The Reproductive Biology of Rambutan, *Nephelium lappaceum* L. (Sapindaceae)

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Abstract

Nephelium lappaceum produces either male or bisexual flowers. The anther development in both types of flowers is the same but those in the bisexual flowers do not dehisce even though their pollen is viable. The anther is tetrasporangiate and its wall development conforms to the basic type. Cytokinesis in microspore mother cells is simultaneous, forming tetrahedral tetrads. The mature pollen grains are tricolpate and two-celled. Only pollen grains from the male flower germinate in the conventional media.

The ovule is anacampylotropous, bitegmic, crassinucellate and the micropyle is formed by the inner integument only. The embryo sac development is of the monosporic *Polygonum* type.

Flower anthesis is at 0900-1100 hours and pollination is entomophilous. Preliminary flower bagging experiments show that fruit formation is dependent on pollination. The average normal flower and fruit drop are 40% and 90% respectively.

The endosperm development is *ab initio* Nuclear and cell formation commences at the micropylar end, proceeding towards the chalaza. The outer layers of the outer integument differentiate into the edible flesh of the fruit. The testa is formed mainly from the inner part of the outer integument and the few remaining layers of the inner integument at the micropylar region.

The seed is non-endospermous and shows hypogeal germination. In fresh seeds, the average percentage germination is 96%, of which 2% of the seedlings give multiple shoots.

Introduction

In Malaya, several species of *Nephelium* produce edible fruits. Those common in cultivation are the Rambutan *(N. lappaceum L.)*, Pulasan (*N. mutabile* Bl.) and Mata kucing (*N. malaiense* Griff.).

Nephelium lappaceum L. is known as Rambutan to the Malays because of its hairy fruits; "rambut' in the Malay language means "hair". Whitehead (1959) recognised different clones based on size and taste of fruits, nature, colour and texture of the soft spines of the rind. The Rambutan is delicious when eaten fresh but it can also be canned or made into an excellent jam. A wine made from it was exhibited at the Colonial and Indian Exhibition in London in 1886 (Burkill, 1935) but the practice never seems to have caught on. The fruit wall, roots, leaves and bark are said to have medicinal value.

Materials and Methods

Field observations on phenology, floral anthesis and pollination, and collection of plant materials were undertaken at weekly intervals or more often as required, in the fruit-tree nursery of the Ministry of Agriculture in Serdang about 20 km from the University of Malaya campus. A voucher specimen *KLU 18610* was deposited in the Herbarium, Botany Department of the University of Malaya. The buds and flowers were fixed in formalin-propionic-alcohol while the fruits were fixed in Craf III. Routine methods of microtechnique were employed to obtain sections 8-15 μ thick. Fruits in wax blocks had to be immersed for periods up to a month in a softening solution of Molifex (B.D.H. Co., U.K.) before they could be sectioned. The

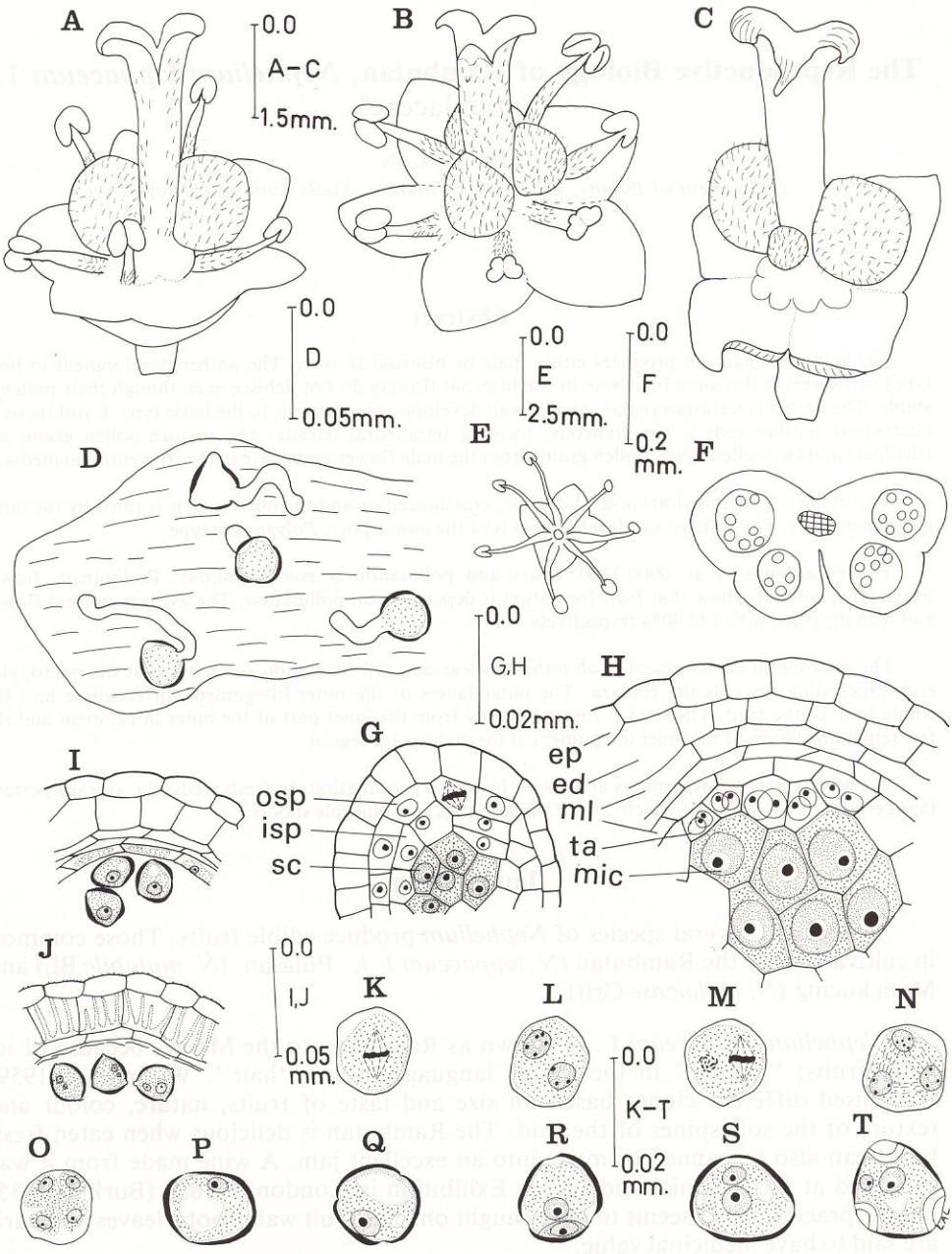

Fig. 1. Floral morphology, microsporangium, microsporogenesis and microgametophyte. (*ed,* endothecium; *ep,* epidermis; *isp,* inner secondary parietal layer; *mic,* microspore mother cell; *ml,* middle layers; *osp,* outer secondary parietal layer; *sc,* sporogenous cell; *ta,* tapetum).
A & B, bisexual flower; *C,* bisexual flower after pollination; *D,* pollen grains germinating on stigma; *E,* male flower, *F,* t.s. tetrasporangiate anther; *G-J,* anther wall at different stages of development; *K-O,* meiosis in microspore mother cells; *P-T,* microspore and a two-celled pollen grain.

mounted fruit sections had to be bleached in a solution made up of potassium dichromate (1 gm), chromic acid (1 gm), glacial acetic acid (10 c.c.) and distilled water (90 c.c.) before staining in safranin. Otherwise the whole embryo sac stains dark purple and this is caused by tannins and other cell inclusions, which mask the cellular organisation. Various concentrations of "Clorox", a commercial bleach, were tried but proved unsatisfactory.

To test pollen viability, the pollen grains from the bisexual and male inflorescences were germinated in various concentrations (2-20%) of sucrose and lactose solutions. The pollen grains from the male inflorescence were used immediately after anthesis while those from the bisexual flowers were released by cutting open mature anther sacs. The pollen grains were examined and pollen tubes measured at 12-hour intervals.

Seed germination and seedling morphology were studied by sowing fresh seeds in garden soil.

Observations and Results

Floral and Fruit Morphology

Flowers are borne on axillary or terminal panicles. The greenish flowers are minute (less than 3 mm wide), without petals (fig 1A, B) and have a pleasant scent. The trees bear either male or bisexual flowers (androdioecious). In a male flower, there are 5-8 anthers supported by white hairy filaments while the gynoecium is small and rudimentary (fig. 1E). In the bisexual flower, the anthers are 5-7 in number and the gynoecium is very well developed with a 2- or rarely 3-locular ovary (fig. 1A, B, C).

The bunched fruits are borne on woody stalks. Depending on the clone, each fruit is oblong to nearly round and it ripens to a red or, less commonly, yellow colour. The rind is covered with thick, soft spines (fig. 4D, F). The edible pulp is white and the taste ranges from sour to sweet. Sour taste and difficulty in detaching pulp from seed are considered poor qualities.

The non-endospermous seed is normally rounded at the micropylar end and pointed at the opposite end. It has a fibrous testa enclosing an embryo with two unequal cotyledons.

Phenology

Depending on the clone, as well as soil and climatic conditions, the tree starts to bear flowers and fruits after 3-5 years. Two distinct flowering seasons are observed in the Malay Peninsula. The first season starts at the beginning of April and the fruits are harvested at the end of July. The second begins mid-August and the harvest is mid-December. The seasonality of the fruits can easily be upset by any change in the pattern of wet and dry season. Most individual trees, however, produce fruits only once yearly; some during the first season and others during the second. Some trees in Serdang are peculiar in that while one side can be laden with ripe fruits, the other half can be just beginning of flower.

After the appearance of the inflorescence, the floral buds (average width 1 mm) take only 3 weeks to develop into mature flowers (average width 3 mm). They open acropetally. Both male and bisexual plants flower synchronously and the flowering period lasts 2-3 weeks. Anthesis is between 0900 and 1100 hours. Ten days after anthesis, the stamens in the bisexual flowers drop off and usually one of the ovules enlarges to form a young fruit (average width 4 mm) (fig. 3C). These fruits mature 12 weeks later and by then the average width is 3.5 cm and length 5.0 cm. The

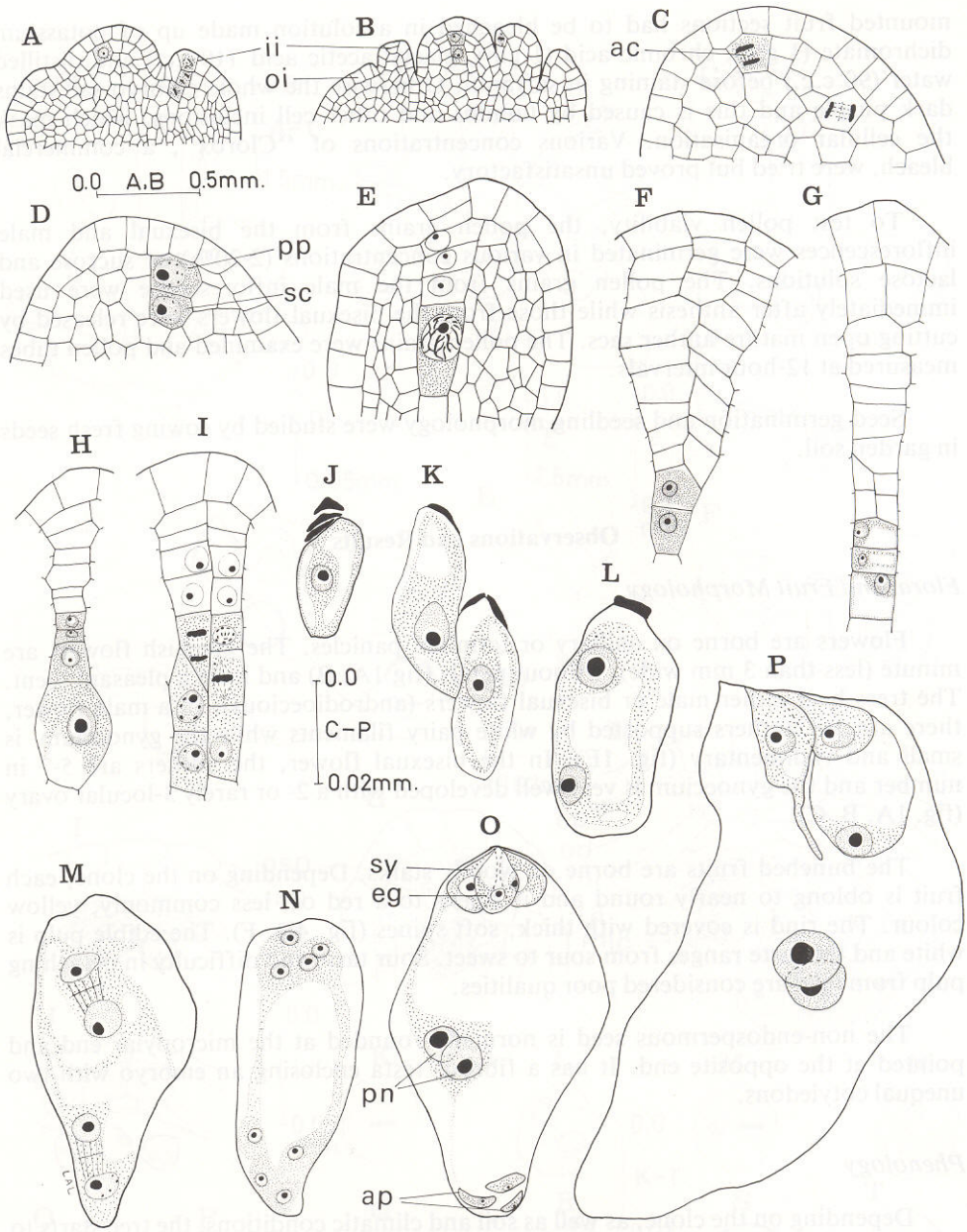

Fig. 2. Megasporogenesis and development of megagametophyte. (*ac,* archesporial cell; *ap,* antipodal; e.g., egg; *ii,* inner integument; *oi,* outer integument; *pn,* polar nucleus; *pp,* primary parietal cell; *sc,* sporogenous cell; *sy,* synergid).
A & B, development of integuments; *C, D,* formation of sporogenous cell; *E-H,* megasporogenesis; *I,* twin tetrads; *J,* functional megaspore; *K,* twin megaspores; *L-O,* development of megagametophyte; *P,* embryo-sac after the degeneration of antipodals.

observation of 10 samples of randomly tagged floral buds, 200 per sample, showed that the average flower abortion was 40% and fruit drop 90%.

Anther Development

The anther development in both male and hermaphrodite flowers is found to be similar except that dehiscence does not occur in the latter. Hence the bisexual flowers are found to be functionally female. The anther is tetrasporangiate and the

anther-wall development conforms to the basic type of Davis (1966). The archesporial cells divide periclinally to form the primary parietal and sporogenous cells. The latter differentiate into microspore mother cells while the former divide to form the outer and inner secondary parietal cells. The endothecium and a middle layer are derived from the outer secondary parietal while the inner middle layer and the tapetum are derived from the inner secondary parietal (fig. 1G, H, I). The tapetum is secretory and includes at first uninucleate cells which become binucleate just before the microspore mother cells undergo meiosis.

Simultaneous cytokinesis accompanies meiotic divisions in the microspore mother cell (fig. 1K-O). The tetrads formed are usually tetrahedral but sometimes isobilateral. Stages of development varying from late prophase to microspore tetrad phase had been observed within the same flower. In addition, different locules of the same anther may exhibit different stages of development such as a locule with microspore mother cells at metaphase I while another locule shows microspore mother cells at anaphase II.

Soon after the tetrads are formed, the microspores separate out and at this time, the tapetum and middle layers begin to degenerate (fig. 1I). The nucleus migrates to the periphery of the microspore, giving the latter the characteristic signet ring shape (fig. 1P, Q). It then divides to form a small lenticular generative cell and a large vegetative cell (fig. 1R). At maturity, the pollen grain is binucleate (fig. 1S, T). By the time the microspores become mature pollen grains, the tapetum and the middle layers have degenerated, leaving only the fibrous endothecium and the epidermis in the anther wall (fig. 1J).

The mature pollen grains are smooth, triangular, tricolpate and measure 15-18 μ in diameter. Both male and bisexual flowers produce similar pollen grains. However, most pollen grains in the functionally female flowers are devoid of nuclei and hence are non-viable.

Pollen Germination

Pollen grains from functionally female flowers did not germinate in the conventional media of sucrose or lactose solutions. Those from male flowers showed maximum germination of 39% in 10% sucrose and 56% in 10% lactose solution. The control sample gave 19% germination in distilled water. Further, at optimum sugar concentrations (10% sucrose and 10% lactose), the pollen tubes were longer, i.e., an average length of 0.1 mm while after 24 hours' incubation the average pollen tube length in distilled water was 0.02 mm. Though the pollen grain is tricolpate, germination is monosiphonous.

Anthers from functionally female flowers were squashed to release the pollen grains, which were then dusted on to the stigma of another flower either of the same or a different tree. The inflorescences were bagged before and after the transference of pollen grains to prevent contamination by pollen grains from other flowers. This was performed on flowers *in vivo* because cut inflorescences tend to dehydrate very fast. After 4 hours the flowers were harvested, fixed in polyvinyl lactophenol and stained in lactophenol cotton blue. The nucleate pollen grains could be germinated on the stigmatic tissue (fig. 1D). However, the percentage germination was not calculated as the sample used was small.

Development in Ovule

Within each loculus of the ovary only one ovule, mounted on a thick funicle, is present. The ovular primordium develops from the placenta. The differentiation of the inner integument is followed by that of the outer (fig. 2A, B). Simultaneously one of the hypodermal nucellar cells enlarges to form the archesporial cell (fig. 2C).

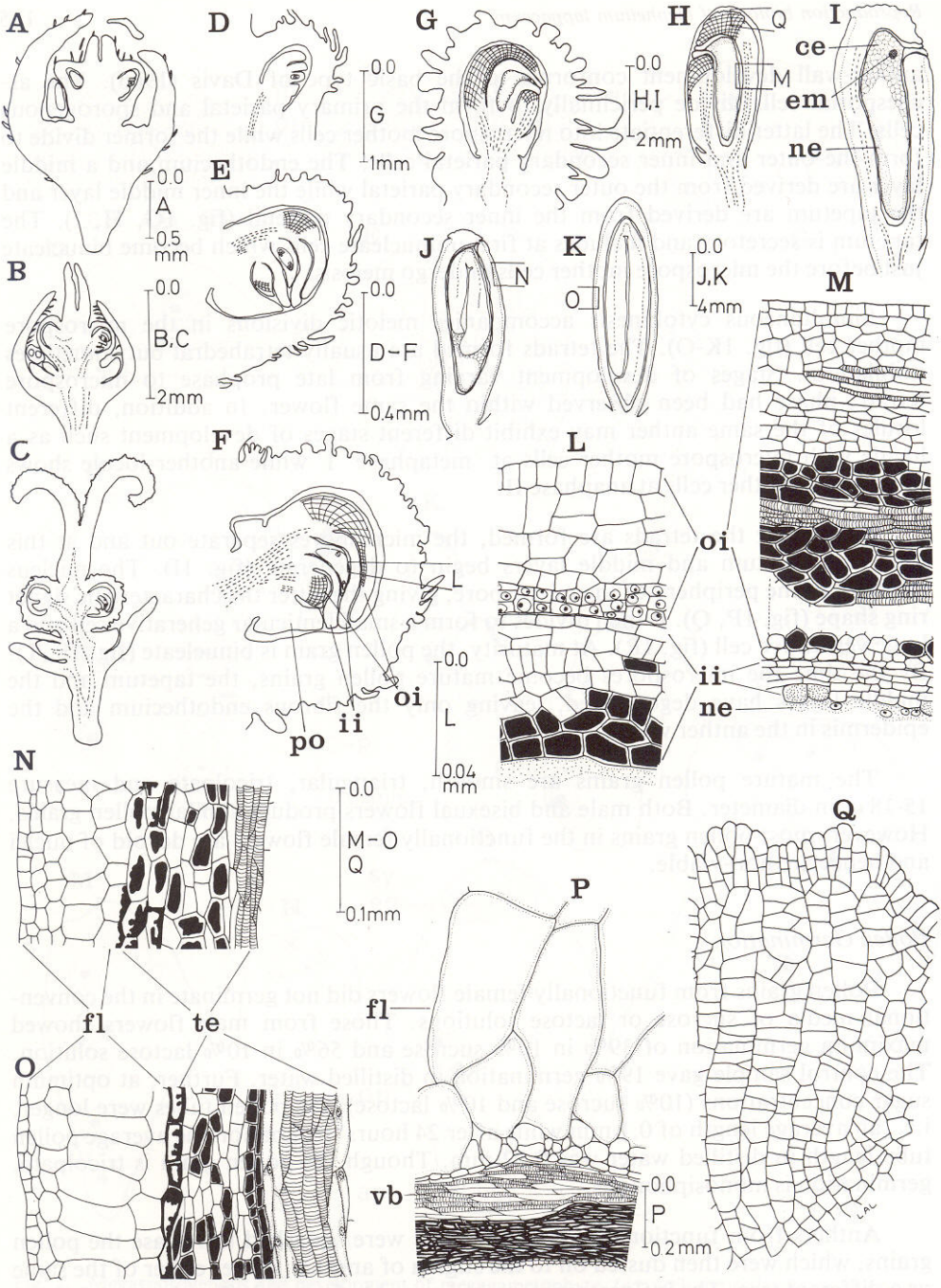

Fig. 3. Development of embryo, fleshy part of fruit, and testa. (*ce,* cellular endosperm; *em,* embryo; *fl,* fleshy part of fruit; *ii,* inner integument; *ne,* nuclear endosperm; *oi,* outer integument; *po,* placental outgrowth; *te,* testa; *vb,* vascular bundle).
A-C, l.s. flower showing ovule development; *D-F,* ovule development; *G & H,* seed differentiation; *I,* globular embryo in seed; *J, K,* dicotyledonous embryo; *L,* anatomy of integuments at mature embryo-sac stage; *M,* anatomy of integuments at globular embryo stage; *N-P,* differentiation of testa and fleshy region of seed; *Q,* anatomy of outer integument near micropyle of *H.*

The mature ovule is anacampylotropous, bitegmic, crassinucellate and the micropyle is formed by the inner integument alone (fig. 3E). A placental outgrowth is present at the chalazal end of the ovule (fig. 3F).

The archesporial cell divides periclinally, giving rise to the sporogenous cell and the primary parietal cell (fig. 2C, D) which undergoes further divisions resulting in

the crassinucellate ovule. As its cytoplasm becomes denser and the nucleus enlarges, the sporogenous cell becomes the megaspore mother cell (fig. 2E). Following the first meiotic division in the megaspore mother cell, a pair of dyad cells are formed, of which the lower divides further to give a three-celled stage (fig. 2F, G). Later, the smaller, upper, dyad cell undergoes a second meiotic division to give a linear tetrad (fig. 2H). Within an ovule, usually only one embryo sac develops; however, exceptional cases of developing twin embryo sacs had been observed (fig. 2I, 2K). At the completion of meiosis, only the chalazal megaspore differentiates to form the female gametophyte while the other three megaspores degenerate soon after formation (fig. 2J). After three successive nuclear divisions, the megaspore gives rise to the mature eight-nucleate embryo sac (fig. 2L-N). Its development conforms to the monosporic *Polygonum* type. The free nuclei are at first arranged in two groups of four each at opposite poles of the embryo sac. One from each group migrates to the centre (the two polar nuclei) and the remainder organises into the egg, flanked by two synergids at the micropylar end, and by the three antipodals at the other end (fig. 2O). Soon after formation, the antipodals degenerate while the two polar nuclei fuse to form a large secondary nucleus (fig. 2P).

Pollination and Fertilization

N. lappaceum is entomophilous. Though the individual flowers are small, less than 4 mm wide, they are grouped into prominent panicles. Bees and butterflies are attracted by the nectar and presumably also by the sweet fragrance of the flowers. The visits of these insects had been observed to be most abundant during floral anthesis i.e., between 0900-1100 hours.

Preliminary bagging experiments, before and after anthesis, were conducted to determine whether fruit production is dependent on pollination. As the anthers in bisexual flowers do not dehisce, the inflorescences were bagged without the removal of anthers. The flowers are very small and several attempts to remove the anthers at the bud stage fatally damaged the buds. Ten random samples, each of 200 young floral buds (average diameter 1.0 mm), were bagged in butter-paper. All the flowers in these samples dropped off and no fruits were formed. Ten other random samples, each of 200 flowers (average diameter 3 mm), were bagged 5 days after anthesis. These samples did produce fruits and the average percentage of fruit abortion was 92%, very near to the average fruit drop (90%) in separate phenology studies. This shows that there is no significant difference between the fruit set from flowers bagged after anthesis and that from unbagged ones. Bagging thus has no marked deleterious effect on fruit development. In addition, flowers bagged before anthesis could not have been pollinated whereas those bagged after anthesis could have been pollinated by pollen grains from the male trees nearby. This strongly suggests that fruit production is dependent on fertilization or at least pollination stimulus.

Though actual pollen-tube growth and fertilization were not seen, the degeneration of one synergid occurs soon after the fusion of the polar nuclei. Later, only the egg and the secondary nucleus remain.

Endosperm

The development of the endosperm is of the *ab initio* Nuclear type. Just before the primary endosperm nucleus divides, the embryo sac enlarges (fig. 3F). The primary endosperm nucleus undergoes several mitoses and the resulting free nuclei occupy mainly the micropylar region and a position around the periphery of the enlarging embryo sac (fig. 4A). Corresponding to the increase in the number of endosperm nuclei, the embryo sac increases in size at the expense of the nucellus and later of the inner integument. When the embryo sac is about 2 mm long, there are only 3-4 layers of the inner integument at the sides but more at the micropylar

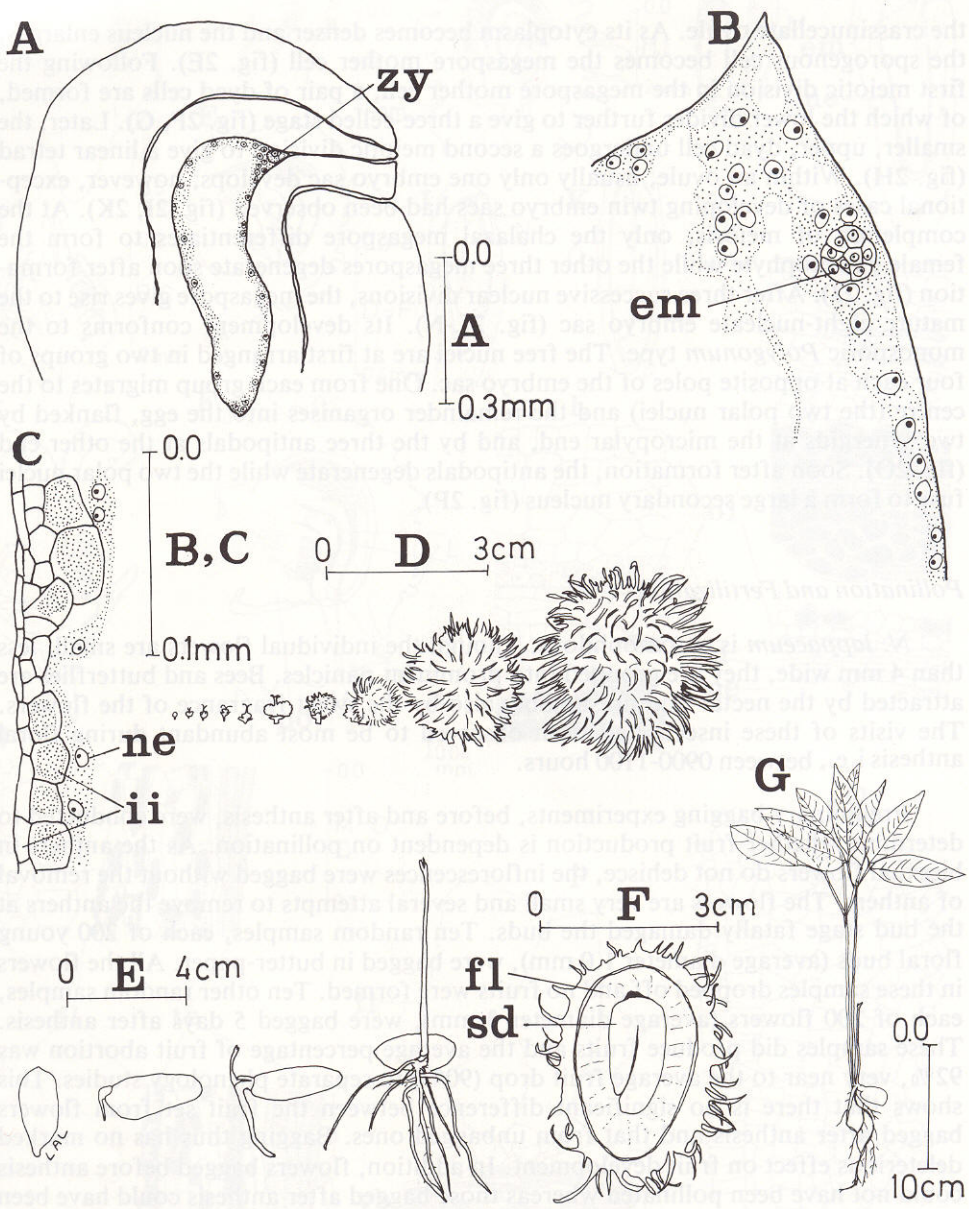

Fig. 4. Embryo, fruit development and seed germination. (*em*, embryo; *fl*, fleshy part of fruit; *ii*, inner integument; *ne*, nuclear endosperm; *sd*, seed; *zy*, zygote).
A & B, nuclear endosperm; *C*, degenerating inner integument cells; *D*, fruit development; *E*, seed germination, *F*, l.s. fruit; *G*, multiple-shoot seedling.

and chalazal regions (fig. 3H, M).

At the chalazal end of the embryo sac, a few cells of the inner integument enlarge to twice or thrice their normal size (fig. 4C). Some of these cells degenerate and release into the embryo sac the contents, which stain darkly with safranin and fast green. The contents are a mixture of tannin, resin and oil. When the embryo sac is 5 mm long, cell formation in the coenocytic endosperm commences at the periphery of the micropylar region and proceeds towards the chalazal end. At the young, globular embryo-stage (± 0.1 mm in width), only a quarter of the embryo sac is filled with cellular endosperm (fig. 3I). Most of the endosperm has become

cellular when the embryo is dicotyledonous (fig. 3J), but it is completely absorbed when the embryo matures (fig. 3K).

Embryo

The division of the zygote occurs much later, compared with the formation of the nuclear endosperm. The earliest stage observed is a small globular embryo, 0.02 mm wide, surrounded by numerous endosperm nuclei (fig. 4B). The globular embryo increases in size and later differentiates into a heart-shaped embryo which then forms the mature straight embryo with two unequal cotyledons (fig. 3I-K). Degeneration of the embryo sacs was frequently observed. Often, the fruits increased in size while the embryo sacs remained small and eventually degenerated.

Seed Coat and Flesh of the Seed

The edible flesh of the fruit is derived from the outer integument while the testa is derived from both the outer integument and the remaining inner integument. The inner integument is initiated around the ovular primordium at the archesporial cell stage (fig. 2A), followed by the development of the outer integument (fig. 2B). Both integuments are already prominent at the megaspore mother-cell stage (fig. 3A, D). At the mature 8-nucleate embryo sac stage, the inner and outer integuments are respectively, 6-7 layers and 5-6 layers thick. The subepidermal cells of the outer integument near the chalaza and placental outgrowth have divided such that it is 10-12 cells thick (fig. 3B, E). The vasculature to the integuments is prominent and abundant.

After the degeneration of the antipodals and just before the division of the primary endosperm nucleus, meristematic activity spreads to the innermost cells on the lateral sides of the outer integument (fig. 3F, L). All these cells divide periclinally, hence they are arranged in rows which fan out radially. Simultaneously, cells of the inner integument also divide in that it becomes 10-13 layers thick. Periclinal meristematic activity of the outer integument continues from the chalazal to the micropylar region of the seed during nuclear endosperm formation (fig. 3G). The epidermis of the outer integument, so far, has only undergone anticlinal divisions.

Before the zygote divides, when the seed is about 1 mm long, the outer integument is 15-30 cells thick. The embryo sac has enlarged at the expense of the nucellus and the inner integument and by then the nucellus has been completely absorbed. The outermost cells of the inner integument elongate while those next to the embryo sac degenerate as this increases in size.

When the seed is about 5 mm long, the inner integument is only 3-4 cells thick along the periphery of the embryo sac though it is much thicker at the chalazal and micropylar ends. Meanwhile, rapid cell divisions, which may produce irregular folds, occur at the micropylar end of the outer integument (fig. 3H, Q). The epidermis of the outer integument now divides both anticlinally and periclinally. These cells contain tanniniferous materials. They then enlarge, become turgid with a juicy fluid and the tannin content disappears during ripening.

The seed continues to grow at the expense of the inner integument which is now only 2-3 layers along the wall of the embryo sac, and 5-6 layers at the micropylar end. When the seed measures to 6-8 mm long (at the globular embryo stage) the cells of the outer integument differentiate into an outer region of thin-walled parenchymatous cells and an inner region of sclerenchyma cells, traversed by vascular tissues (fig. 3I). The outer 6-7 layers of cells increase in size and differentiate into the fleshy part of the fruit (fig. 3M-P). The inner layers of the outer integument and the remaining inner integument become compressed to form the long

fibres, tanniniferous cells and vasculature of the testa (fig. 3P).

The placental outgrowth of the ovule, very prominent at the mature embryo-sac stage, contributes neither to the formation of the testa nor to the fleshy part of the fruit.

Seed Germination

Fresh seeds take only 7-10 days to germinate and germination is hypogeal, in which the hypocotyl is undeveloped and the cotyledons remain within the testa. The first sign of growth is detected when the cotyledons split and the radicle emerges, growing downwards, while the plumular shoot emerges above the soil level (fig. 4E). It is recurved at first, later growing upright. Two axillary shoots develop from the base of the shoot system but these die off one month after germination. When the seedlings are about 2 weeks old i.e., when the stem is about 8 cm long, the first pair of leaves unfold.

The average percentage of germination of 200 fresh seeds sown in garden soil is 96%. Of the seedlings, 2% possess 2 or 3 shoots which emerge from the same point of the seed and they share one root system (fig. 4G). Probably more than one shoot apex are in the embryo.

Discussion

Nephelium lappaceum is a common, indigenous Malaysian fruit tree with great economic potential. The external morphology has been described by Corner (1952) and Allen (1967).

The plants are functionally dioecious and are either male or bisexual. The stamens in the bisexual flowers have been called 'staminodes' (Ochse, 1961). The term seems inappropriate since the present study shows that though the anthers do not dehisce, they do produce viable two-celled pollen grains which could germinate on a living stigma.

Corner (1952) reports that in *Nephelium,* the relation between the male and bisexual trees is not known. He states "it seems therefore that the male trees are useless though it is possible that the bisexual flowers must be cross-pollinated from the male trees to set fruit". This present study on the bagging of the flowers before and after anthesis strongly suggests that fruit production in *N. lappaceum* is indeed dependent on fertilization or at least pollination. Self pollination cannot occur as the anthers of bisexual flowers are not able to release its viable pollen grains. This seems an effective barrier against inbreeding of the species.

Heterostyly is more elaborate in *Cardiospermum halicacabum* (Nair and Joseph, 1960) and *Litchi chinensis* (Banerji and Chaudhuri, 1944). Both bear 3 types of flowers, which differ from each other mainly in the degree of sexual development. These flower types appear consecutively on the same panicle and are designated as Type I, II and III according to the chronological order of the development (Mustard, 1960). Type I functions as male since the gynoecium is rudimentary, Type II as female as the androecium is underdeveloped and Type III, an intermediate of the two, normally functions as male. The only difference between *N. lappaceum* and *L. chinensis* is that in *N. lappaceum,* the 2 types of flowers are borne on different trees. Yet Whitehead reports (1959) that "the cultivated rambutan is usually monoecious, flowers of both sexes being borne on the same inflorescence".

A large proportion of the flowers and fruits of the Rambutan degenerate during development. Khan (1939) and Mustard (1960) also noted such high percentages of flower and fruit abortion in *L. chinensis.* Khan (1939) reported that only a very

small ratio (1:78) of female flowers set fruit. Mustard (1960) was able to reduce total degeneration of embryo sac from 63.1% to 41.0% by partial defloration. The decrease in degeneration in partially deflorated as compared to non-deflorated panicles indicates a competition among flowers. She suggested that water and nutrient deficiencies may be contributing factors, not only to the degeneration of megagametophytes but also the problem of fruit set in *L. chinensis*.

Studies on the embryology of the members in the Sapindaceae are scanty and incomplete except in *L. chinensis* and *Cardiospermum halicacabum*. This present study shows that the anther of *N. lappaceum* is tetrasporangiate and the wall development conforms to the basic type. In the functionally female flowers, degeneration of the pollen grain is common at the various stages of development.

The ovule is bitegmic and crassinucellate and the embryo sac development conforms to the monosporic *Polygonum* type as in other species in the family already studied (Davis, 1966).

The details of embryogeny in *N. lappaceum* are masked by the dense, free-nuclear endosperm and the darkly staining resinous and tanniniferous content of the embryo sac. Within the family the embryogeny of *C. halicacabum* only has been investigated and reported as the Asterad type by Nair and Joseph (1960) but as the Onagrad type by Kadry (1946).

The fleshy pulp of the fruit in Sapindaceae has generated much controversy over the years. Radlkofer (1933) said that the edible fleshy part of *N. lappaceum* is an aril which adnates to the testa. Van der Pijl (1957) and this study show that the fleshy layer is the swollen outer integument and the dry, protective seed coat originates from the innermost layers of the outer integument and the inner integument. In contrast, the edible, fleshy layer of *Nephelium longana* and *L. chinensis* are considered as a free aril (Radlkofer, 1933) or an arillode (Van der Pijl, 1957). The differentiation of the flesh around the micropyle observed here is the same as the exotestal patch described by Corner (1976).

Acknowledgements

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