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THE MORPHOGENESIS OF THE INFLORESCENCE, FLOWER AND FRUIT OF PYRUS NIVALIS JACQUIN VAR. ORIENTALIS TERPÓ

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1. INTRODUCTION

In his articles on the physiology of fruit development, NITSCH (1953, 1965) rightly observes that fruit growth does not begin at pollination of the flower but at an earlier stage during initiation of the floral primordia. He distinguishes two important periods of growth in the life-history of the fruit, viz.:

1. the period of pre-bloom development when growth mainly occurs through cell division;
2. the post-fertilisation period when cell enlargement is the most important factor.

These two periods are separated by the critical phases of anthesis and pollination.

As far as the first period is concerned, flower initiation has been studied in extenso (HILLMAN, 1962; LANG, 1965; SALISBURY, 1963). Many research workers believe that after initiation of the floral primordia the differentiation and development of the various parts of the flower is a more or less automatic process following a well-marked pattern. Owing to this misconception the study of these subjects has been greatly neglected.

The second period is one of substancial growth of the young fruit, which explains why this is often the only period considered in fruit-growth studies. As a result certain important facts providing a better understanding of the nature of fruit growth may well have been overlooked.

The object of the present study of the growth of the fruits of *Pyrus nivalis* Jacquin, a wild species of pear distributed over Central Europe, the Danube countries, the Balkan Peninsula and Asia Minor, is to place proper emphasis on the morphogenesis of both the flower and fruit so as to provide the fullest possible information on this subject.

The literature contains no references to the fruit development of wild pear species, the only comparable literature available relating to the fruit development of cultivars. Furthermore, compared with other fruit-trees, surprisingly little research work has been done on pears. This may be illustrated by the bibliography by SCARAMUZZI (1953) who studied the bud development of the plum, peach, cherry, apple and pear. Out of a total of 237 bibliographical references, 50 relate to the apple, two to apple and pear together, but only five to the pear alone. Out of a total of 370 references in NITSCH (1953), 30 relate to the apple, 6 to apple and pear, and only three to the pear alone.

As regards the study of *Pyrus nivalis*, the following topics will be discussed in succession:

1. the initiation of the flower primordia;
2. the differentiation of the various parts of the flower;
3. the development of the ovary prior to flowering;
4. anthesis;
5. the development of the ovary and any other parts of the flower to the ripe fruit.

2. MATERIAL AND METHODS

2.1. MATERIAL

A very old pear-tree may be seen on the rampart of the Leiden Botanical Gardens. In a plan drawn by H. WITTE in 1868 the tree shown on this site is termed *Pyrus sinaica* (VEENDORP and BAAS BECKING, 1938), and this name occurs earlier in catalogues of the Botanical Gardens, i.e. in BRUGMANS' catalogue (1819) under the author's name Desf., in REINWARDT's catalogue (1831), and in a manuscript catalogue dated 1861 under the author's name THOIN. The tree was probably planted in the newly acquired part after the fifth extension in 1816.

Grafts from the tree were brought to the Arboretum 'De Dreijen' at Wageningen in 1935. The tree that developed from a graft was determined by HENSEN (1962), with the assistance of TERPÓ's article (1960), as

Pyrus nivalis Jacquin var. orientalis Terpó.

Besides this tree Wageningen has three young specimens of the same variety in the Belmonte Arboretum. These young trees, which were planted in 1957, were also determined by HENSEN (1962). One of the three, hereafter referred to as tree I, bears a striking resemblance to the Leiden tree. The two other young trees, II and III, are somewhat different (among other characters the flowers and fruits are larger). Moreover the vegetative growth of trees II and III is far greater than of tree I whose shoots, like those of the Leiden tree, only rarely make considerable extension growth. The vigorously growing trees were possibly raised from seed, whereas the slowly growing tree I may come from a graft taken from the large tree at Leiden.

Material from the large tree at Leiden was measured and sampled from 1958 to 1963. The Wageningen material was used for research in 1964 and subsequent years.

Close to the large tree on the rampart at Leiden is a smaller pear-tree named *Pyrus nivalis*. According to HENSEN's (1962) determination it should be known as *Pyrus austriaca* Kern. (Syn. *P. nivalis* Jacq, f. austriaca (Kern.) Schneid.). In size and structure of its fruits it differs from the large tree.

A few complementary studies have been devoted to other pear-tree species found in the Belmonte Arboretum. The names accompanying the trees in the Arboretum have been adopted in the present publication without modification. The species in question are:
Pyrus amygdaliformis Vill.,
Pyrus austriaca Kern.,
Pyrus calleryana Dcne,
Pyrus elaeagrifolia Pall.,
Pyrus domestica Med.,
Pyrus pyrifolia (Burm. fil.) Nak. var. culta (Makino) Nak.,
Pyrus salicifolia Pall., and
Pyrus ussuriensis Maxim. var. ovoidea (Rehd.) Rehd..

2.2. Sampling, measurements and observation

In their study of the apple Tukey and Young (1942) found that it is much more difficult to secure samplings of this fruit as uniform as possible than those of the cherry, for example. Close inspection of the fruits, the buds, inflorescences and flowers of *Pyrus nivalis* also reveals fairly great differences. Although a great many samples should be taken for this very reason, relatively little material was collected to avoid damaging the plant and upsetting the balance. This is particularly true of fruits whose small number in certain years of the study was due to a poor fruit-set. Samples were therefore not taken at random; instead the specimens selected were, as far as possible, representative of the development. After sampling, the buds, inflorescences, flowers and fruits were fixed in 70% alcohol, a formol – alcohol – acetic acid solution (FAA) in which half the acetic acid is sometimes replaced by propionic acid (FAPA), or in a chromic acid – acetic acid – formol solution of varying ratios of constituents (Craf I–V in Sass, 1961).

For the detailed anatomical study a further selection was made from the samplings.

A general impression of the development of the fruit was obtained by extensive observations of living material on the trees. At Leiden an 18-foot scaffold had to be erected for the purpose. At Wageningen the observations could be made from the ground, the measurements being made with a vernier caliper. Measurements and counts were also made of flowers and fallen fruits.

By combining all observations it is possible to obtain a fairly good conspectus of the morphogenesis of the fruit of *Pyrus nivalis*.

2.3. Microtechnique

Large numbers of microscope slides had to be prepared for studying the internal structure of the bud, flower and fruit. Rauh and Reznik (1951) and Zeller (1960–I) report difficulties experienced in cutting apple and pear buds. These are due to the presence of hairs, often highly lignified, between the soft meristematic tissues in the bud. They are one reason why practically no developmental studies of the pear bud have been available up to now.

After several difficulties in the initial stage of the study, a method was eventually developed that enables the buds of *Pyrus nivalis* to be cut at any stage of growth without loss of a single section. It is roughly the same as that described by Sass (1961). After the material had been fixed in FAA, FAPA or a Craf modification, the tertiary butyl alcohol (TBA) method was used for dehydrating. The block of solid paraffin wax (a Fisher 'tissue mat') containing the material was cut with a rotary microtome on the same day as the buds were embedded, it having been repeatedly found that mishaps occurred when cutting was deferred. Instead of the heavy microtome knife an extra-hard safety-razor blade was used for cutting. Although these blades do not exhibit a particularly well finished cutting edge when examined under the microscope, they usually give a clean and rapid cut. The wax sections were flattened out on the surface of wa-

ter of a suitable temperature, i.e. 52 °C, for paraffin wax with a melting point of about 61 °C. After some trials this method of flattening out sections in a water-bath proved to be more satisfactory than other flattening-out methods. A properly cut ribbon is obvious essential for this method. The great majority of sections were stained with safranin – fast green.

On the whole flowers and fruits can be cut fairly well up to a fruit diameter of about 10 mm. With larger fruits a few sections can only be obtained with the greatest difficulty and usually it is quite impossible to cut a single section. The trouble is caused by the extremely hard groups of sclereids in the material, these being embedded in a tissue of thin-walled parenchymatous flesh cells. Not only are these sclereid clusters lifted out of the wax block by the blade, but the blade edge is irreparably damaged even at the first section. New techniques will have to be developed for cutting this material. The cutting of cultivated pears does not appear to present such a problem; at any rate, BAIN (1961) and STERLING (1954) report no difficulties, and MITCHELL (1950) expressly chose for his study a pear cultivar with few sclereid clusters in the fruit.

In addition to SASS's work (1961) referred to above, the works of CONN, DARROW and EMMEL (1962), CONN (1961), GURR (1965) and JOHANSEN (1940) were consulted for the microtechnique study.

3. GENERAL SECTION

3.1. CLASSIFICATION

The Rosaceae family is divided into four sub-families (ENGLER, 1964), one of which is formed by the Maloideae or Pomoideae. All members of this sub-family bear the characteristic pome fruit, *Pyrus* and *Malus* being the most familiar genera. HENSEN (1962) provides a short survey of the genus *Pyrus*. It can be divided into four sections, the section Pashia being regarded as the most primitive. The species in this section have fruits with a caducous calyx; the eastern Asiatic species have 2–5 carpels, whereas western Asiatic, European and north-west African species invariably have 5 carpels. The other three sections, Achras (Pyrus according to the International Code of Botanical Nomenclature since *P. communis* L., the type species, belongs to this section), Xeropyrenia and Argyromalon, include species that always have 5 carpels and fruits with a non-caducous calyx. The species in the section Argyromalon are found in the mountainous regions of southern Europe and around the Black Sea. One of the species in this section is *Pyrus nivalis* which is distributed over central Europe, the Danube countries, the Balkan Peninsula and Asia Minor. The first known description of *Pyrus nivalis* is by JACQUIN in the Florae Austriacae (1774).

Crossing and breeding of different species of wild pear have resulted in the cultivated European forms of pear. *Pyrus pyraster* of the section Achras, *Pyrus syriaca* of the section Xeropyrenia, and *Pyrus nivalis* of the section Argyromalon are probably important ancestors of the cultivated pear.

The term 'cultivated pear' will be frequently used in this publication, since the name *Pyrus communis* L. is incorrectly applied to the cultivated pear. *Pyrus communis* L. is a species of wild pear from central Europe. The collective name for the cultivated forms of pear should be *Pyrus domestica* Med. (ENGLER, 1964; HENSEN, 1962; SCHWANITZ, 1967). But the name *Pyrus communis* L. is still employed for the cultivated pear in new impressions of handbooks (STRASBURGER, 1967; WILLIS, 1966). Whenever the name *Pyrus communis* L. is used in this publication it denotes that the author referred to probably meant the central European species of wild pear.

As stated earlier (p. 2), the trees from which material was used for the study were determined by HENSEN (1962). The name is

Pyrus nivalis Jacquin var. orientalis Terpó.

A description of this variety was published by Terpó in 1960.

The cultivated forms of pear are vegetatively propagated, so that all specimens form a single clone. Although the term 'variety' (German 'Sorte', French 'variété') is still in fairly common use for these forms of pear, the correct term 'cultivar' will be employed in this publication. In many cases more than one name is used for the same cultivar. Usually the name is only a translation, especially a German translation of a French name. Occasionally the name is entirely changed; for instance 'Bon Chrétien William' ('Williams Bon Chrétien' 'Williams Christ', 'Williams') is known in the United States as 'Barlettt'.

3.2. Morphology

3.2.1. *Structure of the tree*

Pyrus nivalis Jacquin var. orientalis Terpó is a tree that may attain a height of about 10 metres with a compact, thick-set crown. The branches are thick-set crooked, and dark or almost black in colour. They do not bear thorns.

Not only the flowers and fruits, but practically all the leaves are borne by short or dwarf shoots (virgulae). Long shoots (virgae) determine the structure of the branch system. The large tree at Leiden forms few long shoots; during the period 1964–1966 tree I in the Belmonte Arboretum formed no long shoots and in 1967 only two. Trees II and III started to grow vigorously in 1966 when all branches formed new long shoots. This development continued in 1967. Figure 1 shows diagrammatically how short shoots on the two latter trees can develop from a long one. The long shoot is produced at blossom in the spring; it increases rapidly in length and throughout the summer continues to grow at the top and to produce new leaves. The leaves on the long shoot are relatively large with stipules. With the exception of a few lower leaves, the leaves produce in their axils a short shoot with small narrow lanceolate leaves. A long shoot of this kind is shown on the left-hand side of Figure 1. In the following spring the next generation of branches is formed from the one-year-old long shoot. These branches are shown on the right-hand side of the Figure and numbered 1 to 5.

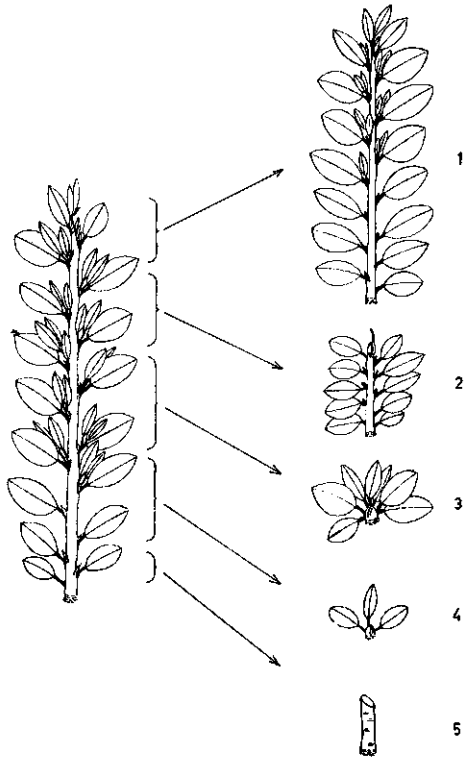


Fig. 1. Diagrammatic representation of the vegetative development of the shoot of *Pyrus nivalis*.

The buds at the top of a shoot, including the terminal, give rise to new long shoots. A number of buds underneath produce a batch of shorter shoots (2) that might be designated short-long shoots or long-short shoots (LUYTEN and DE VRIES, 1926). These shoots do not continue to grow in the spring and are terminated by an aborted leafy flower bud. Highly developed short shoots with abundant foliage are formed on the middle of the original long shoot (3). The more basal short shoots grow smaller (4) and finally a number of dormant buds remain on the lower end of the long shoot (5).

The variously shaped leaves on these shoots are very noticeable. Four types may be clearly distinguished:

1. large coarse leaves with permanent stipules on the long shoot;
2. small narrow lanceolate leaves on the shoots in the axil of the first type of leaf;
3. oval to inverted ovoid leaves on the base of the highly developed short shoots;
4. broad lanceolate leaves at the top of the highly developed short shoot and on the poorly developed short shoots.

No stipules occur on the leaves of types 2–4. The underside of all leaves is covered with downy hairs. A fifth type of leaf may be found on the young seedling, viz. a deeply incised hand-shaped lobate leaf. BEZRUCHENKO (1958) mentions a leaf of this shape in the juvenile stages of *Pyrus communis* L., and HEGI (1935) reports two shapes of leaf in *Pyrus nivalis* which he terms *Pyrus communis* L. subsp. nivalis (Jacq.).

The leaves on the long shoots are arranged in a $^2/_5$ spiral; owing to the thick-set structure of the short shoots it is difficult to determine how their leaves are arranged, but all their lateral organs are neatly arranged in the bud. Consequently the leaf arrangement of the short shoots is readily observed in transverse sections of the bud. In small buds. viz. buds of short shoots with few lateral organs, the leaves are arranged in a $^2/_5$ spiral. In large buds the $^2/_5$ phyllotaxy at the base of the short shoot often gradually passes over into a $^3/_8$ arrangement. Both left-handed and right-handed spirals are found. The lateral organs of the flowerbearing (generative) short shoot have the same spiral arrangement as the vegetative short shoot.

A $^3/_8$ phyllotaxy has been noted for the inflorescence of the cultivated pear (HEINRICH, 1959; RUDLOFF and WUNDRIG, 1939). Like *Pyrus nivalis*, the inflorescence of the apple, which usually has fewer flowers than the pear, also has a predominantly $^2/_5$ spiral arrangement (VISSER, 1955).

The highly developed lateral branches of the one-year-old long shoot (often the long-short shoots) of the cultivated pear may terminate in a flower. In a few cases even more than one flower may develop on the shoot. Usually these flowers bloom later than those of the normal inflorescences (later or June flowering) (LUYTEN and DE VRIES, 1926; RIVALS, 1967). In the apple more or less complete inflorescences may occur on one-year-old long shoots. The flowers of these inflorescences are generally misshapen and have fewer stamens and styles than those of normal inflorescences (ZELLER, 1960–I, II).

These bibliographical details elucidate the flower-bud-like nature of the terminal bud of the long-short shoot of *Pyrus nivalis*.

3.2.2. *Inflorescence structure and type*

With a few exceptions (p. 7), pear flowers are only found on short shoots. Only the upper part of these mixed short shoots, viz. the flower-bearing part, should properly be termed the inflorescence. The inflorescence consists of a number of lateral flowers and is closed by a terminal flower. According to the classical descriptive method (cf. TROLL, 1964), despite the terminal flower this single inflorescence is a raceme (racemus, botrys, Traube). This pear raceme is termed an umbellate cluster (corymbus simplex, Doldentraube) from its shape. It is said to be formed by reduction from a panicle (panicula, Rispe), a composite inflorescence with racemose partial inflorescences.

The classification of Angiosperm inflorescences has created difficulties for 200 years (RICKETT, 1944). Inflorescences with a terminal flower as in *Pyrus* and *Malus* have added to the confusion. TROLL (1964) solves the problem by separating the 'Deskriptive Morphologie der Infloreszenzen' from the 'Typologie der Infloreszenzen'. The 'Typologie der Infloreszenzen' of TROLL and co-workers arrives at a 'natural' classification of Angiosperm inflorescences into two types, the 'polytelic inflorescences' and the 'monotelic inflorescences'. In polytelic inflorescences the top of the floral axis bears a 'florescence' only composed of of lateral single flowers or cymose flowering systems ('partial-florescences') and not ending in a terminal flower. Below this 'main florescence' there may be some branches which repeat the structure of the main stem by producing florescences ('co-florescences') themselves. In the 'monotelic inflorescence' the main axis ends in a terminal flower. The latter group of inflorescenses include those of the Rosaceae and hence *Pyrus* (WEBERLING, 1964).

The morphology of the pear inflorescence is best studied in the cultivated pear from which the *Pyrus nivalis* inflorescence differs but little. The number of flowers in each inflorescence varies from 6 to 11, although there are usually 9 flowers, viz. one terminal and 8 lateral. Proceeding from the terminal flower to the base of the inflorescence, the flowers are successively numbered 1 to 9. Flowers 2 to 5 are situated in the axil of a bract (bractea, brakteoses Hochblatt) and flowers 6 to 9 in the axil of an ovate foliage leaf (frondoses Hochblatt, Kleinlaubblatt). Between the bracts and the foliage leaves, i.e. at point 5 or 6, there is often a transitional leaf in the form of a small, permanent foliage leaf with a long dorsiventrally flattened petiole or a bract with a small lamina at the top. This bract, like the others, falls off immediately prior to or at blossom.

Below the inflorescence one or more foliage leaves are arranged on the short shoot. A short shoot bearing two lateral prophylla and 3 to 5 lanceolate foliage leaves is to be found in the axil of the topmost foliage leaf. Often two foliage leaves underneath the inflorescence have a shoot of this kind. These shoots, which are not usually found in the cultivated pear, produce a new generation of short shoots capable of bearing flowers only a year after. It is for this reason that *Pyrus nivalis* blossoms so luxuriantly every year without unproductive

years (at least as regards flowers). Usually a transitional leaf is also found below the foliage leaves with the shoots. This transitional leaf is small and unlike the other leaves in the inflorescence it bears two stipules fused to the petiole. Underneath are the scars of the bud scales, of which *Pyrus nivalis* has about 24, which is twice the number found in the cultivated pear.

Each of the lateral flowers has two bracteoles or prophylls (bracteolae or prophylla, Vorblätter) on the pedicel. In exceptional cases the two lower flowers of the inflorescence have three such bracteoles. As in the cultivated pear, 1 to 3 organs of foliar origin are found on the stalk of the terminal flower. TROLL (1964) refers to sterile bracts in the cultivated pear and calls them 'Zwischenblätter'. He points out that others, e.g. VELENOVSKÝ (1905–1913), incorrectly name these organs 'Vorblätter' (prophylla). Like the bracteoles and bracts, the 'Zwischenblätter' of *Pyrus nivalis* fall off just before or at blossom.

Figure 2 is a diagrammatic representation of the flowering short shoot of *Pyrus nivalis*.

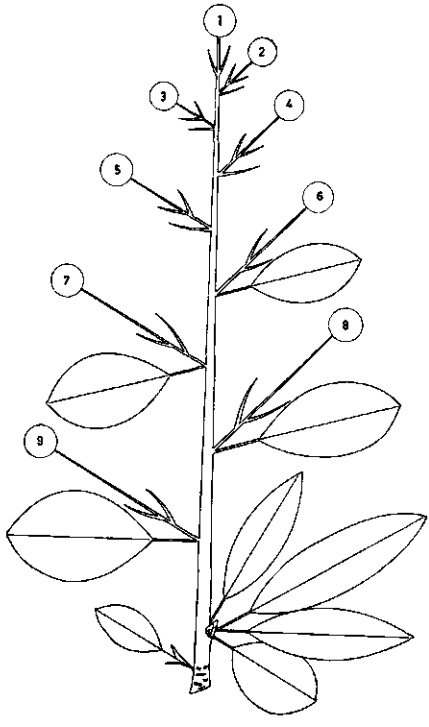


FIG. 2. Diagrammatic representation of the flowering short shoot of *Pyrus nivalis*. Note the ovate leaves on the axis of the inflorescence and the lanceolate leaves of the secondary lateral shoot.

One of the differences between the flowering short shoot of *Pyrus nivalis* and that of the cultivated pear is the presence of leafy shoots below the inflorescence. The cultivated pear usually has buds at these points and only exceptionally 'sylleptic' shoots (LUYTEN and DE VRIES, 1926; ZELLER, 1954). A check made in 1960 showed that the wild pear species studied in the Belmonte Arboretum (cf. p. 2) generally have a shoot of this kind underneath their inflorescence.

Another difference is in the secondary flowers that frequently occur in the cultivated pear, particularly in the axils of the bracteoles of the basal flowers. Together with the frequent occurrence of bud primordia in the axils of the bracteoles and 'Zwischenblätter', these secondary flowers are said to be evidence of the composite character of the pear inflorescence (ZELLER, 1960–I). *Pyrus nivalis* rarely has bud primordia in the axils of the bracteoles, although they do occur in the axils of the 'Zwischenblätter' (cf. p. 14). The latter buds are often distinctly recognizable as undeveloped flowers, so that TROLL's (1964) view that the bracteoles of the terminal flower are sterile bracts appears to be correct. The bud primordia of *Pyrus nivalis* are chiefly found in poorly developed inflorescences (cf. § 3.2.3.). True secondary flowers are not found in *Pyrus nivalis*, although in some years it is common to find that the shoot underneath the inflorescence blossoms together with the main inflorescence instead of a year later. Morphologically this flowering shoot is not homologous with an inflorescence, or a part of an inflorescence, but with an entire flowering short shoot. When the flowering shoot is poorly developed the situation resembles that of the inflorescence with secondary lateral flowers of the cultivated pear. In this case it is difficult to decide whether one or two inflorescences are involved.

Lastly, the inflorescence of the cultivated pear differs from that of *Pyrus nivalis* in that the ordinary foliage leaves of the latter have no stipules. As the microscope slides show, it is only rarely that these are even initiated.

3.2.3. *Initiation and development of the inflorescence*

The pear inflorescence is initiated in the summer and autumn of the year preceding bloom. After differentiation of the floral primordia the sepals, petals, stamens and carpels are formed in succession. In this way a complete inflorescence develops inside the bud before the onset of winter. In the spring the flowers continue to develop. Pollen meiosis takes place about a month before bloom, and the egg-cell is not formed until anthesis starts at the end of April or the beginning of May.

The literature unfortunately contains few references to the initiation of the inflorescence of the cultivated pear. LUYTEN and DE VRIES (1926) made a detailed study at Wageningen of the pear cultivar 'Beurré Hardy'. According to these authors the inflorescence is initiated in August. In 1923 initiating took place some days later than in 1922. In both years juvenile development phases of the inflorescence occurred up to November. FELIUS (1954) gives information dating from 1952 on the flower initiating of six pear cultivars ('Beurré Hardy', 'Clapp's Favourite', 'Comtesse de Paris', 'Conference', 'Légipont' and 'Précoce de Trévoux') for the north, centre and south of Holland. Differences in the initiation date of the pear cultivars were two to three weeks in the same district, so that a distinction may be drawn between early and late cultivars. In all pear cultivars initiation in the south was about a fortnight earlier than in the north. The dates given by FELIUS (1954) (from 16th July to 13th August) represent the approximate period of initiation.

The development of the inflorescence of three pear cultivars was studied by

ZELLER (1958) at Hohenheim, western Germany, for a period of five years. The initiation date varies considerably from year to year. Differences of nearly a month were found in the same cultivar. Differences between the cultivars during the same research year amounted to nearly six weeks. Depending on the research year and the cultivar, the inflorescence is initiated at Hohenheim from the beginning of July to the beginning of September.

In Holland the earliest date of initiation of the inflorescence of *Pyrus nivalis* is the first half of August (Belmonte Arboretum, 1966), although it is generally much later, in September or October, and may continue to November. The obvious reason for such late and irregular initiation is the unfavourable weather conditions, although it would seem that a number of internal factors also have a great influence.

The direct result of irregular initiation is the development of variously shaped inflorescences. In Figure 3 an attempt is made to show the direction in which the inflorescence may develop. On the left is a well-developed short shoot of which the apex usually becomes generative, and in the centre of the figure a normally developed flowering short shoot. The same type of shoot was shown above in Figure 2. The ovaries of the flowers show clearly observable differences in diameter (§ 4.3.1.). The two sub-apical flowers (2 and 3) are particularly small and blossom late. The secondary shoot underneath the inflorescence is moderately well developed. 'Anomalous' flowering short shoots can be seen on the right-hand side of Figure 3.

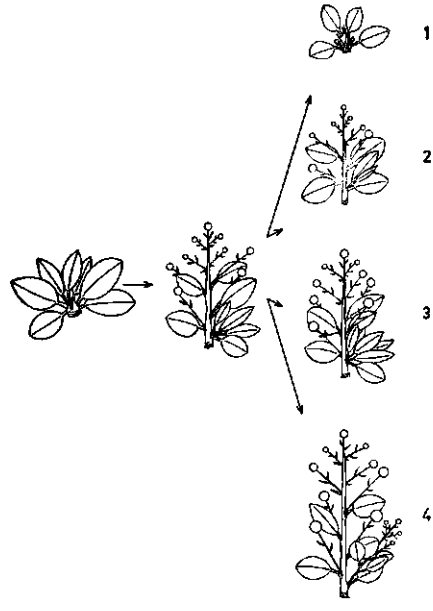


FIG. 3. Diagrammatic representation of the generative shoot development of *Pyrus nivalis*.

1. When the inflorescence is initiated late it may happen that the flowers are not ready to blossom in the spring. Depending on the time-lag, either the entire inflorescence may die off or only the top. In the latter case the remaining flowers are small and misshapen. The flowers bloom later than those of the

normal inflorescence. The ovate leaves of the most poorly developed short shoots of this type are the only feature that distinguishes them from the purely vegetative short shoots with lanceolate leaves.

Since in such cases secondary shoots are almost or entirely absent below the inflorescence and the apex disappears as the inflorescence dies off, this type of short shoot produces no inflorescence in the following years.

2. A less serious developmental lag results in an inflorescence with few flowers. They are comparatively small and substantial differences in size exist within the same cluster. The small, poorly developed flowers, particularly the subapical ones, blossom at a much later date then the large flowers and may sometimes wither and fall off before blossom. Abnormal flowers are the rule, and small buds frequently occur in the axils of the 'bracteoles', especially those of the terminal flower. These buds, which have mixed characteristics of flowers and vegetative shoots, exhibit two clearly visible bracteoles and prophylls. Hence the prophylls of the vegetative shoot are probably homologous with the bracteoles of the flower. In this second type of generative short shoot the lateral shoot underneath the inflorescence is poorly developed.
3. This type of short shoot is initiated earlier and is better developed than the normal one. The inflorescence contains no small or abnormally developed flowers. The flowers are large and there are only minor differences in size and date of flowering. The vegetative shoot underneath the inflorescence is better developed than in the normal flowering short shoot.
4. Instead of a vegetative shoot, some of the early-initiated flowering short shoots may bear a small secondary generative short shoot in the lowermost leaf axil. This shoot somewhat resembles the first type of short shoot, except that the terminal flower is the one best developed. This kind of secondary inflorescence blooms later than the main inflorescence and the flowers are misshapen (cf. p. 27). In a few cases an extra leaf has been observed underneath the secondary generative short shoot from whose axil a vegetative shoot develop.

Some years are characterised by an abundance of short shoots of the first two types, so that a small average number of flowers are found in each inflorescence. Conversely, in other years types 3 and 4 abound, giving a higher flower average to each inflorescence. Despite these observations it is impossible to determine exactly what effect the weather has on the initiation and development of the inflorescence.

Such external factors as temperature and day-length have a marked indirect effect on the initiation and development of the inflorescence of the cultivated pear and apple. This is clearly shown by the fact that in young apple trees the periodicity of the development may be absent, with the result that inflorescences may be initiated practically throughout the year (ZELLER, 1960–I, II). In a number of apple cultivars it was found that the photoperiod had some effect on flower initiation (GORTER, 1965; HILLMAN, 1962), but on the other hand other cultivars showed no response to differences in day-length (GORTER, 1955).

The internal factors affecting the flower initiation of fruit trees have been dealt

with in extenso by KOBEL (1954). Generally speaking, vigorous vegetative growth goes with a poor and irregular initiation of inflorescences. Inhibited growth leads to good and regular initiation, as is also the case with *Pyrus nivalis.*

Tree I in the Belmonte Arboretum initiates its inflorescences much earlier and far more regularly than trees II and III. Usually inflorescences are said to be initiated some weeks after the long shoots have finished growing. In regions with a continental climate two flowering periods may occasionally occur. In this case it is assumed that high temperatures lead to a 'summer dormancy' in the year preceding blossom and that inflorescences are initiated before and after this 'dormant period'. It was long thought that the ratio in which carbohydrate and nitrogen (C/N) are available to a bud is the factor determining vegetative or generative development. But this theory is not supported by detailed studies. The theory is, however, true as a general statement applied to an entire tree. To ensure a good initiation of the inflorescences a certain equilibrium should exist between the nitrogen uptake of the roots and the carbohydrate supply via the leaves. The initiation of inflorescences is inhibited both by a low and a high nitrogen dressing. Some researchers have found that in flower-producing shoots of the apple the starch content is higher than in other shoots. They consider that one requirement for flower initiation is a certain amount of starch below the growing point, and a further requirement would be the impulse provided by a flowering hormone from the leaves (in this connection cf. KOBEL, 1954). According to FULFORD (1965, 1966–II, III, and IV) no flowering hormone is involved. He writes: 'Flowering in apple buds is more likely to be due to the removal of factors inhibiting reproductive development than to the synthesis of a specific flower inducing substance as such'. Flowering can be almost entirely suppressed by the artificial shading of trees. The screening of a single shoot prevents flowering at this point and afterwards may even cause the shoot to die. The surrounding shoots show no response. Apparently certain substances which the leaf produces in the light are fairly immobile or rapidly broken down.

Of the cultivated pear, practitioners say that four or more leaves on the short shoot are a guarantee it will flower in the following year. LECRENIER (1962) checked this rule of thumb by studying 9 pear cultivars ('Bon Chétien William', 'Jules d'Airoles', 'Durondeau', 'Beurré Alexandre Lucas', 'Beurré de Naghin', 'Doyenné du Comice', 'William's Duchess', 'Précoce de Trévoux' and 'Triomphe de Vienne') at Gembloux from 1944 to 1957. He found that the relationship between the number of leaves and the incidence of flowering is a factor of minor importance compared with the processes associated with flowering. But the chances of flowering are increased when the short shoot has many leaves, so that a relatively greater number of inflorescences are formed in terminal buds of short shoots with four or more leaves than in those of short shoots with less than four leaves. It very frequently happens that the buds below the inflorescence of the cultivated pear (cf. p. 9) may become generative in the same year. This means that a short shoot initiates an inflorescence in its terminal bud without ever having borne leaves. This method of initiating an inflorescence is

described by ZELLER (1958) as a normal developmental process.

Young trees usually produce no inflorescences, apparently because the physiological equilibrium between vegetative and generative growth has still to be reached (cf. KOBEL, 1954). In older trees (despite considerable differences between cultivars) most inflorescence buds are usually formed on the short lateral shoots of two-year-old branches. Four to six year and older branches bear relatively fewer mixed buds. The quality of the buds on branches of differing ages is, however, practically the same. In a tree ('Williams Christ') with little young wood in the crown, the differences in bud-number between young and old branches are small, possibly because of the absence of competition of young long shoots (FEUCHT, 1961–a).

It seems that owing to the production of auxins, such growth centres as rapidly growing shoots, apical meristems (apical dominance), fruits, and in some cases leaves, have an inhibiting effect on flower induction and development (FEUCHT, 1961–b). ZELLER (1954) found that the fruit had no effect on the initiation of inflorescences.

Much of the published evidence on the initiation and development of the pear inflorescence is either difficult to combine or contradictory. There are some subjects, such as the development of the flower under varying conditions, that have hardly been studied at all. But in order to assess the value of new horticultural methods, especially sprays of growth-retarding compounds (GRIGGS, IWAKIRI and BETHEL, 1965; JONKERS, 1965; STUURSTOFFEN-SYMPOSIUM, 1967), we need a thorough insight into the morphogenesis of the inflorescence and flower, and hence the fruit, since it is precisely the development of these that is influenced by such methods.

The irregular initiation and development of the inflorescence of *Pyrus nivalis* fits well into the uncertain pattern given of the inflorescence of the cultivated pear. The morphogenesis of the inflorescence will be dealt with more fully in the next chapter.

3.2.4. *The flower*

The great variability of the flower, especially the gynoecium of the Rosaceae, has resulted in numerous studies. A great deal of literature has been devoted to the problem of the inferior ovary of the Pomoideae. MACDANIELS (1940) discusses three different theories as to the origin of the inferior ovary, viz.:

1. The axial, or receptacular, theory.

The inferior ovary mainly consists of axis tissue in the shape of a cuplike receptacle enclosing the carpels. The sepals, petals and stamens are embedded in the upper edge of this floral tube.

2. The appendicular theory.

The tissue surrounding the carpels is formed by fusion of the bases of the sepals, petals and stamens, so that the cup is leaf-like rather than axillar.

3. A combination of 1 and 2.

The tissue surrounding the carpels may be partly axial and partly appendicular in origin.

Both MACDANIELS (1940) and EAMES (1961) consider the vascular bundle pattern of the apple and pear flower to be evidence for the appendicular origin of the cup. Other workers accept the receptacular theory (BAIN, 1961; MITCHELL, 1950). Studies of the flower and fruit of *Pyrus nivalis* have not brought to light any fresh information that would warrant the outright adoption of any one of these three theories.

A general survey of the theories relating to the inferior ovary is given by DOUGLAS (1944, 1957). JUEL's (1918) article shows the importance of attending to nomenclature when perusing older literature. In his anatomical study of the flower of the Rosaceae he describes certain details of the species *Pyrus malus* L. and *Pyrus arbutifolia* (L.) L. fil. Neither species is now representative of the genus *Pyrus* according to the present-day definition. The apple, *Pyrus malus* L., now belongs to the genus *Malus* and apparently *Pyrus arbutifolia* (L.) L. fil. should be known as *Aronia arbutifolia* (L.) Pers.

Few studies have been concerned with the development of the pear flower.

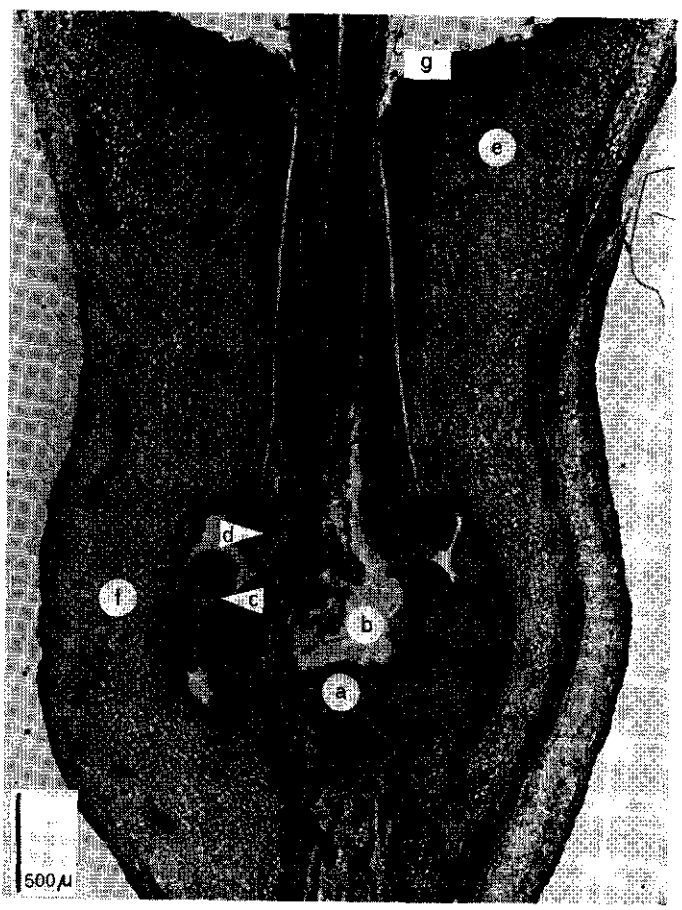


FIG. 4. Median longitudinal section of the inferior ovary of a *Pyrus nivalis* flower (13th May, 1958, stage 11).

a. apex; *b.* cavity above the apex; *c.* ovule (embryo sac containing 8 nuclei); *d.* attachment of the free style; *e.* annular (toral) nectary; *f.* future flesh (cells in longitudinal rows); *g.* for detail see Figure 5.

LUYTEN and DE VRIES (1926) describe a number of developmental phases of the flower of the pear cultivar 'Beurré Hardy'. ZELLER (1958) also gives a survey of the development of the pear flower. The work done by these authors will be considered in further detail in the next chapter. RAUH and REZNIK (1951) carried out a comparative study of the development of the cuplike axis of inflorescences and flowers, including the pear flower.

A brief description of the flower of *Pyrus nivalis* in the blossoming period is given below. The inferior ovary, the most important part of the flower, is shown in longisection in Figure 4. The bisexual actinomorphic flowers are pentamerous. The floral axis is continued in a cuplike receptacle. The sepals and petals, like the 20 odd stamens, are situated on the edge of the cup. The bottom of the cup still contains the remainder of the apical meristem from which the floral parts were formed. Surrounding the growing point are five carpels each facing a sepal. The upright carpels each containing two ovules are fused dorsally with the inner wall of the cuplike receptacle. The ventral suture of the carpels is never entirely closed. The interior of the loculi is in open communication with the atmosphere via the space above the growing point. The five free styles are attached to the ventral side of the carpels. Shortly before bloom the part of the cup bearing the sepals, petals and stamens grows upward. The greater part of the cup wall is formed by this 'intercalary' growth. The growing point and carpels remain in situ and in their deep recess form the inferior ovary together with the cup wall. The inside of the cup wall has developed into a nectariferous tissue (according to FAHN (1967) an 'annular-toral-nectary'). Finally the nectary encloses the free styles like a tube over a considerable portion of their length. Stomata are to be found in the epidermis of the horizontal part of the nectary, around the point at which the styles extend outward (Figure 5). The nectar with its characteristic aminic odour exudes through the apertures of these stomata.

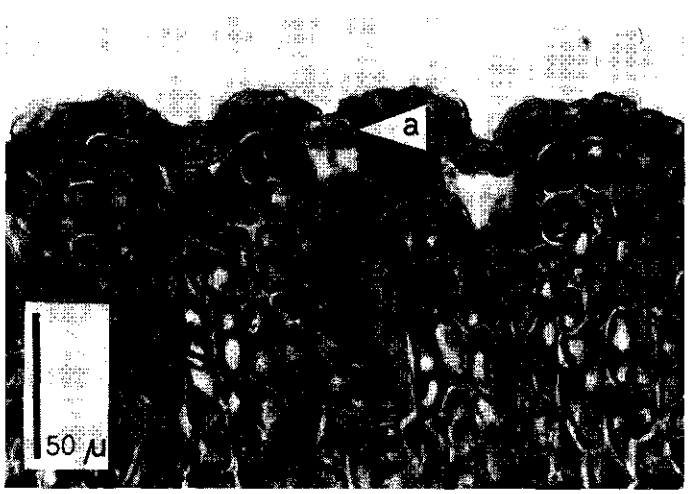


FIG. 5. Detail of nectary.

a. stoma.

3.2.5. *The fruit*

The fruit of the pear, unlike that of the apple, is characterised by the presence of stone cells (brachysclereids) in the flesh. (But there are also one or two apple species containing stone cells in the flesh (KONOVALOV, 1946; MACDANIELS, 1940)). In the pear the stone cells are tightly bound aggregates of varying sizes ('nests' or clusters). These clusters are particularly abundant in a layer surrounding the core and in a layer just below the epidermis. It is these clusters that are responsible for the pear's grittiness. The succulent parenchyma flesh cells containing sugars are arranged around the hard clusters in a radial pattern (Fig. 6). These cells are the only ones that contribute to the pear's nutritive value; it is therefore difficult to understand why so little research has been done on the structure and size of the sclereid clusters and the ratio of stone-cell tissue to parenchyma tissue in the flesh of the pear. Such an investigation made by VAN BLARICOM and BRITTAIN (1961) on behalf of food manufacturers is practically the only one of its kind.

Important modern anatomical and morphological studies of the fruit of the cultivated pear have been undertaken by BAIN (1961), MITCHELL (1950),

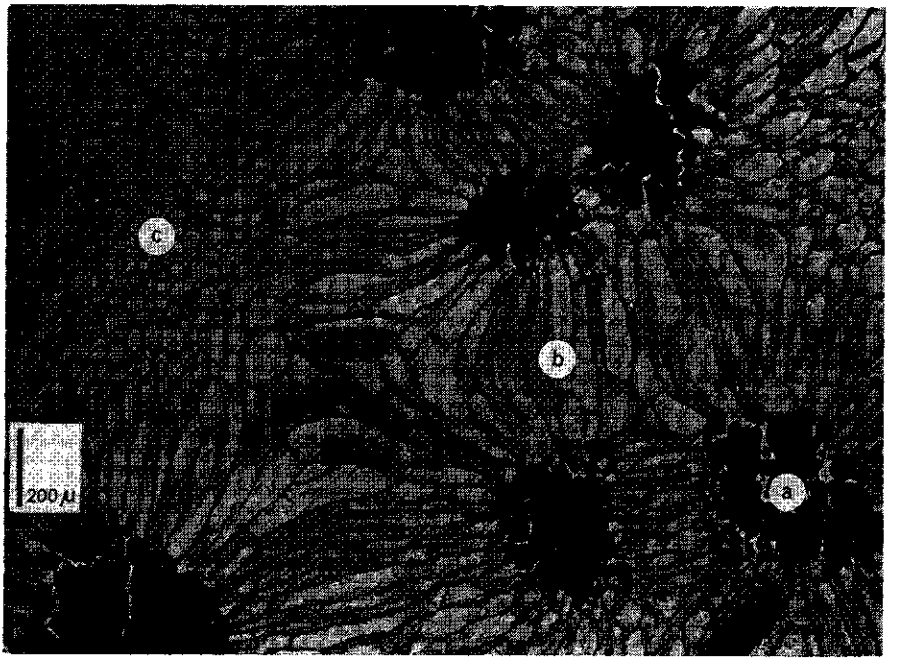


FIG. 6. Flesh of a ripe pear.

a. sclereid cluster
b. elongated parenchyma cells, only 2 to 3 between two adjacent clusters of sclereid
c. at this point the microtome knife has passed between two sclereid clusters, producing a transverse section of the elongated parenchyma cells

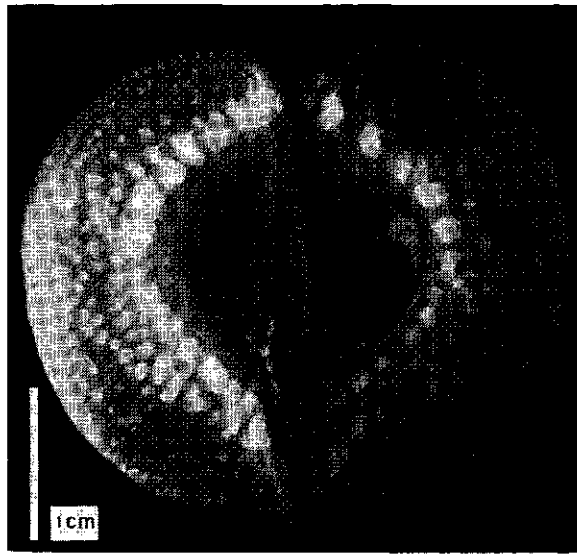


FIG. 7. Median longitudinal section of a ripe fruit of *Pyrus nivalis*. The white patches in the photo are sclereid clusters.

ROSPER (1957) and STERLING (1954). All four give fairly extensive reviews of the older literature.

The fruit of *Pyrus nivalis* is not of the well-known pyriform shape but practically spherical, its diameter not usually exceeding 30 to 40 mm. The longisection of a ripe fruit is shown in Figure 7. The chief characteristic of *Pyrus nivalis* is the layer of closely-knit sclereid clusters around the core and the comparatively small number of fairly large sclereid clusters in the flesh. After the pears have been boiled and pureed, the sclereid clusters can be separated from the other solid constituents of the fruit by centrifuging. Table 1 shows the result of a rough analysis of this kind. It can be calculated from the data supplied by VAN BLARICOM and BRITTAIN (1961) that depending on the cultivar investigated, the stone cell content may amount to 7 to 14 weight per cent. of the dry matter. Compared with this the stone cell content of the ripe fruit of *Pyrus nivalis* is at least $2\frac{1}{2}$ times as high.

TABLE 1. Composition of the dry matter of a fruit of *Pyrus nivalis*.

	Weight per cent.
Sugars and other water-soluble materials	49
Stone cells (clusters)	37
Residual tissue of epidermis, core and flesh	10
Stalk	2
Seeds	2

The fruit has a remarkably good flavour, especially when it has been laid down for some time and has become over-ripe. The sclereid clusters are the only reason why the fruit is unacceptable to the average consumer.

4. THE DEVELOPMENT OF THE INFLORESCENCE AND FLOWER

4.1. INTRODUCTORY

The *Pyrus nivalis* blossom is usually abundant and uniform, all flowers appearing to be exactly alike. For this reason the developmental study of the fruit was first based on the assumption that the starting point, i.e. the inferior ovary, is so much the same in each fruit that any differences between fruits must be due to other factors. Later, however, it was noticed that the growth curves of individual fruits rarely intersect (§5.3.11.). This means that original differences in the size of young fruits or ovaries are perpetuated during development. In fact, an agreement was found between the distribution of large and small flowers in the inflorescence (§ 4.3.1.) and that of large and small fruits on the short shoot (§5.3.7.). DENNE's (1963) and VISSER's (1955) studies of the apple point in the same direction. This makes it a difficult matter to compare fruits sampled at random, and it also disproves the assumption that individual differences in the size of the inferior ovary may be ignored. The frequent occurrence of tri- and quadri-locular fruits in *Pyrus nivalis* points to morphological differences which it should already be possible to observe in the flower. Quadri-locular fruits are also frequently found in the cultivated pear, so much so that EICHLER (1875–1878) draws a quadri-locular ovary in his floral diagram of '*Pyrus communis*'. The literature contains sporadic references to the occurrence of abnormal numbers of locules in the pear fruit. Their origin has not been the subject of any study. Particular attention is devoted to this phenomenon in the present study of the flower and inflorescence.

4.2. THE INITIATION AND DEVELOPMENT OF THE MIXED BUD

4.2.1. *Survey of the development*

COUTIN (1959) describes a number of developmental phases of the mixed bud and the inflorescence of the pear. His sub-divisions are an amplification of FLECKINGER's (1946) and like the latter is entirely based on external morphological characters. These sub-divisions are used for such purposes as indicating the correct time for using sprays for the control of fruit pests and diseases which are closely allied to a specific level of development of the flowering shoot. In a survey extending over a 20-year period (1944–1963), SOENEN (1964) gives for 31 apple and 25 pear cultivars the time at which the relevant developmental phases are reached.

Before these external changes become visible, the apex of the short shoot has already developed into a complete primordial inflorescence inside the bud. LUYTEN and DE VRIES (1926) distinguished eight different developmental phases in stripped mixed buds of the pear 'Beurré Hardy' in the year preceding blossom. ZELLER (1955) distinguishes twelve developmental stages from initiation to blossom. She afterwards published an article (ZELLER, 1960–I) showing micro-

photographs of developmental phases of the apple. Both in LUYTEN and DE VRIES (1926) and ZELLER (1958) only the first two developmental phases relate to the inflorescence as a whole, the other phases being concerned with the separate flower. Since the initiation and development of the individual flowers are not synchronous, LUYTEN and DE VRIES's (1926) classify the inflorescence according to the phase of one flower only, i.e. the second from the bottom, ZELLER (1958) uses the average of the phases of all the flowers in each inflorescence. The sub-divisions of LUYTEN and DE VRIES (1926) and ZELLER (1955, 1958, 1960–I) are shown below side-by-side:

LUYTEN and DE VRIES		ZELLER	
I	Leaf formation	0	Vegetative phase
II	Expansion of the growing point (primordia of the first flowers + bracteoles appear in the form of a single growing point)	1	Commencement of the generative phase ('Pflockstadium')
III	The first primordia differentiate into bracteoles and the primordium of the actual flower	2	Differentiation of the bracteoles (ZELLER, 1955)
IV	The sepal primordia are initiated (the terminal growing point of the inflorescence continues to split off bracts)	3	Sepal differentiation
V	The petal primordia are initiated (the terminal flower is now formed)	4	Petal differentiation
VI	The 10 primordia of the first whorl of stamens are initiated	5	Stamen differentiation
VII	The primordia of the second (5) and third (5) whorl of stamens are initiated		
VIII	The 5 primordia of the carpels are initiated	6	Carpel differentiation
		7	Archesporium differentiation in the anther sacs
		8	Differentiation of pollen mother cells and ovules
		9	Differentiation of the pollen tetrads
		10	The pollen grains are separated; differentiation of nucellus and integuments in the ovules
		11	Differentiation of the embryo sac + egg-cell (anthesis).

The pre-winter development of the inflorescence takes about three months from the initiation to phase VIII ('Beurré Hardy') or to phase 6–7 ('Gellerts Butterbirne', 'Williams Christ'). This is followed by a period of from four to five months in which the inflorescence only continues to develop at a slow rate. From March to April the inflorescence passes through phases 6 to 11 in rapid succession, followed by bloom.

In *Pyrus nivalis* the same developmental phases of the inflorescence may be distinguished as in the cultivated pear. ZELLER's (1955, 1958) sub-divisions will also be adhered to for *Pyrus nivalis* (Figures 8–15, 4 and 23).

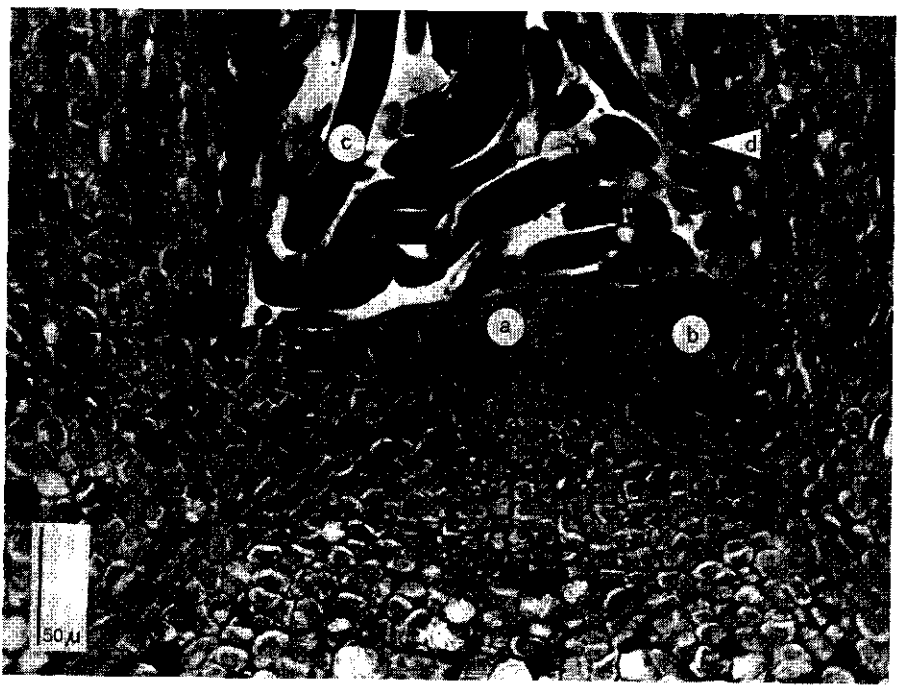


FIG. 8. Apex, vegetative phase (0).

a. the flat apex with at least four tunica layers
b. primordium
c. heavily lignified hair
d. hair insertion

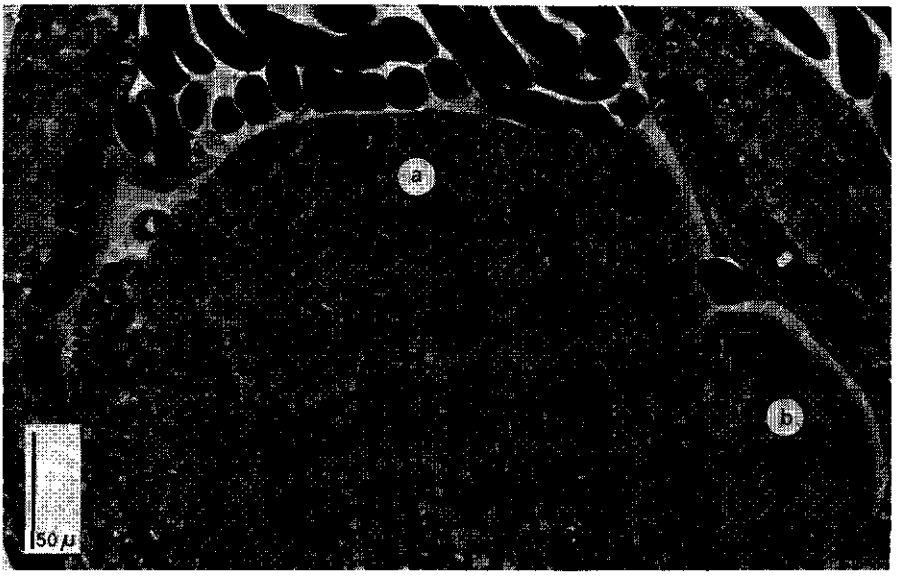


FIG. 9. Apex, beginning of the generative phase (1).
a. expanding apex, two or three tunica layers
b. primordium of a lateral flower with bracteoles or a primordial vegetative lateral shoot

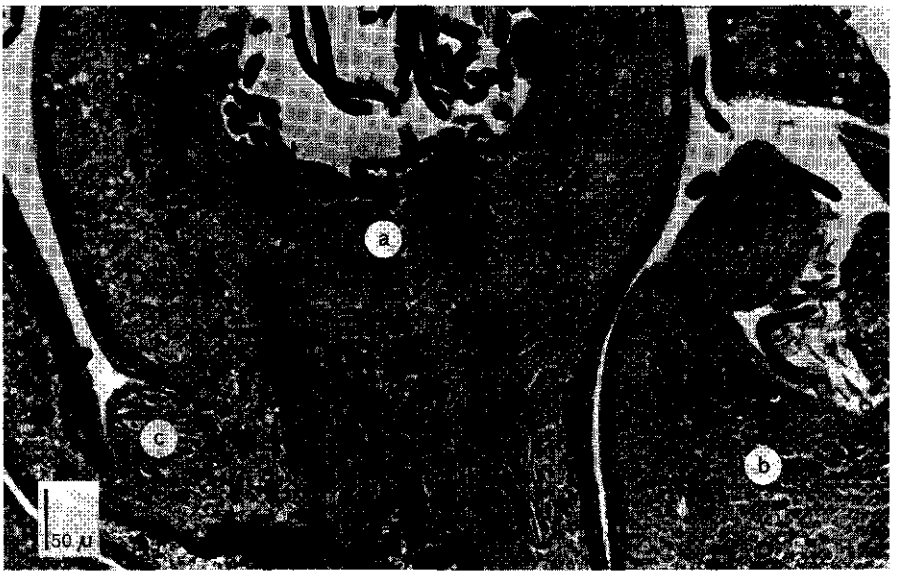


FIG. 10. Upper part of a developing inflorescence (12th November, 1958).
a. apical flower, petal and stamen differentiation (stage 4–5)
b. lateral flower, sepal differentiation (stage 3)
c. undeveloped flower primordium in the axil of a bract

FIG. 11. Upper part of a developing inflorescence (4th January, 1965).
a. apical flower, carpel differentiation (stage 6) the pedicel begins to form; *b.* lateral flower, petal differentiation (stage 4); *c.* lateral flower, stamen differentiation (stage 5); *d.* undeveloped flower primordium in the axil of a bract

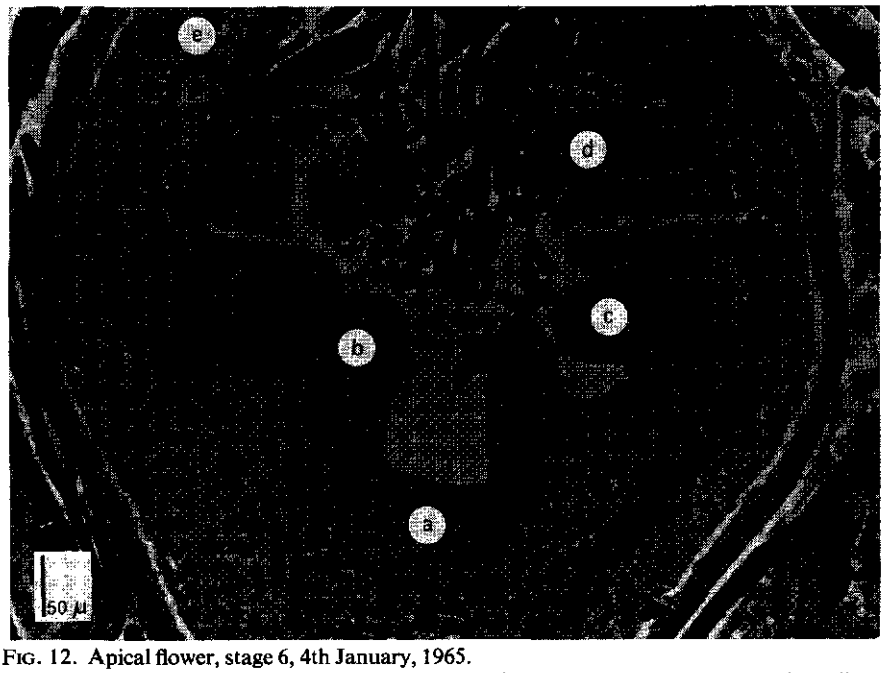


FIG. 12. Apical flower, stage 6, 4th January, 1965.
a. apex with two tunica layers; *b.* carpel primordium; *c.* stamen primordium; *d.* petal primordium; *e.* calyx lobe covered with hairs

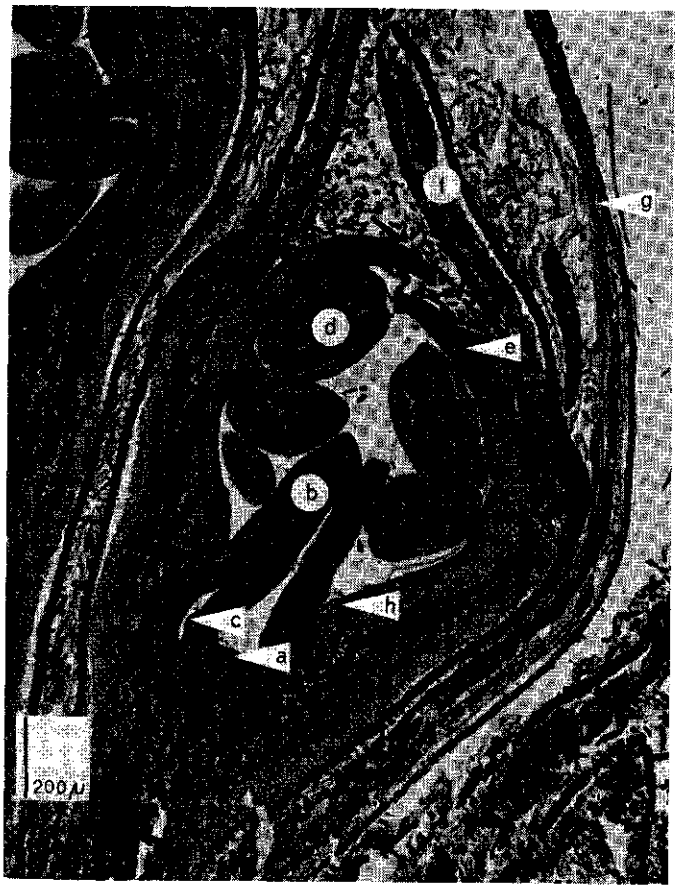


FIG. 13. Lateral flower, stage 8, 28th March, 1958.
a. apex
b. style
c. ovule primordium
d. stamen, the pollen mother cells have been formed
e. petal
f. calyx lobe
g. bract
h. differentiation of nectary

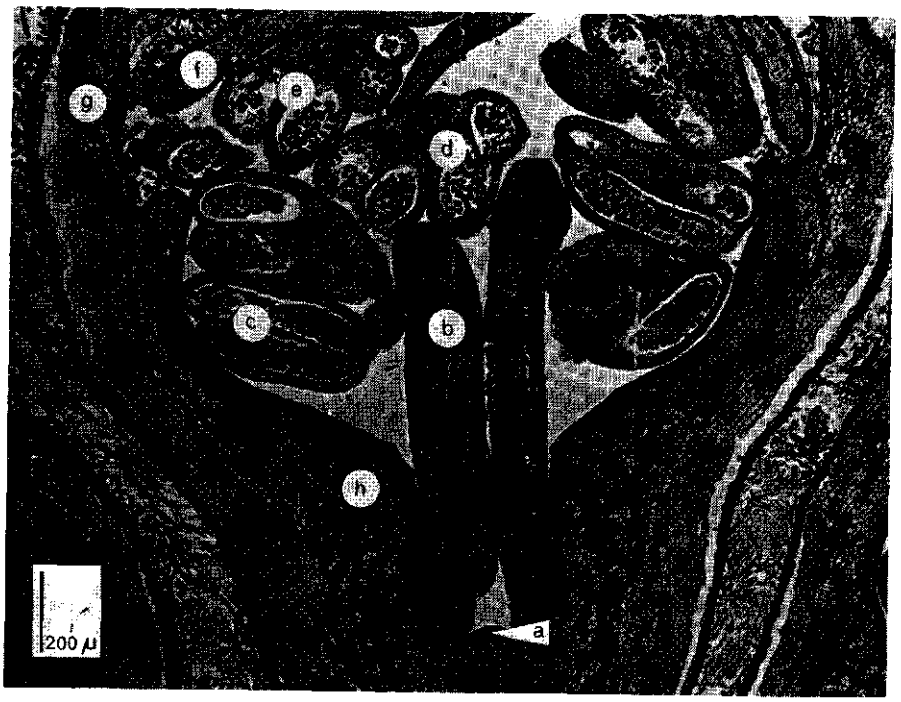


FIG. 14. Apical flower, stage 9, pollen meiosis, 14th April, 1958.
a. apex
b. style
c. longisection of anther (approx. pachytene)
d. transverse section of anther (approx. diakinesis – prophase II)
e. transverse section of anther, tetrads formed
f. petal
g. calyx lobe
h. nectary

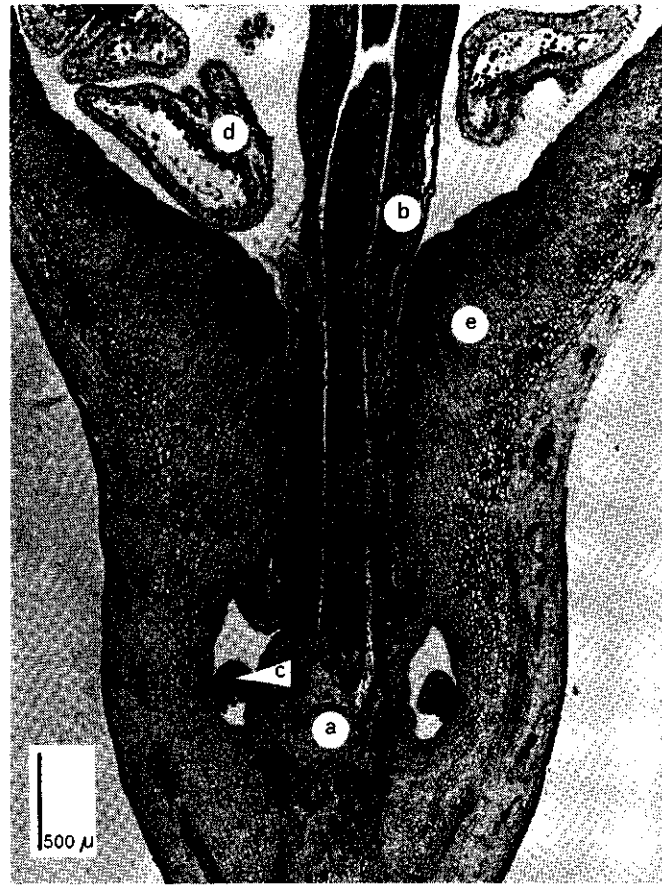


FIG. 15. Flower in balloon stage (stage 10) 2nd May, 1958.
a. apex, in the cavity above hairs inserted at the bases of the styles; *b.* style; *c.* ovule, the integuments have developed; *d.* anther, the pollen grains are detached; *e.* nectary, forms a large part of the ovary
N.B. Cf. Figure 15 (stage 10) with Figure 4 (stage 11)

4.2.2. *The vegetative phase*

Sooner or later each short shoot of the pear will initiate an inflorescence in its terminal bud, so that the term 'vegetative short shoot' as employed in § 3.2.1. is not strictly correct and it is preferable to refer to a short shoot in the vegetative phase or vegetative stage. This phase lasts from the initiation of the short shoot to the first initiation of an inflorescence in the terminal bud.

Short shoots may assume the form of lateral shoots of long shoots (Fig. 1), lateral shoots of long-short shoots (B-Kurztriebe, ZELLER, 1954), or lateral shoots of the ordinary thick-set short shoots (A-Kurztriebe, ZELLER, 1954). The latter type are mostly found in the somewhat older pear trees of the kind investigated. The secondary short shoot is the sympodial continuation of the primary short shoot when the apex of the terminal bud becomes generative or

is lost as a result of injury. The vegetative phase of such a secondary short shoot commences in the bud when the primordia of two prophylla are formed in the axil of the developing foliage leaf just below the initiating inflorescence, and are followed by the primordia of 3–5 foliage leaves. This takes place in the late summer and autumn and coincides with the initiation and development of the inflorescence. The lateral shoot opens at bloom in the following spring (Fig. 2).

After bloom the growing point of these young secondary short shoots continues to split off primordia. Those of the 24 bud scales are first formed, followed by those of the foliage leaves below and on the inflorescence. As soon as the growing point starts to expand the vegetative phase is completed and the generative phase begins. The earliest date at which this occurs in *Pyrus nivalis* is the first half of August, when a new short shoot is initiated simultaneously with the new inflorescence. Hence the vegetative phase of a short shoot of *Pyrus nivalis* normally lasts exactly twelve months. Often an inflorescence is not initiated directly, but another rosette of foliage leaves is developed from the terminal bud, these usually being more numerous than the year before. In this case no new secondary short shoots are formed and the vegetative phase lasts two years, or may even extend over three or more years.

As in the cultivated pear, the number of leaves on the shoot is probably a factor determining the initiation or non-initiation of the inflorescence (LECRENIER, 1962). In exceptional cases the apex of a young secondary short shoot may become generative immediately after the formation of the foliage leaf primordia. Consequently this secondary inflorescence (Figure 3) is formed in the same period, but a little later than the inflorescence of the primary short shoot. In this case the vegetative phase only takes a few weeks or months.

Such secondary inflorescences are also found in the cultivated pear. In some varieties of pear these 'Nachinfloreszenzen' may result in a second flowering period (HEINRICH, 1959), although usually no more than 0.1%–0.5% of the inflorescences have such a secondary inflorescence (ZELLER, 1954). Secondary inflorescences were first observed in *Pyrus nivalis* in 1967. Sixty-seven inflorescences were found on one branch, and 7 of these, or over 10%, bore a secondary inflorescence.

The duration of the vegetative phase depends, among other factors, on the state of the tree. Buds of trees that exhibit vigorous vegetative growth, e.g. trees II and III, generally end their vegetative phase later in the season than those of such poorly growing trees as tree I.

During the vegetative phase the apical meristem of the short shoot is small, narrow and flat. As in the apple (HILKENBÄUMER and BUCHLOH, 1954), four tunica layers are present.

4.2.3. *Commencement of the generative phase*

The generative phase of the short shoot commences when the apical meristem widens and the two innermost tunica layers are disturbed. The entire meristem starts to expand and becomes spherical, bract primordia are split off, and single

primordia, which will subsequently form the flower together with the bracteoles, are produced in the axils of the foliage leaves already initiated in the vegetative phase.

Flower initiation is generally equated with flower formation BÜNNING, 1953; SALISBURY, 1963), but conditions conducive to flower initiation may often be unfavourable for flower development. It is therefore desirable to distinguish a number of phases of generative development, most of which partially overlap, viz.:

1. development of the inflorescence (in *Pyrus nivalis*, of the flowering shoot);
2. development of the vegetative parts of the flower;
3. development of the carpels and stamens;
4. 'sexualisation' of the carpels and stamens.

These four phases are closely allied but one does not necessarily pass over into another. The absence of such a transition is to be regarded as a response to less favourable internal or external conditions.

Thus in the first phase a meristem may be initiated which is capable of forming an inflorescence. Owing to certain factors such a meristem develops into a vegetative shoot instead of into a generative short shoot, for instance the long-short shoots of which the bracts become foliage leaves and the flower primordia vegetative buds.

Something of the kind may occur in the second phase during floral initiation. After the bracts have been split off, the sepal primordia follow in the same order as the foliage leaf primordia of a short shoot. The initiating flower may pass over into a short shoot, e.g. in the lateral shoot below the inflorescence, the bracteoles then become the prophylla of the shoot and the sepals become foliage leaves. Since flower primordia with such tendencies form new parts at a slower rate than those with vigorous generative development, they can be distinguished at an early stage. When the flower primordium fails to pass over into a short shoot, the ovary remains smaller owing to the somewhat inhibited development, and flowering occurs at a rather later date than would otherwise have been the case. If the flower primordium becomes vegetative, its wide apical meristem with the whorls of primordia shows that a flower should actually have been formed at this point. The generally later flowering and reduced size of the lowermost flower in the inflorescence is due to the fluctuating development which is a frequent phenomenon here.

The third phase is marked by the development of the carpels and stamens. This development may also be partly or entirely absent without upsetting the preceding flower development. Ten inflorescences of *Pyrus austriaca* were examined in 1966; in two of the 82 flowers there was a complete absence of carpels. These flowers have a fairly normal appearance but they are without the characteristic thickening of the inferior ovary. *Pyrus pyrifolia* has a number of flowers with only four or five stamens. In 1966 a small number of stamens to a flower was the rule for *Pyrus pyrifolia*, but it was exceptional to find less than five styles.

The converse was true of the other wild pear species examined *(P. amygdaliformis, P. elaeagrifolia* and *P. austriaca)*. As in *Pyrus nivalis*, it was precisely the number of carpels that was reduced, the number of stamens not being noticeably different. The cause of this difference was not investigated, although it was observed that *Pyrus pyrifolia*, unlike the other pear species, had little or no foliage leaves in the inflorescence.

The fourth developmental phase is termed 'sexualisation'. In this phase egg-cells and pollen grains begin to develop in the ovules and stamens. Full generative development is not accomplished until the egg-cells and pollen grains are capable of generative propagation. The absence of this final part of the 'sexualisation' phase is difficult to establish. It may possibly be absent in the flowers of 'Nachinfloreszenzen', since no trace of seeds or even a core is hardly ever discoverable in the fruits produced by these flowers (HEINRICH, 1959).

FEUCHT (1961–b) notes that the flowers of the highly vegetative inflorescence of the apple and pear (pome fruits) develop a greater number of carpels than the flowers of cherry and plum (stone fruits). Since the inflorescences of stone fruits are found at points of poor growth, the flowers apparently tend to produce far more stamens than those of pomefruits. Moreover (still quoting FEUCHT) the more vigorously vegetative, i.e. the more female the inflorescences, the later they flower. These correlations are said to be associated with growth-regulating hormones (auxins, growth retardants, growth regulators). Apparently a lower auxin level is required for optimum development of stamens than for the formation of carpels. According to FEUCHT (1961–b) the correlations are not only true of fruit-trees in general but also of the individual tree and a separate shoot.

Some observations were already made in § 3.2.3. on the factors influencing flower initiation; it emerged that the factor or combination of factors responsible for this flower initiation are still not exactly known. Nothing was found in *Pyrus nivalis* that throws any further light on this problem.

In 1966 a number of buds exhibiting initiation of the inflorescence were found as early as August. In other years this initiation was later and early developmental stages of the inflorescence were noted from September to the beginning of December. Hence *Pyrus nivalis* is somewhat comparable to the pear cultivar 'Beurré Hardy' that also exhibits late initiation of the inflorescence. ZELLER (1954) found that after the inflorescences of the pear cultivar 'Herzogin Elsa' had been initiated in the normal fashion in July, a few buds in the first developmental phase were subsequently discovered in September. 'Nachinfloreszenzen' are initiated in October, November, January, February and March. As a rule the inflorescences on two-year-old short shoots (A-Kurztriebe) are initiated one to three weeks later than those on one-year-old short shoots. One-year-old short-long shoots (B-Kurztriebe) are in turn somewhat later than the one-year-old short shoots. According to ZELLER, for the one-year-old short shoots of either apple or pear it is immaterial whether a fruit is absent or present above the bud. This is in contradistinction to the data given by FEUCHT (1961–b) according to whom the proximity of fruits inhibits or prevents initiation of inflorescences.

The examination of the buds of *Pyrus nivalis* was not extensive enough to confirm any of these statements. It would seem that the fruits of tree I have no effect on the date on which the inflorescence is initiated. Initiation is so irregular in trees II and III that no single conclusion can be drawn.

4.2.4. *Autumn development of the inflorescence*

Initiation of the inflorescence of the cultivated pear is succeeded by rapid development. Before winter sets in the flowers reach the stage at which the carpels are initiated (ZELLER's stage 6 or 7). A 'winter dormancy' is then said to commence which is not broken until the spring.

Only a few workers have tested the accuracy of this statement (PUDOC, 1967). Except in the late pear cultivars 'Beurré Hardy' and 'Légipont', in 1953 the flowers had formed the carpels as early as October, even in the north of Holland where initiation starts about a fortnight later than in the south (FELIUS, 1954). As LUYTEN and DE VRIES (1926) have shown, in the pear cultivar 'Beurré Hardy' inflorescences may be found in stage V (1922) or stage IV (1923) up to November. The later the date of sampling the greater are the differences in development. LUYTEN and DE VRIES measure the developmental stages of the inflorescence by the development of the second flower from the bottom, when the other flowers in the inflorescence are less forward. For instance, the terminal flower begins to develop about a month later than the second flower from the bottom of the inflorescence. LUYTEN and DE VRIES (1926) observed that in the flowering period only about four of the lowermost flowers of many inflorescences blossomed, the others only being represented by scars. Sometimes the terminal flower and the lowermost flowers exhibited good development but one or more flowers below the uppermost flower had already disappeared during bloom. They query whether the vanished flowers may not have been those that had not completed their development before the winter (stage VIII) and whether there were any other inflorescences that completely failed to develop.

A detailed study was made of the development of the *Pyrus nivalis* inflorescence. Slides were made of a large number of peeled buds. The most fully developed flower was taken as the criterion for determining the developmental stage of the inflorescence. The observations are summarised in Table 2. The figures denote the number of inflorescences of a specific stage on each sampling date. The letters L and W indicate whether the buds were sampled at Leiden (L) or Wageningen (W).

It can be seen from the Table that *Pyrus nivalis* inflorescences also reach stage 6 before the winter, although in some years (1958, 1962), as in the pear cultivar 'Beurré Hardy', backward inflorescences can be found late in the year. In these inflorescences the differences in development between one flower and another are greater than in early inflorescences. The flowers at positions 2 and 3 in the inflorescence are particularly backward, and even when the inflorescences develop well in the autumn the flowers formed at these points may have carpels that do not start developing before the winter.

TABLE 2. Stage of development of a number of inflorescences in the autumn of 1957, 1958, 1962, 1963, 1964 and winter of 1965. For stages 2–7, the stage reached by the most developed flower is invariably considered to determine the entire inflorescence.

Date	Stage 0	1	2	3	4	5	6	7	
19 Sept. 1962	2	–	–	–	–	–	–	–	L
4 Oct. 1962	3	1	1	–	–	–	–	–	L
16 Oct. 1962	1	2	2	–	–	–	–	–	L
21 Oct. 1964	–	–	–	–	–	1	1	–	W
2 Nov. 1964	–	–	–	–	–	2	2	–	W
7 Nov. 1963	–	–	–	–	–	2	1	–	L
12 Nov. 1958	5	–	–	2	1	–	2	–	L
23 Nov. 1964	–	–	–	–	–	–	4	–	W
4 Dec. 1962	–	–	2	1	–	–	–	–	L
14 Dec. 1964	–	–	–	–	–	–	–	4	W
20 Dec. 1957	–	–	–	–	–	–	4	–	L
4 Jan. 1965	–	–	–	–	–	–	2	1	W

L = Leiden W = Wageningen

4.2.5. *Winter development of the inflorescence*

Like most other deciduous trees, pear and apple trees pass through a period of winter dormancy in these latitudes. It is not broken until the buds have been exposed to a certain period of low temperatures.

The term 'winter dormancy' is in fact a misnomer, no real dormancy being involved. Development continues slowly and surely inside the bud (ZELLER, 1955). New developmental stages may be reached in backward flowers, and flowers exhibiting no further 'development' may grow heavier and larger. In some cases entirely new inflorescences may even be initiated (ZELLER, 1954, 1960–I, 1960–II).

In order to gain some impression of the winter development of *Pyrus nivalis*, the developmental stages were determined of the individual flowers of a number of inflorescences. The data is summarised in Table 3. In addition to the progressive development, the Table clearly shows how the degree of flower development may vary in a bud, depending on its position in the inflorescence. On 4 February two of the eight inflorescences had not yet reached stage 6, and in 34 out of 62, or 55%, of the flowers the carpels had still not been initiated. By 25 February only one of the 11 inflorescences had failed to reach stage 6, and the carpels only failed to develop in 21 out of 93, or 23%, of the flowers. By 18 March this only applied to 1 out of 75 flowers, and in 5 out of 9 flowers pollen meiosis had already taken place in a very forward inflorescence.

During the autumn and winter there is a slow but noticeable change in the external shape and dimensions of the mixed buds. The mutual differences are very great, not only between trees or branches but also from year to year. In November the buds are sometimes nothing more than a conical extension of the short shoots and do not become longer and thicker until December or January, when a constriction is formed between the bursa and bud. In other years buds

TABLE 3. The development of individual flowers of a number of inflorescences in the winter of 1966.
Developmental stages 2–9 are described on page 20.

Date	Position of the flower in the inflorescence									
	1	2	3	4	5	6	7	8	9	10
4 February	6	3	4	4	5	5	–	–	–	–
(8 buds)	5	2	3	3	3	3	5	5	–	–
	6	2	5	?	?	?	6	6	6	–
	6	4	5	5	6	6	6	6	6	6
	6	3	4	5	5	5	6	6	–	–
	6	4	5	6	?	?	6	6	6	–
	5	3	3	3	4	4	4	5	–	–
	6	5	6	6	6	6	6	6	6	–
Mean	5.8	3.3	4.4	4.6	4.8	4.8	5.6	5.7	6.0	6.0
25 February	8	5	7	7	7	7	7	7	–	–
(11 buds)	7	5	5	6	6	6	6	6	–	–
	7	3	3	5	6	6	6	6	–	–
	7	6	6	6	7	7	7	7	8	–
	7	6	6	6	6	?	?	7	7	–
	6	3	5	5	6	6	6	6	–	–
	7	6	6	6	6	6	7	7	–	–
	7	5	6	6	6	6	6	6	7	–
	7	6	6	6	6	6	7	7	7	–
	5	2	2	3	3	4	5	5	5	5
	7	2	6	6	6	6	6	6	7	–
Mean	6.8	4.5	5.3	5.6	5.9	6.0	6.3	6.4	6.8	5.0
18 March	8	7	7	7	8	8	8	8	8	–
(9 buds)	7	2	6	6	6	6	7	7	7	–
	8	7	7	8	8	8	8	8	8	–
	8	7	7	7	7	8	8	–	–	–
	8	6	7	7	7	8	8	8	–	–
	8	7	7	8	8	8	8	8	–	–
	9	7	8	8	8	9	9	9	9	–
	8	7	7	7	8	8	8	–	–	–
	8	7	7	8	8	8	8	8	8	–
Mean	8.0	6.3	7.0	7.3	7.6	7.9	8.0	8.0	8.0	–

? indicates that the flower was lost during microtechnical manipulations.

of this shape and dimensions are found as early as September. Naturally a relationship exists between this external development and the internal development of the bud.

Table 4 shows the changes in dimensions of a number of buds, including those in Table 3. The slight elongation of the buds in February is revealed by a white point at the top. Bud elongation was fairly well avanced by 18th March, which is early in the year for *Pyrus nivalis*.

TABLE 4. Average diameter of the bursa, and average diameter and length of buds in the winter of 1966.

Date	ø bursa (mm)	ø bud (mm)	length of bud (mm)
4 February (17 buds)	4.5	5.2	9.5
25 February (20 buds)	4.5	5.1	11.5
18 March (20 buds)	4.9	6.1	17.0

4.2.6. *Spring development of the inflorescence*

The buds of *Pyrus nivalis* begin to produce shoots in the spring. The innermost light-coloured bud scales begin to extend at the base and appear at the top in the form of a white point (mid-March – beginning of April). The slightly more peripheral bud scales also begin to extend at the base, thereby revealing a light-coloured zone between the brown points of these scales and the unextended outermost bud scales. In this way the bud telescopes outward without breaking the protective layer of bud scales. The innermost bud scales may reach a length of about $2\frac{1}{2}$ cm. The short shoot develops rapidly inside the bud, and after a time the first foliage leaves, covered in woolly hairs, pierce the layer of bud scales (the growers 'mouse-ear' stage). The flower buds are next to appear. At first the individual flower buds are greyish-green, the colour of the woolly sepals bent over the other parts of the flower. Later on the petals become visible; these are first pink, but just before blossom they envelops the stamens and styles in the form of a white balloon. The balloon stage is followed by anthesis. The main blossoming period of *Pyrus nivalis* is between the last week of April and the end of May. The date at which bloom begins and its duration depends on the weather and on the rate and uniformity of the preceding development. Under optimum conditions a tree may finish flowering a week after bloom commences, whereas in unfavourable conditions it may take as much as six weeks to reach the end of the flowering period. The differences between the flowers in the inflorescence are maintained during spring development and are sometimes even accentuated. As a result in subapical flowers, for instance, meiosis of the pollen mother cells occurs at a later date than in basal flowers of the inflorescence. This also means that the flowers of the inflorescence bloom in a specific order. The lowest flower or the second from the bottom is the first to bloom (cf. page 28). The other lateral flowers successively open from the base to the apex. The apical flower opens when one or more basal flowers are already in bloom. The rate at which the flowers succeed each other in blooming depends both on the weather and differences in development. If the flowers at positions 2 and 3 are very backward, which frequently happens in certain years, they open several days later than the other flowers in the inflorescence. Sometimes the flower buds at these positions wither even before reaching bloom.

The flowering period of a single flower lasts about three days from the balloon stage until the petals fall off. In the balloon stage the stamens are bent inward. The 10 outermost stamens are usually the first to extend and open

their pollen sacs, followed by the 10 remaining stamens in two groups of five.

RUDLOFF and WUNDRIG (1939) have studied the order in which the inflorescence of cultivated pear blooms. They were able to give a characteristic bloom formula for each of the cultivars studied. Three different types may be distinguished in these formulas. In the first type the apical flower is the first to bloom and is much more advanced than the other flowers; the remaining flowers do not bloom until later, i.e. first the lowermost ones, then those above, and finally the subapical flower. In the second type the basal flower blooms first, followed by the flowers above it, the apical flower blooming very late and only being followed by the two flowers below it. The third type corresponds to the order of blooming in *Pyrus nivalis;* the basal flowers bloom first, followed by the other lateral flowers in the direction of the apex of the inflorescence, while the apical flower starts blooming when a few basal flowers have already opened.

Well developed *Pyrus nivalis* inflorescences bloom early, uniformly and rapidly. There is probably no question of the bloom of the subapical flowers being repressed by the apical flower, although it is possible that the apical flower may inhibit development of flowers 2 and 3. Poorly developed flowers bloom late.

The number of poorly developed flowers was comparatively small in 1967, for instance only 7% of the flowers of tree I had four styles (§ 4.3.3.). It would seem that the anomalies noted are peculiar to late blooming flowers, since when flowers (of tree II) which had just opened were examined at the end of the blossoming period it was found that all these flowers had only four or less styles.

When the weather prevents fruit setting at any given part of the blossoming period, only a limited group of flowers are left for fruit production.

4.3. CORRELATION BETWEEN FLOWER CHARACTERISTICS AND POSITION IN THE INFLORESCENCE

4.3.1. *Correlation between ovary diameter and position in the inflorescence*

During the investigation a number of different measurements were made of the flower. It was found that the ovary diameter is a reasonably good index of flower size. It was noticeable that practically no increase in ovary diameter can be observed during the blossoming period. Tables 5 and 6 give a survey of the ovary diameter in relation to the position of the flower in the inflorescence. The average values for each position in the inflorescence in 1958 and 1962 are plotted in the form of a graph in Figure 16.

The graph shows quite clearly that the developmental differences (Table 3) and differences in bloom (§ 4.2.6.) are in marked agreement with the differences in flower size. Flowers at the bottom of the inflorescence are formed early, develop rapidly, grow large, and bloom early. Although the apical flower is initiated fairly later, it can grow larger and bloom earlier because a large part of the original meristem becomes available for the formation of this flower and it develops earlier and more rapidly than a number of flowers situated below.

It seems likely that the differences in order of blossoming in the pear cultivars examined by RUDLOFF and WUNDRIG (1939) are due to differently oriented

TABLE 5. Diameter of the ovary in mm during the 1958 blossoming period.

Date	Position of the flower in the inflorescence										Total	Average
	1	2	3	4	5	6	7	8	9	10		ø
9 May	2.9	2.7	2.6	2.9	2.9	3.0	3.1	3.1	3.0	–	26.2	2.9
	2.9	2.3	2.5	2.8	2.8	2.9	3.0	–	–	–	19.2	2.7
13 May	2.8	2.2	2.5	2.7	2.8	2.6	2.9	3.0	–	–	21.5	2.7
	2.8	2.3	2.8	2.7	2.6	2.9	2.9	–	–	–	19.0	2.7
	3.1	2.5	2.8	3.0	3.0	3.2	3.5	3.3	3.3	–	27.7	3.1
	3.0	2.6	2.7	2.8	2.9	3.1	3.1	3.1	3.2	–	26.5	2.9
16 May	2.7	2.3	2.6	2.5	2.6	2.7	2.7	–	–	–	18.1	2.6
	2.8	2.4	2.5	2.7	2.9	3.0	3.1	–	–	–	19.4	2.8
	2.8	2.4	2.5	2.8	3.0	3.0	3.2	3.2	2.5	–	25.4	2.8
	2.7	2.3	2.5	2.5	2.9	2.8	2.9	3.1	3.0	–	24.7	2.7
20 May	3.0	2.6	2.7	2.8	3.0	2.9	3.2	3.2	3.1	–	26.5	2.9
	3.0	2.3	2.7	3.0	3.0	3.0	3.2	3.2	3.3	–	26.7	3.0
	3.0	2.6	3.0	3.0	3.2	3.3	3.4	3.5	3.5	3.0	31.5	3.2
Total	37.5	31.5	34.4	36.2	37.6	38.4	40.2	28.7	24.9	3.0	312.4	–
Average ø	2.9	2.4	2.6	2.8	2.9	3.0	3.1	3.2	3.1	3.0	–	2.9

TABLE 6. Diameter of the ovary in mm during the 1962 blossoming period.

Date	Position of the flower in the inflorescence										Total	Average
	1	2	3	4	5	6	7	8	9	10		ø
19 May	3.0	2.8	2.8	3.0	3.2	3.2	–	–	–	–	18.0	3.0
	3.0	2.5	2.8	2.8	3.0	3.0	3.0	3.0	–	–	23.1	2.9
26 May	3.1	2.9	3.0	3.2	3.1	3.2	3.3	3.3	–	–	25.1	3.1
	3.2	2.8	2.9	3.0	3.0	3.2	3.4	3.4	–	–	24.9	3.1
30 May	3.1	2.8	2.9	3.0	3.0	3.4	3.3	–	–	–	21.5	3.1
	2.7	2.5	2.4	2.6	2.8	2.8	3.0	2.9	–	–	21.7	2.7
Total	18.1	16.3	16.8	17.6	18.1	18.8	16.0	12.6	–	–	134.3	–
Average ø	3.0	2.7	2.8	2.9	3.0	3.1	3.2	3.2	–	–	–	3.0

distribution of the meristematic mass forming the future inflorescence. If this is true, any apical dominance exerted by the apical flower is heralded by a genetically oriented fragmentation proces giving rise to a larger or smaller meristematic remnant acting as a growth centre.

It can be seen from the graph in Figure 16 that in 1958 the average size of the flowers was less than in 1962, that deviations from the average were greater in 1958 than in 1962. For 1958 it can also be stated that when an inflorescence has only a few flowers these were usually small. It will also be noted that the blossoming period was longer in 1958 than in 1962. All this data lends support to the general picture of the inflorescence given in § 3.2.3. Only one fact is at variance,

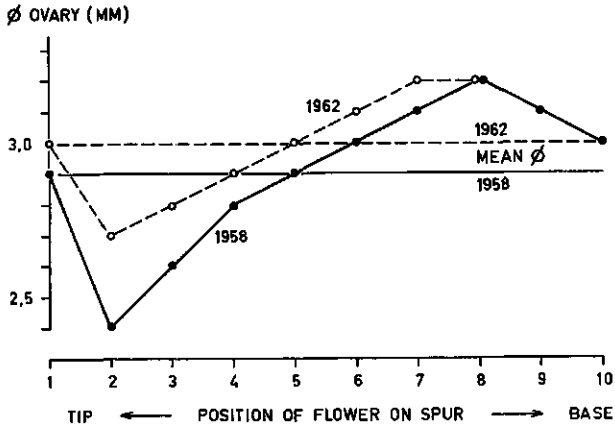


FIG. 16. Ovary diameter in relation to position in the inflorescence.

viz. that the average number of flowers to an inflorescence was smaller in 1962 than in 1958.

4.3.2. *The number of stamens per flower*

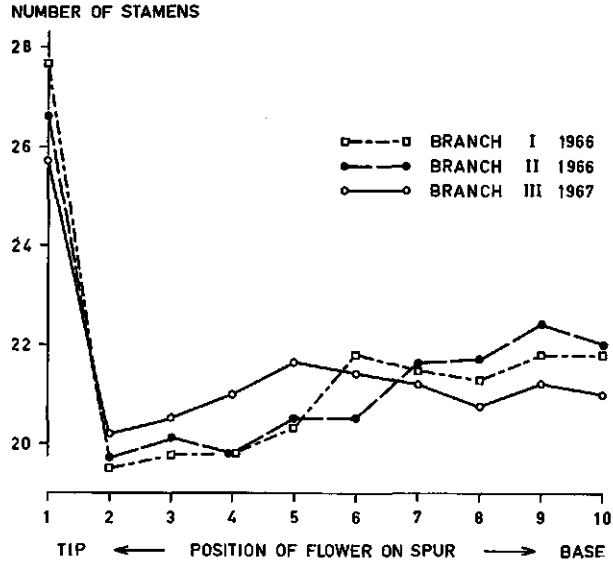
According to the literature the number of stamens in the cultivated pear is always in the region of 20 per flower. HEINRICH (1959) found no differences in the same inflorescence; he also mentions the occurrence of cultivars with a significantly greater or smaller number of stamens per flower, and that the number of stamens probably varies from year to year. HASKELL (1954) assumes a priori that flowers of the same cultivar are essentially alike, since he only took ten flowers at random from a tree and based his survey on this scanty material. In his work on the pear MORRISON (1964) never found more than twenty stamens per flower and assumes this number to be determined genetically and not influenced by environment.

In 1966 and 1967 an examination was made of the flowers of three branches of tree I in the Belmonte Arboretum, Wageningen. Branch I bore 13 inflorescences with 117 flowers, branch II 8 with 67 flowers, and branch III 64 of which 50 were examined bearing 428 flowers. The results of the stamen counts are summarised in Table 7 and plotted in the graph in Figure 17. It would seem that in

TABLE 7. Average number of stamens per flower in relation to position of the flower in the inflorescence.
In 1966 thirteen inflorescences were counted on branch I and eight on branch II; in 1967 fifty inflorescences were counted on branch III.

	Position of the flower in the inflorescence									
	1	2	3	4	5	6	7	8	9	10
1966 Branch I	27.7	19.5	19.7	19.8	20.3	21.8	21.5	21.3	21.8	21.8
Branch II	26.6	19.7	20.1	19.8	20.5	20.5	21.6	21.7	22.4	22.0
1967 Branch III	25.7	20.2	20.5	21.0	21.3	21.4	21.2	20.7	21.2	21.0

FIG. 17. Number of stamens per flower in relation to position in the inflorescence.



Pyrus nivalis the ratios differ from those of the cultivated pear. On average the apical flower has over 25 stamens, flowers 2–5 in 1966 and 2–3 in 1967 averaged about 20, and the flowers underneath had 21–22 stamens. Moreover in 1967, which may be called a year of well-developed flowers, none were found with less than 20 stamens.

4.3.3. *Number of styles per flower*

The styles of the flowers on branches I, II and III were counted in addition to the stamens. The differences occurring between 1966 and 1967 are both notable and interesting. In 1966 only 56% of the flowers were normal, i.e. provided with five styles, the others having four or less. In 1967 93% of the flowers had five styles, one had six, and the remaining 30 flowers four styles. The average values are listed in Table 8 and Figure 18. In view of the small number of abnormalities

TABLE 8. Average number of styles per flower in relation to position of the flower in the inflorescence.
In 1966 thirteen inflorescences were counted on branch I and eight on branch II; in 1967 fifty inflorescences were counted on branch III.

	Position of the flower in the inflorescence									
	1	2	3	4	5	6	7	8	9	10
1966 Branch I	5.0	4.2	4.4	4.8	4.8	4.3	5.0	4.4	4.5	4.3
Branch II	4.6	3.4	4.3	4.4	4.4	4.3	4.8	3.9	4.4	4.0
1967 Branch III	5.00	4.86	4.94	4.98	4.96	4.94	4.88	4.90	4.93	5.00

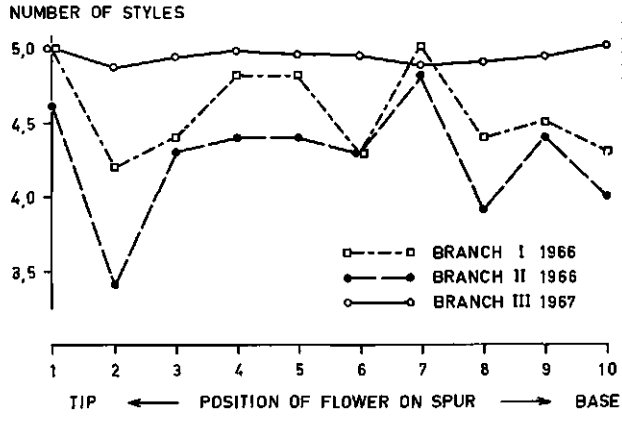


FIG. 18. Number of styles per flower in relation to position in the inflorescence.

in 1967 the results for this year need not be considered. In 1966 the number of styles per flower does not appear to be greatly dependent on the position in the inflorescence, although it is remarkable that both branches show the same tendency. The apical flower and flower 7, the second flower in the axil of a foliage leaf, tend most to have the normal number of styles. The subapical flower is clearly in an unfavourable position, but this is also true of flowers 8 and 10.

As regards the differences between flowers in 1966 and 1967, the latter might again be called a year of well-developed flowers, as in the discussion of the number of stamens per flower, and characterised by great uniformity of the number of styles, the number hardly ever differing from five. The 1966 results are a complete contrast with great variations in the number of styles, the level of five only being reached in a few positions in the inflorescence.

Possibly what is involved in this case is the responses of floral primordia to unfavourable weather conditions at a certain developmental stage, considering the same pattern shown by the two different branches.

Further data pointing in the same direction are given in the following paragraphs.

4.3.4. *Number of styles in the flower in relation to the number of locules in the fruit*

In 1966 a count was made of both the styles of flowers and the locules in ripe fruits. Some data referring to tree I are summarised in Table 9. The percentages of five-styled flowers differ considerably between branch I and branch II, branch II being selected for the counts because at first sight this branch appeared to have many three-styled flowers. Branch I was chosen at random. However, all flowers were investigated on both branches. Since flowers 6, 7 and 8 in the inflorescence have the best fruit set, as will be discussed below in § 5.3.8., the data for these flowers is included separately in Table 9.

Each carpel of the pear flower bears one style, so that it might be expected that the percentage of five-styled flowers would correspond to the percentage of

TABLE 9. Number of flowers with five styles and number of fruits with five locules on tree I in 1966.

	Total	Of which with five styles or locules	Percentage
All flowers			
Branch I	117	73	62
Branch II	67	30	45
Branches I and II	184	103	56
Flowers 6, 7 and 8			
Branch I	38	26	68
Branch II	23	11	48
Branches I and II	61	37	61
Fruits	105	41	39

five-loculed fruits. It can be seen from Table 9 that this is not the case and that far fewer five-loculed fruits occurred than five-styled flowers. For positions 6, 7 and 8 the difference is as much as 22%, or $1\frac{1}{2}$ times as many five styled flowers as five-loculed fruits. It seems unlikely that flowers with less than five styles have a better fruit set than normal flowers, so that we can only assume that some of the five-styled flowers have less than five locules. It will be shown in the succeeding paragraphs whether this conclusion is in fact correct.

4.3.5. *Number of styles and locules in flowers of developing inflorescences*

A great number of buds were cut with the microtome with a view to following the development of the *Pyrus nivalis* inflorescence. In the slides of the last developmental phases of the inflorescence it is possible to calculate the numbers of styles and locules in the flower buds. The results of the counts of a number of years are summarised in Table 10. The number of flowers counted is stated in

TABLE 10. Number of flowers with five styles and the number thereof with less than five locules of developing inflorescences in 1958, 1964–1965 and 1966 as compared with the number of flowers with five styles during bloom in 1966 and 1967.

Date	Number of flowers examined	%	5 styles	%	5 styles but fewer locules	%
21 March' 58–6 May '58 (10 inflorescences)	82	100	41	50	9	11
23 Nov. '64–4 Jan.'65 (5 inflorescences)	32	100	32	100	0	0
25 Feb. '66–18 March '66 (20 inflorescences)	140	100	77	55	25	18
2, 4 and 5 May 1966 (21 inflorescences)	184	100	103	56	–	–
5, 8 and 10 May 1967 (50 inflorescences)	428	100	397	93	–	–

the first column of the table, in column 2 the number of flowers with five styles, and lastly in column 3 the number of flowers with five styles but less than five locules.

The table does in fact show that in 1958 and 1966 a fairly large percentage of the flowers with five styles had less than five locules. It is noticeable that in 1964–1965 not a single abnormal flower was observed. It looks as though the formation of normal flowers is correlated to a very early occurrence of the developmental stages of the flower buds in which both styles and locules are present. As a matter of fact in 1958 and 1966 no counts could be made in January and the beginning of February because the inflorescences were still too insufficiently developed (cf. Table 3).

The agreement found in the 1966 material between five-styled buds cut with the microtome and opened flowers, viz. 55% and 56% respectively, was extremely encouraging.

The number of flowers with five locules in the developing inflorescences in 1966 was 55% minus 18% = 37%. The latter percentage shows remarkably good agreement with the percentage of five-loculed fruits found on tree I in 1966 (39%) (cf. Table 9 and § 5.3.10.). In conclusion it can be said that the establishment of the existence of five-styled flowers with less than five locules and its quantification afford a ready explanation of the discrepancy between the percentages of five-styled flowers and five-loculed fruits.

4.3.6. *The formation of quadriloculate flowers with five styles*

The manner in which the normal number of locules is reduced to four or sometimes even less can be studied by means of microscope slides. Three types of reduction were encountered (cf. Figures 19 and 20):

1. One style and one corresponding locule are completely absent. The flower is four-styled and quadriloculate.
2. The fifth style is present but terminates in a protuberance at the site of the locule. The flower is five-styled but quadriloculate.
3. Two of the five carpels are laterally joined.

a. The styles and locules may be completely joined together, in which case a thick style is formed with a large locule underneath. The flower is four-styled and quadriloculate.

b. The styles and locules may be partially joined together. The flower may have four styles, one of which is furciform, and quadriloculate, or else it may have five styles and four locules, one of which is large and usually contains a remnant of a partition. All manner of intermediate forms can be found in the slides, but the styles are never joined to the apex only; this could only be ontogenetically explained by post-genital fusion, which is a very unlikely occurrence.

The latter type of reduction is particularly interesting. During development the apices of the carpels, the future styles, are first formed, as is also the case with leaf primordia. Under favourable conditions the carpels are initiated prac-

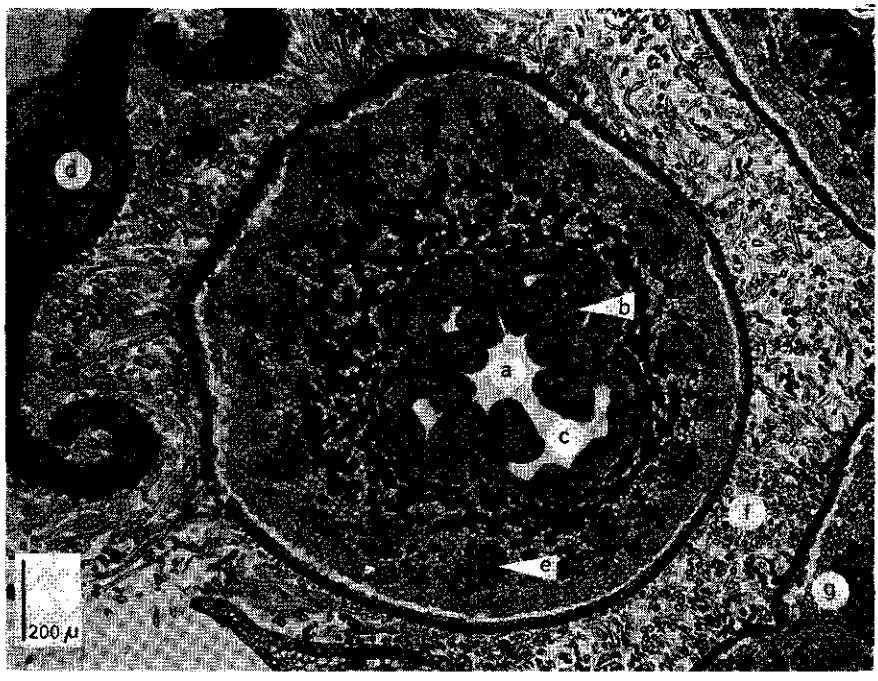


FIG. 19. Transverse section, immediately above the apex, of a developing flower (No. 7) with four locules and four styles, case 3 a, page 40, 14th April 1958. Flower No. 6 of the same inflorescence has four locules and five styles, case 3 b, page 40.
a. cavity above apex
b. normal locule with two ovule primordia and one vascular bundle in the dorsal suture
c. large locule formed by the fusion of two carpels, two ovule primordia and two vascular bundles on the dorsal side
d. foliage leaf bearing the flower in the axil
e. one of the 10 sepal and petal vascular bundles
f. lignified hairs
g. axis of the inflorescence

tically simultaneously. Should conditions be less favourable the carpel primordia are formed at ever increasing intervals. In the latter case it seems clear that development is suddenly inhibited or dislocated by some internal or external factor, as a result of which a development begun in one direction is deflected into others. The various types of carpel reduction may arise in this way. Furciform styles are also found in the cultivated pear (HASKELL, 1954), so that presumably it is subject to the same kind of carpel reduction as *Pyrus nivalis*.

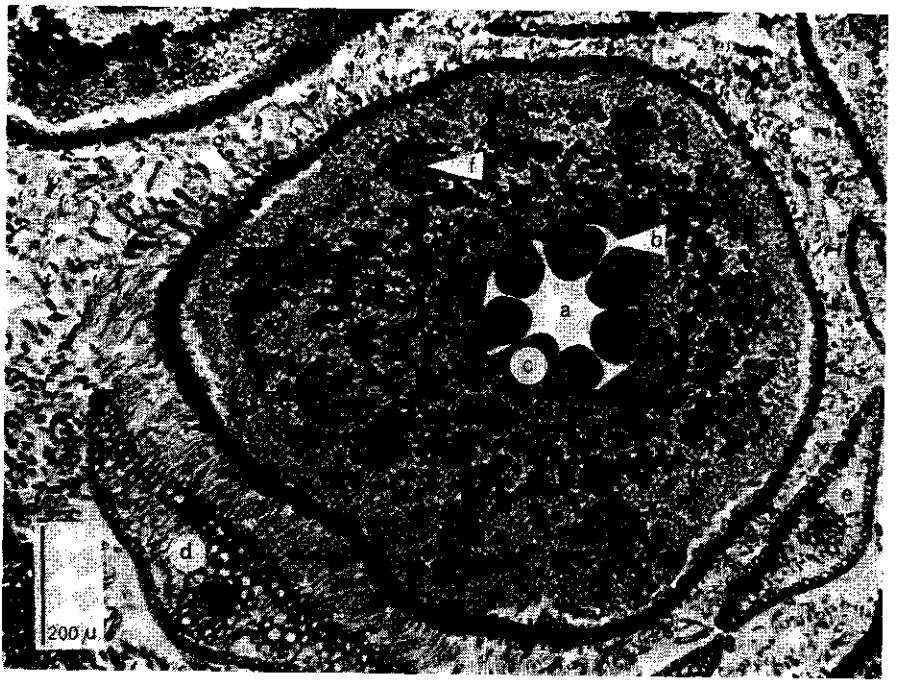


FIG. 20. Transverse section of a developing flower (No. 3) with three locules and four styles, a modification of case 2, pag. 40, 8th April 1958.

a. cavity above apex; *b.* normal locule with two ovule primordia; note the open ventral suture; *c.* lower part of the style, locule not developed; *d.* bract; *e.* bracteole; *f.* one of the 10 sepal and petal vascular bundles; *g.* axis of the inflorescence

4.4. SURVEY OF THE DEVELOPMENT OF THE INFLORESCENCE AND FLOWER

It was found that the flowers of *Pyrus nivalis* differ from each other in various ways, although a certain regularity may be discerned which is often supported by published evidence on the cultivated pear and apple.

1. The relationships between blossoming sequence and size of the flowers are fairly constant within the individual inflorescence (cf. also HEINRICH, 1959; RUDOLFF and WUNDRICH, 1939). This constancy probably depends on a very sharply defined developmental pattern of the inflorescence meristem.
2. Despite this oriented development the number of flowers to an inflorescence is variable.

a. At certain points in the tree predominantly underdeveloped inflorescences will be produced with only a few flowers (cf. also FEUCHT, 1961; ZELLER, 1960–I and –II). The short shoots which form such poor inflorescences may be distinguished at least a year before the actual initiation of the inflorescence

through having formed fewer foliage leaf primordia than short shoots producing well-developed inflorescences.

b. Alongside this early predestination, one or more subapical flowers originally initiated are unable to develop during the later development of the inflorescence. The bracts of such flowers appear in the form of bracteoles of the apical flower.

3. The flowers of poorly developed inflorescences are smaller, bloom later and exhibit a greater tendency to reduce the number of stamens and styles in each flower than do well-developed inflorescences (cf. also RUDLOFF and FEUCHT, 1957).

4. The presence or absence of reductions in the flower chiefly depends on external factors. The position of the inflorescence in the tree is merely of secondary importance. Thus in one year the reductions in *Pyrus nivalis* may be very frequent and in another sporadic. Such reductions as occur are mainly in subapical flowers and the flowers of weak inflorescences. The same rule applies to the initiation or non-initiation of the inflorescence (cf. also LECRENIER, 1962 – 'La liaison recherchée feuilles/fleurs est subordonnée à la floraison' – 'Les conditions extérieures à l'arbre, particulièrement les facteurs climatiques, influent sur la floraison et la non floraison').

5. In view of the great differences occurring from year to year and manner in which the carpels are reduced, it seems likely that such conditions may arise suddenly, e.g. as a reaction to unfavourable changes in the weather.

From this data it is possible to deduce the life history of the pear inflorescence.

In the pre-floral stage the position of the short shoot on the tree determines whether the inflorescence will be poorly developed or well-developed.

The number of leaves on the short shoot may be an indication of the future development. The number of flowers in each inflorescence is determined by the size of the apical meristem during and immediately after initiation of the inflorescence. Under favourable conditions the floral primordia of an inflorescence expand into well-developed flowers that only slightly differ in size and always in accordance with a fixed pattern. In unfavourable conditions the differences between inflorescences and between the flowers of the inflorescence constantly increase during the subsequent development. Inflorescences and flowers may become vegetative again in an early developmental stage or fail to develop further. At a later developmental stage parts of the inflorescence or separate flowers may die off. Reductions in the number of stamens and carpels are a sign of poor development. Such reductions are chiefly found in flowers in an unfavourable position. ZELLER (1960–I) found that poorly developed flower buds mainly die off during the initiation of the stamens and carpels and during pollen meiosis and the formation of the embryo sac. This lends weight to the theory that the flower develops in phases (p. 28).

The next chapter discusses the relationships between the characteristics of the flower and the fruit it produces.

5. GROWTH AND DEVELOPMENT OF THE FRUIT

5.1. INTRODUCTORY

5.1.1. *Growth*

The growth of a fruit is usually defined as the constant increase in volume, weight or diameter. Fruit growth can be shown in the form of a graph by plotting volume, weight or diameter against time. Depending on their shape, the resultant curves may be divided into simple sigmoid types of growth curve or double sigmoid growth curves (CRANE, 1964; DENNE, 1963; NITSCH, 1965). In some cases the double sigmoid growth curve is explained by assuming that the seed or embryo expands at a given period to the detriment of fruit growth. In this connection it is very interesting to note that the fig syconium grows in the form of a double sigmoid curve both in parthenocarpic and seed-producing cultivars. The importance of the division of the growth curves into two types should not be overestimated. Fruit growth is extremely complex and is influenced in various ways by internal and external factors that give rise to irregular growth curves from year to year, from tree to tree and from fruit to fruit.

Hence it is not surprising that different growth curve shapes are found for the fruit of the cultivated pear. CRINS (1950) finds for the fruits of the cultivar 'Précoce Trévoux' a regular increase in diameter decreasing towards maturity (measured from ⌀ 35 mm). On the other hand MITCHELL (1950) reports a double sigmoid growth curve for the cultivar 'Bartlett' (= 'Bon Chrétien William' = 'Williams Bon Chrétien' = 'Williams Christ'). RADU and GHERGHI (1966) describe the growth curve of the pear fruit as being more or less sigmoid ('comme unités biologiques'). But their graph representing ten growth curves of six pear cultivars shows single, double and triple sigmoid curves.

The pear and apple usually increase their volume and diameter at night (HENDRICKSON and VEIMEYER, 1941; TUKEY, 1959). Moisture is removed from the fruit during the day with the result that the volume is generally reduced during the morning. This diurnal rhythm should be taken into account when measuring fruits on the tree.

The apple increases in volume towards maturity through the formation of large intercellular spaces, thereby considerably lowering the specific gravity. This is not true of the pear, or only to a very slight extent (BAIN, 1961).

5.1.2. *Development*

The fruit development of the pear following bloom may be divided into two periods (BAIN, 1961). The first period is one of cell division during which the fruit shape alters considerably. In the second period fruit growth is solely determined by enlargement in the volume of the cells already formed. TOYAMA and HAYASHI (1957–I) estimate the cell division period at 25–30 days for an early pear cultivar and at 45 days for a late one. STERLING (1954) mentions for the 'Bartlett' cultivar a period of 6–8 weeks for the mass of the fruit flesh and 12 weeks for the outside layer of the fruit. BAIN's (1961) results, working with the

same cultivar, show substantial agreement with STERLING's, but she places more emphasis on the continuation of the cell division activity in the outer cell layers of the fruit until maturity (c. 20 weeks).

CRINS (1950) and DENNE (1960) observed that the effect of thinning out apple fruits is more vigorous development of the remaining fruits. According to DENNE (1960) the cell division period is lengthened as a result and the fruit flesh parenchyma cells expand more than in fruits of unthinned trees.

5.1.3. *Morphogenesis*

The morphogenesis, or process by which the pear fruit obtains its shape, has hitherto received little attention. There are occasional references in the literature to factors influencing the shape of the fruit. GRIGGS, IWAKIRI and CLAYPOOL (1957) report that in the 'Bartlett' cultivar parthenocarpic fruits are relatively longer than seeded fruits.

RODRIGUES and MENEZES (1951) and SCHANDER (1954, 1955) describe how the shape of the fruit depends on the number of seeds to a fruit. Pears with only a few seeds are elongated, whereas those with an abundance of seeds are round.

SCHANDER's (1955) observations of a number of apple cultivars are particularly interesting with regard to what is found in *Pyrus nivalis* (§ 5.3.3.). He remarks that in elongated apples (length/diameter > 1), as in pears, fruits with few if any seeds are relatively longer than fruits with a large number of seeds. The converse is true of extremely flattened apples (length/diameter < 1) in which fruits with a large number of seeds are less flattened, viz. longer than fruits with few if any seeds.

However, the seed's role as a growth centre should not be overestimated. Several investigators, including ROSPER (1957) and VARGA (1963), have found that when seeds are removed from the apple after the June drop the fruit still continues to develop in the normal way despite the serious injuries it has sustained. Hence the unilateral position of apple seeds does not invariably mean that the fruit will develop more vigorously on this side. According to SCHANDER (1955) 71 % of a sample of fruits with a regular structure should be unsymmetric owing to irregular distribution of the seeds. But since unsymmetric fruits usually have seeds on the thick side, SCHANDER still adheres to the view that seeds cause local expansion of the fruit. He is of the opinion that the fruit may also exhibit more vigorous local development as a result of light and gravity. Apparently these three factors (seed, light and gravity) compete with each other, so that the effect exerted by the seed is not always visible.

The unilateral position of seeds in *Pyrus nivalis* may cause local enlargement of the core. Since the layer of flesh outside the core is uniformly thick, a rather asymmetric fruit is in fact formed. These anomalies are not very noticeable because each separate fruit has a slightly irregular structure. As many as 68 % of the seeded fruits of trees I, II and III were found to contain one seed only (§ 5.3.9.). Outwardly these fruits are impossible to distinguish from others containing more seeds. They are all practically spherical, unlike seedless fruits whose flattened shape usually distinguishes them from seeded ones.

But if at an early developmental stage the outermost cell layers of the pear have been slightly injured the layer of flesh below the injury stops growing, whereas the core continues to grow unhindered. If a small part of the surface remains uninjured in the middle of an injury the flesh will continue to develop at this point. Probably therefore the outermost cell layers of the pear are of prime importance for the development of the underlying flesh. These cell layers contain chlorophyll and continue to produce new cells for a long period.

Gibberellic acid (GA_3) in given concentrations promotes longitudinal fruit growth, so that elongated pears with long stems are formed (GRIGGS and IWAKIRI, 1961; VARGA, 1963). Growth-retarding compounds such as Alar, also known as 'B-Nine' (N-dimethyl amino succinamic acid) result in malformed pears with short, thick stems (GRIGGS, IWAKIRI and BETHELL, 1965).

The effect of the position of the fruit in the cluster in the apple has been studied by DENNE (1963), VISSER (1955) and others. Fruits on the tip of the spur were usually found to be larger and longer than the others. According to DENNE (1963) a positive correlation exists between the diameter of the short shoot and the size of the fruits formed on it. VISSER (1955) found that inflorescences with five flowers (weak inflorescences) produce lighter fruits than inflorescences with six flowers (vigorous inflorescences). Moreover the fruits at the tip of weak inflorescences contained more malformed specimens (beaked fruits) than the fruits of vigorous inflorescences. The weak and vigorous inflorescences may probably be compared with inflorescences 2 and 3 of *Pyrus nivalis* shown in Figure 3, p. 11. VISSER (1955) did in fact find that weak inflorescences flower at a later date than vigorous ones. It is interesting to note that the malformation of beaked fruits is due to an irregularity in the vascular bundle system that must have originated during floral initiation (VISSER, 1954).

5.1.4. *Histogenesis (sclereid clusters, intervening parenchyma cells)*

The sclereids in the pear fruit are practically isodiametric and free from sharp protuberances. This type of sclereid is termed a brachysclereid to distinguish it from others. The conglomeration of cells forming the sclereid clusters indicates the homogeneity of the sclerenchyma tissue.

The first sclereids are formed directly the fruit starts to develop. OSTERWALDER (1910) found them only three days after fertilisation in the expanding ovary of the 'Gute Louise' cultivar. STERLING (1954) and BAIN (1961) observed the first sclereids in the 'Bartlett' cultivar about two weeks after flowering.

Sclereids are found in *Pyrus nivalis* 10 days after flowering. The first are formed as a result of lignification of parenchyma cells in the immediate vicinity of the core and in the eye. After sclereids have been formed in a scattered pattern in the flesh, usually from fairly large parenchyma cells, the surrounding cells also begin to lignify, producing small sclereid clusters. Around such a cluster is then formed a meristem producing new cells which also lignify. The latter cells are arranged in a radial pattern around the first-formed small sclereid cluster. Sclereid clusters positioned near each other may coalesce and produce a single large sclereid cluster. After the mitotic activity has ceased the

remaining cells of the meristem around the cluster begin to extend, forming the very large radially oriented parenchyma cells of the flesh.

From the anatomical viewpoint the development of the young fruit is particularly interesting. The cells in the young ovary are arranged lengthwise, just as they were formed from the wide shoot apex. The eye, which only developed about a month before blossom, also has a longitudinal cell arrangement. The first-formed sclereids, i.e. those in the eye and immediately surrounding the core, retain this longitudinal arrangement. Shortly after fruit set begins the direction of division of the parenchyma cells of the flesh is completely changed. Rows of cells are now formed radiating outward with the core as the centre. This implies that this arrangement is still to be found in the nucleus of subsequently formed sclereid clusters. Lastly, the cells are arranged in a radial pattern with the nucleus of the sclereid clusters as the centre (this applies both to the last-formed sclereids and the succulent parenchyma cells; cf. Figures 21 and 6). The developmental process is more complex in the parts of the fruit surrounding the stalk insertion and the eye.

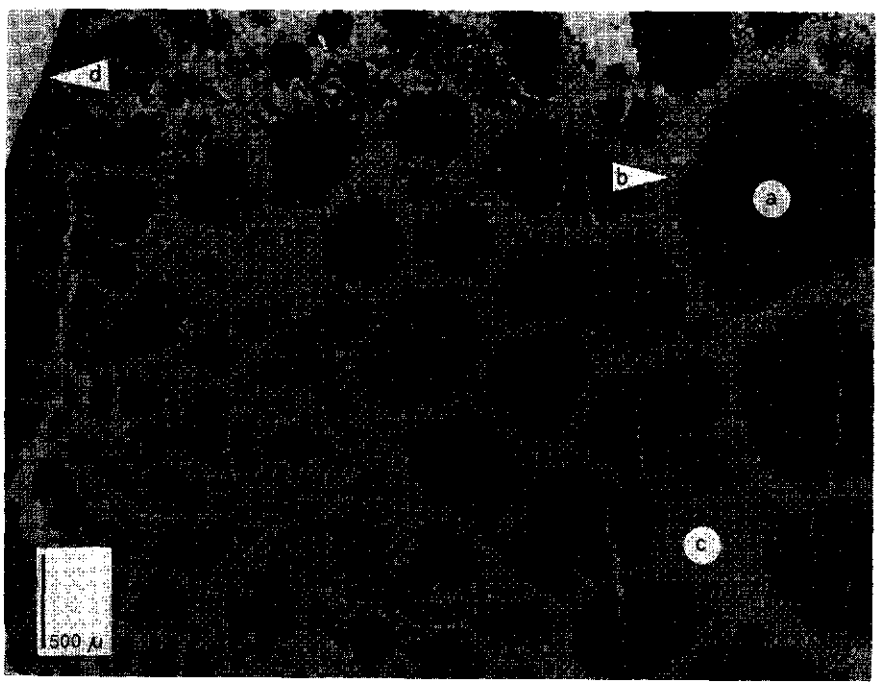


FIG. 21. Transverse section of a young fruit at the end of the cell-division period, 14th August 1962.

a. large sclereid cluster close to the core, the outermost layers of sclereids are arranged radially

b. meristem

c. point at which the microtome knife has passed between two sclereid clusters

d. epidermis

Since pears grow softer and sweeter during maturation, some investigators have thought that the sclereid material might be converted into sugars. ALEXANDROV and DJAPARIDZE (1927) did in fact observe that after two to three months the walls of sclereids of *Cydonia vulgaris* (quince) became thinner and lost their lignin.

Their experiments on the pear failed because the stored fruit began to rot.

CRIST and BATJER (1931) noted that the lignocellulose content of the pear reaches a maximum at an early developmental stage and then falls off considerably. The sugar content shows a marked increase just after the peak of this maximum has been reached. They considered this a clear indication that lignocellulose was converted into sugars. SMITH (1935) proved however that the amount of lignocellulose in each fruit does not decrease, but even increases slightly after the maximum percentage has been reached. STERLING (1954) adduces anatomical grounds for proving the absence of delignification during the developmental process of the fruit.

The fruit of *Pyrus nivalis* also showed no anatomical indications of decomposition of cell-wall material of the sclereids.

5.2. FRUIT GROWTH

5.2.1. *Increase in diameter*

In 1962, 1963 and 1964 individual fruits were regularly measured on the trees by means of a vernier caliper (accuracy of reading 1/10 mm). In 1962 and 1963 it was the fruits of the large tree at Leiden that were measured, and in 1964 all fruits of tree I in the Belmonte Arboretum, Wageningen. The observations are illustrated graphically in Figure 22. The first five points of observation of the 1962 curve are connected by a broken line because the first four points relate to the transverse diameters of ovaries of randomly selected flowers not belonging to the fruits measured later on in the season.

During the observation years there can be observed halfway through the growing period a temporary reduction in the rate of growth and flatter curves, so that a double S curve also occurs for the fruit growth of *Pyrus nivalis*. MITCHELL (1950) concludes from his observations of the 'Bartlett' cultivar that the temporary decline in rate of growth is associated with the concomitant rapid elongation of the embryo in the seeds of the fruit. Embryo elongation in *Pyrus nivalis* also approximately coincides with a decline in the rate of growth of the fruit. It can be seen from Table 11 and Figures 23–27 that in 1962 elongation of the embryo mainly occurred between mid-August and mid-September. But having regard to the high frequency of parthenocarpic fruits in the pear a different explanation would appear more likely. MITCHELL (1950) himself notes that eights weeks after full bloom cell division ceases in the fruit flesh. In his investigations this important moment of fruit growth coincides with the period at which the rate of growth starts to decline. This radical change in the pattern of growth is probably more important for fruit development than the effect exerted by the embryo.

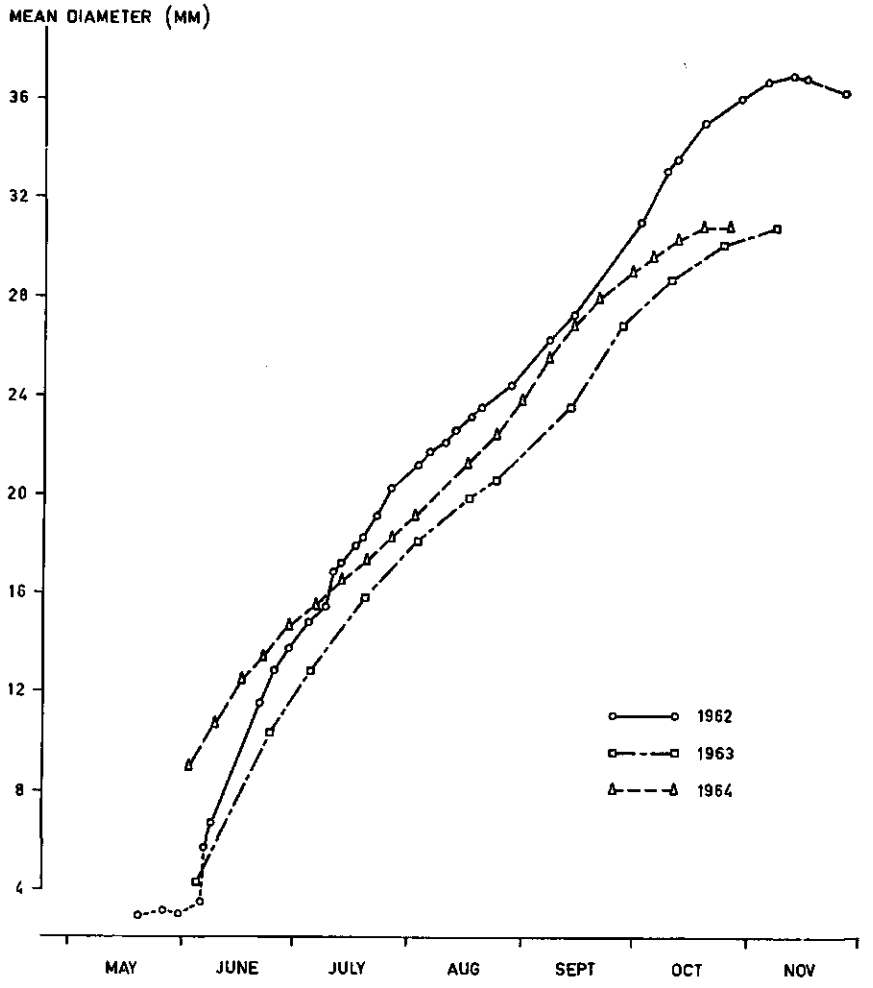


FIG. 22. Increase in the fruit diameter (transverse) during the growing season.

Apart from the decline in the rate of growth, it is noticeable in the graph in Figure 22 that the diameter of the ovary shows no increase during the May bloom, and that during the last days of the growing period the fruits actually grow smaller. This is probably due to loss of moisture through evaporation. Many different kinds of factors could possibly inhibit the transport of water to the fruit while evaporation is in progress, for instance the effect of the abscission layer in the fruit stalk, the fall of the leaves, or too low a temperature.

The curve of the Wageningen tree (1964) differs from that of the Leiden tree (1962 and 1963), the point of transition of the two S curves forming the curve being situated far more towards the middle of the growing period than in the other two curves, where this point of transition comes later. The difference be-

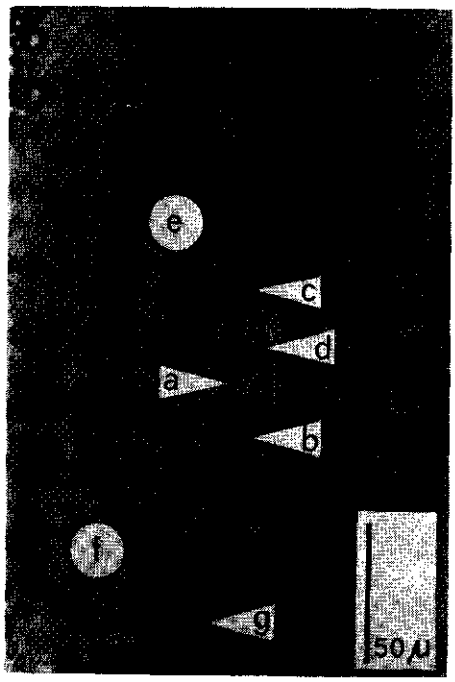


FIG. 23. Embryo sac formed, stage 11, 13th May 1958.
a. embryo sac
b. ovum and synergids
c. antipodal cells
d. polar nucleus
e. nucellus
f. inner integument
g. micropyle

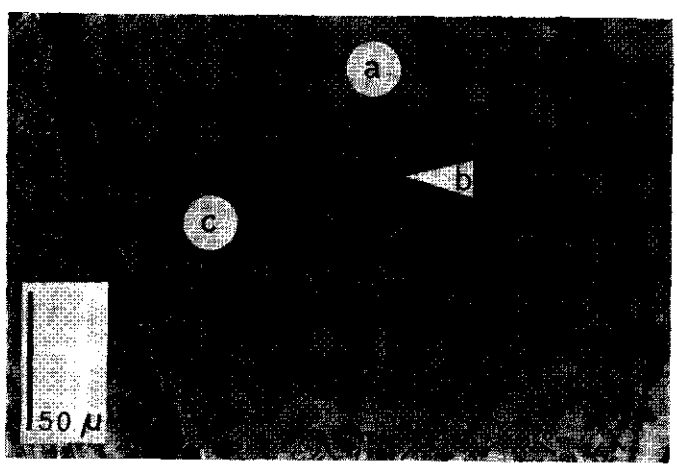


FIG. 24. Proembryo, 13th June 1962.
a. embryo sac
b. proembryo
c. nucellus

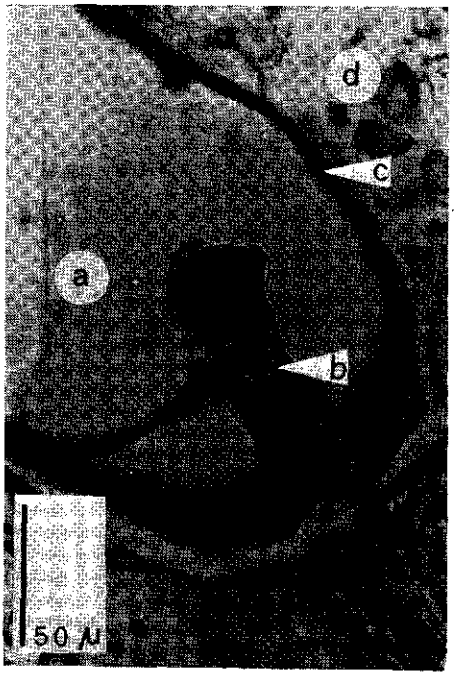


FIG. 25. Embryo, 3rd July 1962.
a. embryo sac; *b.* embryo; *c.* endosperm; *d.* nucellus.

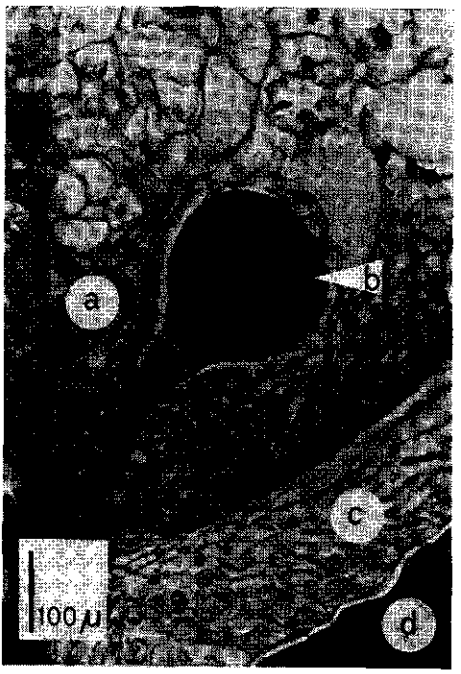


FIG. 26. Embryo, 6th July 1964.
a. embryo sac with endosperm; *b.* embryo; *c.* nucellus; *d.* seed coat.

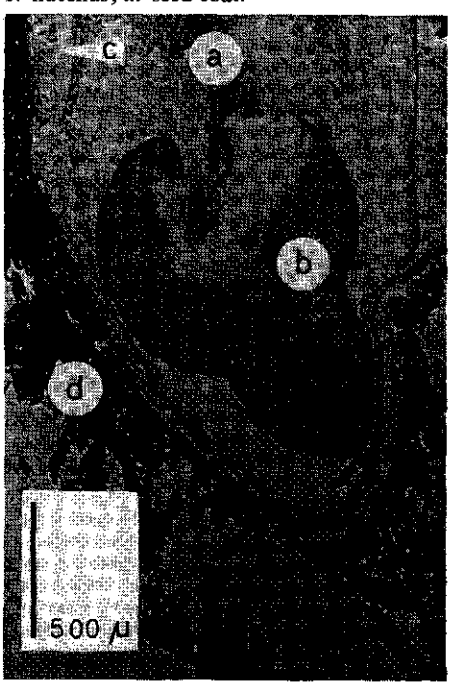


FIG. 27. Embryo, 14th August 1962.
a. embryo sac; *b.* embryo; *c.* nucellus; *d.* seed coat.

TABLE 11. Length of the embryo in 1962 (cf. also Figures 23–27).

Date	Length
13th June	60 μ
3rd July	100 μ
14th August	1,330 μ
19th September	c. 6 mm

tween the growth curves may be genetic, depending on differences in the ages of the trees, or it may be merely due to a difference in the weather conditions during the observation years. But it may also be possible that, as DENNE (1960) found for the apple, the fairly light crop borne by the Leiden tree during these years led to an extension of the period of cell division of the fruit. This would also explain why the average size of the 1962 fruits was so much greater than of the Wageningen tree in 1964.

5.2.2. *Increase in volume*

Since the increase in volume is three-dimensional it provides a more complete picture of fruit growth than the increase in diameter. But volume measurements are attended by a great drawback. They usually necessitate picking the fruits off the tree, which means that it becomes impossible to measure the growth of individual fruits on the tree. Moreover picking or thinning the fruits often leads to more rapid growth of the remaining fruits. Lastly, volume measurements are fairly complicated and rough. For instance, during the present investigation the liquid displacement had to be measured in 96% alcohol because the fruits are not properly wetted with water and too many air bubbles cling to the greasy surface of the fruit.

Rapid and reliable measurements of the diameter are not attended with the same difficulties as measurements of the volume. A very good impression of the fruit growth may be obtained by regular measurements of both the transverse diameter and the length of the fruit. With the aid of a formula ROEMER (1966) was able to make an approximate calculation of the volume of apples on the tree from these two dimensions.

The length and diameter components may also be considered in relation to each other. Thus the length/diameter ratio supplies data on the shape and changes in the shape of the fruit during development (§ 5.3.5.).

Pyrus nivalis was examined in 1962 with a view to ascertaining whether the volume of the fruits could be calculated. Since these fruits have a practically spherical shape, it was assumed that the formula $^1/_6\ \pi\ \varnothing^3$ would give a reliable value for the volume. To test the accuracy of this hypothesis, the measured and the calculated volume of the same samples were plotted side-by-side in graph form (Fig. 28).

It can be clearly seen from the graph that the volume increases almost rectilinearly up to the end of August. From the beginning of September the rate of

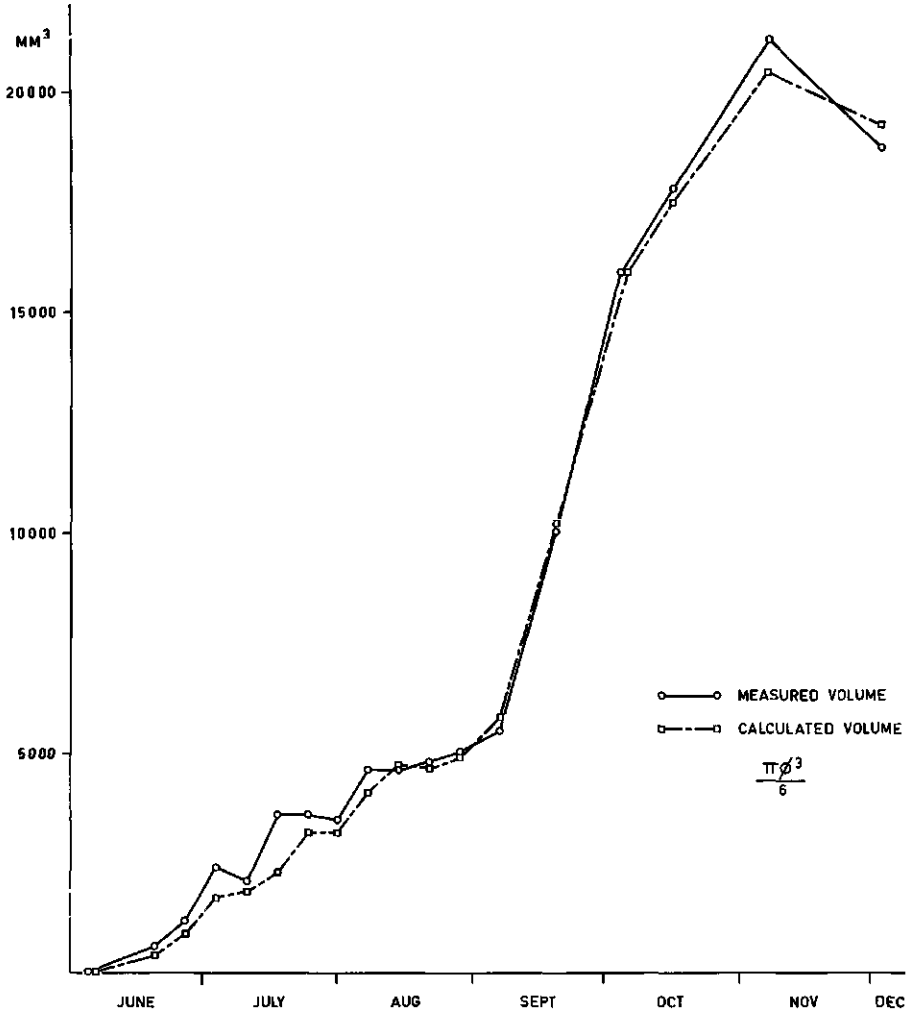


FIG. 28. Measured and calculated volume of picked fruits in 1962.

increase is suddenly much accelerated, but this second part of the curve is also approximately rectilinear. The result is a curve more or less consisting of two straight lines. The transition from one straight line to the other in the curves in Figure 28 corresponds to the point of deflection of the 1962 diameter curve in Figure 22. The reduction in volume at the end of the growth period is particularly notable in Figure 28.

A calculation was also made of the volume of the fruits measured on the tree, shown in Figure 22. These calculated volumes are plotted in the graph in Figure 29. The curves are more flowing than in Figure 28, although in this case

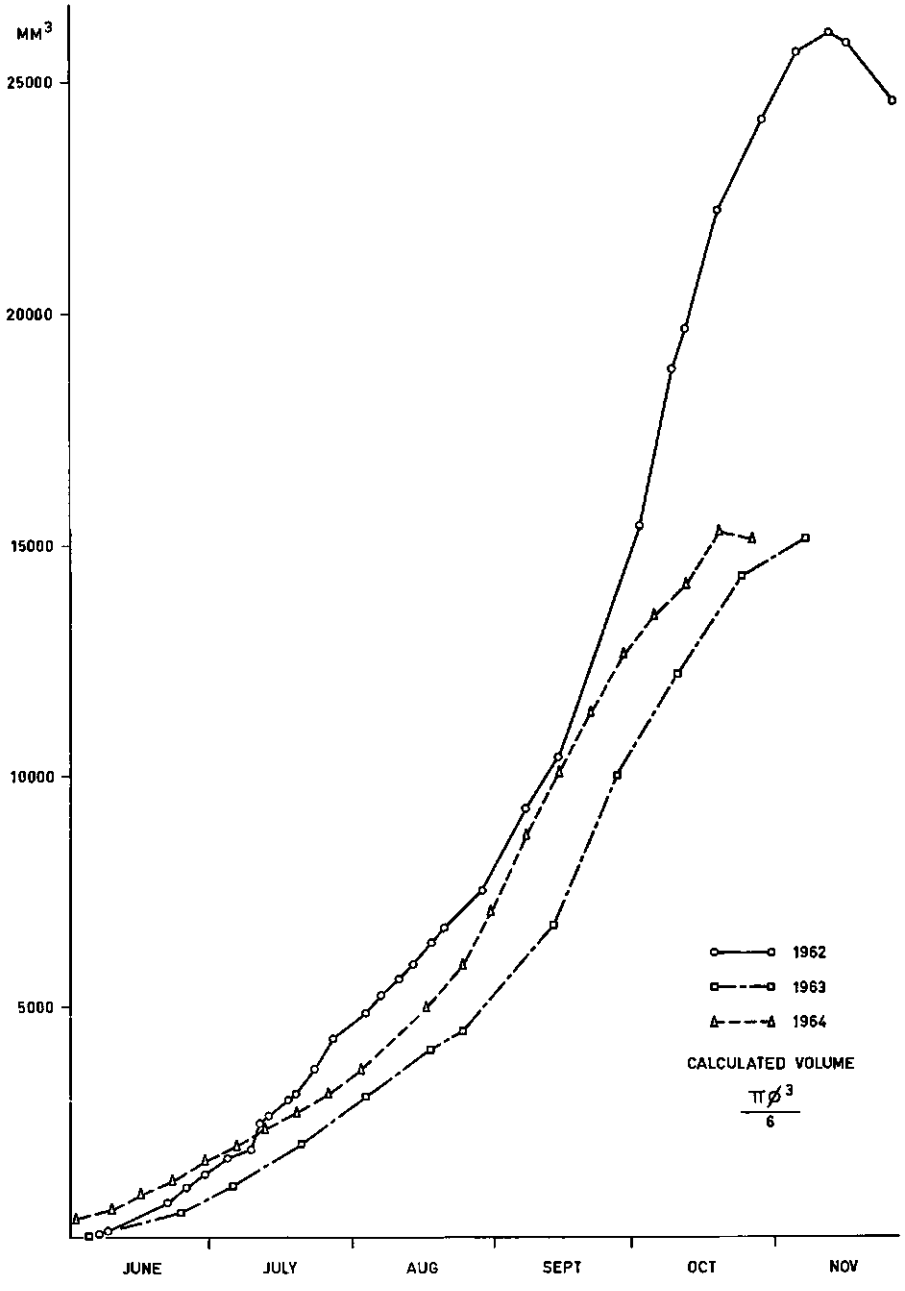


FIG. 29. Calculated volume of fruits measured on the tree (identical with those in Figure 22).

also we observe a pattern consisting of two straight lines. The first straight part of the curve coincides with the period of new cell formation, the second straight part with the period in which the fruit grows almost exclusively as a result of cell extension.

A comparison of Figs. 22 and 29 shows why volume curves have advantages over diameter curves. From the diameter curve it would appear as though fruit growth has reached the half-way line as early as the end of July, whereas according to the volume curve this point is not reached until the beginning of September. A large increase in diameter at the beginning of the growth period only corresponds to a small increase in volume, whereas vice versa a small increase in diameter at the end of the growth period results in a very substantial increase in volume.

5.2.3. *Fresh weight and dry weight*

Increase in volume is not an ideal index of fruit growth which is due, among other causes to the above-mentioned daily fluctuations in fruit volume. Perhaps the best criterion is the increase in dry weight, but the determination of this is also attended with a number of difficulties. As in the case of volume determination, the fruit has to be picked off the tree. Relatively too low or too high dry-weight values may be found as a result of the escape of volatile components, the occurrence of oxidation processes, and moisture remaining in bound form during drying.

The mean fresh and dry weights per pear of fruit samples collected in 1962 are plotted in graph form in Figure 30. In addition to these two data, the diameter curve of the same fruits is also included in the graph.

The kink in the latter curve is rather more marked than that of the fruits measured on the tree in 1962 (Fig. 22), so that the double S shape is more in evidence. The shape of the fresh-weight curve is practically identical with the volume curves in Figure 28 derived from the same material. The dry-weight curve exhibits some remarkable features. About half the material is formed in the fruit during June and July and the other half in September. No increase in dry weight occurs in August, October and November. On the other hand the fresh weight goes up by about a quarter in October but loses much of its increase in November. Evidently the moisture content of the fruit changes during the growth period. The dry-weight content variation can be clearly seen when the fresh weight/dry weight ratio is shown in percentages (cf. Figure 31). Like the ripe fruit, about 20% of the ovary consists of dry matter. But at the end of July and in the first two weeks of August the dry matter reaches the very high figure of 43%. The percentages are lower for the cultivated pear. For the 'Kieffer' cultivar SMITH (1935) reports a dry-matter content of 15.13% at the beginning of fruit development in 1931 (2nd June), the peak being reached in July with 24.15%, finally falling to 17.00% for the ripe fruit on 10th November. For 1933 the contents were 11.1% (20th May), 23.6% (7th July) and 17.4% (9th October).

Thus approximately the same development takes place in the 'Kieffer' culti-

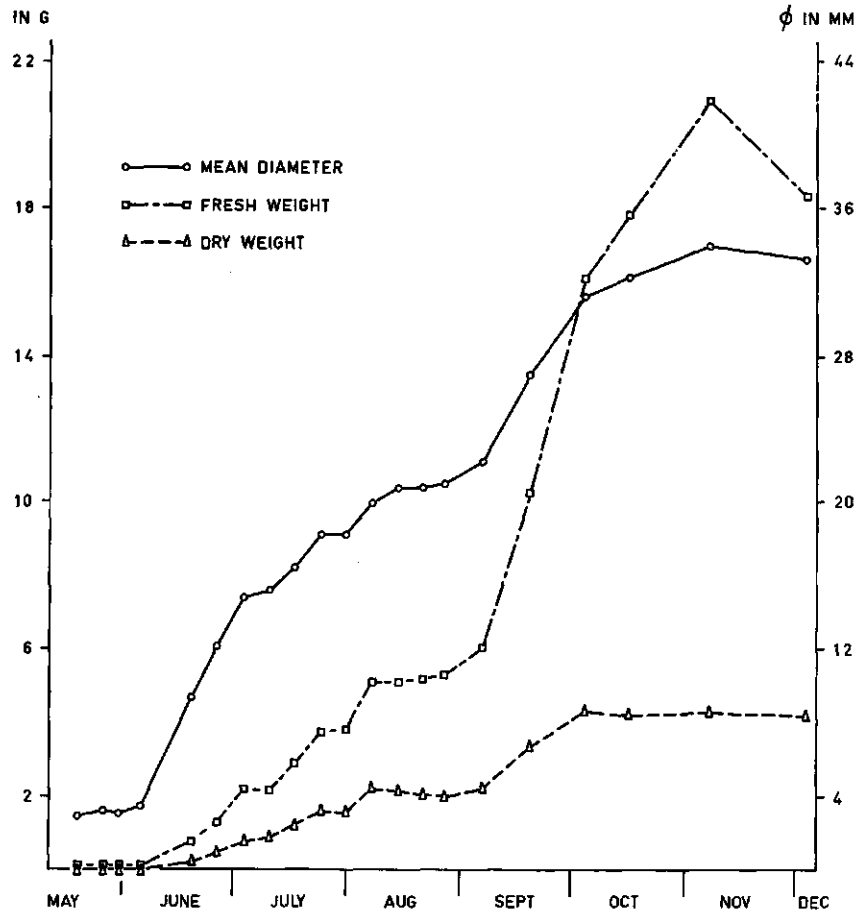


FIG. 30. Mean dry and fresh weight of fruits in 1962.

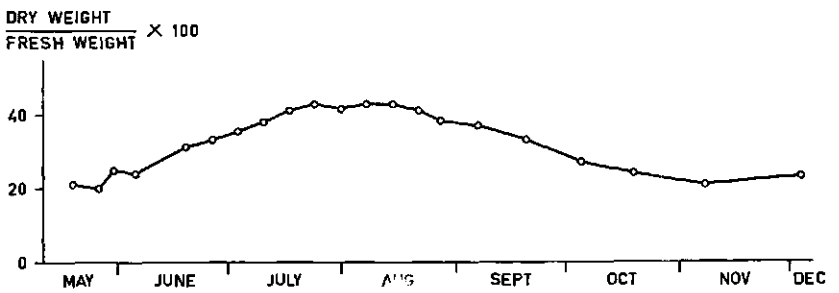


FIG. 31. Dry weight in percentages.

var as in *Pyrus nivalis* but, probably due to the lower sclereids content, with lower percentages of dry matter.

On the other hand RADU and GHERGHI (1966) discovered no optimum curve. In their series of observations the dry-matter content steadily increases during fruit development, reaching its maximum in the ripe fruit. In the 'Leipziger' cultivar which has the lowest dry-matter content, the figure increased in 1953 from 9.70% (fruit diameter 11 mm) to 13.76% (⌀ 45 mm), and in the 'Untuosa Hardenpont' cultivar which had the highest dry-matter content, from 16.88% (⌀ 21 mm) to 23.48% (⌀ 67 mm) in 1959 and from 15.42% to 22.20% in 1960.

5.3. MORPHOGENESIS

5.3.1. *Parthenocarpy*

GORTER and VISSER (1958) observe that the term 'parthenocarpy' is often employed in cases where 'seedlessness' is meant. Parthenocarpy means that the fruits develop without the influence of fertilised ovules. In addition to the absence of fertilised ovules, seedlessness may also be caused by early embryo abortion.

In contradistinction to the apple, a high percentage of seedless fruits is a common phenomenon in the cultivated pear. VON KARNATZ (1963) mentions an average of 20.9% seedless fruits in the pear as against an average of only 0.5% in the apple in the cultivars he examined over a period of ten years. The highest yearly average for pears and apples respectively was 74.4% and 1.5%, the lowest 5.6% and 0.1%. A factor increasing the probability of formation of parthenocarpic fruits is the pear's high degree of self-sterility. This is more in evidence in the pear than in the apple, so that covered inflorescences of the apple only produce 63% seedless (parthenocarpic) fruits as against 98% for the pear.

Self-sterility is also true of wild pear species. ZIELINSKI (1965) found that only one (*Pyrus faurei* Schneid.) of 15 species examined (amongst them *Pyrus nivalis* Jacq.) produced fruits following artificial self-pollination. These fruits contained seeds, so that in this experiment no parthenocarpic fruits were formed.

The tendency to form parthenocarpic fruits is not explained by this self-incompatibility, but it is understandable that in the absence of good pollen suppliers, wild pear varieties (as for instance *P. nivalis* Jacq. var. orientalis Terpó) may also have a great many parthenocarpic fruits owing to the combination of these two characters. In 1966, when the *P. nivalis* trees in the Belmonte Arboretum at Wageningen did not bear a very abundant crop, it was found that 177 or 44% of the 402 fruits contained no seeds. Since it was not noted whether fertilisation actually took place, according to GORTER and VISSER (1958) this would be a case of seedlessness and not of parthenocarpy.

5.3.2. *Seedlessness and dimension*

When the fruits of *Pyrus nivalis* are divided into weight classes many seed-

TABLE 12. Division into weight classes of the 1966 pear harvest and percentage of seedless fruits in each weight category.

Weight class (g)	Tree I			Trees II + III			Total		
	No.	of which seedless	%	No.	of which seedless	%	No.	seedless of which	%
0.01– 5.00	3	3	100	–	–	–	3	3	100
5.01–10.00	16	13	81	1	1	100	17	14	82
10.01–15.00	31	20	65	14	11	79	45	31	69
15.01–20.00	23	10	43	47	33	70	70	43	61
20.01–25.00	13	6	46	69	42	61	82	48	59
25.01–30.00	13	5	38	70	26	37	83	31	37
30.01–35.00	5	1	20	41	5	12	46	6	13
35.01–40.00	–	–	–	32	1	3	32	1	3
40.01–45.00	1	0	0	14	0	0	15	0	0
45.01–50.00	–	–	–	7	0	0	7	0	0
50.01–55.00	–	–	–	1	0	0	1	0	0
55.01–60.00	–	–	–	1	0	0	1	0	0
Total	105	58	55	297	119	40	402	177	44

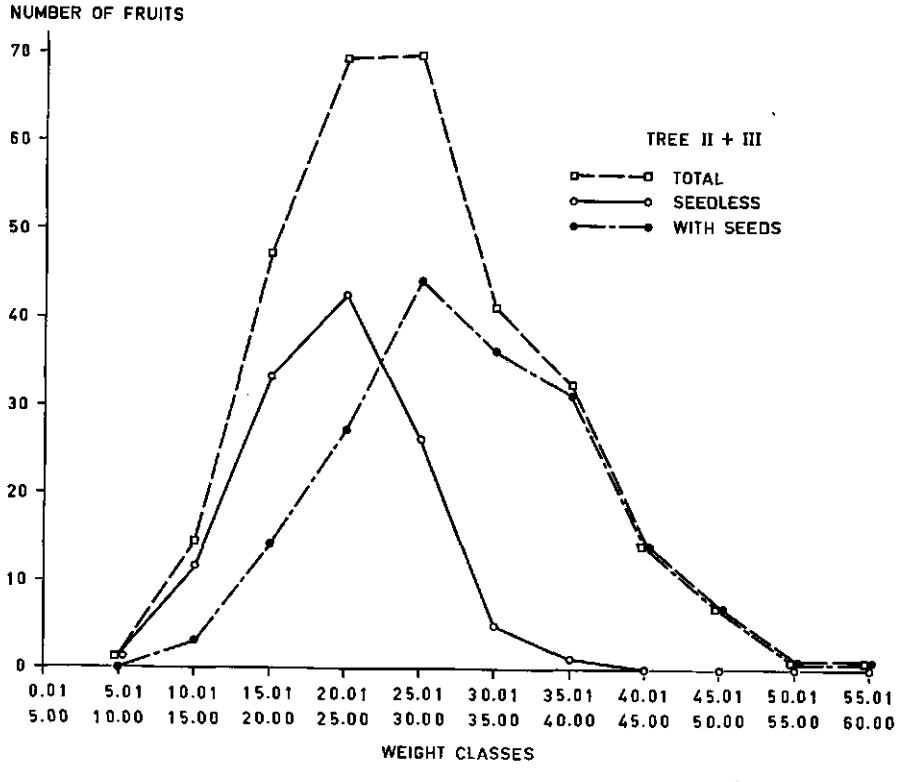


Fig. 32. Distribution over the weight classes of seeded and seedless fruits of trees II and III.

less specimens are found among the small fruits, but only a few among the large ones. The observations of material collected from tree I and trees II and III in 1966 are separately specified in Table 12. The data of trees II and III together are illustrated graphically in Figure 32. It is particularly clear from the table that seedless fruits of tree I are smaller than those of trees II and III. The percentages of seedless fruits are respectively 55 and 40.

The drop of ripe fruits is not noticeably accelerated or retarded by the presence or absence of seeds. In October 1966 73 fruits were gathered under trees II and III; 41 % of these were seedless. In November 1966 157 fruits were collected of which 43 % were found to be seedless. Fruits damaged by feeding insects or birds are not included. It is noticeable that six of the eight last fruits on the trees finally picked on 18th November 1966 proved to be apical fruits (occupying position 1 in the inflorescence). No marked abscission layer is present in these fruits and when they are picked the vascular cylinder is broken, probably at a predetermined point.

5.3.3. *Seedlessness and shape*

The length/diameter ratio provides some insight into the shape of the fruit. Of the cultivated pear it is usually true to say that this ratio is greater than unity. But the ripe fruits of *Pyrus nivalis* are almost invariably somewhat more wide than long, so that the length/diameter ratio is less than unity.

This length/diameter ratio was determined of undamaged fruits of trees II and III collected in November 1966. The values found are plotted in the graph in Figure 33.

Unlike the cultivated pear, seedless fruits of *Pyrus nivalis* are more highly flattened than the seed-bearing ones. All seedless fruits have a length/diameter

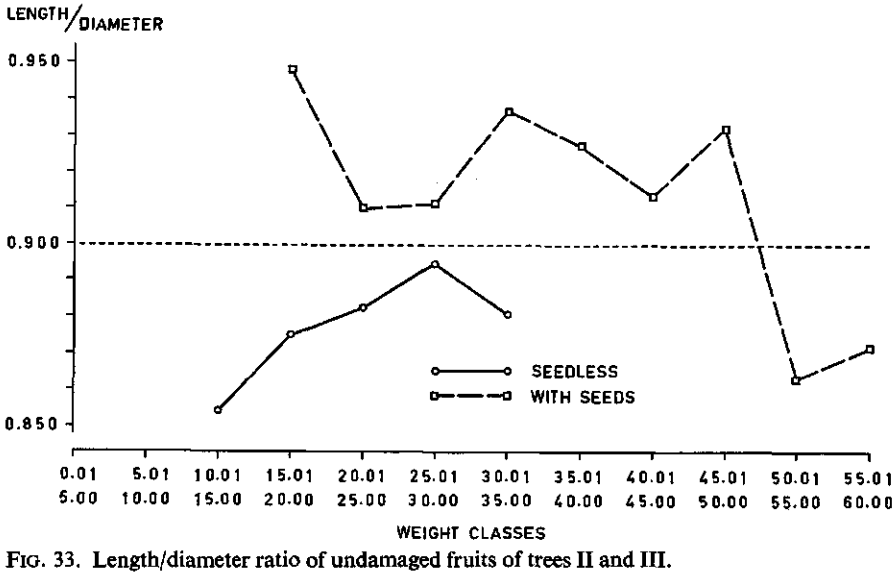


FIG. 33. Length/diameter ratio of undamaged fruits of trees II and III.

ratio of less than 0.900 and except for the largest fruits, the seed-bearing ones reach higher values. Hence flattened *Pyrus nivalis* pears have the same characteristics as flattened apples of which the seedless fruits are also more highly flattened than those bearing seeds (SCHANDER, 1955). The extremely flattened shape of the largest fruits is explained in § 5.3.5.

5.3.4. *Seedlessness and core size*

One naturally assumes that the core of seedless fruits will be smaller than that of seed-bearing ones. In the fruit of *Pyrus nivalis* the core is clearly surrounded by a layer of thick sclereid clusters. All material inside this layer belongs to the core and no sclereids are found in this part. The core of every fruit is practically spherical. The transverse diameters of the core of undamaged fruits of trees II and III collected in November 1966, are shown in graph form in Figure 34.

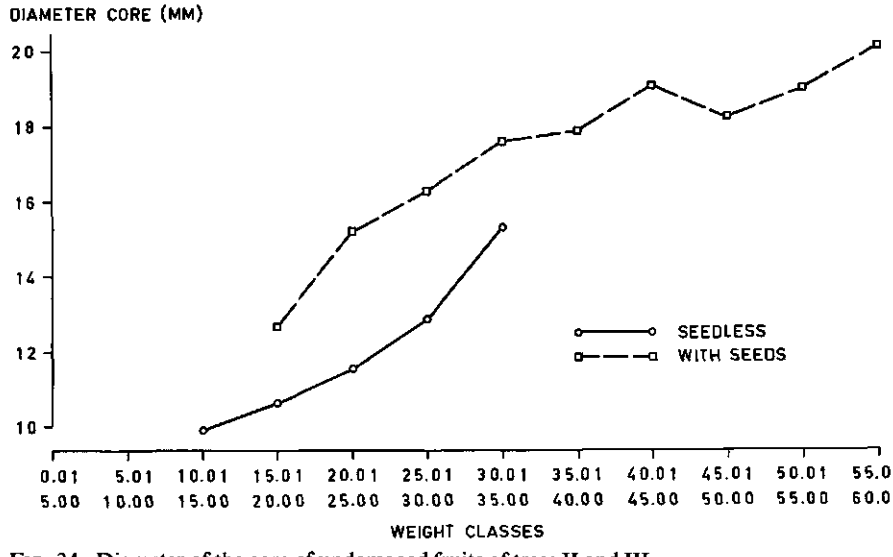


FIG. 34. Diameter of the core of undamaged fruits of trees II and III.

Considered by weight class, the cores of seedless fruits are distinctly smaller than those of seed-bearing fruits. But irrespective of whether the fruits are seedless, the diameter of the core increases with increasing weight of the fruit. The distances from the insertion of the stalk to the core and to the original vegetative apex (inside the core) are the same for seed-bearing and seedless fruits (Figs. 35 and 36). These distances also increase with increasing size of the fruits but to a far less extent than the diameter of the core. It seems very likely that the presence or absence of seeds in the fruit of *Pyrus nivalis* solely affects the growth of the core. Other parts of the fruit develop in the same way or at most adapt themselves to a large or small core. If this assumption is correct the greater flattening of the seedless fruits could be explained by means of differences in core-size as compared with seed-bearing fruits.

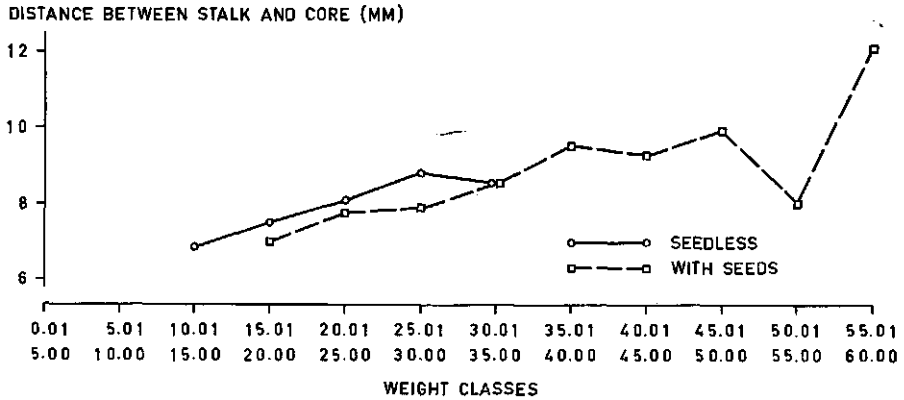


FIG. 35. Distance from the insertion of the stalk to the base of the core in undamaged fruits of trees II and III.

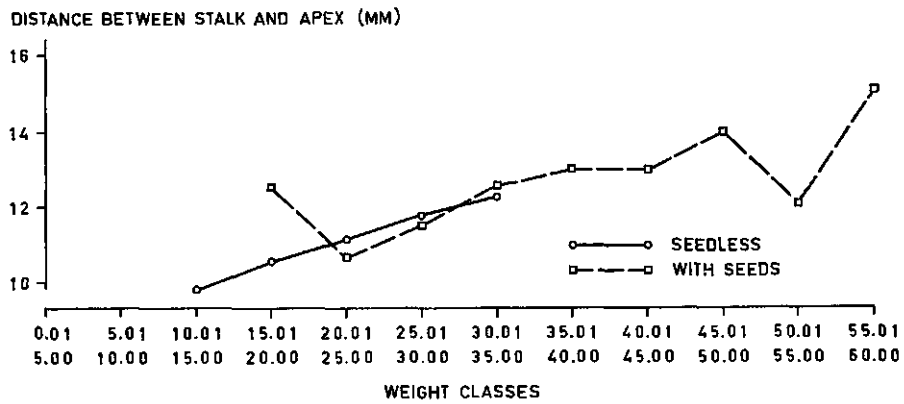


FIG. 36. Distance from the insertion of the stalk to the original apex in undamaged fruits of trees II and III.

5.3.5. *The cause of flattening of seedless fruits*

A comparison of the various developmental stages of the fruit shows that longitudinal growth takes place quite differently from diametrical growth. The development of the ovary to a fully-grown fruit is illustrated in Figures 37 and 38. The contours of the longisections of fruits 0, 29 and 36 days after anthesis are reproduced on the left-hand side of the first figure. The original apex of the flower is taken as the centre of the coördinate axes. The subsequent development of the fruit is shown on the right-hand side of Figure 37. The longisection of the 36-day-old fruit is here shown reduced in the centre of the figure; surrounding it are the contours of fruits 71, 121 and 172 days after blossom. In this case the point at which the vascular bundles meet just below the vegetative apex is taken as the centre of the coordinate axes, the vegetative apex of slightly older fruits not always being so clearly visible as that of young fruits. It is often surrounded and occasionally forced upward by outgrowths of tissue.

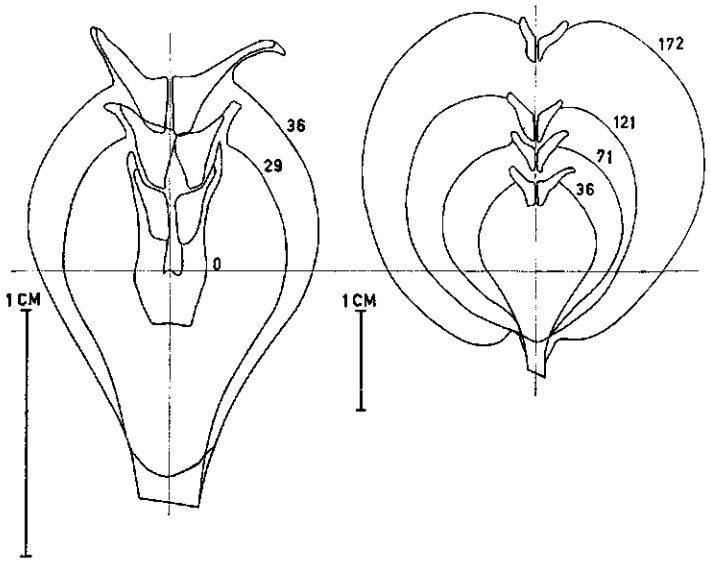


FIG. 37. Development of the fruit with the original apex as the centre. The numerals denote the age of the fruits in days after blossom,

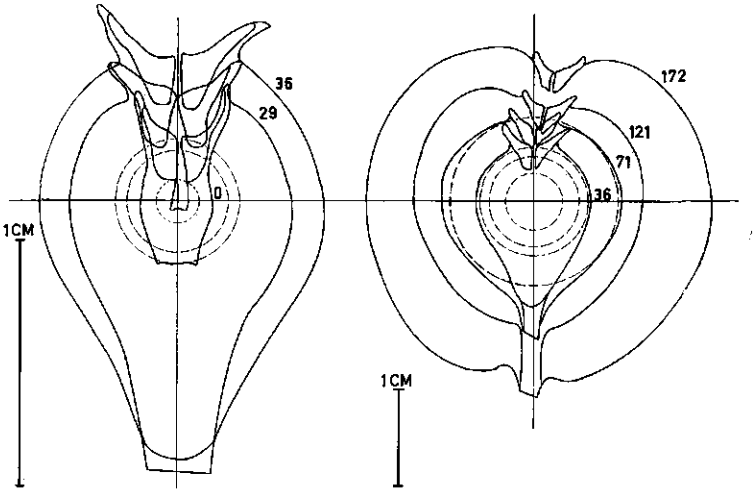


FIG. 38. Development of the fruit with the middle of the core as the centre. The numerals denote the age of the fruits in days after blossom.

The same fruit contours are shown in Figure 38 in which, however, the centre of the core is taken as the centre of the coördinate axes. In each cross-section the peripheries of the cores are indicated by a broken circular line.

In theory there are three points at which the fruit could grow along the longitudinal axis, viz.:

1. At the eye end. Since the eye cells lignify only a few days after fruit growth commences, longitudinal growth is quite out of the question at this point. It can be seen in Figure 7 (p. 18) that in the ripe fruit the eye is inserted in a layer of thick sclereids in the form of a wedge.
2. In the core. The part mainly growing here is that situated between the eye and the original vegetative apex. The styles, of which the dried-up tips extend beyond the eye, develop lengthwise on the base and therefore continue to grow at the same rate as the surrounding core tissue. The core develops no further than is required by the size of the seeds it contains. In some cases it develops so little that owing to lack of space some of the seeds in the locule burst through the open ventral suture into the space above the apex.
3. In the part between the insertion of the stalk and the core. This part develops very rapidly in the first few weeks after fruit set, so that both in *Pyrus nivalis* and the cultivated pear (cf. ROSPER, 1957) there is first a rapid increase in the value of the length/diameter ratio, after which it steadily falls until the fruit is ripe. BAIN (1961) found that the ovary of the 'Bartlettt' cultivar had a length/diameter ratio of 1.1 at blossom. Fourteen days later this ratio increased to 2.7, after which it fell to 1.3 for harvest-ripe fruits 133 days after blossom.

As the fruit develops the flesh is forced upward around the eye in the form of a wall, so that it drops down as it were into a cavity in the fruit. This wall, like one sometimes formed around the insertion of the fruit-stalk, is always included in length measurements, thus adding to the length of the fruit.

Figure 37 clearly shows that the longitudinal growth discussed under 3 ceases in *Pyrus nivalis* only a month after blossom. Thereafter longitudinal growth is almost wholly due to the development of the core.

It is still not entirely clear how longitudinal growth occurs between the core and the insertion of the fruit stalk.

In both the cultivated pear and *Pyrus nivalis* a part of the pedicel just below the ovary seems to thicken into fruit tissue and be thus absorbed in the fruit (cf. ROSPER, 1957). But in *Pyrus nivalis* only about 2½ weeks after blossom scalariform vessels are found in the fruit stalk at the point of insertion 3 mm from the original apex. Over a month later pitted vessels occur in the fruit stalk, and here and there scalariform vessels in its extension inside the fruit up to half-way the distance from the core. Scalariform vessels only appear in the vascular bundless of the flesh three months after blossom. These only occur at the points where vascular bundless branch and where vascular bundless pass close by or through a sclereid cluster. Throughout fruit growth the main mass of the metaxylem of the vascular bundles in the flesh always consists of very wide spiral vessels. It is clear that longitudinal growth ceases at the points where the rigid scalariform and pitted vessels are encountered. No torn scalariform or pitted vessels are found in the extension of the fruit stalk inside the fruit, but only stretched spiral vessels. Since the original apex is 1–2 mm from the pedicel insertion in the ovary of the flower, and since scalariform vessels in a young fruit are found at 3 mm from the apex, in *Pyrus nivalis* not more than 1–2 mm

of the fruit extension can be attributed to the absorption of a part of the fruit stalk by the fruit. Consequently the remainder of the longitudinal growth described under 3 is due to elongation of the basal part of the ovary below the apex (cf. also ROSPER, 1957).

In order to obtain an idea of the growth of the rest of the pear, the core, which expands spherically throughout the developmental stages, is taken as the centre of growth (Fig. 38). The circumference of the core is indicated by a broken circular line. It is noticeable that in each developmental stage the flesh forms a practically concentric zone around the core, the only exceptions being the stalk and eye ends. It appears as though the entire fruit expands spherically from the centre of the core, but that this expansion is inhibited by the eye end, with the result that first the fruit is flattened at this point and later even dented, causing a reduction in the length /diameter ratio. In the first instance there is no growth inhibition at the stalk end. It is only when the flesh grows thicker than the distance from the stalk end to the base of the core that the same phenomenon occurs at this point as at the eye end, viz. growth retardation close to the stalk where it causes flattening and afterwards a cavity. It is only in very large fruits that the flesh may become so thick as to cause a flattening of this kind. As a result the length/diameter ratio is sharply reduced at the end of the growth period; this explains the different value of this ratio for the large seed-bearing fruits in Figure 33.

The relatively marked flattening of seedless fruits can also be readily explained. In these the core remains small so that longitudinal growth is comparatively slight; in fact, about one month after blossom it is solely due to the expansion of the core. The flesh does not appear to respond to the absence of seeds and grows at the same rate as in seed-bearing fruits. Consequently the diameter, which depends on the growth of both the flesh and core, increases far more rapidly than the length, for which core growth alone is responsible. If the core

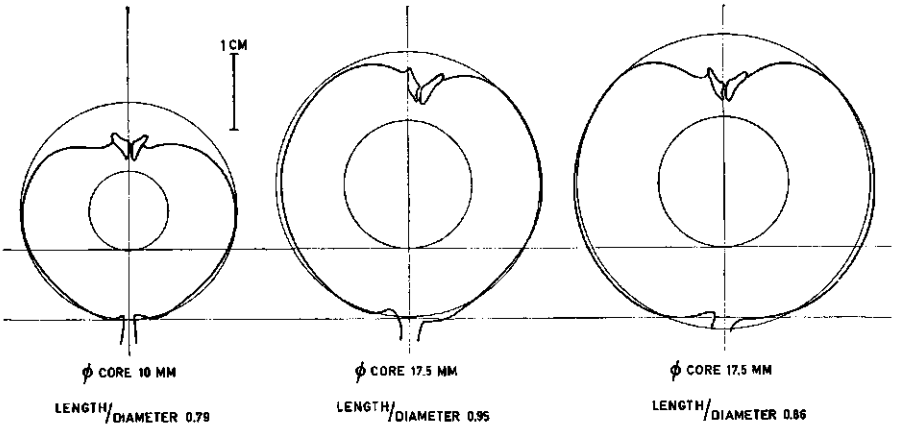


FIG. 39. The shape of a seedless, normal and extremely large fruit.

remains small this has a far more direct effect on longitudinal than on latitudinal growth. As a result a relatively marked flattening is soon reached in seedless fruits.

To illustrate this interpretation, Figure 39 shows side-by-side a parthenocarpic fruit (length/diameter = 0.79), with a small core, a medium-sized fruit (length/diameter = 0.95) with the same thickness of flesh, but with seeds and hence a large core, and a large fruit (lenght/diameter = 0.86) with a core of the same size and a thicker layer of flesh. The flattening of the fruits is shown up by the circumscribed circle.

5.3.6. *Formula for the length/diameter ratio*

The data in the previous section provides a simple formula for the length/diameter ratio of fruits of *Pyrus nivalis*.

$$\text{length/diameter} = \frac{X + Y + E}{X + 2Z}$$

wherein X = the diameter of the core (Fig. 40), Y = the distance from the insertion of the stalk to the base of the core (after a month this distance reaches a constant value of about 9 mm; cf. Figure 35), Z = the thickness of the flesh, and E = the length of the sclerified plug (eye), a constant of about 4 mm.

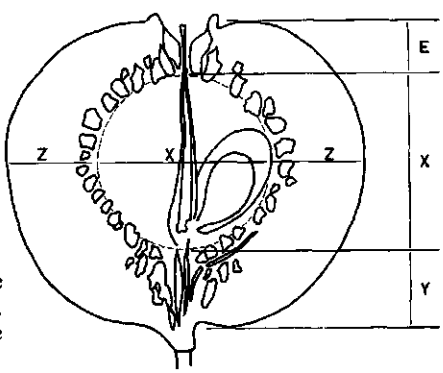


FIG. 40. Longisection of a ripe fruit. X = diameter of the core; Y = distance from the insertion of the stalk to the base of the core; Z = thickness of the flesh; E = length of the sclerified plug (eye), constant c. 4 mm.

If in this formula we substitute values of 8, 9 and 4 mm for Z, Y and E respectively and X = 6, X = 11, X = 17 and X = 20 mm, then the length/diameter ratios are respectively 0.86, 0.89, 0.91 and 0.92. As can be seen in Figure 34, the values 11 mm and 17 mm show good agreement with the average value for the diameter of the core of a seedless and a seed-bearing fruit. In Figure 33 the calculated length/diameter ratios of 0.89 and 0.91 would certainly not be wide of the mark.

If X = 20, Y = 9 and E = 4 and the flesh thickness Z is successively 9 and 10, as may be the case in extremely large fruits, then the length/diameter ratios are successively 0.87 and 0.83. This formula is obviously only a rough approximation; for instance, no account is taken of the invariably measured increase in

length of the fruit resulting from the expansion of the flesh to an annular wall surrounding the eye and stalk ends. Nevertheless this simple formula does provide some idea of the growth pattern of the fruit of *Pyrus nivalis*.

According to the literature (SKENE, 1966) it has been observed that unlike the pear, it is precisely the part between the eye end and the core of an apple that exhibits marked longitudinal growth. This difference in morphogenesis between the two fruits is revealed by an inspection of young apple and pear fruits. Young apples are thickest and roundest on the stalk side and the fruit usually tapers in the direction of the eye end. The converse is true of young pears.

In view of the above it would be interesting to examine whether such substances as gibberellic acid or growth inhibitors such as B-Nine which regulate longitudinal growth would have any effect at these points in the apple and pear.

Moreover it is probable that the effect of seeds on fruit growth has also been greatly overestimated (cf. p. 45). But the presence of the epidermis and a number of underlying cell layers is essential to the expansion of the flesh (cf. p. 46).

This outermost fruit layer is also the one that remains active for the longest time, so that an investigation into its effect on fruit growth might produce some interesting data.

5.3.7. *Correlation between fruit size and position in the inflorescence*

In theory every ovary in the *Pyrus nivalis* inflorescence (for the structure cf. § 3.2.2. and Fig. 2) is capable of expanding into a fruit. But in a part of the inflorescences there is a complete absence of fruit set, and of the others usually only one or two fruits reach the developmental stage (cf. RUDLOFF and HERBST, 1939).

If no apical pear (position 1) is formed, the apical portion of the short shoot falls off gradually owing to the formation of a succession of abscission layers until the pear or foliage leaf in the highest position (usually position 6) has been reached. This explains why in ripe pears it is practically impossible to determine the original position on the short shoot when the apical pear is missing. Consequently of the pears picked in 1958 and 1962 during fruit development, the position could only be determined of a few, chiefly collected from abundant inflorescences. The fruits from positions 2 and 3; 4, 5 and 6; and 7, 8, 9, like the samples picked at various dates, are therefore summed to enable a determination to be made of the average diameter (as a criterion of the size) of a reasonably large number of fruits. This number is shown in brackets next to each diameter in Tables 13 and 14 in which the results are summarised.

The results clearly illustrate that fruits in positions 2 and 3 are small as compared with the remainder. Pears occupying positions 7, 8 and 9 were largest in 1958, and also very large at the beginning of 1962. This would be different in the apple in which the king fruit, i.e. that formed from the terminal flower of the inflorescence is the largest. Since the 1958 and 1962 data are mainly taken from abundant inflorescences the results give a distorted picture which is only applicable to these particular inflorescences.

For this reason, in 1964 data was again assembled on the possible relationship

TABLE 13. Correlation between the mean diameter of pears in mm and the position in the cluster during their development in 1958. The figures in parentheses indicate the numbers investigated.

Month	Position of the fruits in the inflorescence				Total mean
	1	2 + 3	4, 5 + 6	7, 8 + 9	
May	3.0 (27)	2.6 (58)	3.0 (87)	3.4 (71)	3.0 (243)
1st–15th June	7.0 (1)	5.4 (1)	7.0 (2)	7.5 (5)	7.3 (9)
16th–30th June	–	9.9 (2)	10.6 (6)	12.0 (8)	11.2 (16)
July	20.0 (2)	17.3 (1)	18.1 (19)	18.9 (12)	18.4 (34)
August	19.3 (9)	18.0 (1)	21.5 (17)	22.2 (15)	21.2 (42)
September	22.0 (1)	21.3 (1)	26.7 (1)	26.8 (1)	24.2 (4)
October	–	28.7 (1)	30.4 (1)	37.2 (2)	33.4 (4)

TABLE 14. Correlation between the mean diameter of pears in mm and the position in the cluster during their development in 1962. The figures in parentheses indicate the numbers investigated.

Month	Position of the fruits in the inflorescence				Total mean
	1	2 + 3	4, 5 + 6	7, 8 + 9	
May	3.0 (6)	2.8 (12)	3.0 (18)	3.2 (9)	3.0 (45)
1st–15th June	4.4 (6)	2.8 (10)	3.8 (18)	4.2 (14)	3.8 (48)
16th–30th June	11.7 (4)	7.9 (5)	10.3 (4)	11.5 (8)	10.5 (21)
July	16.4 (8)	15.1 (13)	16.4 (18)	18.4 (15)	16.7 (54)
August	19.8 (10)	19.5 (6)	19.8 (24)	19.7 (13)	19.7 (53)
September	23.3 (5)	23.1 (7)	24.0 (11)	24.3 (4)	23.7 (27)
October	32.4 (1)	28.6 (1)	29.4 (4)	33.0 (3)	30.8 (9)
November	35.4 (2)	29.0 (3)	35.5 (6)	35.3 (2)	33.9 (13)

between fruit size and the position of the fruit in the inflorescence. In this year measurements were regularly taken of all fruits, including single fruits and fruits from clusters with low fruit numbers, from tree I in the Belmonte Arboretum, Wageningen. The average diameters are listed in Table 15. The latest observations, made on 26th October, are shown in graph form in Figure 41. In view of the 1964 observations, when the position of each fruit in the inflorescence was determined directly after blossom, it can be stated that basal pears in positions 7, 8, 9 and 10 are the largest and that pears 2 and 3 remain the smallest. The combination of an apical fruit and a fruit from group 2 and 3 on the same shoot only occurred once in 1964. The subapical fruit (2) also dropped off before 22nd July, so that this is omitted from Table 15. The smallness of the fruits in positions 2 and 3 cannot be explained by apical dominance of a growing apical fruit owing to the latter's absence. A comparison of the observations in Table 15 shows that even at the first measurement the fruits differed in size. When the differences are compared with the differences in size found in flowers according to their position in the inflorescence (§ 4.3.1.) it can be seen that the differences in flowers and fruits are exactly parallel, so that it would appear reasonable to attribute the differences in fruit size to differences in flower size (or diameter of the ovary).

TABLE 15. Mean diameter of all fruits in mm on a small tree (tree I) in the Belmonte Arboretum, Wageningen, in 1964. Since pears which dropped off before 2nd August were usually suffering from growth disorders they are not included.

Date	Position of the fruits in the inflorescence				Total mean
	1	2 + 3	4, 5 + 6	7, 8, 9 + 10	
1st–2nd June	8.6	7.1	8.6	9.5	9.0
8th–9th June	10.5	8.6	10.4	11.1	10.7
15th–16th June	12.2	10.5	12.0	12.8	12.4
22nd June	13.3	11.2	13.1	13.8	13.4
29th June	14.5	12.6	14.3	15.1	14.7
6th July	15.4	13.2	15.1	15.9	15.5
12th–13th July	16.4	14.0	16.1	16.9	16.5
19th–20th July	17.2	14.9	16.9	17.7	17.3
26th–27th July	18.1	15.8	17.7	18.6	18.2
2nd Aug.	18.9	16.6	18.6	19.6	19.1
16th Aug.	21.0	18.8	20.7	21.6	21,0
24th Aug.	22.4	19.8	22.0	22.8	22.4
30th–31st Aug.	23.7	21.1	23.3	24.4	23.8
7th Sept.	25.3	22.6	24.9	26.1	25.5
14th Sept.	26.5	23.7	26.1	27.4	26.8
21st Sept.	27.7	25.0	27.1	28.5	27.9
28th Sept.	28.7	26.1	28.3	29.6	28.9
5th Oct.	29.2	26.6	28.9	30.1	29.5
12th Oct.	29.4	26.2	29.5	31.2	30.2
19th Oct.	29.9	26.6	30.1	31.7	30.8
26th Oct.	30.0	25.9	30.2	31.7	30.7

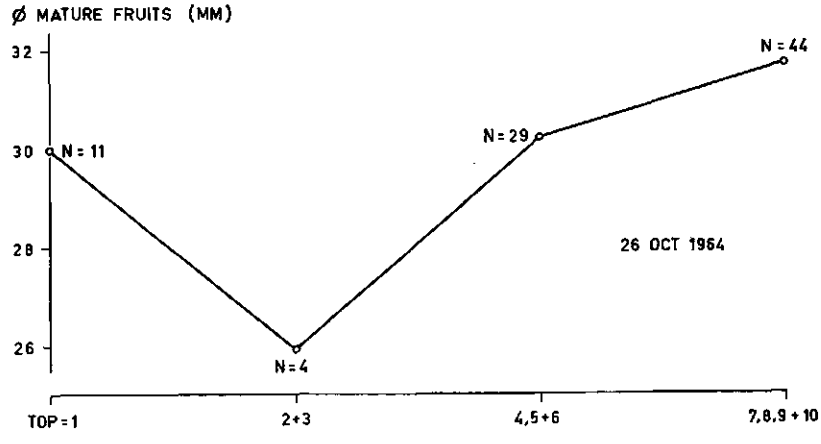


FIG. 41. Correlation between the diameter of the fruit and the position in the cluster. N = number of fruits measured.

5.3.8. *Correlation between fruit production and the position in the inflorescence*

Since the 1964 observations relate to the entire tree it is an easy matter to give a reliable overall picture of the fruit production. During blossom 350 inflorescences were counted on the tree of which only 171 bore fruit on 15th–16th June. Since the number of fruits totalled 298, the average fruit number was $1^3/_4$ per fruit-bearing shoot. Table 16 shows the distribution of the fruits over the branches and over the positions in the inflorescences. The total numbers of fruits per position in the inflorescence are shown in graph form in Figure 42. It can be quite clearly seen that positions 2 and 3 not only produce small fruits but there is only a very slight chance of a fruit being formed in these positions. Position 2 is a particularly unfavourable one. The table shows that of the four fruits originally formed in this position three dropped off before 2nd August. Both the table and graph make it clear that positions 6, 7 and 8 are the most pro-

TABLE 16. Correlation between the fruit set on tree I in 1964 and the position in the inflorescence.

Branch No.	No. of inflor-escences	Number of pears formed at each position in the cluster											Total fruit set
		1	2	3	4	5	6	7	8	9	10	11	
0	8	1	–	1	–	–	2	2	3	2	2	–	
3	3	1	–	1	–	1	2	–	–	–	–	–	
4	2	–	–	–	–	–	1	1	–	–	–	–	
6	2	–	–	–	–	2	–	–	–	–	–	–	
7	3	–	–	1	–	–	1	1	–	–	–	–	
8	4	–	–	–	1	–	1	2	1	1	–	–	
9	19	3	–	2	2	2	4	5	10	7	4	1	
10	7	1	–	–	2	4	4	4	2	1	–	–	
11	12	1	1	2	2	–	5	4	2	2	–	–	
12	2	1	–	–	–	–	1	–	–	–	–	–	
13	1	1	–	–	–	–	–	–	–	–	–	–	
14	27	3	–	2	7	5	7	6	9	8	4	–	
15	3	1	–	–	–	1	1	–	1	2	–	–	
16	1	–	–	–	–	–	–	–	1	–	–	–	
17	1	1	–	–	–	–	–	–	1	–	–	–	
18	1	1	–	–	–	–	–	–	–	1	–	–	
20	15	–	1	–	2	2	2	3	6	4	–	–	
21	13	3	–	–	2	4	1	3	2	4	1	–	
22	3	–	1	–	–	–	1	–	1	1	–	–	
23	10	2	–	–	1	3	4	3	5	3	1	–	
24	5	1	–	–	1	2	3	1	–	1	–	–	
25	17	3	1	–	1	1	3	7	7	2	1	–	
26	12	1	–	1	1	3	5	6	4	1	2	–	
Total infl.	171	25	4	10	22	30	48	48	55	40	15	1	298
Dropped prior to 2nd Aug.		6	3	3	5	9	8	8	16	10	3	0	71
% drop		24	75	30	23	30	17	17	29	25	20	0	24

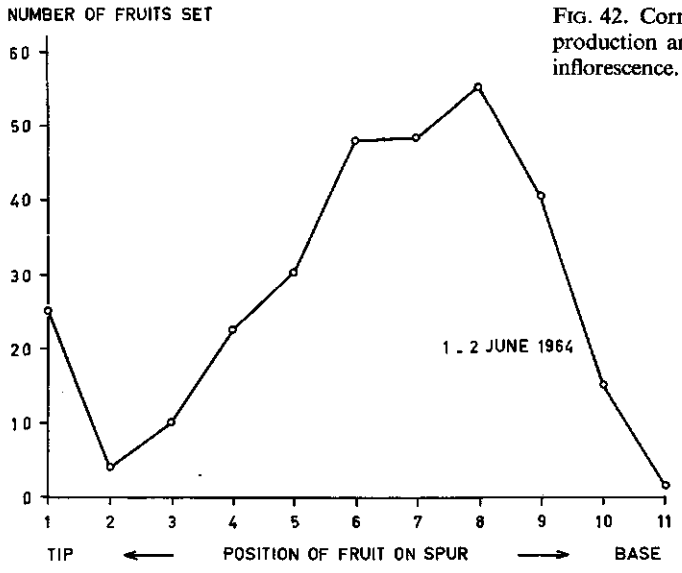


FIG. 42. Correlation between fruit production and the position in the inflorescence.

pitious for fruit setting and that only relatively few fruits drop off before 2nd August. Ultimately the chance of a ripe fruit being formed at positions 6, 7 and 8 is about 40 times as great as at position 2 on the inflorescence. For the sake of completeness it should be added that between 2nd August and 5th October a further three fruits dropped off from positions 6, 7 and 8. After 5th October many of the fruits were already ripe and eaten by birds, so that any further check on early drop is irrelevant. The observations discussed in this section prove that fruit formation in *Pyrus nivalis* is possible at any position in the inflorescence but that most fruits develop at positions 6, 7 and 8.

5.3.9. *Number of seeds in the fruits*

Inspection of Figure 34 (p. 60) shows that the presence or absence of seeds influences the size of the core and hence that of the fruit itself. It seemed an attractive idea to determine the effect of the number of seeds on the fruit size, but since the only data available related to 1966 this project was abandoned.

After discovering the high percentages of seedless fruits it was to be expected

TABLE 17. Number of fruits on tree I and trees II and III with one, two or more seeds in 1966. The percentages compared with seed-bearing fruits are shown in parentheses.

	Total number	Seedless	%	Seed-bearing	%	1 seed	%	2 seeds	%	> 2 seeds	%
Tree I	105	58	55	47	45 (100)	32	30 (68)	12	11 (26)	3	3 (6)
Trees II and III	297	119	40	178	60 (100)	121	41 (68)	45	15 (25)	12	4 (7)
Total	402	177	44	225	56 (100)	153	38 (68)	57	14 (25)	15	4 (7)

that the seed-bearing fruits would only contain few seeds. The data for trees I, II and III are summarised in Table 17. It was in fact found that only a small percentage of the fruits contained more than two seeds. If the percentages of fruits with one, two or more seeds are calculated exclusive of seedless fruits they are found to be the same for tree I and trees II and III; 68% of the fruits contained one seed, 25% two seeds, and only 7% more than two seeds.

5.3.10. *Number of locules in the fruits*

According to its classification *Pyrus nivalis* belongs to a group of pears that should have fruits with five locules. Very often, however, fruits may occur with a different number of locules, usually four. The numbers of locules per fruit of ripe fruits were counted in 1966. Table 18 shows the various numbers of five-chambered seedless and seed-bearing fruits in both types of trees.

TABLE 18. Number of five-chambered fruits on tree I and trees II and III in 1966.

	Seedless			Seed-bearing			Total		
	total number	5 locules	%	total number	5 locules	%	total number	5 locules	%
Tree I	58	21	36	47	20	43	105	41	39
Trees II and III	119	38	32	178	70	39	297	108	36
Total	177	59	33	225	90	40	402	149	37

Both were found to bear very high percentages of anomalous fruits. Only 37% of the harvest of the three trees consisted of quinqueloculate fruits. At this point it might be suggested that quinquelocularity might actually be an anomaly in *Pyrus nivalis*. But in the inflorescence it was already observed that despite the low percentage of five flowers in 1966, quinquelocularity is to be regarded as normal and that a smaller number of locules (< 5) is due to disorders during the morphogenesis of the flowers (§ 4.3.5. and § 4.3.6.).

To judge from the data in Table 18 it would appear that five locules are found rather more often in seed-bearing fruits. This might be due to the fact that owing to the greater number of ovules in the five-chambered flower (10 as compared with 8 in a four-chambered one), the possibility of seed formation is greater than in a flower with fewer locules.

The relationship between quinquelocularity and weight was examined of the fruits of trees II and III. The graph in Figure 43 reveals a very clear relationship between quinquelocularity and weight. It may be inferred from the rising curve that five-chambered fruits are usually heavier than those with fewer locules It should be noted that the last two points of the curve are due to two single fruits.

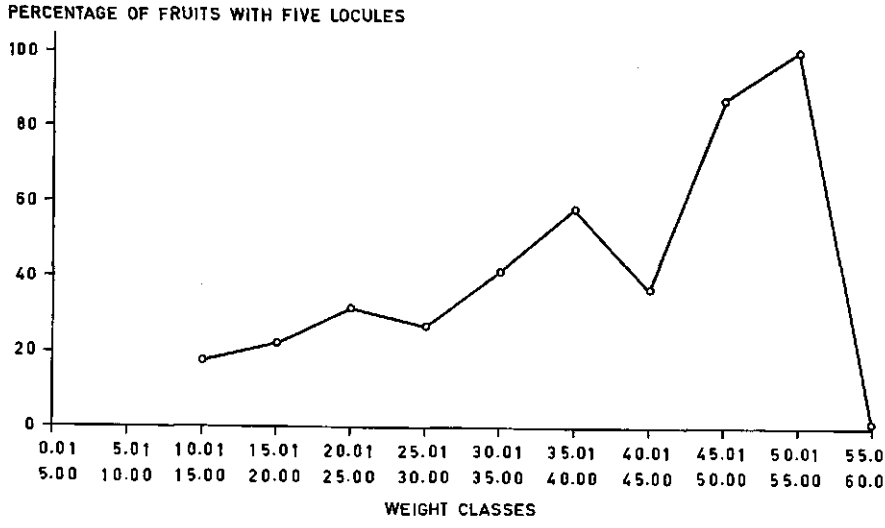


FIG. 43. Fruit size in relation to quinquelocularity.

5.3.11. *Differences in fruit growth on different branches*

Inspection of the growth curves of individual fruits creates the impression that as the growing season advances the curves diverge to an increasing extent; in other words the original difference in size of the young fruit or ovary becomes increasingly larger. The measurements made in 1963 of fruits on the two terminal axes of the same branch prove that in this instance the converse is true.

The mean transverse diameters of the fruits on the two branches are plotted in the graph in Figure 44. Although the curves of the two branches diverge in this case also, there is no question of more rapid fruit growth on branch I. On 4th June, during the first measurement, the mean fruit diameter on branch on branch I was 4.6 mm and that on brach II 3.8 mm, a difference of 0.8 mm or 17%. On 24th October, during the last observation, the difference between branch I with a fruit diameter of 31.4 mm and branch II with one of 28.4 mm was 3.0 mm or only 10%. If the differences are compared with the volume, calculated according to the formula $^1/_6\pi d^3$, the percentages are 44 and 26 respectively. In this case, therefore, original differences in fruit size do not become relatively greater during the growing period but just the reverse.

It was even observed that growth curves of individual fruits may intersect each other, viz. an initially small fruit grows more rapidly than a larger one and eventually exceeds it. This was not often observed and is in contradiction with the data in § 5.3.7. where it was shown that the initial differences are maintained. In some cases this discrepancy can be explained, since when the seeds in a large ovary fail to develop the core of such a fruit remains small, so that the fruit does not develop at the same rate as an initially smaller seed-bearing fruit which eventually grows larger (§ 5.3.2.). In the same way the number of fruits on the short shoot may exert an influence (DENNE, 1960), so that potentially

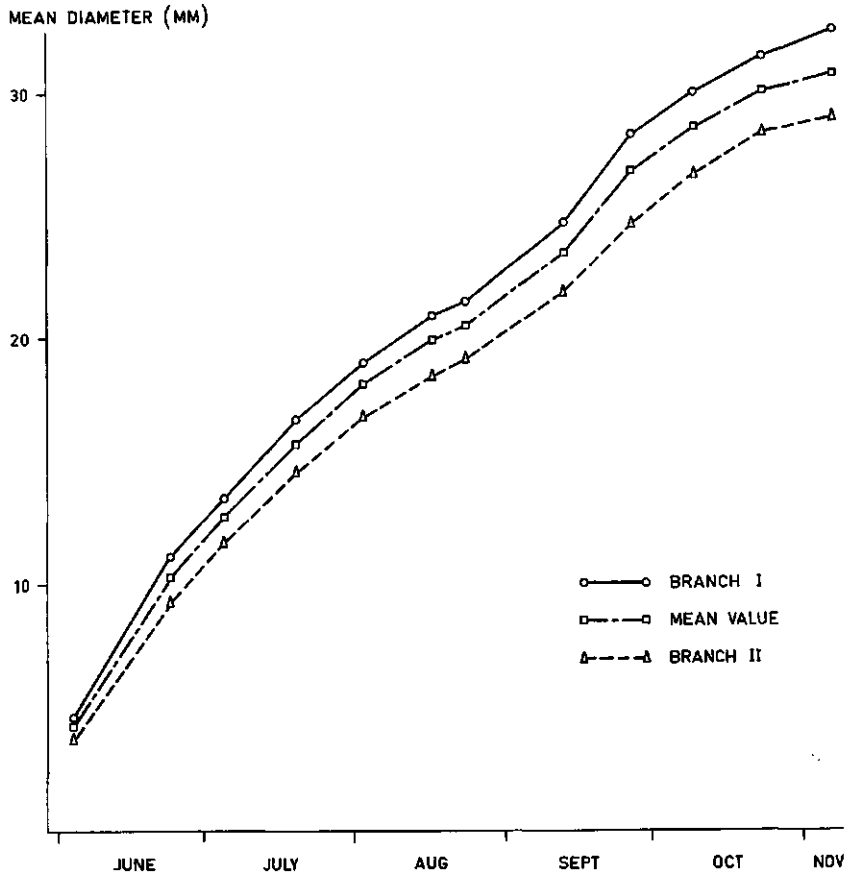


FIG. 44. Differences in fruit growth on different branches.

similar fruits on a shoot with a high fruit set do not develop so well as on shoots with a single fruit. In *Pyrus nivalis*, of which the shoots were not artificially thinned, the fruits on shoots with a high fruit set are certainly not smaller than single fruits. This may be due to the fact that only 'vigorous inflorescences' (VISSER, 1955) are capable of producing an abundance of fruits. 'Weak inflorescences' produce few if any fruits.

5.4. HISTOGENESIS

5.4.1. *Number of sclereid clusters in the ripe pear*

The number of sclereid clusters in the pear may be determined by means of simple techniques. The fruit is cut lengthwise into two parts as near as possible of equal size. One half is stored for microscopic study, the other cut into transverse slices about 1 mm thick. These slices are made transparent by placing them in a solution of 9 parts water and 1 part concentrated bleaching agent hav-

ing a 12% chlorine content. The slices are then rinsed in 50% alcohol and afterwards transferred to 70% alcohol. The sclereids in the slices are counted as carefully as possible with the aid of a stereoscopic microscope. A distinction is drawn between the sclereid clusters surrounding the core, located in the flesh and just below the epidermis. Table 19 lists the results of the counts of two fruits collected on 9th November 1962. The counts are reduced to numbers of sclereid clusters in the entire pear. The numbers of sclereid clusters in the two pears differ considerably. The pear in position 7 in the inflorescence contains over $1^1/_2$ times as many sclereid clusters as the one in position 4.

TABLE 19. Number of scleried clusters in the fruit.

	Pear No. 4 (⌀ 30.0 mm)	Pear No. 7 (⌀ 36.0 mm)
Sub-epidermal	6,130	8,550
Flesh	8,930	14,530
Around core	480	920
Total	15,540	24,000

The distribution of the sclereid clusters in the flesh, around the core and below the epidermis may be determined by means of simple volume and area formulas. The result of the calculations is summarised in Table 20; it is solely a matter of the numbers of sclereid clusters per unit of area or volume. In the table a distinction is drawn between the apical and basal part of the fruit. The plane running through the centre of the core normal to the longitudinal axis of the pear is taken as the separation between the two parts. The figures in Table 20 bear out what is already visible to the naked eye, viz. that the clusters at the eye end are denser than at the stalk end. It is clear that in both pears the concentration of clusters in the flesh is practically the same. This agrees with the observation that large and small fruits are equally succulent. The number of sclereid clusters in the two pears differ considerably. An ontogenetic study on a quantitative basis had to be abandoned because the sclereids are so much more concentrated in young fruits than in ripe ones that it becomes practically impossible to section and to count the clusters.

TABLE 20. Number of sclereid clusters per unit of area and volume.

	Pear No. 4		Pear No. 7	
	apical	basal	apical	basal
Sub-epidermal (sclereid clusters per mm^2)	2.45	1.89	2.25	1.96
In flesh (sclereid clusters per mm^3)	0.87	0.67	0.94	0.63
Around core (sclereid clusters per mm^2)	0.58	0.48	0.79	0.81

5.4.2. *Numbers of sclereids per cluster and estimates of the numbers of sclereids per pear*

Slides for microscopic study could not be prepared from the remaining pear halves referred to in the previous section. However it proved possible to microtome a number of longitudinal sections of another ripe fruit.

In these median sections, as in Figure 7 (p. 18), it can be seen that the sclereid clusters surrounding the core are very large and that the size decreases in the direction of the epidermis.

The sclereids forming a cluster are not all of the same size. Usually several large sclereids are located in the centre, the size of the sclereids decreasing towards the periphery.

Since the sclereid clusters are more or less spherical it is nevertheless possible to calculate the mean diameter of the sclereids and the number in a cluster. If the sclereid cluster may be imagined as consisting of cubic sclereids of the same size with an edge x, n sclereids being situated along the centre line, then the number of sclereids on a median section will be $^1/_4\pi(n.x)^2$. In the slide the number of sclereids in such a cross-section was counted for clusters at different points of the pear. The approximate figure for the number of sclereids in the cluster in question is found by supplying in the formula $^1/_6\pi(n.x)^3$ the calculated value n.x from the formula for the circular cross-section. The diameter of such a sclereid cluster can be measured under the mixroscope, so that the edge x of the imaginary sclereid is known. Measurements of individual sclereids under the miscroscope show that this figure is in fact representative of the mean diameter of the sclereid in a cluster.

The results of the calculations are listed in Table 21. Considering the vast size of the sclereid clusters in the fruit of *Pyrus nivalis*, the large numbers of sclereids per cluster are not surprising; what is noticeable, however, is the great difference in the diameter of the sclereids. The diameter of sclereids in clusters immediately below the epidermis is about half that in clusters encircling the

TABLE 21. Numbers of sclereids and their size for clusters at different points in the fruit (cf. Figures 45 and 46).

	No. of sclereids counted (cross-section)	No. of sclereids calculated	Measured ⌀ of cluster (μ)	Calculated ⌀ of sclereid (μ)
Epidermis				
sub-epidermal	433	6,790	420	18
flesh I	160	1,530	336	23
flesh II	153	1,430	420	30
flesh III	410	6,280	800	35
small cluster adjacent to core	875	19,500	1,200	36
large cluster ↓ adjacent to core	3,500	156,000	2,540	38
Core				

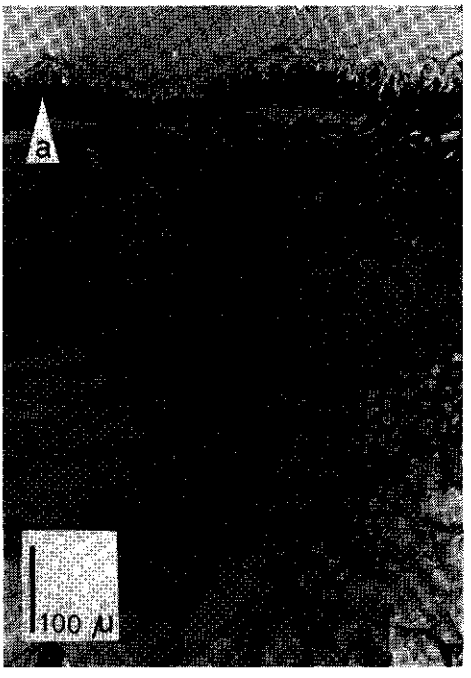


FIG. 45. Sclereid cluster immediately below the skin of a ripe pear. The diameter of the sclereids is about half that of sclereids in clusters close to the core.
a. epidermis

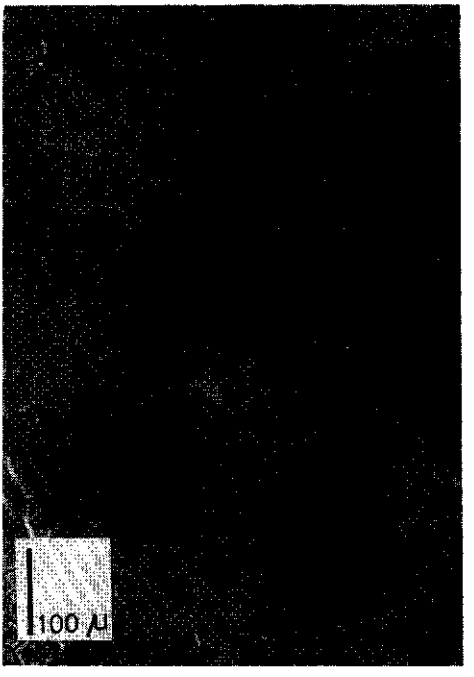


FIG. 46. Part of a sclereid cluster close to the core of the ripe pear shown in figure 45.

Compare the size of sclereids in the photos (same magnification!).

core (Figs. 45 and 46). The diameter of the sclereids of clusters situated between the epidermis and the core increases as the clusters approach the core. The number of sclereids per pear may be determined by combining the counts in the previous paragraph with the calculations given in the present one. The sclereid clusters used for the calculation are those considered to be representative of the three types, viz. those encircling the core, sub-epidermal clusters, and intermediate clusters in the flesh. For the first type, the largest cluster was taken from the flesh with a diameter of over 1 mm, this being more representative of the average size of the clusters round the core than the far larger cluster in Table 21. The results of the calculations for pears 4 and 7 are listed in Table 22. In studying this table it should not be forgotten that the determination of both the number of sclereid clusters per fruit and the number of sclereids per cluster is solely based on two fruits. Depending on the size of the fruit, the number of sclereids per fruit will vary from 100 million to 170 million, it being assumed that large and small fruits contain sclereids of the same size. The eye, which almost entirely consists of sclereids, is not included; however it only contains about 1 million sclereids, a number which hardly affects the total.

TABLE 22. Numbers of sclereids per fruit.

	No. of sclereids per cluster	Pear no. 4		Pear no. 7	
		no. of clusters	sclereids $\times 10^6$	no. of clusters	sclereids $\times 10^6$
Sub-epidermal	6,790	6,130	42	8,550	58
Flesh	6,280	8,930	56	14,530	91
Core	19,500	480	9	920	18
Total		15,540	107	24,000	167

It may be asked how many parenchyma cells responsible for the succulence and flavour of the fruit are contained in the flesh. Microscopic observations show that the sclereid clusters are separated by a few parenchyma cells. Very frequently only two cells are found between adjoining clusters (Fig. 6, p. 17). Since the sclereid clusters are polyhedral at the end of the cell-division period they are densely concentrated. The minimum number of parenchyma cells in the flesh may therefore be reliably estimated by assuming that each sclereid cluster is surrounded by a single layer of parenchyma cells. Using the formula πd^2 for the spherical surface, a rough calculation can be made of the number of parenchyma cells by substituting for d the number of sclereids along the centre line of the cluster plus 2 (for the parenchyma cells at either end of this line).

The numbers of parenchyma cells for pears 4 and 7 were calculated in this way, the result of the calculation being given in Table 23. This calculation, although more or less based on a minimum number of parenchyma cells in the flesh, produces substantial figures, i.e. rather less than one-third of the number of sclereids. Adding together the numbers given in Tables 22 and 23, the total number of cells in the flesh is about 140 million for pear 4 and about 220 million for pear 7.

If the volume of the sclereid clusters in Table 22 regarded as representative is compared with the volume of the flesh of pears 4 and 7, which was calculated earlier, we find that the volume of the parenchyma cells of the flesh is about thrice that of the sclereid clusters. Since the parenchyma cells are the same size

TABLE 23. Numbers of parenchyma cells in the flesh.

	No. of parenchyma cells per cluster	Pear no. 4		Pear no. 7	
		no. of clusters	cells $\times 10^6$	no. of clusters	cells $\times 10^6$
Sub-epidermal	2,040	6,130	12.5	8,550	17.5
Flesh	1,950	8,930	17.5	14,530	28.5
Core	3,950	480	1.9	920	3.6
Total		15,540	31.9	24,000	49.6

as the sclereids at the end of the cell-division period, they must show an approximately tenfold increase in volume from this time until maturation. If we use this data to calculate the diameter of pears 4 and 7 as it would have been at the end of the cell-division period, we obtain 20.3 mm and 23.5 mm respectively. These are values for the diameter reached by comparable fruits by the end of August. At this moment cell-division activity has practically ceased in the flesh, and the fruits start to expand rapidly by enlarging the volume of the parenchyma cells of the flesh (§ 5.2.2.).

By measuring and counting cells in slides under the microscope a rough figure of 1.8 million cells is obtained for the ovary. In about 90 days, the cell-division period in 1962, this number increases to over 200 million. If the mitotic activity of each newly formed cell is unimpaired, seven successive cycles of cell-division would be sufficient for the production of this number of cells. Since sclereids once formed lose their mitotic acitivity and are therefore excluded from the cell-formation process, are even greater number of cell-division cycles needed to reach the figure of 200 million.

In order to determine the number of mitotic cycles the large sclereid cluster in Tables 21 and 23 was considered separately. If we assume that a nucleus of $\frac{1.8 \times 10^6}{24{,}000} = 75$ sclereids required for its formation is derived from cells already present in the ovary, then about 14 concentric layers 1 sclereid thick and surrounding the nucleus are required to form the cluster. Consequently at least 15 cell-division cycles are needed to form the concentric layers of sclereids and the layer of parenchyma cells. But as well as radial growth there is also growth in a tangential direction (dilatation). By determining the number of cells of the successive concentric layers it was calculated that about 5 cell-division cycles would be required for this tangential growth. Hence altogether some 20 cell-division cycles would be needed to form a sclereid cluster of this size.

Since the cell-division period is 90 days, each cell has 4 to 5 days to grow, synthesize proteins, and divide again.

According to BAIN (1963) the cell number in fruits of the 'Bartlett' pear cultivar increase from 5–10 million during blossom to approximately 100 million in the ripe fruit, about 60 million of these being parenchyma cells.

The formulas, combined with the rather inaccurate measurements and counts, must obviously give results that can only be regarded as provisional and a rough approximation. It is probably that far more accurate results could be obtained with an image analysing computer (Quantimet).

5.5. SURVEY OF THE FRUIT DEVELOPMENT

Fruit growth in *Pyrus nivalis*, as in the cultivated pear, may be divided into two stages. During the first, which occupies about 90 days, active cell multiplication takes place in the flesh. Cell-division activity around the core ceases at a fairly early date, but the cells long remain capable of division in the peripheral part of the fruit, thus permitting radial growth. As a result the part of the ovary

peripheral to the sepal and petal vascular bundles is the most highly developed. Consequently these vascular bundles in the ripe fruit are situated just outside the layer of thick sclereid clusters encircling the core (cf. Fig. 7, p. 18). Owing to surface growth, the cells in the outermost layers of flesh cells and the epidermis even continue to divide until the fruit is ripe (about 180 days). Hence any injury to the outermost cell layers of the fruit almost completely arrests further development of the flesh. DERMEN (1965) cites an example in which the surface growth of the skin is out of step with growth in volume, thereby causing cracks in the epidermis (triploid apple cultivar 'Stayman'). The absence of seeds has no harmful effect on the development of the flesh, although the core of such fruits is always smaller than in seed-bearing fruits. The flattened shape of the seedless fruits is associated with this.

The size attainable by the ripe fruit is to a great extent already determined in the ovary. A small ovary develops into a small fruit and a large ovary into a large fruit. As a result the largest fruits develop at the base of the inflorescence, the apical pear and the fruits in the middle occupy an intermediate position, while the two sub-apical fruits are always small. Since poorly developed inflorescences have small flowers with small ovaries, they also produce small fruits (cf. also VISSER, 1955). Fruit set is determined by the same rules, large, well-developed flowers having a better change to develop into fruit than small, poorly developed ones. This can be understood when we consider that the poorly developed generative organs characteristic of poorly developed flowers (cf. also RUDLOFF and FEUCHT, 1957) also lessen the change of pollination and fertilisation. In this connection it should be noted that to judge from ZIELINSKI's study (1965), pollination and possibly also fertilisation may also be necessary for the development of the seedless fruits of *Pyrus nivalis*. In addition the combination of late blossom and the production of inferior pollen constitute additional drawbacks to the fruit set of poorly developed flowers. This late blossom also has a direct effect on the final size of the fruit since the growth period is shorter than in early-set fruits.

But the most important factor in the determination of fruit size is the size of the ovary which corresponds in turn to the number of cells it contains. TOYAMA and HAYASHI's defoliation tests (1957–II) supply clear evidence on this point. Defoliation during flower initiation results in the following year in small fruits consisting of comparatively few large cells. Defoliation during fruit development also results in small fruits, but in this case because the cells fail to expand and remain small. The number of successive cell divisions in the flesh is obviously limited after the fruit set and is probably hardly affected by the presence or absence of leaves. The cell-division period can only be prolonged by heavy thinning of the fruit (DENNE, 1960). But the presence of leaves is important for fruit development by means of cell extension. This means that fruits on trees or branches with a relatively large number of leaves will develop more vigorously and also form larger parenchyma cells of the flesh than fruits on trees or branches with few leaves. In *Pyrus nivalis*, however, no marked difference in growth was found between fruits on branches with many or few leaves.

The sclereids that begin to form in the fruit of *Pyrus nivalis* directly after the fruit set are not uniform in size at all points. The largest are usually found in sclereid clusters surrounding the core. Both the size of the sclereid clusters and that of the sclereids themselves decreases in the direction of the epidermis. In the last clusters formed, just below the epidermis, the sclereids are only half the diameter of those in sclereids surrounding the core.

In the flesh, branching vascular bundles, i.e. lateral branches of the sepal and petal vascular bundles, grow increasingly finer as they approach the epidermis (McALPINE, 1911). The metaxylem of the vascular bundles in the fruit almost entirely consists of spiral vessels. Consequently the vascular bundle system both as a whole and in its constituent elements permits an extensive increase in volume of the fruits.

SUMMARY

A detailed study is made of the structure and development of the inflorescence of *Pyrus nivalis* Jacquin var. orientalis Terpó (this species is regarded as one of the ancestors of the cultivated pear). It was found that the few observations made by other investigators of the cultivated pear and apple largely agreed with my own findings.

The inflorescence is always located on the end of a short shoot which develops from a mixed bud. One or more foliage leaves are found below the actual inflorescence. The axil of one or two of these leaves contains a short shoot with a rosette of 3–5 lanceolate leaves which will form the inflorescence for the following year, or in less favourable cases for the year after. The inflorescence usually has nine flowers, i.e. one terminal flower (No. 1) and 8 lateral ones (Nos. 2–9). Flowers 2–5 are positioned in the axil of a bract, Nos. 6–9 in the axil of an ovate foliage leaf. Abnormal development of flowers and irregularities in the initiation of inflorescences are commonly found. As a result inflorescences are formed of which the flowers either remain small and produce fewer stamens and carpels than usual, or else entirely fail to develop. The differences from one year to another and the manner in which carpels are reduced make it seem likely that anomalies may occur fairly suddenly in response to unfavourable weather conditons, the temperature probably being an important factor. Flowers 2 and 3 in the inflorescence (just below the apical flower) show a particularly marked response. It was observed that small, poorly developed flowers blossom later in the year, the fruit set is poor, and the fruits produced are always small.

It was found that the development of the flower and hence of the ovary is of far-reaching importance to fruit development, the size reached by the ripe fruit being almost solely determined by the size of the ovary. Small ovaries develop into small fruits and large ovaries into large fruits.

The largest fruits are therefore found on the base of the fruit-bearing short shoot, and the smallest in the positions just below the apical pear which itself occupies an intermediary 'position'. Differences in fruit size may be increased or reduced by the development or lack of development of seeds, since seedless fruits develop less vigorously than seed-bearing ones.

The length/diameter ratio is a criterion for the shape of fruit. Certain parts of the fruit (eye, internal extension of the fruit-stalk) are unable to develop longitudinally even shortly after the fruit set. On the other hand the fruit is able to increase in diameter without restriction until maturity. As a result the length/diameter ratio gradually decreases during fruit development.

Most fruits finally have a practically spherical shape; owing to excessive lateral swelling the large fruits acquire a more flattened shape. Seedless fruits are again an exception. Although they are small, there is relatively marked flattening because the core is invariably small. Unilateral development of seeds appears to have scarcely any effect on fruit shape. Fruit development is studied both biometrically and histogenetically.

The inflorescence and flower develop in the same way as in the cultivated pear and apple. Eleven developmental stages may be distinguished. In the autumn of the year preceding blossom flower development does not extend beyond the initiation of the carpel primordia (stage 6). Development continues slowly throughout the winter so that pollen meiosis (stage 9) can take place at the end of March to the beginning of April. Up to the pollen meiosis stage the organs of the flowers are densely concentrated around the apex from which they are formed. It is not until the last month before blossom that a new tissue (annular – toral – nectary) with a different cell arrangement is formed in an intercalary position and encloses the styles in the form of a cup. Part of the original tissue grows upward together with this tissue area, so that calyx lobes, petals and stamens are then borne on the edge of the receptacle.

The embryo sac (stage 11) is not formed until blossom. Up to the date of this development the cells in the ovary are arranged in longitudinal rows.

Cells begin to lignify in the young fruit a number of days after blossom. These are the cells of the annular (toral) nectary which lignify almost completely, thus forming the eye of the pear and cells adjoining the core. The sclereids are still arranged lengthwise in the centre of the sclereid clusters immediately around the core and in the eye. Radial divisions soon begin to dominate in the young fruit, forming radial rows of cells with the core in the centre. This cell arrangement is disturbed by continuous changes in shape and lignification of cells at many points in the young fruit. The cells are still capable of dividing between the resultant sclereid clusters, so that each cluster is surrounded by a kind of meristem. These meristems add new cells to the clusters, the outmost layers of clusters consisting of radial rows of cells.

The large sclereid clusters usually consisting of a great number of sclereids (brachysclereids) are characteristic of *Pyrus nivalis*. It can be seen in a median longitudinal section of a ripe pear (Fig. 7) that very large sclereid clusters (⌀ 1–3 mm; 20,000–150,000 cells) surround the core and that their size decreases (to 0.1–0.4 mm; 100–6,000 cells) in the direction of the epidermis, becoming slightly larger immediately below (0.3–0.5 mm; 7,000 cells). Small groups of sclereids, or only a few are found in the centre of each cluster, while comparatively small sclereids are arranged radially on the outside. A layer of very large thin-walled parenchyma cells of the flesh are also radially arranged about each cluster. Between two adjacent clusters there are only a few parenchyma cells (quite often no more than two layers). It was found that the sclereids in clusters close to the core are twice the size (⌀ 36 μ) of those of clusters directly below the epidermis (⌀ 18 μ).

It was found that a large pear contains about 24,000 sclereid clusters. They are most densely concentrated at the eye end. It can be calculated that such a large fruit contains nearly 170 million sclereids. Including one layer of parenchyma cells surrounding each sclereid cluster, the total number of cells in the flesh is nearly 220 million. Twenty division cycles are needed to produce this number of cells from the ovary (1.8 million cells). Since the cell-division period

of the fruit of *Pyrus nivalis* takes about 90 days, 4 to 5 days are available for each division cycle.

Since the metaxylem of young fruits entirely consists of spiral vessels (that of somewhat older fruits largely consists of such vessels), the vascular bundle system of the fruit forms no obstacle to considerable expansion of the fruit.

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SAMENVATTING

De bouw en de ontwikkeling van de bloeiwijze van *Pyrus nivalis* Jacquin var. orientalis Terpó – de soort wordt beschouwd als één van de stamouders van de gekweekte peer – werd uitvoerig bestudeerd. De weinige waarnemingen van andere onderzoekers aan de gekweekte peer en appel bleken in grote trekken met onze bevindingen overeen te komen.

De bloeiwijze is steeds geplaatst aan het einde van een kort lot, dat uit een gemengde knop tot ontwikkeling komt. Onder de eigenlijke bloeiwijze zijn één of meer loofbladeren aanwezig. In de oksel van één of twee hiervan bevindt zich een kort scheutje met een rozet van 3–5 lancetvormige bladeren dat de bloeiwijze voor het volgende jaar of in minder gunstige gevallen voor een later jaar zal vormen. De bloeiwijze telt meestal negen bloemen, een terminale (no.1) en acht laterale (no's 2–9). De bloemen 2–5 staan in de oksel van een schutblaadje, de nummers 6–9 in de oksel van een eirond loofblad. Abnormale ontwikkeling van bloemen en onregelmatigheden in de aanleg van bloeiwijzen komen veel voor. Hierdoor ontstaan bloeiwijzen waarvan de bloemen òf klein blijven en minder meeldraden en vruchtbladen vormen dan normaal òf zelfs in het geheel niet tot ontwikkeling komen. De verschillen van jaar op jaar en de wijze waarop de reductie van vruchtbladen plaats vindt maken het aannemelijk dat afwijkingen vrij plotseling kunnen ontstaan als reactie op ongunstige weersomstandigheden, waarbij de temperatuur waarschijnlijk een belangrijke rol zal spelen. Vooral de bloemen 2 en 3 in de bloeiwijze (vlak onder de topbloem) reageren sterk. Waargenomen is dat kleine, slecht ontwikkelde bloemen laat bloeien, terwijl de vruchtzetting slecht is en de vruchten die er uit voortkomen klein blijven.

De ontwikkeling van de bloem en daarmee van het vruchtbeginsel blijkt van verstrekkende betekenis voor de vruchtontwikkeling te zijn. De afmeting die de rijpe vrucht kan bereiken wordt namelijk vrijwel uitsluitend bepaald door de afmeting van het vruchtbeginsel. Kleine vruchtbeginsels groeien uit tot kleine en grote tot grote vruchten. De grootste vruchten komen daardoor voor aan de basis van het vruchtdragende korte lot, de kleinste op de plaatsen vlak onder de toppeer die zelf een intermediaire ‚positie' inneemt. De tegenstellingen in vruchtgrootte kunnen verscherpt of verzacht worden door het zich al of niet ontwikkelen van zaden. Vruchten zonder zaden groeien namelijk minder sterk uit dan vruchten met zaden.

Een maatstaf voor de vorm van de vrucht is de lengte/diameter verhouding. Bepaalde delen van de vrucht (kroontje, inwendige voortzetting van de vruchtsteel) kunnen reeds kort na de vruchtzetting niet meer in de lengterichting uitgroeien. In tegenstelling daarmee kan de vrucht tot aan rijpheid onbelemmerd in diameter toenemen. Het gevolg hiervan is dat de lengte/diameter verhouding gedurende de vruchtontwikkeling gestadig afneemt.

De meeste vruchten vertonen uiteindelijk een vrijwel kogelronde vorm, de grote vruchten hebben door excessief zijdelings uitdijen een meer afgeplatte

vorm gekregen. Een uitzondering vormen wederom de vruchten zonder zaden. Hoewel zij klein zijn treedt door het klein blijven van het klokhuis toch een relatief sterke afplatting op. Eénzijdige ontwikkeling van zaden blijkt nauwelijks enige invloed op de vruchtvorm te hebben. De ontwikkeling van de vrucht is zowel biometrisch als histogenetisch bestudeerd.

De ontwikkeling van de bloeiwijze en van de bloem geschiedt op dezelfde wijze als bij de gekweekte peer en appel. Er kunnen elf ontwikkelingsphasen (stadia) worden onderscheiden. In de herfst van het jaar vóór de bloei gaat de bloemontwikkeling niet verder dan de aanleg van de vruchtbladprimordia (stadium 6). Tijdens de winter gaat de ontwikkeling langzaam door zodat eind maart – begin april de pollenmeiose (stadium 9) kan plaats vinden. Tot aan de pollenmeiose blijven de onderdelen(organen) van de bloem dicht om het vegetatiepunt waaruit zij zijn ontstaan gegroepeerd. Pas in de laatste maand voor de bloei gaat zich intercalair een nieuwe weefsel (annular – toral – nectary) met een afwijkende celrangschikking vormen dat als een koker de stijlen gaat omsluiten. Tezamen met dit weefselgebied groeit een gedeelte van het oorspronkelijke weefsel mee omhoog waardoor kelkslippen, kroonbladeren en meeldraden op de rand van een beker (receptaculum) komen te staan.

De vorming van de embryozak (stadium 11) vindt pas tijdens de bloei plaats. Tot aan deze ontwikkeling zijn de cellen in het vruchtbeginsel gerangschikt in rijen die in de lengterichting verlopen.

In de jonge vrucht gaan enkele dagen na de bloei cellen verhouten. Dit zijn de cellen van het ‚annular – toral – nectary' dat vrijwel in zijn geheel verhout en zo het kroontje van de peer vormt en cellen die vlak tegen het klokhuis aan liggen. In het centrum van de steencelnesten vlak om het klokhuis en in het kroontje is de rangschikking van de steencellen in de lengterichting nog aanwezig. Reeds spoedig gaan in de jonge vrucht de delingen in radiale richtingen overheersen. Hierdoor ontstaan radiale celrijen met het klokhuis als centrum. Door voortgaande vormverandering en verhouting van cellen op vele plaatsen in de jonge vrucht wordt deze celrangschikking verstoord. Tussen de gevormde steencelnesten blijven de cellen deelvaardig, waardoor elk steencelnest omsloten is door een soort meristeem. Deze meristemen voegen nieuwe cellen aan de steencelnesten toe zodat de buitenste lagen hiervan bestaan uit radiaal verlopende celrijen.

De grote uit meestal zeer veel steencellen (brachysclereïden) opgebouwde steencelnesten zijn kenmerkend voor *Pyrus nivalis*. In een doorgesneden rijpe peer (fig. 7) is te zien dat rondom het klokhuis een zone van zeer grote steencelnesten (⌀ 1–3 mm; 20.000–150.000 cellen) aanwezig is en dat de afmeting daarvan afneemt (tot 0,1–0,4 mm; 100–6.000 cellen) in de richting van de epidermis om vlak daaronder weer iets groter te worden (0,3–0,5 mm; 7.000 cellen). In het centrum van elk steencelnest zijn groepjes of ook wel slechts enkele grote steencellen aanwezig, terwijl aan de buitenzijde relatief kleine steencellen radiaal gerangschikt liggen. Om elk steencelnest heen ligt eveneens straalsgewijs gerangschikt een laag zeer grote dunwandige vruchtvleesparenchymcellen. Tussen twee aangrenzende steencelnesten is het aantal parenchymcellen klein, heel vaak niet meer dan twee lagen. De steencellen uit een steencelnest

rondom het klokhuis blijken tweemaal zo groot (⌀ 36 μ) te zijn als die uit een nest vlak onder de epidermis (⌀ 18 μ).

Het aantal steencelnesten in een grote peer blijkt ca 24.000 te bedragen. Zij liggen het dichtst opeen aan de zijde van het kroontje. Door berekening kan het aantal steencellen in zo'n grote vrucht worden bepaald op bijna 170 millioen. Met één laag parenchymcellen om elk steencelnest heen wordt het totale aantal cellen in het vruchtvlees bijna 220 millioen. Dat wil zeggen dat voor vorming daarvan uit het vruchtbeginsel (1,8 millioen cellen) 20 delingscycli nodig zijn. Omdat de celdelingsperiode bij de vrucht van *Pyrus nivalis* ca 90 dagen duurt zijn per delingscyclus 4–5 dagen beschikbaar.

Doordat het metaxyleem in jonge vruchten geheel en in wat oudere vruchten grotendeels is opgebouwd uit spiraalvaten vormt het vaatbundelsysteem van de vrucht geen belemmering voor een aanzienlijk uitgroeien van de vrucht.

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