
* $p \leq 0,05$
** $p \leq 0,01$
*** $p \leq 0,001$

TABLE 38.1 Mean values of selected variables

Set	No. of fruit	x_1	x_2	x_3	x_4	x_5	y	z
S70	24	1 462	172	305	1 767	149	1 401	1 550
A69	18	558	273	373	931	-	-	713
A70	14	572	-	576	1 148	46	678	724

TABLE 38.2 Selected total correlations with y, fruit flesh mass

Degrees of freedom ...	S70	A69	A70
	22	-	12
r_{1y}	0,509*	-	0,520‡
r_{2y}	-0,143	-	-
r_{3y}	-0,154	-	0,557*
r_{4y}	0,523**	-	0,727**
r_{5y}	0,552**	-	0,670**

APPENDIX 38 (contd.)

TABLE 38.3 Selected total correlations with z, fruit flesh plus seed mass

Degrees of freedom ...	S70	A69	A70
	22	16	12
r_{1z}	0,584**	0,765***	0,573*
r_{2z}	-0,181	0,320	-
r_{3z}	-0,191	0,478*	0,526‡
r_{4z}	0,589**	0,831***	0,744**
r_{5z}	0,629**	-	0,716**

TABLE 38.4 Selected first order partial correlations with y, fruit flesh mass

Degrees of freedom ...	S70	A69	A70
	21	-	11
$r_{1y,3}$	0,531**	-	0,566*
$r_{1y,2}$	0,545**	-	-
$r_{3y,1}$	0,232	-	0,598*
$r_{2y,1}$	0,266	-	-

TABLE 38.5 Selected first order partial correlations with z, fruit flesh plus seed mass

Degrees of freedom ...	S70	A69	A70
	21	15	11
$r_{1z,3}$	0,602**	0,791***	0,619*
$r_{1z,2}$	0,615**	0,818***	-
$r_{3z,1}$	0,260	0,552*	0,579*
$r_{2z,1}$	0,297	0,533*	-