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Intrinsic and extrinsic factors affecting pollination and fruit productivity in teak (*Tectona grandis* Linn.f.)

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Abstract

The intrinsic and extrinsic factors controlling pollination and fruit productivity in teak (*Tectona grandis* Linn.f.) have been studied in detail in Kerala, India. Though clonal seed orchard establishment has progressed very well in the country, low fruit productivity has hampered the teak improvement programmes to a great extent. The field studies as well as laboratory experiments led to the conclusions that inadequate pollinator activity, low pollen-ovule ratio, self-incompatibility and fruit abortion due to dominance effect of floral and fungal infection are the main causes for low fruit productivity in teak.

Key words: Teak, reproductive biology, fruiting potential, fruit abortion, self incompatibility, factors affecting fruiting, fruit productivity

Introduction

Teak (*Tectona grandis* Linn.f.) is one of the most valuable tropical timber species naturally grown in a number of countries of South-East Asia. Due to its unique wood properties, it also has been widely planted outside its natural range. Today it is of major importance in many plantation programmes throughout the tropics. Teak, being highly adapted to a wide range of climatic and edaphic conditions, is preferred for large scale plantation programmes in India. Teak improvement programmes were started in India during early sixties and through these programmes seed production areas and seed orchards were established through out the teak growing states in India. Open pollinated seeds from these stands are expected to produce high yielding progenies but the low seed production compared to the number of flowers has shattered the expectations of the teak breeders. Though thousands of flowers are produced, less than 1 percent turn to mature fruits, causing shortage of good quality seeds. As a result, the forest managers are forced to raise planting materials from whatever seeds available. In such a situation the breeding programmes will become a futile exercise.

Low seed production in teak has promoted several studies on the reproductive biology of teak [1-9]. Teak was reported to be an insect pollinated species with high degree of self incompatibility based on the studies in Thailand [1, 2]. They also observed intra tree flight as the habitual nature of these insects resulting in geitonogomy or selfing. In Kerala 17 species of insects were reported to visit teak flowers [4]. The low fruit and seed set is attributed to insufficient number of pollinators, insect attack, rain damage and premature fruit abortion due to unknown physiological reasons [2, 10, 11].

Understanding the processes of pollination, fertilization, embryo and seed development, fruit maturation and fruit abortion may reveal the reasons for low fruit productivity. Though a number of workers studied the breeding system in teak, the studies were not complete. Hence, this study was initiated to gather information on the factors affecting pollination of teak and for controlling or boosting pollination and thereby increasing the fruit productivity in seed stands and seed orchards.

Materials and methods

The present study was mainly conducted in the Kerala Forest Research Institute Campus, Peechi, Thrissur District. In addition, observations were taken on the percentage of fruiting and fruit abortion from various forest divisions in Kerala.

Percentage of fruit and seed setting : Ten teak trees were selected and ten inflorescences from each tree were observed for the number of buds, flowers and fruits produced to get an idea of the percentage of fruit setting. In order to study the position effect of flowers on fruit setting three inflorescences from each of the four trees were observed. The pooled data on the number of fruits developed at each position was subjected to analysis of variance and mean comparison test (Duncan's Multiple Range Test) was also carried out. Thirty fruits per tree were cut open and observed for number of seeds developed.

Flower opening, anthesis, pollen load on the stigma and stigma receptivity : The inflorescences in the trees were observed at various intervals to collect the data on time of flower opening, anthesis, falling of flowers and other such floral activities. The pollen grains at various intervals were collected and tested for germination and viability in 14 per cent Sucrose solution [3]. Stigma receptivity at intervals was tested by staining with 1 per cent aqueous solution of Nile blue sulphate and warming in 1% acetic acid. The stigma receptivity was tested from 6 am to 4 pm with an interval of 2 hrs, for which 10 flowers each from 1st, 2nd, 3rd and 4th order branching of the inflorescences were collected. The staining of lipids on the stigmatic surface indicates the stigma receptivity. In order to find out whether enough pollination occurs naturally, the pollen load was estimated during rainy and sunny days by observing the stigmatic surface at the end of the day.

Pollination studies : Artificial pollination studies were conducted to get an idea of the type of mating system. Ladders and towers were used to get an access to the flowering branches.

i) *Natural mode of pollination*: A simple experiment was conducted to assess the role of insect foragers in pollination where three types of inflorescences were kept under observation. a) A few inflorescences were covered with nylon nets thereby preventing the entry of insects. b) Some of the inflorescences with emasculated flowers were kept open for natural pollination. c) Some inflorescences were kept open for natural pollination where the flowers are not emasculated. At the end of the day, 15 stigmas were excised from these three types of flowers to observe the pollination success and pollen load. This was done in order to find out whether insects are inevitable for pollination and for setting of seeds.

ii) *Artificial self pollination*: The flowers were emasculated and dusted with pollen of the same tree at peak pollination time in order to find out whether teak prefers self pollination.

iii) *Artificial cross pollination*: The flowers were emasculated before anthesis and the stigmas were dusted with pollen from other trees to find out the result of cross pollination.

Pollen tube growth in self and cross pollinated flowers : The style and stigma from some of the self and cross pollinated flowers were collected at various time intervals up to 24 hours from pollination for studying the *in vivo* pollen tube germination using fluorescence microscopy. Staining was done with Aniline blue [12]. Pollinated flowers were excised and pistils were fixed in acetic alcohol and then stored in 70 per cent alcohol. They were transferred to 4N Sodium hydroxide, a clearing agent, for overnight. The cleared pistils were then rinsed with double distilled water and kept in decolourised Aniline blue for overnight. The stained pistils were then washed in water and mounted in glycerine. The specimens were observed under fluorescence microscope for pollen tube growth.

Results and discussion

Flowering mainly occurs during rainy season though a few trees erratically flower here and there during summer. In Kerala, peak flowering season is June to August. In other countries also flowering is during rainy season as reported from Thailand [7], Indonesia [6] and Mozambique [8]. This shows that teak flowers during rainy season and fruits mature in 6-8 months during dry period.

The number of inflorescences vary from tree to tree and an inflorescence lasts about one month. The flowers have a short life of 12±1 hr (6 am to 6 pm) after which the petals and stamens fall leaving the calyx and style for some more time. In an inflorescence flowers are in four maturity age groups; flowers at first order branching (P_1), second order branching (P_2), third order branching (P_3) and fourth order branching (P_4) (Fig. 1). Units of 15 flowers are arranged as compound dichasial cyme. They are morphologically similar except in the size of the flower and the stigma lobes in P_3 and P_4 positions.

Regarding the function, the pollen viability and stigma receptivity are almost same in all types.

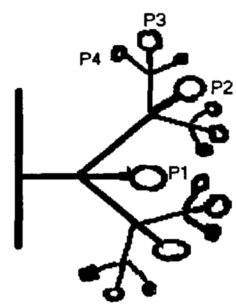

Fig. 1 Position of flowers (P_1, P_2, P_3 and P_4) in a portion of the teak inflorescence

Nectar was produced in the lower half of the corolla tube during early morning hours to afternoon. Pollen was also present in relatively small quantity during morning hours. 95 per cent of the pollen grains were found to be viable.

Local weather has a profound influence on pollination. Continuous rain has been seen to delay the anther dehiscence and stigma receptivity. Periodic drizzles also limit insect visit and foraging activity. During sunny days the pollen load varied from 1-17 while on rainy days it was around 1-2.

Position effect of flowers on fruiting : The statistical analysis of the total fruits produced at different flower positions in the inflorescence revealed that the four positions, irrespective of the trees and inflorescence, differed significantly ($p < 0.01$). Of all the positions, the P_1 position differed significantly from the P_2, P_3 and P_4 positions (Table 1). The third and fourth positions did not differ significantly. The number of flowers in the P_1, P_2, P_3 and P_4 positions are in the ratio of 1:2:4:8 respectively. Even though the number of flowers are far less than the other positions, fruit setting was highest in the P_1 position followed by second. It is clearly seen that the flowers at P_3 and P_4 are less productive than the flowers at the other two positions. The flowers in P_1 position mature first, then P_2, P_3 and P_4 respectively. Many of the P_4 buds do not normally open. Fruits initiated early in the infloreseences are known to have a lower probability of aborting than the fruits initiated late [13]. There was an opinion that large inflorescences are not for production of more fruits but to remain on the male side or more pollen donating side [14]. In teak the later opening flowers in the 3rd and 4th order (P_3 and P_4 flowers) are not producing much seeds though their pollen grains are viable and stigma receptive. Hence, these flowers must be for pollen donation.

Table 1. Percentage of fruit setting at different flower positions in teak

Position	P_1	P_2	P_3	P_4
% of fruit setting	78.25^a	43.08^b	18.25^c	4.42^c

*The values superscribed by the same letter are in the same group

Pollinating agents : It is observed that 80 per cent of the total flowers covered with nylon nets did not receive even a single pollen grain (Table 2) and hence, it is clear that insects are necessary for pollination. However, 20 per cent were self pollinated which might be due to the natural shaking of branches. In open and normal (un-emasculated) inflorescence more than 87 per cent flowers were pollinated while in open and emasculated inflorescences slightly less number of flowers (77%) were pollinated that also with very low pollen load. This shows that a small percentage of flowers are generally pollinated by pollen from the same inflorescence.

The insect activity increased from the morning hours as the temperature increased, till noon. Then it gradually decreased. The maximum active time was from 9 to 12 noon. Various orders of insects include Hymenoptera, Diptera, Coleoptera, Lepidoptera, Hemiptera and Thysanoptera. Of the variety of species represented, the dominant one was from Hymenoptera. These include solitary bees and wasps. The Hymenopteran group of insects were identified as the potential pollinators. There were a variety of insects visiting the trees and most of them spent their time among the inflorescences of a single tree. The only exceptions were bigger wasps which moved very fast among the inflorescences of a single tree as well as to the adjacent trees. Though bees are known pollinators of agricultural crops and other tree crops, their numbers were very few on teak inflorescence. Rainy conditions that dominate during flowering time of teak also brought down the insect activity in general and the role of insects in cross pollination.

Table 2. Insects as pollinating agents in teak

Type of inflorescence	Average number of pollen grains on stigma	Percentage of stigmas pollinated
Inflorescences covered with nylon nets	3	20
Inflorescences open and not emasculated	9	87
Inflorescences open and emasculated	2.9	77

Of the 17 species of insect visitors, reported earlier, to visit teak flowers 13 were hymenopterans, two dipterans and other two were lepidopterans [4]. They have also noted that the hymenopterans particularly the solitary bees, *Prosopsis pratensis, Allodape marginate* and *Halictus* sp., to be the most potential pollinators.

Honey bees are established pollinators in agricultural and horticultural crops and in a variety of tree species. However, only few of these bees were found to visit teak inflorescences. During this study a number of bees were observed to visit the inflorescences. The dominant one was the sting less bee (*Apis florae* Fabr.) followed by *Apis mellifera* Linn., *Apis indica* Fabr., and two species of solitary bees, *Anthophora zonata* (Linn.), and *A. niveo-cincta* Smith. These bees, particularly the solitary bees, carried a load of pollen on the under side of their abdomen and hind legs. They were found to be very active, visiting several inflorescences on the same as well as on different trees in a short time. Most of the bees except *A. mellifera* were present only in small numbers. Although a few colonies of domesticated bees (*Apis indica*) were kept in the vicinity of the trees under observation, no major increase in the activity of honey bees was observed. Probably the bees might have gone to other nectar sources in the area. Hymenopterans in general play a vital role in teak pollination. The main pollinators are some solitary bees like *Halictus tectonae* Narendran and Jobiraj and Wasps.

Pollen load : Pollen load and number of stigmas pollinated vary and it can be seen that during early flowering season when only few trees were in flower, many of the flowers were not pollinated. However, after 2nd week of March more than 80 per cent flowers were pollinated (Table 3). During peak flowering season on sunny days around 95 per cent flowers were found to be pollinated with an average pollen load of 8.25 while on rainy days only 45 per cent were found to be pollinated that also with low pollen load of 1.9. This was because of the low insect activity during heavy rain.

Stigma receptivity : Stigma receptivity started after 8 am and was highly receptive by 12 noon, then slowly the receptivity is lost. The stigmatic secretions reportedly contain lipids, amino acids and perhaps sugars. The lipids are stained blue with Nile blue sulphate. The best colouration was seen from 10 to 2pm, which is the stigma receptivity period. Tangmitcharoen and Owens [7] also reported 11am to 1pm as the most receptive period. Stigma receptivity was expressed similarly by flowers at all the positions.

Table 3. Percentage of stigmas pollinated and the pollen load in teak

Time of observation	3rd week of February	2nd week of March	3rd week of March	4th week of March	1st week of April	July sunny day with intermittent showers	July rainy days
% of stigmas pollinated	65	53	80	80	94	95	45
Average number of pollen grains on stigma	3	3	6	4	9	8.25	1.95

Pollen tube growth in self and cross pollinated flowers : Both cross pollinated and self pollinated pistils were subjected to fluorescent microscopy. The pollen germination and stigma penetration occurred within 45 minutes of pollination. The pollen tubes were seen in the stylar region by 1 hour. There was no inhibition of pollen tubes growing at the stylar region in both the cases. The entry of pollen tubes into the ovules through micropyle occurred within 5-6 hours. In cross pollinated ones there was no obstacle for the entry of pollen tubes into ovules (Fig. 2) while, in self pollinated ones the pollen tubes coiled round the ovary region failing to make an entry (Fig. 3a). In few cases, at the late season, pollen tubes succeeded to enter the ovule after breaking the self incompatibility barrier (Fig. 3b). Hence, teak must have a late acting gametophytic self incompatibility as also reported by Tangmitcharoen and Owens [7]. They also noted pollen tube abnormalities in 20 per cent of the self pollinated flowers. From this it can be seen that teak prefers cross pollination and a certain percentage of self incompatibility is prevalent. Index of self incompatibility (ISI) estimated following the method by Zapata and Arroyo [15] based on artificial self and cross pollination studies showed that this species is partially self incompatible with a value of 0.4.

Artificial self and cross pollination : The percentage of fruit setting in self pollinated and cross pollinated flowers varied much (Table 4).

Table 4. Fruit set in artificial self and cross pollinated flowers in teak

Period after pollination	% of fruiting in open polli-nation	% of fruiting in artificial self polli-nation	% of fruiting in cross polli-nation	% of fruits aborted in selfed fruits	% of fruits aborted in cross pollinated fruits
2 weeks		26	56		
1 month		16	34		
2 months		12	22		
3 months		6	12		
4 months		4	10	85%	82%
$4^{1}/_{2}$ months	1	4	10		

Fertilized ovules were counted after two weeks because some unfertilized ovules also will be retained up to 10 days. While 56 per cent of the cross pollinated flowers were fertilized, only 26 per cent were fertilized out of the total self pollinated flowers.

Fruit abortion : It was found that 85 per cent of the selfed fruits and 82 per cent of the cross pollinated fruits aborted with in 4 months. Palupi and Owens [6] were of the opinion that fruit set depends on food resources and scarcity of food resources leads to fruit abortion. It was also suggested that there is a tendency for fixed abortion providing opportunity for selection at zygotic level either through competition among embryos or by direct control from the maternal plant [16]. Production and nutrient dynamics of reproductive components of teak in the dry tropics was studied by Karmacharya and Singh [17]. Based on a study of 14 to 30 year old teak tree stands in the Chakia Range (Varanasi Forest Division, Uttar Pradesh), they could observe that flower production per tree was positively related to tree size and that only about 0.5-0.7 per cent of the flowers developed into fruits. Immature fruit abscission amounted to 34 and 58 per cent of the total number of fruits. In both stands it was seen that relatively greater amounts of dry matter and nutrients were allocated to reproductive parts in September than in other months. Towards the end of the fruit maturation period, considerable nutrient re-absorption occurred where more than 90 per cent of the nutrients, accumulated in the peduncle, were utilized.

There was also an opinion that the fruit abortion may be due to dominance hierarchy generated among flowers and fruits within an inflorescence as a consequence of ontogenetic difference by which the later developed fruits abort due to shortage of food resources or due to the inhibitory chemicals produced by the dominant fruits [18, 19]. In *Dalbergia sissoo* [20] and *Syzygium cuminii* [21] the dominant fruits produce a diffusate containing a chemical, which inhibited the growth of subordinate ovules leading to abortion.

A good percentage of fruit fall was also due to the fungal infection caused by *Phomopsis* sp. and *Collitotrichum* sp. [22]. A survey conducted at various teak plantations in Kerala showed that the seed infection caused by *Phomopsis* sp. is widely distributed in the state. Trees in dry zones like Chinnar also had fungal infections causing shedding of a large percentage of flowers and fruits. Fungicidal treatments using Mancozeb 75 per cent QP (Indofil M45) @ 0.25 per cent conc. given during the early budding stage till maturing of fruits controlled the infection.

By natural pollination, only about 1 per cent fruit setting could be observed while through artificial self pollination 4 per cent (on repeating the selfing experiment in the successive years fruiting percentage of 6 per cent and 2.67 per cent could be obtained) and by artificial cross pollination 10 per cent fruiting could be obtained which clearly shows that insufficient pollination is one of the reasons for low fruit productivity as suggested by Hedegart [2] and Tangmitcharoen and Owens [7]. Hedegart [2] reported varying fruiting percentage of 0.2 per cent and 1.3 per cent through natural pollination in different years. Through artificial cross pollination he could get 12 per cent fruiting.

The number of seeds per fruit also varied much. About 33.00 per cent of the total fruits were found to be seedless, 45.67 per cent with one seed, 16.33 per cent with two seeds, 5.33 per cent with three seeds and 0.33 per cent with four seeds. The reason for low seed development must be due to the low pollen-ovule ratio found in many cases. Though 4 ovules were present in each flower, the number of pollen grains on each stigma was found to be less than 4 in many cases.

The intra tree flight observed in teak flower visitors effect in geitonogomy, the genetic equivalent of selfing [1, 2]. Teak trees flower strongly over a period of 3-8 weeks and the flowers have a single day life. Teak has a diversity of flower visitors. Willson and Price [14] and Augspurger [23], while working with *Asclepias* sp. and *Hybanthus prunifolius*, have reported that the mass flowering pattern and the inflorescence display size generally attract a number of insect visitors with diverse species, but end up in restricting the flower visitors to a single tree promoting self pollination and inbreeding. This fact holds true for teak also. For a species under low population and high floral density the pressure of geitonogomy is generally high. Tropical trees generally produce large number of flowers sufficient enough to satisfy the nutritional requirement of the pollinators, there by limiting the circulation of most flower visitors to a single tree effecting selfing [24, 25]. Though teak discourages self fertilization through self incompatibility, a small percentage of selfing occurrs in this species. Artificial cross pollination with control measures to check fungal attack will definitely lead to more fruit productivity though artificial cross pollination is not easy in teak.

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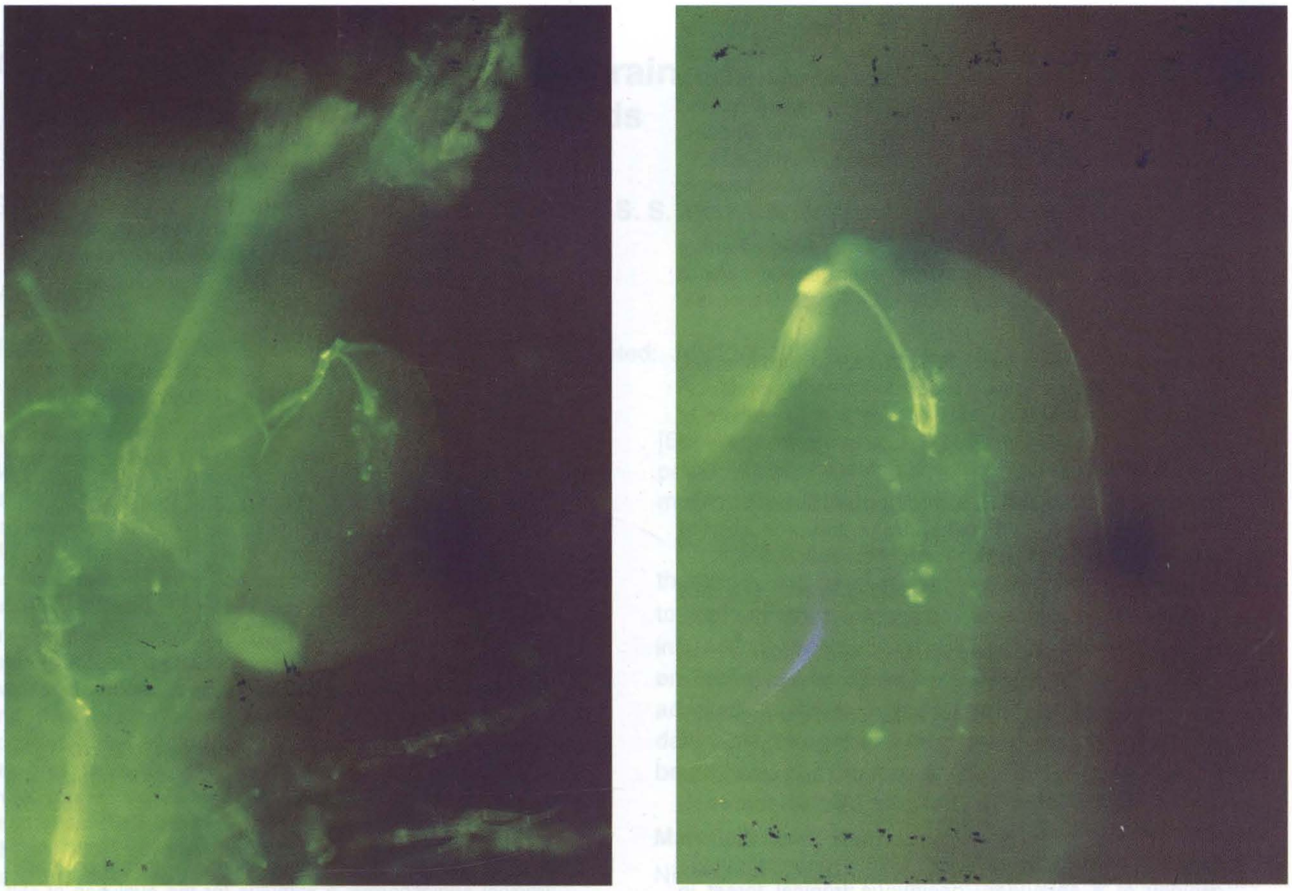

Fig. 2. Pollen tube entry in cross pollinated flower at micropyle region

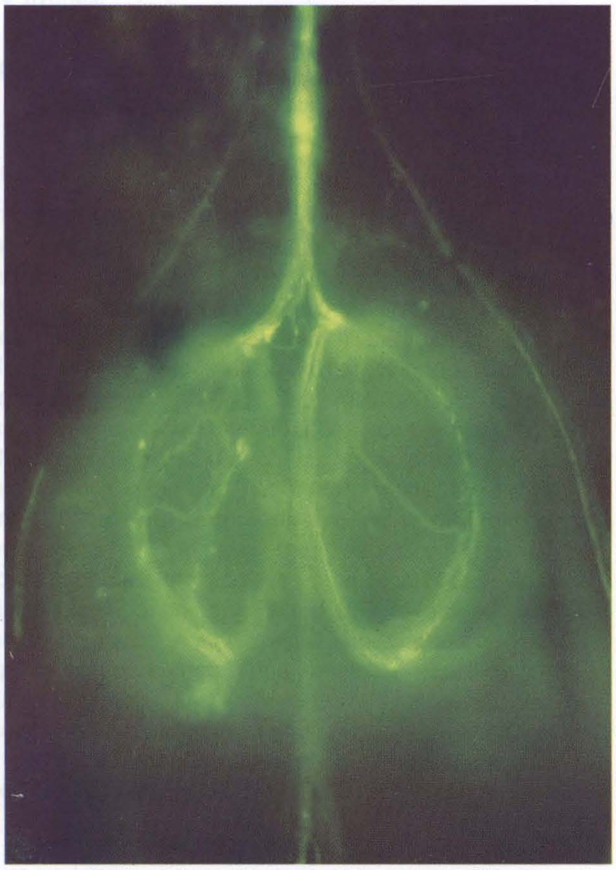

Fig. 3a. Pollen tube coiling round the ovary failing to make an entry in selfing

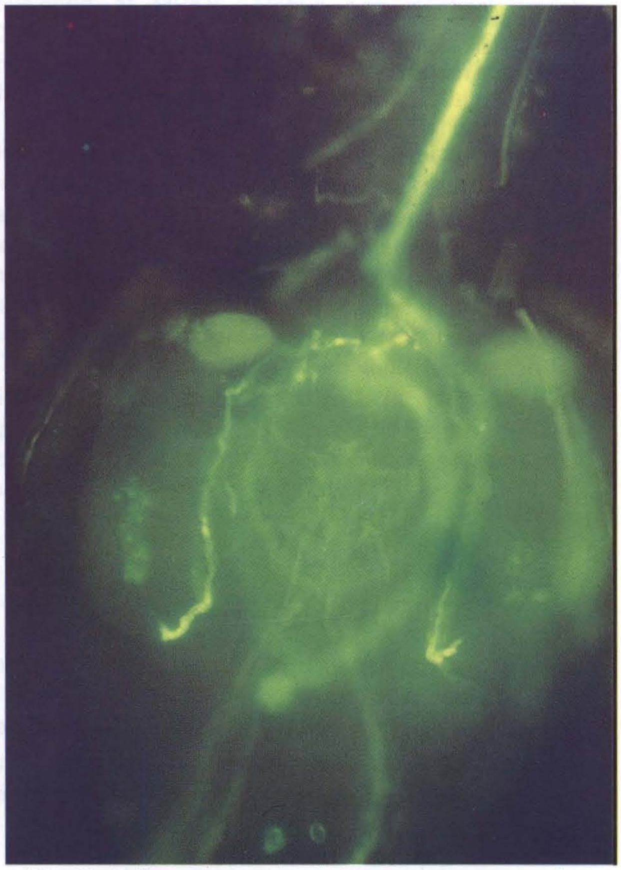

Fig. 3b. Pollen tube entry in selfing at late season after breaking the incompatibility barrier

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