POLLINATION IN THE TROPICS

by Professor John B Free CMG, United Kingdom

Pollination is the transfer of pollen from the anther of a flower to the stigma of the same or another flower. This process begins seed production in flowering plants. In some regions the need for pollination has long been understood: the practices of artificial pollination, and the encouragement of natural pollination originated in the Middle East. Since ancient times humans ensured that female date palms are productive by hand-pollinating them with pollen from male inflorescences. It is a long established procedure for owners of fig groves to introduce capri figs, which although inedible, produce pollen and harbour the tiny wasps that pollinate other fig flowers.

This knowledge of pollination even extended into religious life. An Assyrian Palace relief from 2750 years ago depicts an eagle-headed god who appears to be pollinating a sacred tree with pollen from a fir cone. The bag he is carrying possibly contains more fir cones and pollen. So our subject is not only important to humans, it is a concern of the gods!

In countries with highly mechanised agriculture, the use of bees for pollination has increased greatly during the 20th century and it is now an integral part of crop production. In recent times far less attention has been paid to the pollination of tropical crops. This is partly because other factors, such as inadequate soil, water, and poor soil fertility are also limiting crop production. In these cases pollination as does occur is sufficient to provide for the plant's bearing capacity. With the use of improved cultivars and irrigation, pollination may easily become the limiting factor, leading to increased need for pollinating insects.

Pollination requirements

The effect of pollination on the yield of most crops grown in temperate climates is well-established. There is relatively little information about the pollination of tropical crops. More data is urgently needed, especially as the results of pollination research can be of direct benefit to growers, who can take immediate action without the need for complex equipment, or large-scale investment, and reap an almost immediate reward.

Some flowers self-pollinate without the aid of insect visitors, although their structure indicates that in the evolutionary past they were insect-pollinated. For example, placing bags over flowers (so that insects cannot reach them) of paw paw, sweet pepper, hot pepper and egg plant usually does not decrease fruit set. So growers need not be too concerned about the pollination of these crops: improvement in yield would seem to depend solely upon increasing the bearing capacity of the plant by favourable nutrition and by plant breeding.

Some apparently insect-pollinated flowers are parthenocarpic. Examples are various cultivars of banana and *Citrus*. In contrast, plants traditionally supposed to be wind pollinated may benefit from insect pollination. Thus we now know that the oil palm is primarily insect-pollinated and **not** wind-pollinated as previously supposed.

There are indications that the following tropical crops benefit from insect pollination: allspice, avocado, cashew, coconut, coffee, cotton, lychee, mango, melon, passion fruit, safflower, sunflower, and many varieties of *Citrus* and *Cucurbits*.

It is likely that some (for example safflower, mango, okra, and opium poppy) give only moderately increased yield when pollinated by insects while others (for example cashew and guava) give greatly increased yields. However, more research is needed. The pollination requirements of other crops including tropical legumes, which are beginning to be used in large-scale production, are mostly unknown.

Because of the lack of time and facilities, too many of the studies on tropical crop pollination have been of a preliminary nature only. Careful studies must be instigated to determine:
a) whether fruit or seed set is usually adequate;
b) whether the crops benefit from pollination; and
c) which insects pollinate the flowers.

Does a crop need insect pollination?
A standard method to determine whether a crop benefits from insect pollination is to compare the yields of plants that are grown under three different conditions:
a) covered by nylon screen cages containing honeybee colonies;
b) covered by cages to exclude insects;
c) not caged.

If cages are not available useful information may be obtained by bagging individual flowers or flower heads to exclude pollinating insects. Some of the bagged flowers must be hand-pollinated to find the maximum set possible under these conditions.

Experiments must also determine whether the crops benefit from self- or cross-pollination. Cross-pollination is obviously needed when the sexes are segregated on different plants (for example melon) or by different periods of flowering of the same plant (for example avocado). Cross-pollination may also increase yields of plants that can be self-pollinated.

Cross-pollination can only occur when the insect moves from one plant to another, and this usually happens on only a small proportion of flower visits.

Production of hybrid seed crops on a commercial scale is creating a special need for cross-pollination by insects, and a high population of pollinating insects is needed to carry pollen from rows of male plants to rows of female plants.

Many varieties of fruit tree need cross-pollination. When an insect moves from a tree of a polliniser variety to a tree of a main variety, it pollinates only the first few flowers it visits, so parts of trees adjacent to the polliniser tree get most fruit set. To obtain an even fruit set, orchards should be planned so that the main variety trees are surrounded by polliniser trees.

Availability of pollinating insects
Having considered the need for pollination I wish now to turn to the availability of pollinating insects. Probably humans at first encouraged wild bees and other pollinating insects as primeval forests were cleared, allowing light to penetrate and low growing plant species to multiply.

However in many parts of the world, including the tropics, there is a tendency for populations of wild bees and other pollinating insects to diminish until they are too few for crop pollination. A number of factors have contributed towards this:

1. Intensive cultivation of the land, including the destruction of hedgerows, banks and rough verges has diminished the number of nesting and hibernation sites available;

2. Regular cutting of roadside verges and around field crops and the use of herbicides have destroyed flowering plants that help to provide beneficial insects with food;
3. Use of selective herbicides destroy flowering weeds within crops;
4. Use of insecticides. These are probably the most serious threat to wild pollinators in agricultural areas and provide the greatest deterrent to using honeybees as pollinators.

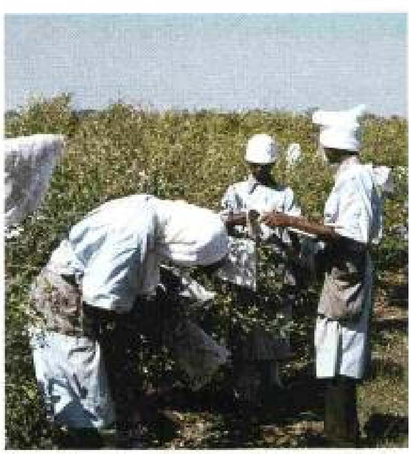
The damage to honeybee colonies differs according to many factors including the insecticide's toxicity, the method and time of day of application, the number of applications, the proportion of foragers visiting the treated crop, the crop and its floral structure, the foraging behaviour of bees on the crop, and the 'drift' of insecticide to other sources of forage.

Too little is known about the toxicity of insecticides to wild bees and honeybees in the tropics, although some information is now being obtained.

Fortunately practices tending to diminish wild bee populations are in general less severe at present in the tropics. But unless care is taken to avoid destroying wild pollinators in tropical countries, pollination will be almost entirely dependent on honeybees. Already, it is supposed that in a number of tropical countries the honeybee bee colonies managed by beekeepers will soon be the major pollinators, although in the past, large areas of vacant bush land, and scattered holdings provided ample nest sites for wild pollinators, including wild honeybees.

Modern agricultural practice not only tends to diminish the numbers of wild pollinators but also tends to increase demand for pollinating insects.

Pollination cages over coffee bushes © JOHN B FREE
Mango flowers bagged and tagged © JOHN B FREE



Mango flowers bagged and tagged © JOHN B FREE

Pollination cages over coffee bushes © JOHN B FREE

Difference between temperate and tropical conditions
Because of different climatic conditions and different insect pollinators it is most unwise to apply findings from temperate countries to tropical ones, or from one hot country to another. For example pollen tube growth is probably faster in the tropics. On the other hand, the tendency for unpollinated flowers to survive longer than pollinated ones is probably greater in temperate regions. Perhaps while the pollen is being transported by insects it becomes desiccated and inviable more quickly in hot countries.

Growers can discover whether their crops are receiving sufficient pollination by hand-pollinating (self- and cross-) a sample of the flowers and comparing their set with flowers left alone.

Research should also determine whether pollination provides advantages in addition to greater seed or fruit yield. Increased pollination can induce a greater proportion of early flowers to set seed, and so give an earlier and more uniform crop, with less loss at harvest.

Pollination can also influence the quality as well as the size of the crop; when pollination is inadequate, small, lopsided, or otherwise misshapen and inferior fruits may be formed.

Wild plants

The pollination needs of many wild plants are unknown. Certainly the pollination of soil enriching and soil stabilising plant species should be encouraged, while the pollination of others such as weeds of agricultural crops should be discouraged. However, it is difficult to decide whether pollination is beneficial or detrimental as far as humans are concerned. Many wild plant species whose fruits and nuts are eaten by birds and small mammals may need pollination; if such food were not available, perhaps the birds and mammals would turn their attention more to agricultural crops; perhaps on the other hand, such animals would not be able to survive until agricultural produce were available to them. Clearly, we have much to discover.

Increased demand for pollinating insects

In temperate countries the gradual increase in field size has increased pollination need while a crop is flowering, thereby decreasing the ability of the local insect population to pollinate it adequately. The tendency to concentrate particular crops in certain areas intensifies the situation. However when the major crop in an area is not in flower, there may be too little forage. Thus, in temperate countries large-scale monocultures increase the demand for pollination, yet also decrease the populations of wild pollinators, and decrease honey crops from honeybee colonies.

With an increase in mechanisation of farming and accompanying field size, a similar dilemma could arise in the tropics. At present, many countries in the tropics and sub-tropics still have small plantations of a variety of crops, that flower at different times, growing in close proximity.

Moreover in the tropics, flowering of crops is more prolonged and less intensive than in temperate regions. Where growing conditions are favourable, farmers may take two or three harvests from the same plots during a year, and at any one time the same crop species may occur in a sequence of growth stages. Many fruit trees also flower and fruit throughout the year, although more abundantly at certain periods. Therefore, forage for bees is often present at all times, and with prolonged crop flowering, fewer pollinators are needed than for temperate climate crops of equivalent size.

However, with increased monoculture in the tropics, flowering will be more concentrated and large pollinator populations will be needed for shorter periods; this is already happening in some locations with some crops. Furthermore, whereas pollen sources that allow cross-pollination are naturally present in small mixed farms, special provisions for crop pollination may be necessary when there are large areas of a uniform crop.

Types of pollinators

Many species of insects visit the flowers of commercial crops to seek nectar or pollen or both. Probably most transfer a few pollen grains and so contribute to pollination. However, relatively few are consistently good pollinators.

The most efficient pollinators carry plenty of pollen on their bodies, brush against the stigmas of flowers transferring the pollen, visit several flowers of the same species in succession, and move frequently from flower to flower and for crops needing cross-pollination, from plant to plant.

To find the pollinating efficiency of a particular type of insect, flowers in clusters should be bagged while still in the bud stage, and when they have opened the bags removed until they are visited by the insect; they are then bagged and the proportion of visited flowers that produce seed determined.

A crop is sometimes dependent on one or a few local insect species of pollination. For example, thrips are the main pollinators of oil palm in Malaysia, and midges are the main pollinators of cocoa.

Many solitary bees show preferences for particular plant species, and are well adapted to pollinate them. For example, in Jamaica a small solitary bee *Exomnolopsis pulchella* appears to be the sole pollinator of hot pepper, sweet pepper and egg plant, while pigeon pea is visited by large solitary bee (*Megachile* spp).

The pollinator of a particular crop may differ in different areas. In Jamaica, skipper butterflies, are the sole pollinators of papaya; they appear in considerable numbers at dusk, forage on both hermaphrodite and male flowers, and move rapidly from flower to flower and from tree to tree, but in South Africa few insects other than honeybees visit the papaya flowers. Again in Jamaica, many wasps visit cashew and mango flowers, whereas in Kenya they are visited by numerous ants but no wasps.

In contrast other crops are visited by many insect species. Probably most transfer a few pollen grains and some may help pollination. But relatively few are consistently good pollinators.

Some insects fail to pollinate because they are unable to release the flower's pollinating mechanism. For example, many forage insects are too small to depress the keel of various leguminous flowers and can only visit those that have already been tripped. Honeybees find difficultly in obtaining nectar and pollen from some flowers with deep corolla tubes, and sometimes they learn to obtain forage without pollinating.

However, in general the honeybees (*Apis mellifera*, *Apis cerana*, *Apis dorsata* and *Apis florea*) whose bodies are covered by branched hairs are our most valuable pollinators. In particular *Apis mellifera* which occurs in many parts of the world, is active throughout the flowering season, visits and pollinates a large proportion of species, although it is not especially adapted to any of them.

Even where numerous insect pollinators occur, honeybees are often the most important.

In Jamaica, four crops (hot pepper, sweet pepper, egg plant and papaya) that either do not need pollination, or whose yield is not limited by lack of pollination, are visited primarily by insects other than honeybees and wasps, whereas crops that benefit from insect pollination (avocado, cashew, *Citrus* sp, coffee, cotton, cucumber, glycerine, mango, okra, pimento, pumpkin) are mostly visited by honeybees and wasps.

Although honeybees were usually less abundant than wasps, they are more efficient at transporting pollen and in pollinating.

The presence of wasps probably discourages the pollination of coconut. Individual wasps tend to remain and forage intermittently on a single female flower for a long time and attack any other wasp or honeybee that alights on it. For much of the day, each female flower has the same individual wasp on it. Honeybees quickly retreat when threatened, although in the absence of wasps, they move readily between flowers and are valuable pollinators. Because the wasps' behaviour is detrimental to pollination, their colonies near coconut plantations should be destroyed.

Providing pollinating insects

Now to consider ways of increasing pollination. Efficient pollinating insects can be encouraged by making the habitat more acceptable for nesting and hibernation, or they can be taken to the vicinity of the crop to be pollinated.

For example, recently the midges that pollinate cocoa have been successfully cultured on a variety of media including rotting fruit and stems, and pod husks from cocoa, and they are then released on plantations where midges are too few. The manipulation of fig wasp populations for pollination has of course long been practised.

Solitary bees are especially valuable for pollinating legumes. However for commercial use a species of solitary bee must be gregarious, rapidly increase its population in man-made nests, be easily manipulated and managed, not be subject to uncontrollable parasites and disease, visit the flowers of a commercial crop in preference to those of other crops, and have a peak of activity coinciding with it.

Among other wild bees deserving of study are the social stingless bees of Central and South America, Africa and Asia. Little is know of their forage behaviour, and their potential use as pollinators of commercial crops is largely unexplored. However the situation will soon be rectified. Meanwhile, it is important to conserve them, and ensure that they have adequate nesting sites.

Using honeybees

In contrast the honeybee, *Apis mellifera* and *Apis cerana* have long been kept for honey production, and techniques of managing their colonies already exist so these species can readily be introduced in large numbers as and where required.

Because there are often insufficient wild pollinators, and because experiments have demonstrated the greater yield of many crops when adequately pollinated, the demand for honeybee colonies for pollination has greatly increased during recent years. Indeed, in many countries the potential need already exceeds the supply.

This has led to research into ways of using the honeybee colonies as efficiently as possible to ensure that the maximum population of pollinating bees visit the crop needing pollination

However, in less advanced agricultural societies, the concept of pollination and the pollinating value of the honeybee is still not widely understood. In situations where individual plots are small it is unlikely that growers would appreciate any lack of adequate pollination, and even if they did so, it would not be economical for them to hire colonies. The presence of bees for pollination would depend on the grower keeping their own colonies, even if the bees fail to produce a honey crop, or, in others keeping colonies in the vicinity for honey production. In such circumstances, government subsidies might be necessary to encourage beekeeping in areas, and so to increase the local populations of pollinators.

Where in contrast, the field size is large and the crops concentrated, it should be economically possible for the grower to import colonies for pollination. Indeed, in arid areas, where irrigation is necessary for crop productivity, there may be not alternative sources of forage, and crop production may be entirely dependent on importing honeybee colonies.

The concentration of colonies required for pollination may well over-exploit the floral resources and the beekeeper will need to charge a fee that compensates for the lack of a honey crop. Over-exploitation of an ecosystem by foraging honeybees will have a detrimental effect on the population of native pollinators; honeybees are usually competitively superior than wild pollinators, so the imported honeybee colonies should be removed directly sufficient pollination has been achieved.

Beekeeping for wax or honey will inevitably help pollination. But beekeeping must no longer be considered in the restricted roles of honey and wax production.

Governments may help in ways other than providing training and financial aid to potential beekeepers.

There are of course, difficulties associated with beekeeping for pollination in tropical countries that do not occur in temperate lands. In several regions of Africa and Asia where bees are kept there is dearth of forage during part of the year and colonies become weak or abscond. Such absconding is often regular and apparently depends on rainfall but research is needed on the causal factors and ways to prevent it. Meanwhile it is important for the beekeeper to know the locations of alternative sources of forage to which colonies may be moved during such dearth periods (and to have this and other equipment suitable for migratory beekeeping). Surveys to map the density and distribution of bee plants could be undertaken with great benefit, in many countries.

Breeding to increase pollination

There are large differences in potential yield for many tropical fruit trees and shrubs; this suggests that the most effective long term way of increasing crops will be by selective plant breeding.

In Jamaica, bagging flowers of papaya failed to decrease set; but contrary to expectation, the fruit set of pistallate flowers was greater that that of hermaphrodite flowers and trees with only pistallate flowers carrying more developing fruits than those with hermaphrodite flowers, presumably the physiological state of the female trees permitted them to bear more. If these results prove to be generally true, female trees should be selected by growers and plant breeders in preference to hermaphrodite ones.

It was also found that for akee, cashew and mango there were considerable differences between different varieties of mango trees in the proportion of their hermaphrodite flowers than natural fruits and in the ratio of female to hermaphrodite flowers. In general, the larger the proportion of hermaphrodite flowers the greater the percentage of fruit set.

The early stages of any breeding programme based on yield would automatically select against plants that have a small proportion of hermaphrodite or female flowers and are unattractive to bees.

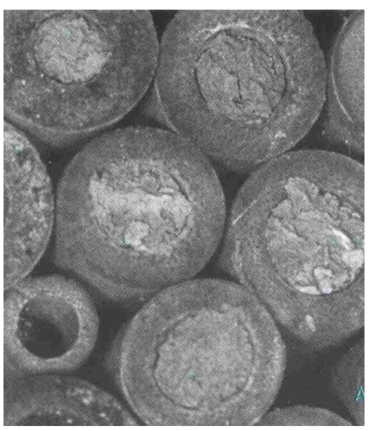
In Kenya, cashew trees that yielded most also had more pollen grains on their stigmas and so were also the most attractive to bees.

Later in a breeding programme it might be necessary to select especially for a high proportion of hermaphrodite or female flower and attractiveness to honeybees. Suitable high yielding cultivars may, of course, need more pollinators, especially if cross-pollination is necessary.

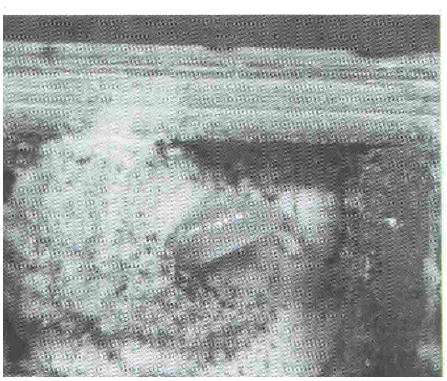
It is satisfying for us to reflect that the finds form fundamental research on the foraging of honeybees and on colony management is applicable wherever in the world there are crops to be pollinated. However intensive and prolonged practical research in the tropics will be necessary before we are able to ensure that tropical crops are being adequately pollinated, and pollination is not the factor limiting seed or fruit production.

More investment in research personnel and equipment is necessary to accelerate progress. Fortunately, many persons in authority now appreciate the importance of maintaining and expanding populations of honeybees, and other useful insects, in order to support the level of fruit, seed, fibre and vegetable oil production to which humans have become accustomed. So hopefully, there will now be increasing support for pollination research and for encouraging beekeeping as an aid to crop pollinating.

Whereas the feeding activities of most insects tend to diminish the amount of plant food available to their succeeding generations, the foraging of pollinating insects increase seed production and hence the amount of forage available to their species.



Bamboo stems holding nests of solitary bees *Osmia rufa*



A bamboo nest split open to show a cell of *Osmia rufa* containing larva and pollen, separated from its neighbour by a mud wall

Ensuring pollination

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By contrast where the field size is large and the crops concentrated, it should be economically possible for the grower to pay beekeepers to provide colonies for pollination. Indeed in arid areas where irrigation is necessary for crop productivity, there may be no alternative sources of forage, and crop production may be entirely dependent on honeybee colonies brought by beekeepers to the crop.

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Because there are often insufficient wild pollinating insects and because experiments have demonstrated the greater yield of many crops when adequately pollinated, the demand for honeybee colonies for pollination has greatly increased during recent years. Indeed, in many countries the need already exceeds the supply.

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Plant breeding to increase production

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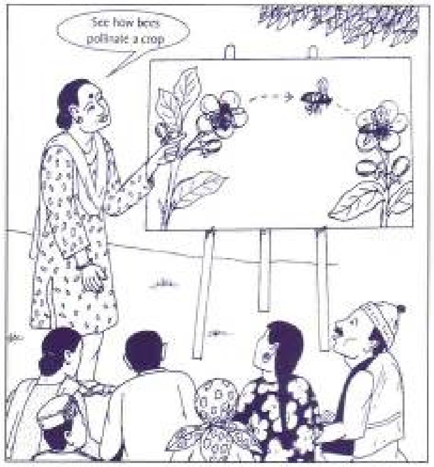
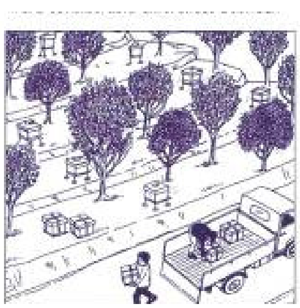
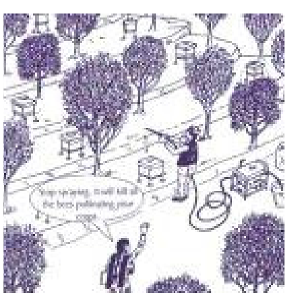


A bee pollinates a crop by transferring pollen from one flower to another of the same or different plant of a crop.



To ensure better pollination of all trees bee hives should be placed evenly in the sunny locations in the orchard and protected from direct wind



To save bees and other insect pollinators from pesticides these should not be sprayed during the flowering period, when the bees and other insect pollinators are visiting the crop

Illustrations are taken from Pollination management of mountain crops through beekeeping*, by Uma Partap.*

EXPLANATION PLEASE!

Cross-pollination: the transfer of pollen from the anther of a flower to the stigma of a flower on another plant of the same species

Parthenocarpic: the ability to produce fruit without fertilisation of the flower

Pollen tube: the tube formed when a pollen grain germinates. The male gametes travel down the tube to the egg.

Self-pollination: the transference of pollen from an anther to a stigma of the same flower, or to the stigmas of flowers on the same plant

Pistillate flowers: flowers containing only pistils (female parts)

Hermaphrodite flowers: flowers that have both pistils and stamens (female and male parts).