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THE VEGETATIVE AND REPRODUCTIVE STRUCTURE OF PAPAYA (CARICA PAPAYA)[1]

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INTRODUCTION

Anatomical and morphological studies of tropical crop plants are widely scattered in journals and reference books. This literature is all too often inaccessible to students and researchers in the developing countries of the tropics. In addition, the structure of many crops has never been carefully studied. These factors present a significant constraint on the teaching of and research in tropical agriculture, since all aspects of agriculture are based ultimately on a firm botanical understanding of the crop and especially its plant structure and function. Therefore, this monograph is presented in an effort to summarize previously published information and to offer new observations on the structure of one crop, the papaya. The format of the present monograph will serve as a basis for what is hoped will be a forthcoming series dealing with different tropical crops. The morphology, anatomy, and cytology of the different vegetative and reproductive parts of the plant are described in detail. The terminology used can be found in an introductory text of plant anatomy (for example Esau, 1977). The author welcomes suggestions or comments that could improve the usefulness of such a reference and could be incorporated in future monographs.

MATERIALS AND METHODS

Observations were made on freehand sections of either fresh or fixed material of several unnamed cultivars of Latin American origin. Drawings were made with the aid of a drawing tube attachment for a Wild M20 microscope.

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The gross morphology of papaya was accurately but only briefly described by Ochse (1931) and Purseglove (1968). These and other published descriptions were combined with original observations to give a complete summary description of the structure of papaya.

CARICA PAPAYA L.

Family - Caricaceae
Common names - Papaya, Pawpaw, Tree-melon, Fruta de Bomba, Papayer, Mamão.
Hawaiian names - Mikana, Milikana, Papaia, He'i.

GENERAL MORPHOLOGY

Seedling: Germination is epigeal; emergence occurs 2-3 weeks after planting. The two cotyledons are ovate with three main veins. The root system is loosely fibrous; one or occasionally more tap root(s) develop. The first or second foliage leaf is three-lobed. Successive leaves are increasingly more lobed.

Adult: Cultivated trees are small, but old specimens can grow 10 m tall. The trunk is monopodial and usually unbranched; inflorescences are lateral. These features define Corner's model in a recent scheme of tree architecture (Hallé, Oldeman and Tomlinson, 1978). The wood of the trunk and tap root is soft and succulent. Internodes are hollow. The 0.6 m long tap root may or may not be branched. Secondary roots arise mainly from the top 15 cm of the tap root and grow up to 4 m long in one-year-old plants. Feeding roots occur at this depth within 3 m of the stem (Swarbrick, 1964). Leaves are alternate and clustered near the apex. The phyllotaxy is a 3/8 spiral on the axis and 5/13 within the bud (Sprecher, 1943). A system of (2+3) or (3+5) contact parastichies is observed on the trunk (Arnold and Baas Becking, 1949). The petiole is hollow and 25-100 cm long. The lamina is 25-74 cm in diameter and palmately 7-11 lobed to varying degrees (Badillo, 1971). Persistent leaf scars (Fig. 6G) change shape with later thickening of the axis (quantitative analysis by Arnold and Baas Becking, 1949). Flower buds are axillary; the first is initiated 4-8 weeks after germination. The single or grouped inflorescences are associated with every leaf after their first appearance. Branch buds are axillary and single on the lower stem region. One or more accessory branch buds occur distal to an inflorescence bud in the upper stem region (Fig. 6G). Branch buds are strongly inhibited but grow out after injury to the shoot apex or with age. Apical bud growth is uninterrupted. The apex lacks protective scales or stipules but has colleters on the young leaves (see *Leaf*-Lamina). New leaves emerge at about 2 per week (Storey, 1969b). Plants are usually dioecious although sometimes hermaphrodite (bisexual) flowers occur primarily within the staminate inflorescence or on separate plants. Inflorescences are cymose. Laticifers occur in all organs.

SEED

Seed Coat: The outer region is fleshy and becomes a gelatinous sarcotesta at maturity (Fig. 1C). It is derived from the multiple outer epidermis of the outer integument of the ovule (Foster, 1943; Roth and Clausnitzer, 1972; Stephens, 1910). The mesotesta is compact, consisting of a series of sculptured, spongy, and hydroscopic longitudinal ridges, derived chiefly from subepidermal layers of the outer integument (Fig. 1A). The inner epidermis of the outer integument remains unchanged except for development of druses. The inner integument produces thin, inner, sclerotic layers of the seed coat with the inner epidermis tanniniferous and subepidermis fibrous. The funicle is stout, its head occasionally enlarged and fleshly as a short aril (Corner, 1976). The funicular vascular bundle (Fig. 1A) extends into the inner integument at the chalazal end where it subdivides.

Endosperm: Cells are thin-walled with abundant oil and aleurone grains; starch is absent at maturity (Fig. 1B).

Embryo: The embryo is straight and median with ovoid and flattened cotyledons (Fig. 1A).

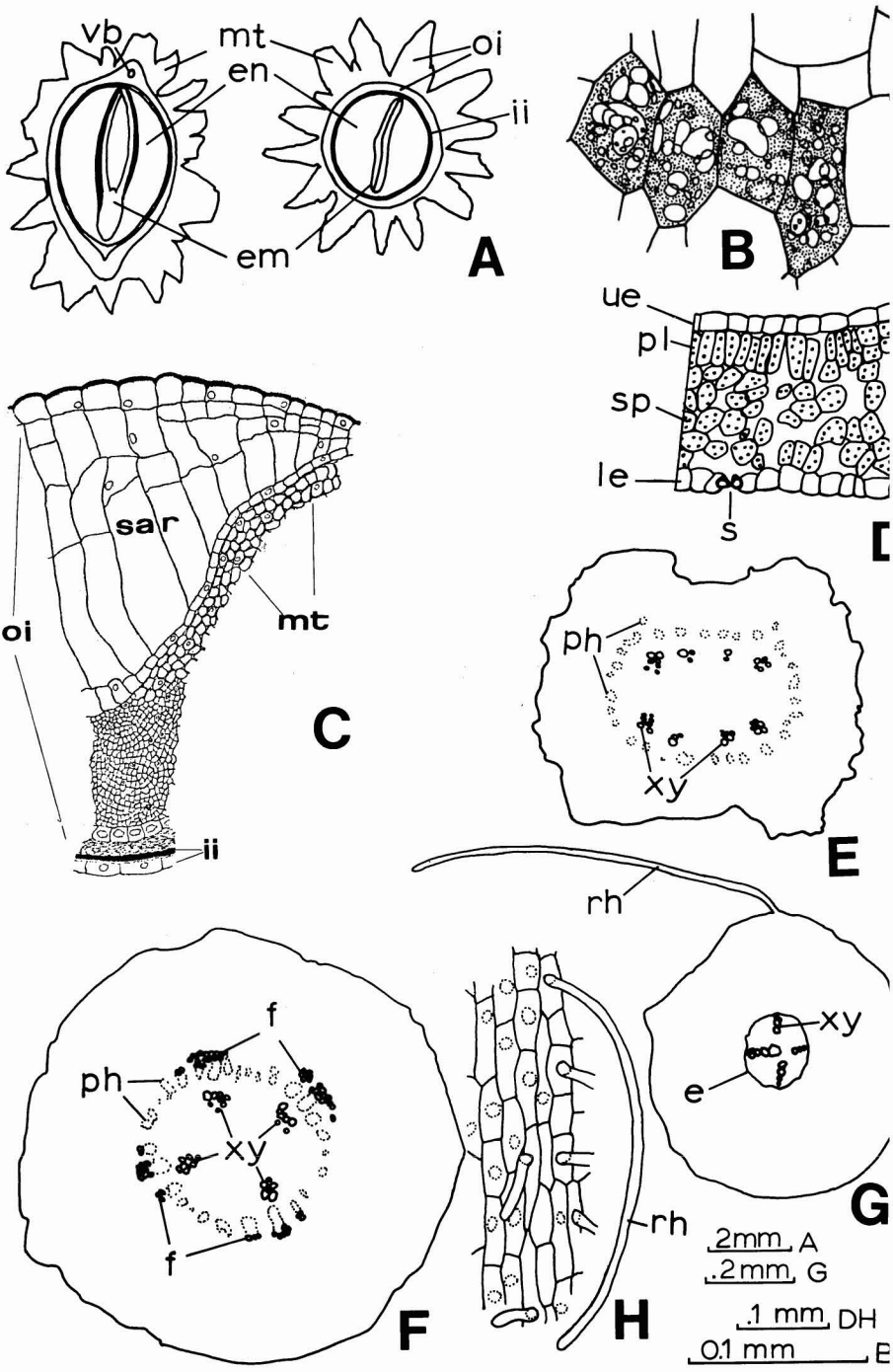
SEEDLING

Radicle: Root hairs arise from adjacent epidermal cells (Fig. 1H); trichoblasts are absent. The cortical parenchyma cells contain starch. The endodermis is thin-walled, the outer tangential and radial walls becoming suberized with age. The pericycle is one to two-layered. Phloem poles alternate with two, three, or four xylem poles. A pith is absent (Fig. 1G).

Hypocotyl: The epidermis has scattered, swollen cells. The cortex is chlorenchymatous with some peripheral angular collenchyma in the upper region of the hypocotyl. The endodermis is poorly developed or absent. Phloem strands lie both opposite and in between the four xylem strands in the lower region (Fig. 1F) and the eight xylem strands in the upper region. The pith is chlorenchymatous and solid.

Epicotyl: The histology is similar to that of the hypocotyl except that four smaller additional xylem strands of the upper hypocotyl region extend into the epicotyl but lack fibers (Fig. 1E), presumably due to the younger age of this region.

Cotyledon: The upper epidermis has scattered stomata (density = 19.6/mm^2) and lacks trichomes. The mesophyll is composed of one layer of palisade tissue and three to four layers of spongy tissue (Fig. 1D).The lower epidermis has trichomes (Fig. 4C, K) and stomata (density = 247.5/mm^2). Guard cells are slightly sunken or level with the surface, and they are larger and contain more chloroplasts than those in the mature leaf lamina. Subsidiary cells are absent.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ADULT - ROOT

The organization of the primary root structure is similar to that of the radicle (Fig. 1G, 2A). A pith is present in the larger roots and may or may not contain scattered small metaxylem elements (Fig. 2B). The primary xylem typically has four to five poles, with 3-10 small metaxylem elements radially aligned. Each pole terminates in protoxlyem (exarch), and alternates with regions of large metaxylem elements. Wide rays are opposite the protoxylem and lack a peripheral cluster of phloem fibers (Fig. 2B). Secondary xylem and phloem tissues are similar to those of the stem. Phloem rays are wide, and radial groups of fibers and sieve tubes alternate with the rays. Phloem fibers occur in more or less discrete groups (Fig. 2B) rather than in radial files as in the stem. The rays expand greatly near the periphery (Fig. 2C), the greatest tangential enlargement occurring in the central ray parenchyma. A periderm is present. Druses are found in the pith and peripheral ray parenchyma cells. Starch is present in the pith and ray parenchyma, and in the xylem parenchyma not adjacent to vessels. Lateral roots originate in the pericycle opposite the protoxylem.

ADULT - SHOOT

Node: The node is unilacunar, with three groups of many leaf traces (Fig. 3D) that become organized into a ring at the base of the petiole. Nodal plates are present in most but not all nodes; they lack vascular tissue and are composed of compact but unlignified parenchyma. Older plates have parenchyma in longitudinal files with multiple subdivisons (Fig. 3H). Druses and cystoliths, with many cell wall extensions (trabeculae), are scattered in older nodes. Starch is absent.

Internode: Primary tissues: The epidermis initially has scattered trichomes (see *Leaf*-Lamina). The outer cortex consists of one to two layers of subepidermal parenchyma and angular collenchyma cells which lie mainly opposite phloem caps (Fig. 3E). The inner cortex (this is referred to as endodermis by Holm, 1915, or pericycle by Arnold and Baas Becking, 1949 and Metcalfe and Chalk, 1950) consists of chlorenchyma cells located between the collenchyma cells of the outer cortex and the phloem sclerenchyma (Fig. 3E). Vascular rays are wide and chlorenchymatous. Collateral vascular bundles are numerous, radially elongated, and organized in a ring, forming a complex network by tangential anastomosing. Phloem fiber caps occur in older regions. The parenchyma region between the primary xylem and phloem contains more laticifers on the inner or xylem side

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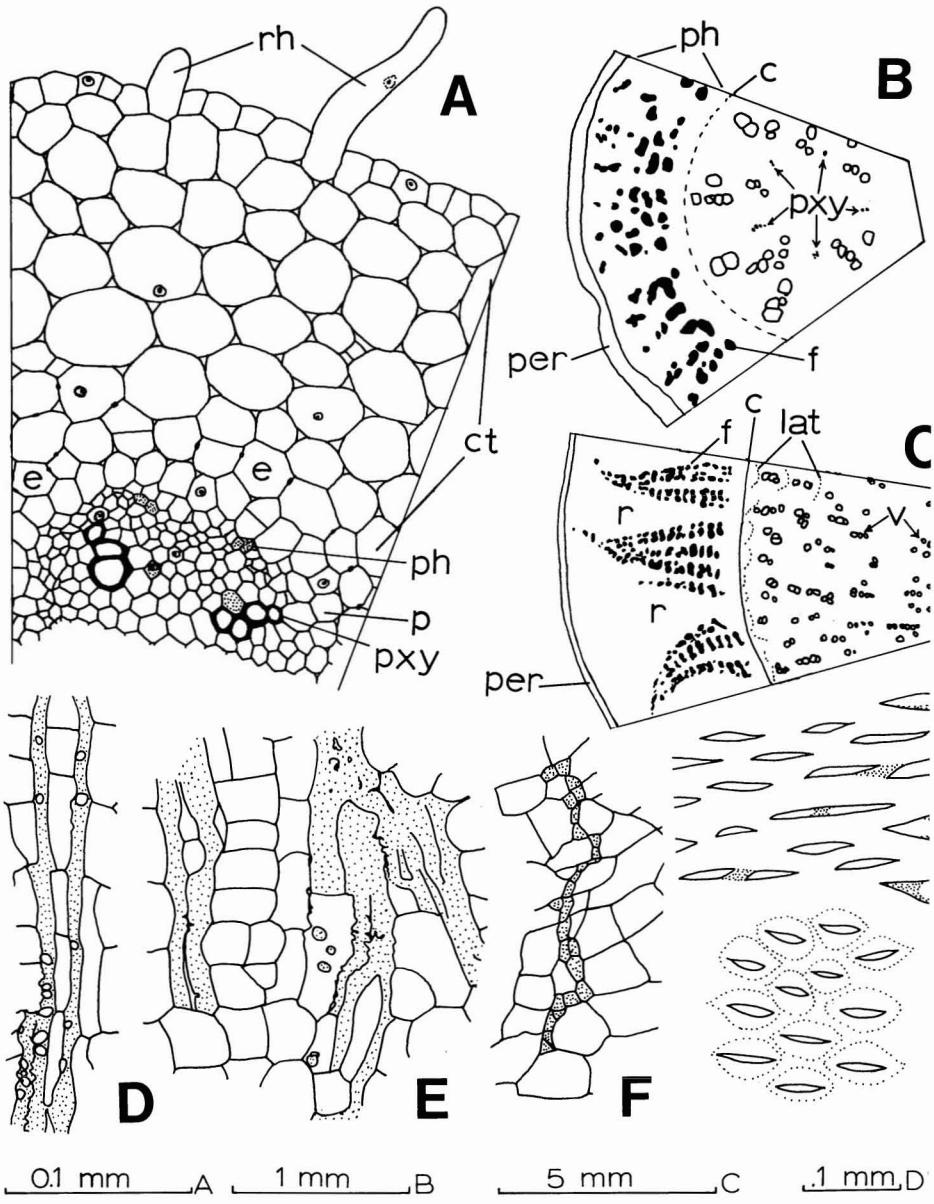
Figure 1. *Seed and seedling.* **A.** Mature dried seeds, T.S. (transverse section) and L.S. (longitudinal section). **B.** Endosperm cells. **C.** Ovule wall of developing seed (after Foster 1943; magnification not given). **D.** Cotylendon, T.S. **E.** Epicotyl, T.S. **F.** Hypocotyl, T.S. of lower region. **G.** Radicle, T.S. **H.** Radicle in surface view, many root hairs broken off.

(e) endodermis, (em) embryo, (en) endosperm, (mt) mesotesta ridge, (f) fibers, (ii) inner integument, (le) lower epidermis, (oi) outer integument, (ph) phloem, (pl) palisade mesophyll, (rh) root hair, (s) stoma, (sar) sarcotesta, (sp) spongy mesophyll, (ue) upper epidermis, (vb) vascular bundle, (xy) xylem.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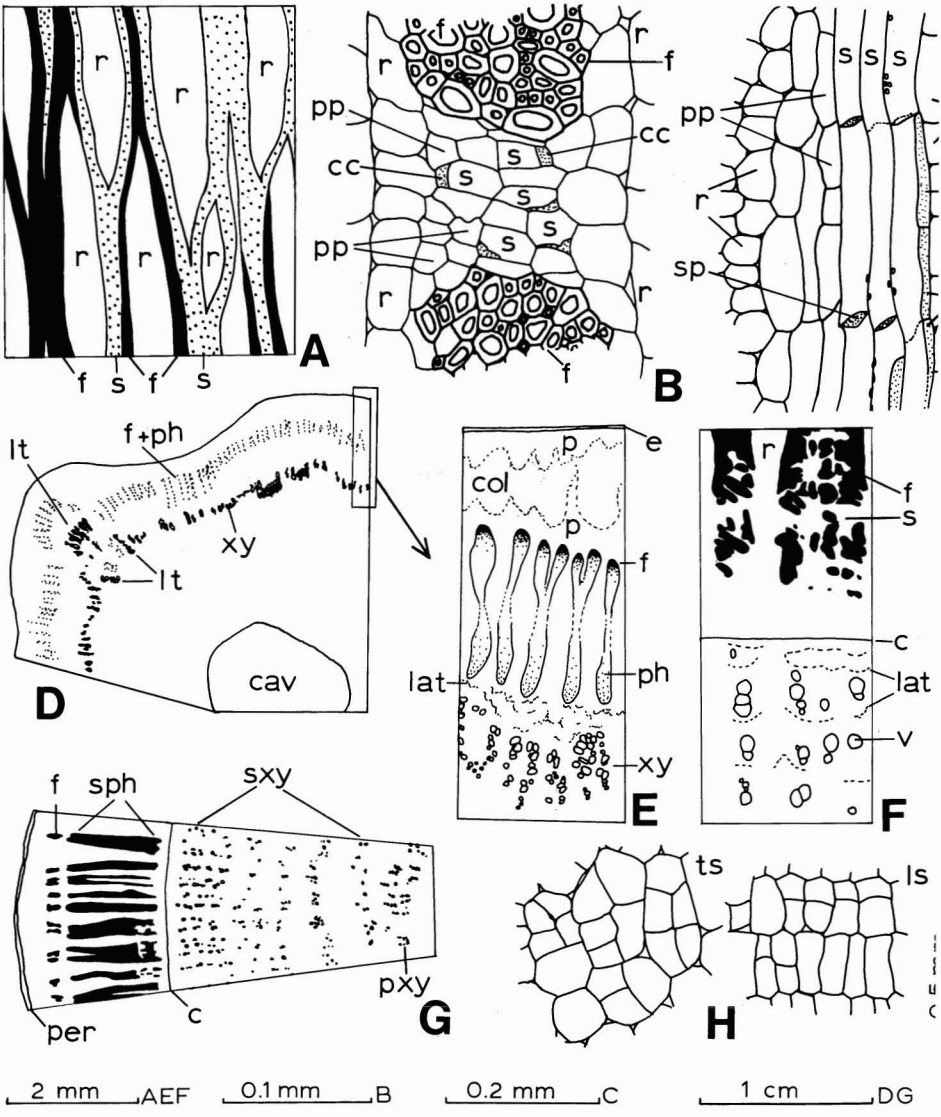
and is perhaps derived from the fascicular cambium which is not well defined at this early stage. The pith is hollow in the center (Fig. 3D).

Secondary tissues: A periderm is present and is initiated in the first cell layer below the epidermis. Sclereids are scattered in the phellem (cork). The outer bark is green due to chlorenchyma cells of the cortex and the peripheral ray parenchyma in older regions. The cortex is persistent, with pockets of collenchyma and primary phloem fiber caps (Fig. 3G). The cortical parenchyma cells divide and become expanded tangentially between pockets of collenchyma. Druses are abundant in the cortex. The cambium is storied although an interfascicular cambium is often undefined. The phloem near the cambium has distinctly storied sieve elements and companion cells (Fig. 3A, C). Sieve plates are transverse, and sieve areas occur on lateral walls. Fiber groups alternate radially with groups of sieve elements, companion cells, and parenchyma (Fig. 3B). Phloem rays are wide (multiseriate) and tall, with uniform ray parenchyma cells (homogeneous) (Fig. 3A). Rays are dilated at the periphery with their central parenchyma cells greatly enlarged. Articulated laticifers are scattered in phloem rays. Laticifers are fused tangentially (Fig. 2D, E, F) and occur throughout the xylem but are more numerous between the rays and near the cambium (Fig. 3F). The early secondary xylem is indistinct from the primary xylem (Fig. 3G). The xylem is composed mostly of unlignified parenchyma, with groups of 1-7 vessel elements (Fig. 3F). Vessel pits are alternate—bordered when in contact with vessels, gash-like and unbordered when in contact with parenchyma cells (Fig. 2G). Perforation plates are simple and transverse. Wood fibers are absent. The parenchyma adjacent to vessel elements is lignified. Xylem rays are wide (multiseriate) and tall. Starch is abundant in the xylem parenchyma cells, especially near vessel elements and cambium; in the phloem near fibers; and at the edges of rays. The development of stem thickening was described, together with quantitative data on surface distortions, by Arnold and Baas Becking (1949).

Leaf: Petiole: The epidermis has scattered 2-3 celled, club-shaped, deciduous trichomes (see *Leaf*-Lamina). Stomata are widely scattered. The subepidermal parenchyma is chlorenchymatous, with scattered red-pigmented cells. Angular collenchyma cells occur in a complete ring within the subepidermal parenchyma (Fig. 4B). The parenchyma interior to this collenchyma is large-celled and is adjacent to a ring of sclerenchyma. Fibers and lignified parenchyma are in alternating groups (Fig. 4B) forming a continous sclerenchyma ring (Fig. 4A). Collateral vascular bundles are radially elongated, occurring in a ring and opposite the fibers. There is no cambium. The pith is hollow in the center (Fig. 4A). Druses are abundant in all collenchyma and parenchyma tissues.

Figure 2. *Root.* **A.** Primary root, T.S. **B.** Root after start of secondary growth, T.S. **C.** Old root in cambium region, T.S. **D, E, F.** Laticifers in young secondary xylem, radial S., tangential S., and T. S., respectively. **G.** Vessel wall pitting patterns, surface view.

(c) cambium, (ct) cortex, (f) fibers, (lat) laticifers, (p) pericycle, (per) periderm, (ph) phloem, (pxy) protoxylem, (r) ray, (rh) root hairs, (v) vessel elements.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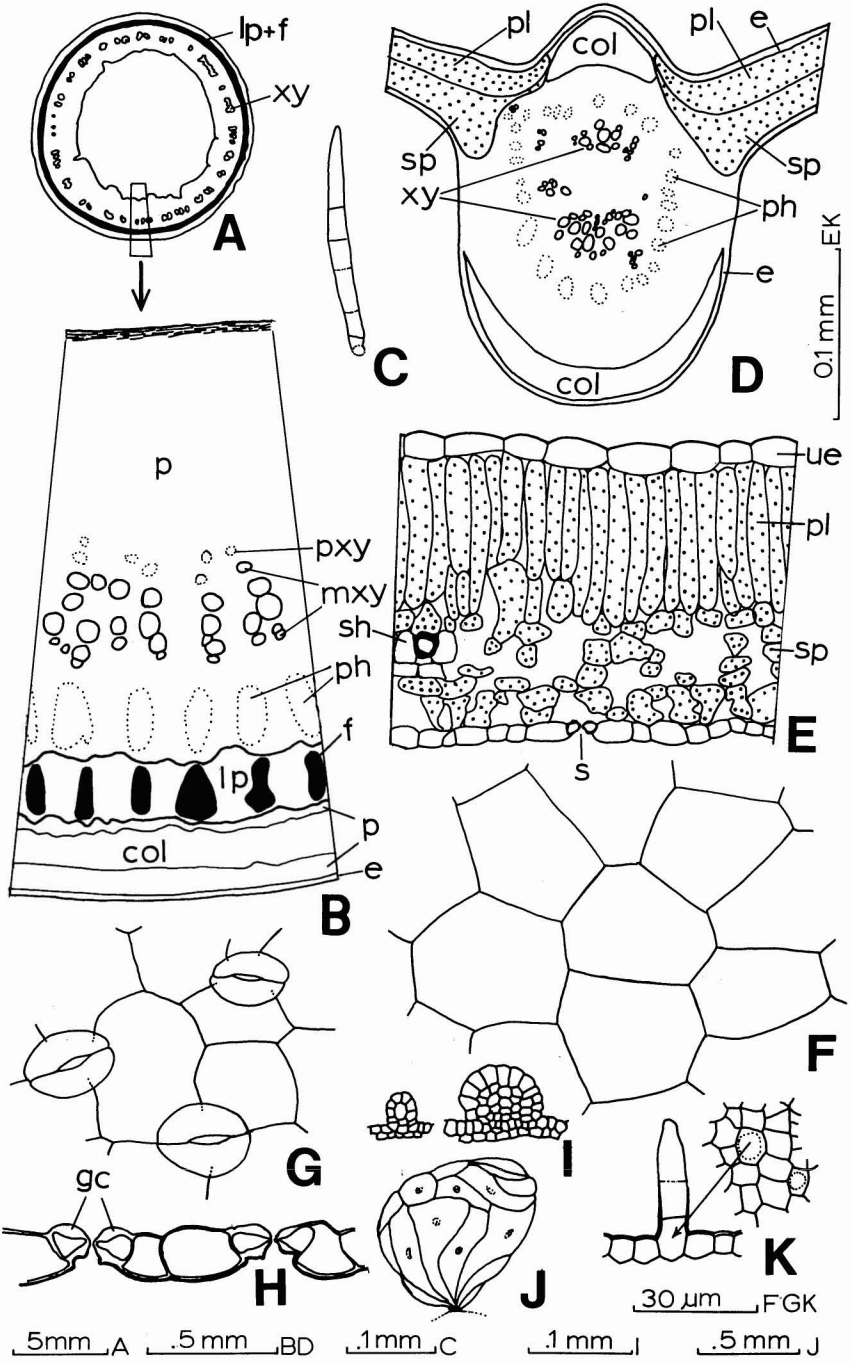
Lamina: Young leaves and other organs have 2-6 celled, simple trichomes (Fig. 4C, K) and multicellular, club-shaped trichomes (Fig. 4J) that were called "intumescence" by Sprecher (1943) and "pearl hairs with oil droplets" by Holmgren (1911) who considered them emergences. The trichomes detach during organ enlargement. Colleters occur at the junction of the petiole and lamina, above and below large veins; they are variously shaped and derived from the epidermis and subepidermal layers (Fig. 4I). Their internal cells contain many druses and secrete slime when young. The protective function and development of the intumescence and colleters were described by Sprecher (1943). The upper epidermis has isodiametric cells in a surface view; these are elongate over the veins; stomata are absent (Fig. 4F). The lower epidermis has smaller cells than the upper and has stomata (Fig. 4G) that are slightly sunken, anomocytic, and have a density of 727/mm^2 (Fig. 4H). Benítez de Rojas (1968) has compared the epidermis in various species of *Carica*. Gum-like deposits frequently occur on the lumen side of the outer epidermal cell wall. Crystals are absent in epidermal cells. The mesophyll consists of one (rarely two) adaxial layer(s) of palisade tissue and 4-6 layers of spongy tissue containing druses (Fig. 4E). Venation is reticulate; small veins may or may not have a parenchyma sheath (Fig. 4E). Large veins have caps of angular collenchyma above and below the vein, with parenchyma occurring between the epidermis and the cap. Vascular tissues of the large veins are arranged in a ring; xylem and phloem groups are wthin a region of collenchyma and parenchyma (Fig 4D). Druses are numerous in these latter two tissues. Chlorenchyma cells are absent in all tissues associated with the largest veins.

FLOWER

The inflorescence is a cyme, much branched and elongated in the staminate (male) and reduced in the pistillate (female) plant. The inflorescence axis is hollow and similar to the petiole in structure but with litle collenchyma. There are three basic flower types, although Storey (1958) reported a single pistillate, 15 staminate, and 15 hermaphrodite forms. A detailed description of floral morphology was given by Sprecher (1943), Hofmeyr (1938), and Storey (1969a). The time from flower bud emergence to anthesis is 45-47 days in both staminate and pistillate flowers; the hermaphrodite shows a two-day delay. Maximum anthesis for male and female flowers occurs at 6-8 pm (Mekako and Nakasone, 1975).

Figure 3. *Stem.* **A.** Secondary phloem, tangential S. **B.** Secondary phloem, T.S. **C.** Secondary phloem, tangential S. **D.** Internode with hollow pith and leaf trace, T.S. **E.** Internode detail at end of primary growth, T.S. **F.** Old stem, detail of cambium region, T.S. **G.** Old stem, T.S. **H.** Nodal plate, L.S. and T.S.

(e) epidermis, (c) cambium, (cc) companion cells, (col) collenchyma, (f) fibers, (lat) laticifers, (ls) L.S., (lt) leaf trace, (p) parenchyma, (per) periderm, (ph) phloem, (pp) phloem parenchyma, (pxy) primary xylem, (r) ray, (s) sieve tube member, (sp) sieve plate, (sph) secondary phloem, (sxy) secondary xylem, (ts) T.S., (v) vessel member, (xy) xylem.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Staminate flower: The calyx cup is 5-toothed (Fig. 5A). The corolla is tubular and 5-lobed. There are 10 stamens inserted at the throat of the corolla: 5 alternating with petals, 5 opposite petals with shorter filaments (Fig. 5B). Anthers and filaments have long, rope-like, unicellular trichomes (Fig. 6D). Anthers have four (two at dehiscence) locules (Fig. 6A). The endothecium has helical thickenings; dehiscence is longitudinal. A rudimentary pistil is present. The calyx and corolla are dehiscent. The pedicel is similar to the petiole but solid, without sclerenchyma, and with collenchyma in a complete ring.

Pollen: Development is described by Asana and Sutaria (1929) and Allan (1963). The microspore mother cell forms four microspores by furrowing after meiosis. The pollen grain has three apertures (tricolporate), each aperture consisting of a long, external colpus and a short, perpendicular, internal os (Fig. 6B). The pollen surface is finely reticulate. Grains are 32-39 μm in diameter and spherical when wet (28.5 μm diameter was given by Eng and Rao (1968)). Shed pollen appears to be uninucleate although Kumar, Abraham, and Srinivasan (1945) reported that it is two-celled. The course of the pollen tube was briefly described by Traub and O'Rork (1939). Hormonal effects on pollen growth were given by Eng and Rao (1968). The pollen tube enters the ovule 2-10 days after pollination (Allen, 1963; Foster, 1943). The development of sperm has not been described. The pollination mechanism is unclear, but some insects are indicated (reviewed by Free, 1975), and Baker (1976) proposed a breeding system with mistaken pollinators in which the staminate flower is mimicked by the stigma of the pistillate flower.

Pistillate flower: The calyx cup is 5-toothed and persistent (Fig. 5C). Sporne (1977) reported that the vascular supply to the sepals come from "girdling bundles" which arise from 5 trunk bundles. The corolla has 5 petals which are twisted, inconspicuously fused at the base, and slightly adnate to the ovary base. Stamens are absent. The ovary is 5 carpellate, slightly inferior, and hollow with parietal placentation. A diagram of floral vasculature and carpel limits is given in Fig. 6C. The ovary is terminated by 5 sessile, deeply cleft stigmas. The stigmatic surface has many unicellular hairs whose tips are swollen. Vascular bundles are numerous and in two rows in each stigmatic lobe. The stylar canal is short and lined with stigmatic hairs and mucilage. The pedicel structure is similar to that of the petiole, but solid. Collenchyma cells are absent in the pedicel. Certain strains commonly produce teratological internal ovaries which originate from either the pla-

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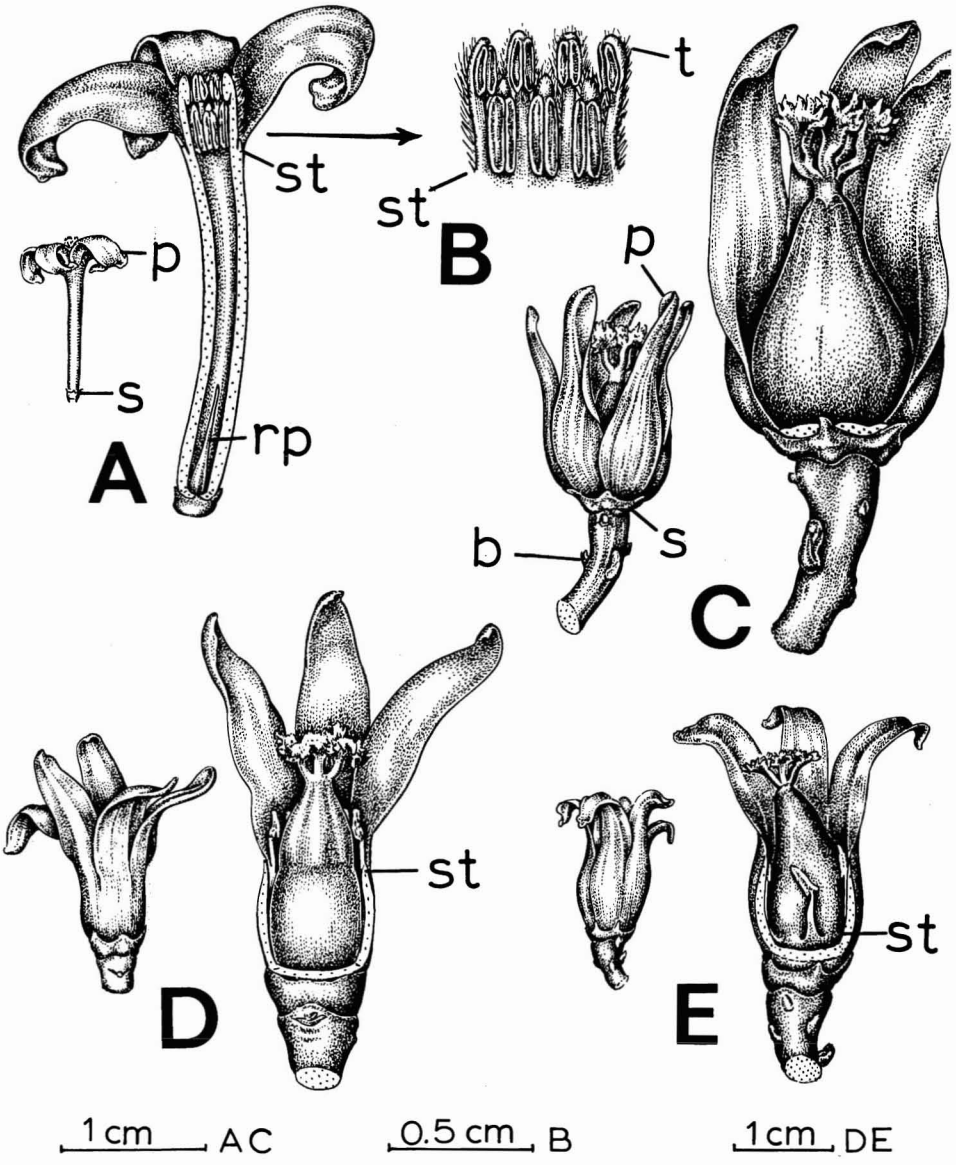
Figure 4. *Leaf.* **A.** Petiole with hollow center, T.S. **B.** Petiole in detail, T.S. **C.** Trichome from young leaf. **D.** Main vein of lamina, T.S. **E.** Lamina with small vein, T.S. **F.** Upper epidermis, surface view. **G.** Lower epidermis with stomata, surface view. **H.** Stomata on lower epidermis of lamina, T.S. **I.** Colleter of young leaf, two stages of development (after Sprecher, 1943). **J.** Intumescence of young internode, side view. **K.** Trichome from young petiole, surface and side views.

(col) collenchyma, (e) epidermis, (f) fibers, (lp) lignified parenchyma, (mxy) metaxylem, (p) parenchyma, (ph) phloem, (pl) palisade mesophyll, (pxy) protoxylem, (s) stoma, (sh) sheath cell of vein, (sp) spongy mesophyll, (ue) upper epidermis, (xy) xylem.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centa or from rudimentary pistils which arise from the receptacle (Nakasone and Arkie, 1971).

Ovule: Development was described by Agharkar and Banerji (1935), Foster (1943), Kratzer (1918), Kumar et al. (1945), and Singh (1960). The ovule is anatropous and has two integuments. Four megaspores are produced. The embryo sac is 8-nucleate and is derived from the chalazal (basal) megaspore. Antipodal cells disintegrate almost immediately. The endosperm is presumably 3n. It is initially free-nuclear and becomes cellular 79 days after pollination, starting at the micropylar end. The development of the embryo is relatively slower than of the endosperm [see Foster (1943) for details].

Hermaphrodite flower: The size is intermediate between staminate and pistillate flowers. Elongata type: The corolla is united for one-third of its length (Fig. 5D), and its lobes are not twisted. The 10 stamens are arranged the same as in male flowers. The pistil is functional and elongated. Pentandria type: The corolla tube is short (Fig. 5E). Five stamens with long filaments are attached to the base of the ovary, and lie in furrows of the ovary. The pistil is functional and not elongated. Carpelloid forms occur which are very variable. In these forms some to all of the stamens become carpelloid, producing irregular ovaries. Storey (1969a) gives details of vasculature in carpelloid flowers to show the origin of the pistillate flower from a hermaphrodite ancestor.

FRUIT

The ovary develops into a fleshy berry. Fruit shape is spherical when developed from female flowers, pyriform to cylindrical from the elongata type, and cylindrical and 5-furrowed from the pentandria type. The central cavity is 5-angled and contains 300-700 viable seeds arranged in 5 rows on the ovary wall. Fruit weight is correlated to seed number and seed weight (Allan, 1969) but pollination is not necessary factor for fruit set (Free, 1975).

Immature fruit: The epidermis has scattered stomata (Fig. 6H). There are no trichomes. The pericarp lacks sclerenchyma. Vascular bundles and laticifers form an anastomosing network throughout the parenchyma, and are most numerous in the periphery of the fruit where calls are smallest (Fig. 6E). Abundant white latex flows freely from surface wounds. Tracheary elements of the vascular bundles have helical thickenings. The smaller

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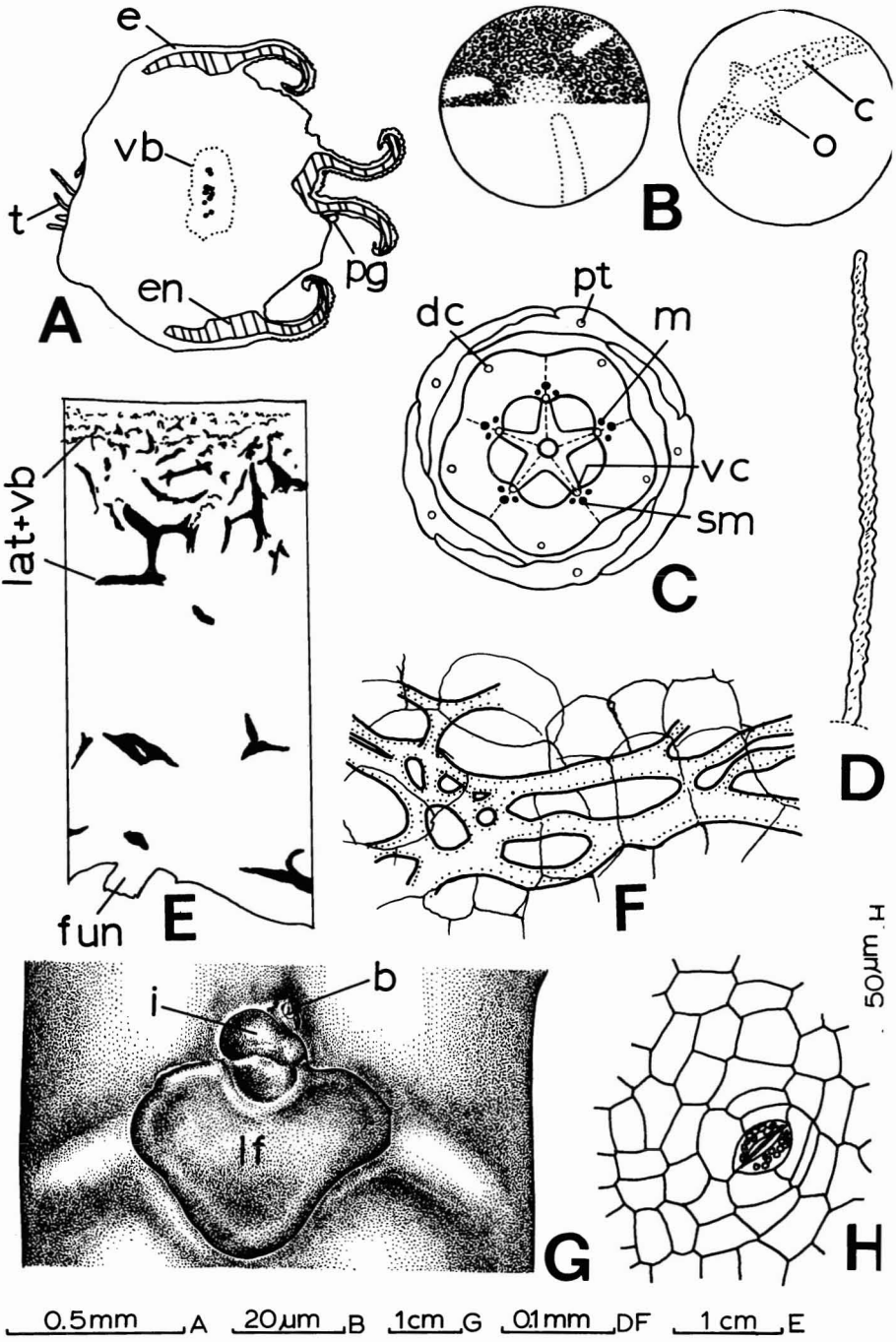
Figure 5. *Flowers.* **A.** Staminate flower, two petals removed in enlargement. **B.** Stamens at top of corolla tube. **C.** Pristillate flowers, two petals removed in enlargement. **D.** Hermaphrodite flower, pentandria type, two petals removed in enlargement. **E.** Hermaphrodite flower, elongata type, two petals removed in enlargement.

(b) bud of undeveloped flower, (p) petal, (rp) rudimentary pistil, (s) sepal, (st) level of stamen insertion, (t) trichomes.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xylem elements are adjacent to an associated laticifer. Tanniniferous cells are scattered near the central cavity. A single vascular bundle is present in each funiculus. Changes in the pericarp (fruit wall) during development are briefly described by Roth and Clausnitzer (1972). Resistance of young fruit to anthracnose was correlated with ability of wounded tissues to produce a periderm that was initially suberized and later was lignified (Stanghellini and Aragaki, 1966).

Mature fruit: The epidermis has a thick culticle with wax deposits on its surface view. Stomata are widely scattered, and trichomes are absent (Gassner, 1973). Chromoplasts are elongate and needle-like. They are present in all of the mesocarp parenchyma giving an orange color to the tissue. Starch is absent. There is no sclerenchyma. Laticifers occur throughout the mesocarp tissue (Fig. 6F), often paralleling vascular bundles, but the latex becomes granular and is not white or freely flowing as in the green, immature fruit.

CYTOLOGY

The somatic number is 18; n = 9 (Asana and Sutaria, 1929; Foster, 1943; Siguara, 1927). Sex types of flowers are unrelated to chromosomal morphology (Kumar et al., 1945) but are determined by gene loci (Storey, 1969b). Chromosome lengths may vary with variety (Datta, 1971).

DISTINCTIVE FEATURES

Laticifers (Fig. 2D-F, 3F, 6F) are found in all organs. They are articulated, anastomosing, multinucleate at maturity (easily seen in mature fruit), and especially common in the periphery of green fruit from whch latex is collected commercially (Fig. 6E). Latex is white and contains a proteolytic enzyme, papain. Latex is absent in ripe fruit (Griebel, 1928).

Figure 6. *Flower, fruit, and buds.* **A.** Anther at dehiscence, T.S. **B.** Pollen, freshly shed, surface view. **C.** Diagram of pistillate flower in T.S., dotted lines show limits of carpels (from Storey, 1969a). **D.** Trichome from stamen. **E.** Ovary wall, ovule not shown on funiculus (fun), T.S. **F.** Laticifers in mature fruit wall, tangential S. **G.** Node of stem showing leaf and inflorescence scars. **H.** Epidermis of young fruit, surface view.

(b) bud of undeveloped flower, (c) colpus, (dc) dorsal carpellary bundle, (e) epidermis, (en) endothecium, (fun) funiculus, (i) inflorescence scar, (lat) laticifers, (lf) leaf scar, (m) marginal bundle, (o) os, (pg) pollen grain, (pt) petal trace, (sm) submarginal bundle, (t) trichomes, (vb) vascular bundle, (vc) ventral carpellary bundle.

PROPAGATION

New plants are produced predominantly from seed. Grafting is possible either by cleft grafting, using seedling stock and a scion taken from newly released lateral bud of a decapitated tree (Fairchild and Simmonds, 1913; Lange, 1969), or by budding (Sookmark and Tai, 1975). Stem cuttings have been rooted (Traub, 1937). Clonal propagation has been successful using tissue culture techniques, either from existing apical meristems (Litz and Conover, 1978; Yie and Liaw, 1977) or from callus-derived embryoids (De Bruijne, De Langhe and Van Rijck, 1974).

REFERENCES

Agharkar, S. P., and I. Banerji. 1933. The development of the embryo sac in *Carica papaya.* J. Dept. Sci. Univ. Calcutta 10: 1-8.

Allan, P. 1963. Pollen studies in *Carica papaya.* I. Formation, development, morphology, and production of pollen. S. Afr. J. Agric. Sci. 6: 517-530.

Allan, P. 1969. Effect of seeds on fruit weight in *Carica papaya.* Agroplantae (S. Afr.) 1: 163-170.

Arnold, G. H., and L. G. M. Baas Becking. 1949. Notes on the stem structure of *Carica papaya.* Ann. Bot. Gard., Buitenzorg 51: 199-230.

Asana, J. J., and R. N. Sutaria. 1929. A cytological study of pollen development in *Carica papaya.* J. Indian Bot. Soc. 8: 235-244.

Badillo, V. M. 1971. Monographia de la familia Caricaceae. Assoc. de Profesores, Univ. Central de Venezuela, Maracay.

Baker, H. G. 1976. "Mistake" pollination as a reproductive system with special reference to the Caricaceae. Pp. 161-169. *In* J. Burley and B. T. Styles (Ed.). *Variation, Breeding and Conservation of Tropical Forest Trees.* Academic, London.

Benítz de Rojas, C. E. 1968. Caracteres microscópicos de la epidermis foliar en Caricaceae. II. Género *Carica.* Universidad Central de Venezuela, Instituto de Botánica Agrícola, Maracay. (also: 1974. Rev. Fac. Agron. Univ. Cent. Venez. 7: 195-274.)

Corner, E. J. H. 1976. The seeds of dicotyledons. 2 vols. Cambridge University Press, Cambridge.

Datta, P. C. 1971. Chromosomal biotypes of *Carica papaya* Linn. Ctyologia 36: 555-562.

De Bruijn, E., E. De Langhe, and R. Van Rijck. 1974. Actions of hormones and embryoid formation in callus cultures of *Carica papaya.* (Int. Symp. Fytoform. Fytiat.) Meded. Fac. Landbourwwet. Rijksuniv. Gent 39: 637-646.

Eng, L. L., and A. N. Rao. 1968. Pollen germination and formation of callose plugs in papaya pollen tubes. Curr. Sci. 37: 690-692.

Esau, K. 1977. Anatomy of seed plants. 2 ed. J. Wiley and Sons, New York.

Fairchild, D., and E. Simmonds. 1913. The grafted papaya as an annual tree. Circular 119, 13 pp. U.S. Bur. Plant Industry.

Foster, L. T. 1943. Morphological and cytological studies on *Carica papaya*. Bot. Gaz. 105: 116-126.

Free, J. B. 1975. Observations on the pollination of papaya (*Carica papaya* L.) in Jamaica. Trop. Agr. 52: 275-279.

Gassner, G. 1973. Mikroskopische Untersuchung pflanzlicher Lebensmittel. 4. Aufl. Bearb. von F. Bothe. Fischer, Stuttgart.

Griebel, C. 1928. Über den mikroskopischen Bau einiger tropischer Früchte and ihren Nachweis in marmeladenartigen Zubereitungen wie "Lukutate-Mark". Zeitschr. Untersuch. Lebensmittel 55: 89-111.

Hallé, F., R. A. A. Oldeman, and P. B. Tomlinson. 1978. Tropical trees and forests: an architectural analysis. Springer Verlag, Berlin.

Hofmeyr, J. D. J. 1938. Genetical studies of *Carica papaya* L. I. The inheritance and relation of sex and certain plant characteristics. II. Sex reversal and sex forms. Sci. Bull. Dept. of Agr. S. Afr. 187, 64 pp.

Holm, T. 1915. Medicinal plants of North America. 90. *Carica papaya*. Merck's Report 24: 136-140.

Holmgren, I. 1911. Några iakttagelser öfver förekomsten af pärlhår hos tropiska växter. Svensk Bot. Tidsk. 5: 197-216.

Kratzer, J. 1918. Die verwandtschftlichen Berziehungen der Cucurbitaceen auf Grund ihrer Sammenentwicklung mit spezieller "Berücksichtigung der Caricaceen, etc. Flora 110: 275-343.

Kumar, L. S. S., A. Abraham, and V. K. Srinivasan. 1945. The cytology of *Carica papaya* Linn. Indian J. Agr. Sci. 15: 242-253.

Lange, A. H. 1969. Reciprocal grafting of normal and dwarf Solo papaya on growth and yield. HortScience 4: 304-306.

Litz, R. E., and R. A. Conover. 1978. In vitro propagation of papaya. HortScience 13: 241-242.

Mekako, H. U., and H. Y. Nakasone. 1975. Floral development and compatibility studies of *Carica* species. J. Amer. Soc. Hort. Sci. 100: 145-148.

Metcalfe, C. R., and L. Chalk. 1950. Anatomy of the dicotyledons. 2 vol. Clarendon Press, Oxford.

Nakasone, H. Y., and T. D. Arkie, Jr. 1971. Development of intra-ovarian ovaries in *Carica papaya* L. J. Amer. Soc. Hort. Sci. 96: 550-553.

Ochse, J. J. 1931. Vegetables of the Dutch East Indies. Archipel Drukkerij, Buitenzorg.

Purseglove, J. W. 1968. Tropical crops. Dicotyledons. 2 vols. Longmans, London.

Roth, I., and I. Clausnitzer. 1972. Desarrollo y anatomía del fruto y de la semilla de *Carica papaya* L. (Lechosa). Acta Bot. Venez. 7: 187-206.

Siguara, T. 1927. Some observations on the meiosis of pollen mother cells of *Carica papaya,* etc. Bot. Mag. (Tokyo) 41: 219-224.

Singh, D. 1960. Studies on endosperm and development of seeds in *Carica papaya* L. Hort. Adv. 4: 89-96.

Sookmark, S., and E. A. Tai. 1975. Vegetative propagation of papaya by budding. Acta Horticult. 49: 85-90.

Sporne, K. R. 1977. Girdling vascular bundles in dicotyledon flowers. Gardens' Bull. (Singapore) 29: 165-173).

Sprecher, A. 1943. Beitrag zur morphologie von *Carica papaya* L. Ber. Schweiz. Bot. Ges. 53A: 517-549.

Stanghellini, M. E., and M. Aragaki. 1966. Relation of periderm formation and callose deposition to anthracnose resistance in papaya fruit. Phytopathol. 56: 444-450.

Stephens, E. L. 1910. The development of the seed coat of *Carica papaya.* Ann. Bot. 24: 607-610.

Storey, W. B. 1958. Modification of sex expression in papaya. Hort. Adv. 2: 49-60.

Storey, W. B. 1969a. Pistillate papaya flower: a morphological anomaly. Science 163: 401-405.

Storey, W. B. 1969b. Papaya. pp. 389-407. *In* F. P. Ferwerda and F. Wit (Ed.) *Outlines of perennial crop breeding in the tropics.* Misc. Papers 4. Landbouwhogeschool, Wageningen.

Swarbrick, J. T. 1964. The growth and root distribution of some temporary shade plants of cocoa. Trop. Agr. 41: 311-323.

Traub, H. P. 1937. Rooting of papaya cuttings. Proc. Amer. Soc. Hort. Sci. 34(1936): 291-294.

Traub, H. P., and C. J. O'Rork. 1939. Course of pollen tube in *Carica papaya* and *Cucurbita.* Nature 143: 562.

Yie, S. T., and S. I. Liaw. 1977. Plant regeneration from shoot tips and callus of papaya. In Vitro 13: 564-568.