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Pollination and Pollen-pistil Interaction in Oil Palm, *Elaeis guineensis*

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Structural and cytochemical aspects of the pistil and details of pollination and pollen-pistil interaction were investigated in the African oil palm (*Elaeis guineensis* Jacq.), an important perennial oil crop. The stigma is trilobed, wet and papillate. The branched papillae are confined to a narrow linear zone on each stigmatic lobe. Each stigmatic lobe harbours a deep stigmatic groove, which runs adaxially along the surface. The stigmatic groove is bordered by a well-defined layer of glandular cells, each of which has a pectinaceous cap on the inner tangential wall. The style is hollow. The canal cells show thickenings on the inner tangential wall. The stigmatic groove and stylar canal contain an extracellular matrix secreted by the canal cells which is rich in proteins, acidic polysaccharides and pectins. The canal cells at the base of the style are papillate and loosely fill the stylar canal. The stigma becomes receptive when the stigmatic lobes separate, and remains so for 24 h. Pollination is mediated by weevils as well as by the wind. Under natural conditions the pollination efficiency was 100 %. Pollination induces additional secretion in the stigmatic groove and stylar canal. During post-pollination secretion, the pectinaceous caps of the cells lining the stigmatic groove are degraded. Pollen grains germinate on the stigmatic papillae and tubes grow on the surface of the papillae, entering the stigmatic groove and advancing along it into the stylar canal to eventually gain access to the locules. Pollen tubes are seen in the ovules 18–20 h after pollination.

Key words: Arecaceae, *Elaeis guineensis*, African oil palm, pollination, stigmatic grove, stylar canal, Tenera hybrid, weevil.

INTRODUCTION

Elaeis guineensis Jacq. is the highest oil-yielding perennial crop grown on a commercial scale throughout much of Malaysia and Indonesia (Purseglove, 1975; Hartley, 1988). This plantation crop has recently been introduced to southern parts of India (Rethinam, 1992). The fibrous mesocarp is the source of palm oil and the seed yields palm kernel oil. The total oil yield depends upon fruit production. Of the hybrid varieties, Tenera is preferred for commercial plantations owing to its thinner shell and thicker mesocarp (Cobley and Steele, 1976). Numerous studies have been carried out into its floral biology and pollination efficiency (Sayed, 1979; Pillai and Ponnamma, 1992). Pollination occurs via wind and weevils (Sparnaaij, 1969). As pollination is a recognized constraint in plantations of younger palms, manual pollinations are often carried out to sustain yield (Hartley, 1988). Detailed information on the structure of the pistil and pollen-pistil interaction is needed for a rational approach to yield improvement. To the best of our knowledge no such studies have been carried out on the oil palm despite its economic importance.

This paper describes structural and cytochemical features of the pistil, pollination and pollen-pistil interaction in Tenera hybrid (var. Dura × var. Pissifera).

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MATERIALS AND METHODS

Investigations were carried out on 5–10 year old palms raised in and around Bhadrawati (13·52°N 75·40°E), Karnataka State, India. Observations of floral biology, anthesis and anther dehiscence were made in the field.

Non-specific esterases on the stigmatic surface were localized using α-naphthyl acetate (Mattson *et al.*, 1974) and phosphatases using α-naphthyl acid phosphate (Scandlios, 1969) as substrates. Stigma receptivity and temporal details of post-pollination events were studied by pollinating excised pistils implanted on 1 % agar medium in Petri dishes (Shivanna and Rangaswamy, 1992). Pollen germination and pollen tube growth were studied using the aniline blue fluorescence method (Shivanna and Rangaswamy, 1992).

Pollinated and unpollinated pistils were fixed in 2·5 % glutaraldehyde-paraformaldehyde prepared in 0·1M cacodylate buffer (Karnowsky, 1965) for 3 h. The fixed material was dehydrated through 2-methoxy ethanol, ethanol, n-propanol and n-butanol. Infiltration and embedding were carried out in glycolmethacrylate monomer mixture (O'Brien and McCully, 1981). Semi-thin (2, 3 and 4 μm) sections were cut with glass knives.

Sections were used to localize various components. The cuticle was localized using 0·02 % auramine O (Heslop-Harrison, 1977), proteins with Coomassie brilliant blue R (Fisher, 1968), insoluble polysaccharides with PAS reagent (McGukin and Mackenzie, 1958), pectins with alcian

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blue (Heslop-Harrison, 1979), and lipids with auramine O (Heslop-Harrison, 1977).

For scanning electron microscopy, pistils were fixed in 2 % glutaraldehyde for 12 h. The fixed material was dehydrated through an ascending series of cold acetone (10–100 % for 10 min each), critical point dried, mounted on aluminum stubs and coated with gold particles and studied in an LEO VP 45 scanning electron microscope.

Natural pollination efficiency was calculated by counting the number of pollen grains on stigmatic lobes ($N = 50$). For this purpose, flowers (2–3 d after anthesis) were brought to the laboratory in plastic screw cap bottles (20 ml) containing absorbent cotton soaked in FAA (5 ml formaldehyde : 5 ml acetic acid : 90 ml 50 % ethanol) fixative. Pistils were deliberately not collected in a liquid fixative to prevent pollen being dislodged from the stigma. The stigmatic lobes were stained with auramine O and observed under the fluorescence microscope; the number of pollen grains (which fluoresced brightly) present on each stigmatic lobe was counted.

To study pollen density in the air, glycerine-coated slides ($N = 78$) were exposed for 24 h on female inflorescences. An area in the plantation was selected in which a palm in the male phase was surrounded by rows of palms in the female phase. The slides were stained with 0·2 % auramine O and observed under the fluorescence microscope with UV illumination. Pollen grains could be clearly distinguished from the debris, and the number of pollen grains cm^{-2} was computed.

Pollen grains were tested for the presence of reserve material. Lipids were localized using a mixture of Sudan III + IV (Dafni, 1992) and starch with I_2KI solution.

Temporal details of weevils visiting female flowers were recorded by continuous observations. The number of weevils visiting freshly opened bunches of female flowers was recorded from 0600 to 1800 h on 2 d. Foraging behaviour and flower handling times were also recorded.

RESULTS

Elaeis guineensis is a monoecious species in which male and female inflorescences are borne alternately in cycles of varying periods. On average, each year an individual palm bears $10 \pm 2{\cdot}5$ male inflorescences and 7 ± 2 female inflorescences (1·4 male : 1 female). Both types of inflorescence are compound spikes. Each female spikelet bears four–14 flowers, which are arranged spirally around the rachis. The centrally positioned spikelets have a greater number of flowers (12–14) than those at the base and apex (four–eight) of the inflorescence. The total number of female flowers in an inflorescence is approx. 900; of these, 150–250 open in a day. The female flowers are sessile. The pistil is columnar and is the most conspicuous part of the flower (Fig. 1A). The pistil and rudimentary androecium are enclosed by six sepaloid perianth lobes (in two whorls of three) enveloped by two bracteoles and an elongated spinuous bract. The style is not clearly defined and extends for 8–10 mm from the ovary, terminating in a fleshy, trilobed stigma. The gymnoecium is tricarpellary and syncarpous and the ovary is superior and trilocular. There are three deep-seated orthotropous ovules, one in each locule. Placentation is axile (see Hartley, 1988).

Anthesis occurs acropetally in both the male and female inflorescences. In any inflorescence all the female flowers open in 3 d and the male flowers in about 4 d. Male flowers open between 0800 and 0930 h and female flowers from 0900–1000 h.

Pistil

The three lobes of the stigma are appressed to one another in the younger stages of pistil development and spread out during the receptive stage. The receptive surface is confined to a narrow linear zone on the adaxial surface of each lobe (Figs 1A and 2A). The receptive surface is papillate and wet, though the amount of exudate is limited. Most of the papillae are unicellular but some are multicellular and many of them are branched (Fig. 1B). During the earlier stages papillae are covered with a cuticle (Fig. 2B). At the receptive stage the cuticle becomes disrupted in places, particularly at the bases of papillae through which the exudate is released. Localization of esterases and phosphatases on the stigma indicated that their activity was maximal at the receptive stage. The non-receptive surface of the stigma lobes is smooth.

A deep longitudinal groove is present along the length of the papillate region of each stigmatic lobe. We termed this a 'stigmatic groove' (Figs 1B, 2C and D). The groove is lined with a clearly defined layer of glandular cells, similar to the canal cells of hollow styles (Figs 1B, 2C and D). Each glandular cell is capped with a thickening (Fig. 2D and E), that stains distinctly with alcian blue and mildly with PAS reagent indicating its predominantly pectic nature. Stigmatic lobes are heavily vascularized; six–18 vascular bundles are present in each lobe around the stigmatic groove.

The three stigmatic lobes converge and the respective grooves also join to form the stylar canal (Figs 1A–E and 2F). The latter is lined with a layer of canal cells (Figs 1C, D and 2F), which are similar to the glandular cells lining the stigmatic grooves. The canal cells do not have a pectinaceous cap on the inner tangential wall but they do have PAS-positive thickenings (Fig. 2F and G). The canal cells and the groove cells lack a cuticle on the inner tangential wall at the receptive stage (Fig. 2C).

The stigmatic groove and the stylar canal are filled with a secretion product containing pectic substances, insoluble polysaccharides and proteins. The peripheral cells of the cortex of the stigma and style accumulate phenolic compounds, oils, lipid globules and raphides. Transverse sections of the pistil show numerous vascular bundles in the stylar cortex.

The upper portion of the stylar canal has three deep grooves corresponding to the three stigmatic lobes. The lower portion of the stylar canal is more or less circular. Interestingly, the canal cells in the lowermost 5–6 mm of the style protrude into the stylar canal in the form of papillae and loosely fill the lumen of the canal (Figs 1E, 2H and 4I). In the lowermost portion of the style, the stylar canal diverges into three narrow canals with papillate canal cells, each leading to a locule of the ovary.

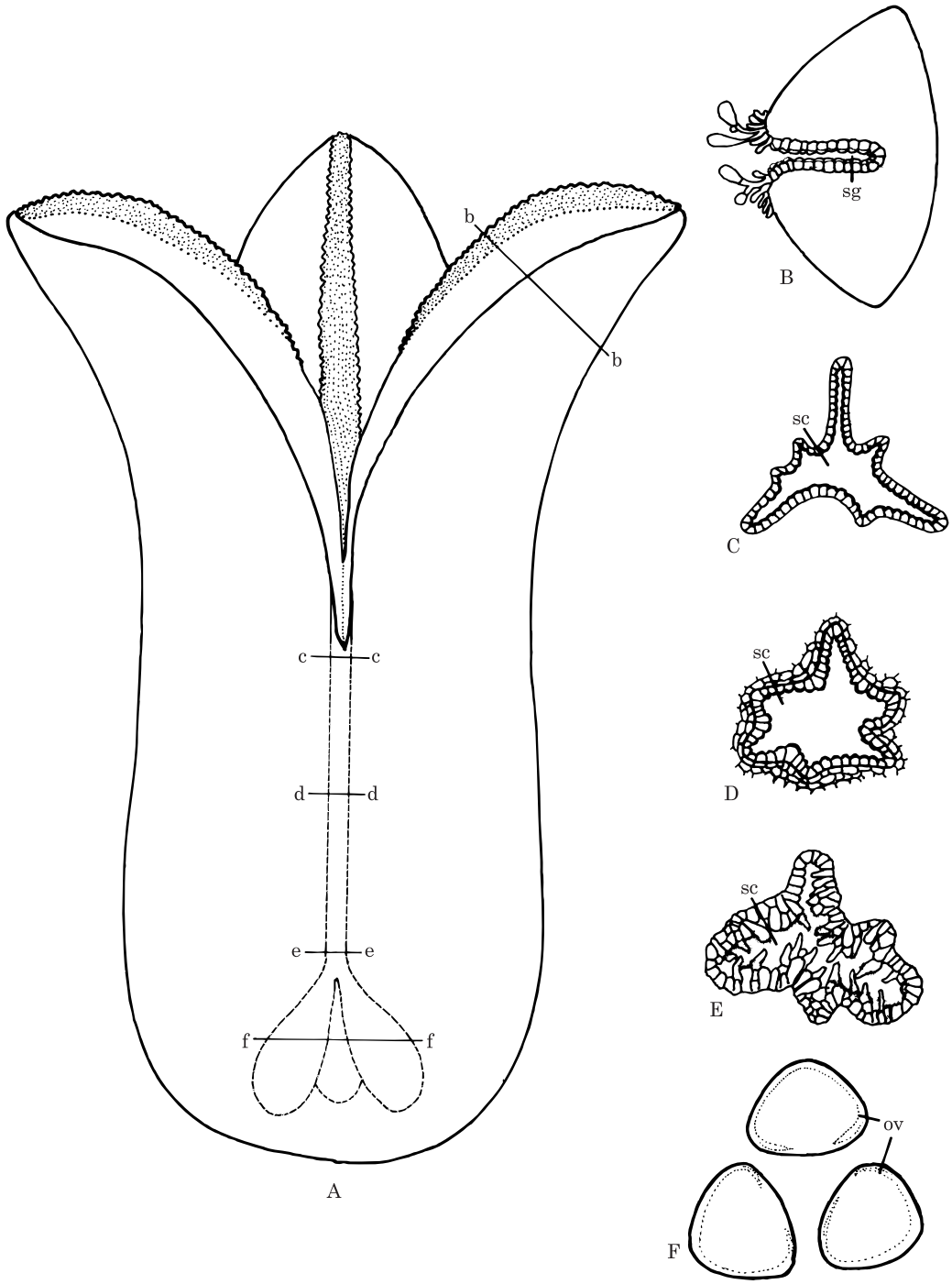

FIG. 1. A, Diagrammatic representation of the pistil showing the three stigmatic lobes, an indistinguishable style and ovary. The dotted region on the adaxial surface of each stigmatic lobe represents the receptive, papillate region. Broken lines in the style and ovary indicate the stylar canal and the locules. B–F, Transverse sections of a stigmatic lobe (B), stylar canal (C–E) and locules (F) taken at the points shown in A. Note that the glandular canal cells in the lower region of the style are papillate. ov, Ovule; sg, stigmatic groove; sc, stylar canal.

Pollination

Pollen grains contain starch and constitute the major food source of weevils, which inhabit the male inflorescences in large numbers (2000–3000 per inflorescence) during the pollen shedding stage. The weevils actively forage in the region of freshly opened male flowers in each spikelet. They do not visit the older parts of the male spikelets which have no pollen remaining.

Although the total number of male flowers in bloom per day is very high (approx. 2500 per inflorescence d^{-1}), competition for pollen grains is always intense. After consuming pollen from one inflorescence weevils search for further male inflorecences on other palm individuals,

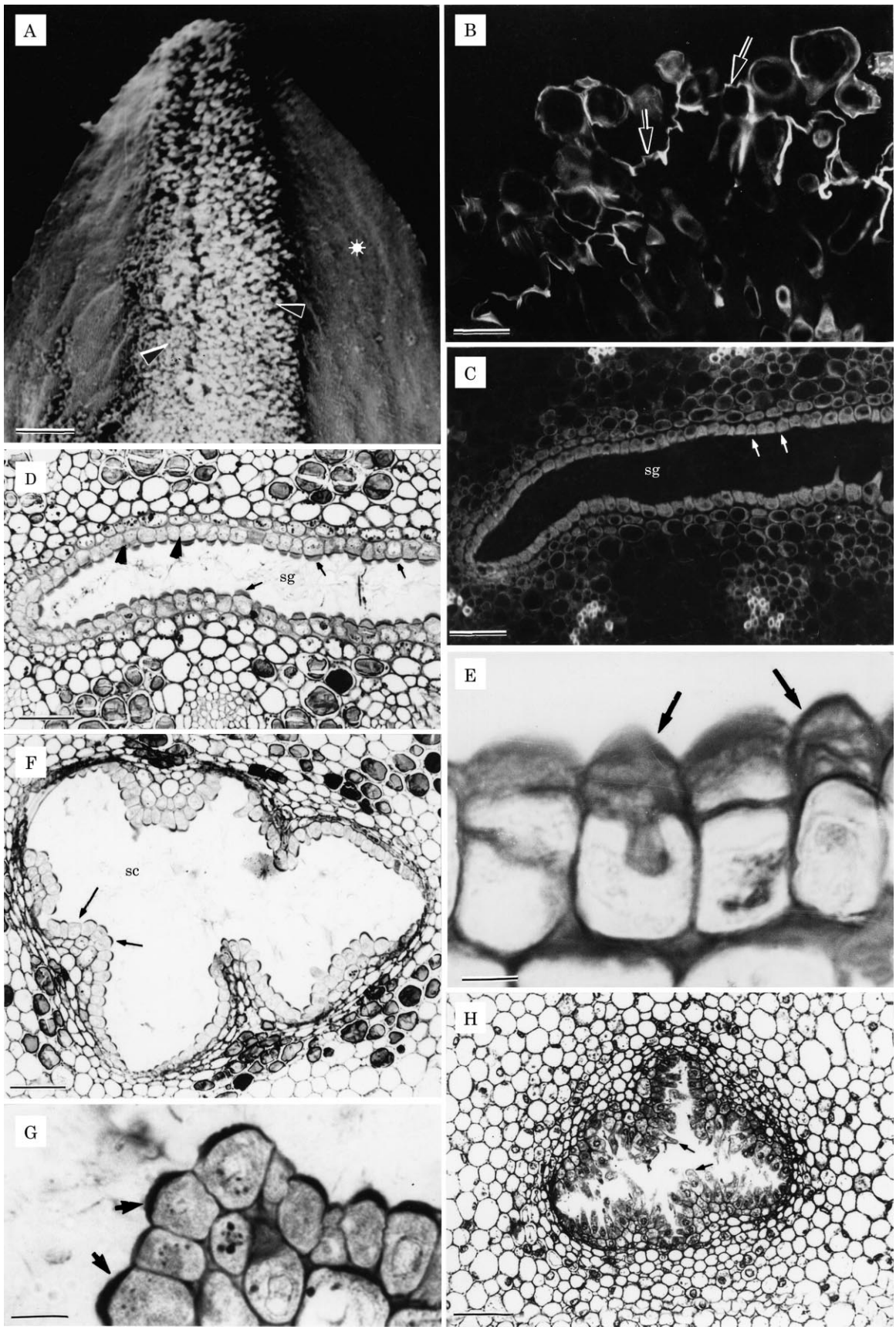
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TABLE 1. *Results of manual pollination of pistils (N = 25 pistils for each stage)*

Developmental stage of the flower	Pollen germination on stigmatic lobes (%)	Extent of pollen tube growth
10–14 h before stigmatic lobes are fully opened	15–26	Confined to stigmatic papillae
Stigmatic lobes fully opened	67–76	In the style
24 h after anthesis	0–13	Confined to stigmatic papillae

Incubation period: 5 h.

which they locate by the intense fennel-like fragrance. Weevils carry numerous pollen grains all over their body. As freshly opened female flowers also emit a similar fennel-like fragrance, weevils also land on receptive female flowers and effect pollination. Lack of rewards in the female flowers reduce the flower handling time by the weevils (3·13 ± 1·28 s per flower). Visitation of weevils to female inflorescences starts around 0700 h and continues until 1500 h (Fig. 3); maximum activity was observed between 1100–1200 h.

Pollination efficiency under natural conditions was 100 %, although on average only eight pollen grains were found per stigma (comprising three lobes). Pollen density in the air was considerably lower (4·83 ± 4 grains cm^{-2}) when the majority of the plants in the plantation were in the female phase. When the male phase dominated, pollen density increased to 35·72 ± 13·12 pollen grains cm^{-2}. The movement of pollen in the air was limited to a distance of about 30 m from the pollen source.

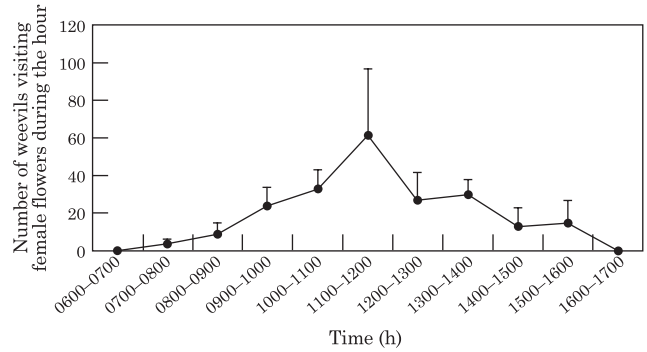


FIG. 3. Temporal details of weevil visits to female inflorescences recorded between 0600 and 1800 h.

Pollen germination and pollen tube growth

The perianth lobes are small and do not show any visible change during floral development. However, the stigmatic lobes, which are appressed to each other in the flower bud, open and spread out for a day exposing the receptive surface. After 24 h, the stigmatic lobes develop anthocyanin. The period of stigma receptivity was determined by studying pollen germination and pollen tube growth following manual pollinations (Table 1). Although some pollen germination was oberved on the stigma when the lobes were partially open, maximum pollen germination was recorded when stigmatic lobes were fully opened and stigmatic exudate was visible. Pollen grains failed to germinate after the stigma lobes developed anthocyanin (24 h after anthesis), indicating the loss of receptivity.

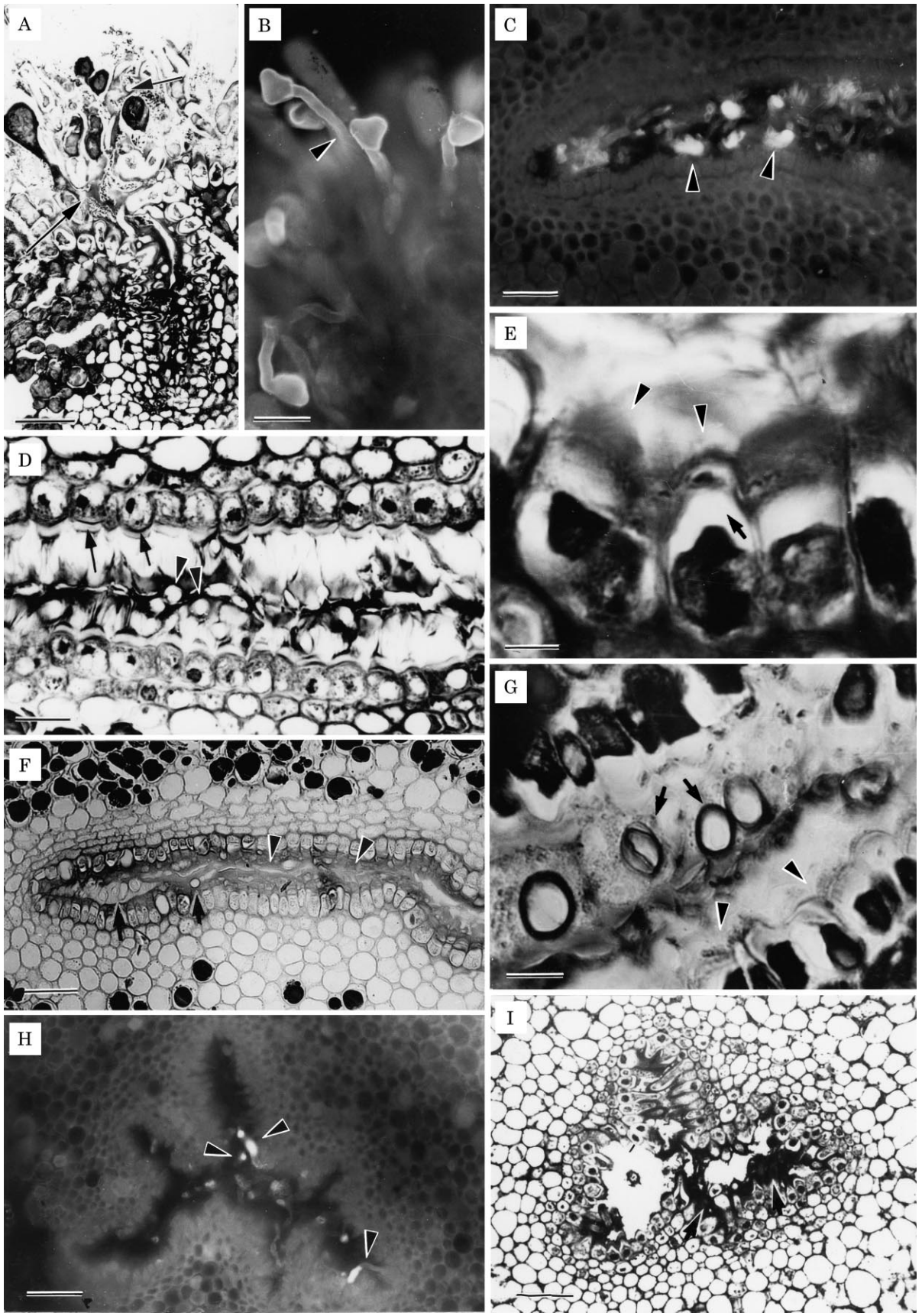
Pollen grains germinate within 2 h after pollination. Pollen tubes grow down the surface of the stigmatic papillae (Fig. 4B) and enter the stigmatic groove (Fig. 4C, D and F), reaching the middle portion of the stigma within 3 h of pollination and entering the style by 5 h after pollination (Fig. 4H). Pollination induces additional exudation from the stigmatic groove. The post-pollination exudate is copious, filling the stigmatic groove (Fig. 4D–G) and reaching the papillate region of the stigma (Fig. 4A). During post-pollination secretion, the pectin-rich cap on the groove cells breaks down (Fig. 4E) and the secretion stains intensely with alcian blue (Fig. 4E and F). Subsequent to pollen tube growth, the glandular cells of the groove become vacuolated and show signs of degeneration (Fig. 4D, E and G). The stylar canal also shows massive post-pollination secretion and vacuolation of canal cells similar to those lining the stigmatic groove. Eighteen hours after pollination, pollen tubes enter the locules of the ovary.

The fruit is a sessile drupe, attaining maturity within 180 d of pollination. Oil starts to accumulate in the mesocarp 140 d after pollination. By the time fruits mature (180 d after pollination), the mesocarp contains mineral crystals and mucilaginous cavities in addition to oil.

DISCUSSION

This is the first comprehensive study of pistil and pollen-pistil interaction in oil palm. The stigma of *Elaeis guineensis* is wet and papillate (Heslop-Harrison and Shivanna, 1977). The three divergent stigmatic lobes and extensive papillate region on each lobe provide a large receptive area for the

FIG. 2. A, Scanning electron micrograph of terminal part of the adaxial surface of a stigmatic lobe showing a papillate receptive area (arrowheads) and smooth non-receptive area (asterisk). Bar = 120 μm. B, Fluorescence micrograph of a portion of a receptive surface of an unpollinated stigma stained with auramine O showing a brightly fluorescing cuticle (arrows) around stigmatic papillae. Bar = 640 μm. C and D, Portions of the stigmatic groove (sg) stained with auramine O (C) or PAS (D). Note the absence of the cuticle on the inner tangential walls of the groove cells (arrows). The groove (sg) is bordered by a well-defined layer of glandular groove cells (arrowheads in D) and the latter have caps on the inner tangential wall (arrows). Bars = 640 μm. E, Groove cells at a higher magnification stained with PAS showing the cap lightly stained for polysaccharides (arrows). Bar = 60 μm. F, Transverse section of the stylar canal (sc) in the mid stylar region showing canal cells (arrows). Bar = 320 μm. G, A portion of F showing densely stained PAS-positive thickenings (arrows) on the inner tangential wall (inset). Bar = 170 μm. H, Transverse section of the lower region of a stylar canal. Canal cells are papillate (arrows) and loosely fill the canal. Bar = 640 μm.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receipt of airborne pollen grains. Receptivity of the stigma is associated with opening of the stigmatic lobes and secretion of a limited amount of exudate. As in other wet-papillate systems, the papillae of younger stigmas are covered with a cuticle. At the time of receptivity the cuticle-pellicle layer shows disruption through which the limited amount of exudate is released onto the stigmatic surface.

The wet-papillate stigma of oil palm shows distinct differences when compared to other species with wet stigmas. The papillate region of each stigmatic lobe leads to a well-defined longitudinal groove, the structure of which is comparable to the stylar canal. The presence of a stigmatic groove is unique to oil palm. In other species with hollow styles, the papillate zone of the stigma continues until it becomes continuous with the stylar canal. The stigmatic groove mentioned in *Rhododendron* (Palser *et al*., 1992) is dissimilar to the structures seen in oil palm. In *Rhododendron*, the grooves represent depressions in the stigmatic surface; structurally, the surfaces of these grooves are similar to other parts of the stigma and do not exhibit the specialization seen in the oil palm stigma. Anatomical details of the stigma have not yet been described for any other palm. However, Uhl and Moore (1971) have presented transverse sections of the stigma of several species of Arecaceae that show a furrow comparable to the stigmatic groove of oil palm indicating that this may be a general feature of this family.

Post-pollination secretion of the stigmatic exudate has been reported in many species such as *Acacia* spp. (Kenrick and Knox, 1981; Marginson *et al*., 1985), watermelon (Sedgley and Scholefield, 1980) and *Annona squamosa* (Vithanage, 1984). Post-pollination secretion has been suggested to facilitate adequate pollen germination (Sedgley and Scholefield, 1980; Vithanage, 1984). In oil palm, post-pollination secretion is largely confined to the stigmatic groove and stylar canal with a little on the surface of the stigma. Most of the post-pollination secretion in the stigmatic groove derives from the breakdown of pectinaceous caps of the groove cells. Post-pollination secretion obviously provides additional nutrients. Thus, in oil palm, post-pollination secretion appears to be an adaptation to permit pollen tube growth rather than pollen germination.

Caps similar to those present on groove cells have been reported in the stigmatic papillae of some distylous species of *Linum* (Dulberger, 1974). However, these caps do not break down following pollination.

The stylar canal is smooth for most of its length. However, in the lowermost 4–5 mm the canal cells become papillate and loosely fill the lumen. Pollen tubes come into greater contact with the papillae during their growth in this region compared to the upper region of the style. The significance of this papillate region of the stylar canal during pollen-pistil interactions is not clear. Such papillar outgrowths in the lower part of the style have been reported in a few other hollow-styled species such as *Crotalaria* (Malti and Shivanna, 1984), *Arachis* (Lakshmi and Shivanna, 1985) and *Acer* (Peck and Larsten, 1991). In many hollow-styled self-incompatible species such as *Hemerocallis*, *Annona*, *Gasteria* and *Lilium* (see Shivanna and Johri, 1985), self-pollen tubes are inhibited in the lower part of the style or the ovary whereas in solid-styled taxa they are arrested on the stigma or in the style. Based on previous reports, Brewbaker (1957) suggested that intimate contact between pollen tubes and the cells of the transmitting tissue is necessary for effective inhibition of incompatible pollen tubes. As such an intimate contact cannot be established in the stylar region in hollow-styled species, inhibition is delayed until pollen tubes reach the ovary. The lower part of the style with papillate canal cells permits such an intimate contact between the pollen tubes and the canal cells in hollow-styled systems. Therefore, it is possible that the papillate region of the style may screen pollen tubes for self- or interspecific incompatibility.

Oil palm is anemophyllous as well as entomophyllous, although the latter is more prevalent and effective. Rapid consumption of pollen grains by thousands of weevils leads to exploration of other trees for further rewards. The similar fragrance of the male and female inflorescences acts as an attractant to weevils. However, olfactory guidance to female flowers results in pollination by deceit as rewards for weevils are lacking. Pollination by deceit is common, for example in *Myristica insipida* (Armstrong, 1997) and is widespread among taxa with unisexual flowers in which visual or olfactory guides in the non-rewarding female flowers mimic those in the rewarding male flowers.

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FIG. 4. A, Transverse section of part of the pollinated stigmatic lobe in the papillate region stained with toluidine blue O, showing profuse exudation after pollination (arrows). Bar = 640 μm. B, Fluorescence micrograph of a pollinated stigma stained with aniline blue to show pollen germination and pollen tube growth along the papillae (arrowhead). Bar = 640 μm. C, Fluorescence micrograph of a portion of the stigmatic groove 6 h after pollination, stained with aniline blue, showing brightly fluorescing pollen tubes (arrowheads). Bar = 640 μm. D, Transverse section of the stigmatic groove 8 h after pollination stained with toluidine blue O. Glandular cells (arrows) of the groove show massive exudation. Note that the pollen tubes (arrowheads) are growing through the mucilaginous secretion. Bar = 170 μm. E, As for D. The magnified groove cells show vacuolation (arrow) and breakdown of the pectinaceous cap (arrowheads). Bar = 60 μm. F, As for D but stained with alcian blue to show the pectic nature of the post-pollination secretion (arrowheads). Arrows show pollen tubes. Bar = 640 μm. G, Pollen tubes (arrows) in transverse section amidst post-pollination secretion. Pectinaceous cap has loosened (arrowheads) and filled most of the cavity. Bar = 60 μm. H, Fluorescence micrograph of a transverse section of the stylar canal showing pollen tubes (arrowheads) 8 h after pollination. Bar = 320 μm. I, Transverse section of the stylar canal just above the ovary, showing secretion (arrowheads) from the glandular papillae. Bar = 640 μm.

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