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Bees in the pollination of seed crops

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INTRODUCTION

MANY SPECIES of bees are efficient pollinators and bees probably account for 90 per cent or more of all insect pollination. So it is not surprising that much of the new knowledge about pollination of entomophilous crops results from research on bees. Such knowledge is of considerable economic importance, since crops produced with the aid of bee pollination are worth annually many millions of pounds, and at least twenty times the value of the honey and wax obtained from the beehives.

A great deal of research work on the pollination of seed crops has been done in the last ten or twenty years. The original papers are published in many different journals and bulletins, in forty or more languages. Many of the results obtained are, however, accessible to English-speaking readers through books that have recently been published. This review will serve as a guide to these books, as well as giving a more detailed survey of some of the researches on which they are based.

The first of the books, *Pollination of Agricultural Plants*, was published in Moscow in 1956, and it has just been translated into English in the United States Department of Agriculture; copies of the translation are available (ref. 94).

The First International Symposium on Pollination held in 1960, and the Second held in 1964, allowed a vigorous interchange of experience and ideas between entomologists and agronomists in many countries. The Proceedings of each (refs. 81, 82) have been published, as has a full report of the Ninth Pollination Conference in the U.S.A., held in 1970 (ref. 148); this carries the title *The Indispensable Pollinators*. A valuable reference book *Insect Pollination of Crops* by J. B. Free (ref. 47) appeared in the same year. Finally, *Pollination of Seed Crops* was published in 1972 (ref. 34); this is based on publications reported in the journal *Apicultural Abstracts* between 1959 and 1971.

The first book (ref. 94) is a collection of reports by individual Russian scientists on experiments with different crops—many of them legumes grown for seed. At the Pollination Conference (ref. 148) scientists working in the United States similarly reported their findings: legumes are the most important group here, too, but preplanned pollination of cucumber, onion, safflower and cotton, and of such fruits as citrus, blueberry and cranberry, is dealt with extensively.

Free's book (ref. 47) deals systematically with both seed and fruit crops. It describes the flower structure of each, and mechanisms of pollination and fertilisation, and sets out practical ways of ensuring adequate pollination by providing honeybees, or other bees, or other insects such as blowflies. A preliminary section of the book describes the foraging of honeybees, their colony organisation, colony management for pollination, and the utilisation of other bees as pollinators.

In the 1972 book (ref. 34), a third of the 583 publications summarised are on the various legumes. In many countries where experiments have been done, legumes are satisfactorily pollinated by honeybees, provided there is an adequate flying force of them. But lucerne

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(alfalfa) and red clover—especially the tetraploid varieties—have proved more difficult to pollinate, and this has led to interesting new developments which are outlined below. In many countries, studies have been made on identities and populations of wild bees that forage on these and other "difficult" crops, and ways and means have been established for rearing some of the most effective bees in large numbers. For red clover, with its long corolla, long-tongued bumble bees can be used. For lucerne, the commercial use of certain solitary bees has been worked out.

The honeybee is still the most satisfactory all-round pollinator, colonies being brought into the fields during the flowering period. One hazard is that other plants flowering in the neighbourhood may attract the bees away from the crop they are brought in to pollinate: for instance, a field of rape may attract bees away from a field of clover (ref. 57). So allowance must be made for this in deciding how many colonies of bees should be hired. With some crops, one of the chief problems has been the killing of bees by pesticide treatment, but this can be solved if the situation is understood and if proper precautions are then taken.

Various methods of preconditioning honeybees can be useful, and "pollen inserts" which ensure that bees carry pre-selected pollen on their bodies to the flowers, by arranging that they get dusted with the pollen as they leave the hive on each foraging flight (ref. 34). Another successful line of development has been selective breeding of honeybees to provide effective pollination of a specific crop (lucerne); this is summarised later. Similar possibilities for other crops are being explored.

Since the 1950s there has been great expansion of research on the pollination of oilseed and bean crops. Honeybees are among the chief pollinators of many oilseed crops, including rape, sunflower and safflower and the tung tree (ref. 94). A special problem with beans, whose flowers have a long corolla, is that many visiting honeybees collect nectar without pollinating the flowers, by using holes already bitten in the corolla by bumble bees.

Of the beverage, spice, aromatic and other tropical crops (ref. 34), honeybees are shown to be the chief pollinator of coffee (at any rate in Brazil); *Apis florea* of fennel (in India); and thrips of cacao (in Costa Rica). Honeybees increased the yield of pimento in Jamaica; both honeybees and wild bees visit coriander in the U.S.S.R. The part played by honeybees in the production of lavender oil is discussed later.

RED CLOVER AND BUMBLE BEES

Red clover and lucerne (refs. 1, 18, 19, 67) are two important legume crops that are, from the pollination point of view, troublesome.

The main difficulty with the pollination of red clover (*Trifolium pratense*) is that the corolla of the flower is so long that most bees are unable to reach the nectar in it. In Cambridge, Hawkins (ref. 63) found that if the open surface of the nectar was more than 7mm down the corolla, honeybees could not suck the nectar out. He discussed the possibility of breeding bees with a longer tongue or, what was more likely to be effective, plants with a shorter corolla. Bond and Fyfe, also working in Cambridge (ref. 25), had some success with F_1 red clover; they also found that plants of English origin tended to have higher and more accessible nectar, and hence more visits from bees and a greater seed yield, than plants of continental origin. A survey of red clover seed production in twenty European countries (ref. 2), presented to the Second International Symposium in Pollination (ref. 82), showed that the length of the corolla tube of red clover *decreases* from north to south in Europe, whereas the tongue length of honeybees *increases*. This may well account for the relative usefulness of honeybees for pollinating red clover in southern Europe and the difficulties encountered in the north.

These difficulties have been tackled in a number of ways. In Czechoslovakia (ref. 65) it is considered necessary to make the nectar more accessible and attractive, as in second-crop flowering, which honeybees often work quite readily. In Denmark (ref. 58) emphasis has been put on planting trees and bushes to shelter the bees from wind. Experiments in Finland (ref. 132) showed that high soil moisture gave a higher sugar content per head of red clover than low soil moisture. In 1955, a favourable summer, the flower corolla was shorter, and the amount of nectar and its sugar content were distinctly higher, than in 1954 and 1956. Results were as follows:

	1956	*1954*	*1955*
Flowering period (days)	58	29	42
Number of "pollinating bee units" (in 1000s per hectare)	67	180	454
Seed yield (kg/ha, i.e. approx. lb/acre)	86	459	612

The seed yield, like the number of bee units, was about 7 times higher in the best year than in the worst.

The concept of the "pollinating bee unit" takes into account the fact that some bees are more efficient pollinators than others (refs. 36, 107, 126). A honeybee is given the base value of 1 unit; even short-tongued bumble bees such as *Bombus terrestris* rate higher (1·5 units), and long-tongued species (*B. agrorum*, *B. hortorum*, *B. lapidarius* etc.) higher still (2·5 units). These ratings are for "positive" bees which visit the flower in the normal way. A "negative" bee, which gets nectar from a hole that she or some other bee has bitten in the side of the corolla, rates 0 units. (Honeybees cannot bite the holes, but they can and do suck nectar through holes bitten by bumble bees.) Pollen-collecting bees are in general more effective as pollinators than nectar collectors (ref. 46).

We have seen that the problems with red clover pollination are most acute in northern Europe. There, with the long hours of sunshine in midsummer, a long corolla develops, but the local honeybees have shorter tongues than in southern Europe. One obvious answer is the use of certain species of native bumble bees, whose tongues are long enough to reach the nectar. This possibility has been extensively investigated, for example in Belgium (ref. 101), England (refs. 61, 62), Finland (ref. 186), Norway (ref. 107), Poland (ref. 14), Rumania (ref. 8), Sweden (ref. 73), U.S.S.R. (ref. 56), Canada (ref. 68), U.S.A. (ref. 146), New Zealand (ref. 124).

In tetraploid red clover the pollination difficulties are intensified. The tetraploids produce more nectar, but the corolla is longer (ref. 169). The value of bumble bees, and of pollen-collecting honeybees, is even more important than with diploid varieties (ref. 37). In Denmark, for instance, tetraploids attracted only half as many "pollinating bee units" as diploids (ref. 36). In the United States, as in Europe, the more attractive a variety was to bees, the higher was its seed yield (ref. 21).

REARING BUMBLE BEES

The great potential of bumble bees for pollinating red clover (refs. 62, 107) has led to attempts in many countries to *rear* suitable species for taking to the field during flowering. Several methods have been developed. The most straightforward is to seek out nests in spring and transfer them to nesting boxes (Poland, ref. 194; U.S.A., ref. 87). Alternatively empty nesting boxes are put out in likely places in the hope that queens will find them and be sufficiently attracted to occupy them (Denmark, refs. 76, 77; Canada, refs. 71, 72; New Zealand, ref. 134). Queens can be captured in spring and put into the boxes, where they may or may not stay to found a nest (France, ref. 153; Sweden, refs. 51, 52, 60). A final alternative is to capture young queens in autumn, overwinter them in an incubator or suitable greenhouse and, when they become active in spring, to put each into a nesting box (Czechoslovakia, ref. 197; Denmark, refs. 76, 77; Switzerland, ref. 78). In nature each queen winters on her own in a "hibernaculum" she digs out (ref. 5).

General or more extensive accounts of rearing bumble bees have been published in Canada (ref. 147), Czechoslovakia (refs. 113, 196), Denmark (ref. 75) and England (ref. 123). Attention has been paid to the use of the bees in greenhouses, especially in Czechoslovakia (ref. 109) and the Netherlands (ref. 93). Diseases that reduce the success of rearing bumble bees have had to be investigated (ref. 170); parasites include nematodes (refs. 4, 150, 151, 152), mites (ref. 80) and parasitic wasps (ref. 3).

SUMMARY OF POLLINATION METHODS

To summarise, the following are some of the approaches to the problem of getting red clover pollinated, with references to aspects of the subject not dealt with above.

(1) making conditions on the crop suitable for bees to forage
(2) taking honeybee colonies to the crop
(3) removing competing bee forage from the area
(4) using suitable honeybees (ref. 171), especially races with relatively long tongues (72, 173)
(5) making colony conditions suitable (refs. 32, 161, 189)
(6) "training" the bees to the crop by feeding scented syrups (refs. 65, 154, 155)
(7) using other species of bees that have long tongues
(8) making the clover attractive to bees, i.e. secreting more nectar, containing more sugar (ref. 35)
(9) using red clover with a shorter corolla, either second-cut or by plant breeding (refs. 172, 173, 174).

LUCERNE AND GREGARIOUS-NESTING BEES

Lucerne or alfalfa (*Medicago sativa*) presents a different pollination problem. As with red clover, bee pollination is essential for a satisfactory seed yield—in Germany honeybees alone increased the crop 5 times (ref. 156). But honeybees tend to be unwilling to forage on lucerne flowers or, if they do visit them, they contrive to do so without pollinating them because of the behaviour of the flowers themselves (see e.g. ref. 47). The staminal column of the flower (which supports the pollen-bearing anther) is held under pressure within the keel petal by interlocking projections from this petal and the two wing petals. When the tension is released, the staminal column snaps forward against the standard petal, causing the pollen to be dispersed. This process is called "tripping", presumably from a mechanical or electrical analogy.

TRIPPING THE FLOWER

If a bee alights on the keel petal seeking pollen or nectar, her weight presses the petal down and thus trips the flower. The column then strikes the underside of the bee's head at the base of her proboscis, where a small ball of pollen accumulates. Whichever way it is brought about, the tripping process is irreversible, and the staminal column does not return again to the keel petal. A bee visiting a lucerne flower to collect pollen works from the keel petal, bracing herself with her two middle legs on the wing petals; this helps her to force her head into the flower. A nectar forager need only insert her tongue into the flower. Either way, the bee receives a blow from the staminal column as the flower is tripped, and she is trapped momentarily between the column and the standard petal. With experience, a nectar forager learns to avoid being trapped, by working from the side of the flower—and consequently does not pollinate it. A pollen forager can still be an efficient "tripper" even if she learns to avoid being trapped, but the odds are that she will desert lucerne and seek pollen from some other crop.

Few insects other than bees trip lucerne flowers (ref. 24). Attempts at selection of plants for flowers that trip automatically are not rewarding. Methods of mechanical tripping, by beating the plants, dragging ropes across them, or using rubber rollers, are time-consuming and inefficient, and damage the plants (ref. 47). So, as with red clover, the problem must be solved with the aid of bees. Several possibilities have been explored:

(1) plant breeding to make the lucerne more attractive, by increasing the amount of sugar produced, or by producing flowers that do not trap the bees
(2) selective breeding of honeybees to obtain strains that are willing to work lucerne
(3) finding other species of bees that are better adapted to pollinating lucerne.

A detailed study has been made by Pankiw and his colleagues in Canada of the characteristics of lucerne flowers and their seed production (ref. 139). A mutant with only a vestigial corolla (refs. 138, 140) was developed, but this presented difficulties; for instance, a mutant in which certain parts of the flower are missing seems to disorient the bees (ref. 136). Selection for a tubular corolla might be more promising, or for a weak or absent tripping mechanism (as in clover), so that honeybees would not develop the habit of working the flowers from the side. Although in Czechoslovakia "tripping resistance" was not found to influence the frequency of visits by bees (refs. 96, 130), in Canada it was, the bees' preference being correlated with ease of tripping. Their preference was, however, most closely linked with the sugar production of the flowers (ref. 137); the sugar concentration of lucerne nectar has in fact been used successfully as a measure of the pollination obtainable in a lucerne crop (ref. 129). A bee will put up with the unpleasant effect of the tripping if the reward for doing so is high enough.

BREEDING HONEYBEES TO POLLINATE LUCERNE

Meanwhile, a series of experiments was conducted by Mackensen and Nye in the United States, results being published from 1965 to 1969 (refs. 110, 111, 127, 128). These experiments showed that honeybees could be bred to pollinate lucerne. First, it was established (by trapping pollen brought into various hives) that some colonies of honeybees collected a much greater proportion of their pollen from lucerne than other colonies did. Three colonies each of lines collecting high and low percentages of lucerne pollen were selected, and daughter queens from these colonies were instrumentally inseminated (ref. 112) with semen from drones of the same colonies, i.e. from their brothers. Subsequent colonies headed by sister queens proved more alike in the proportion of lucerne pollen they collected than colonies headed by unrelated queens. The tendency to collect (or not to collect) lucerne pollen thus seemed to be inherited. Selections were made through subsequent generations, insemination being done in Louisiana and lucerne trials in Utah. Results were as follows:

Generation	*Percentage of pollen collected that came from lucerne*	
	"High" line	*"Low" line*
2	40	26
3	50	15
4	66	8
5	85	18
6	86	8

The percentages in three separate groups of 5 colonies in the sixth generation were 87·6, 87·5 and 82·2 for the high line, 6·8, 9·0 and 7·6 for the low line. It was concluded that further selection would give no further advantage.

Some other ways of getting honeybees to work lucerne should be mentioned before discussing the use of other bees for the purpose. There must be no other plants in flower that will successfully compete for the bees' visits (refs. 39, 163). Proximity of the colonies to the lucerne field can be important (ref. 106). In large plots in the U.S.A., landmarks that help the bees to find their way are beneficial (ref. 105). Moving colonies to a new site may help to ensure that bees work the area immediately round their hives (ref. 104). In Czechoslovakia switching the position of colonies during the flowering period increased the tripping rate (ref. 95). Experiments in France led to the conclusion that fresh colonies should be brought into the fields several times during the flowering period, so that there is a renewed supply of inexperienced bees; also that a high colony density is needed—up to 15/hectare or 6/acre (ref. 102). In the U.S.S.R. the Caucasian race of honeybees was found to be the most efficient at pollinating lucerne (ref. 164); experiments in other countries have not given such clear-cut results on racial differences.

WILD BEES AS POLLINATORS

The difficulties with honeybees have led to many studies of the wild bees that are attracted by lucerne flowers, and of their relative efficiency as pollinators. Some of the countries where this work has been done are Hungary (refs. 119, 120, 121), Poland (ref. 193), Rumania (refs. 83, 84), U.S.S.R. (refs. 16, 149, 165), Canada (ref. 66), U.S.A. (refs. 26, 114) and New Zealand (ref. 195).

These surveys have shown that some of the bumble bees are useful as lucerne pollinators (refs. 39, 120, 193, 195), but that certain solitary bees are better still. There are about 20,000 species of solitary bees, and they greatly outnumber the social species—so the search is a wide one. *Andrena*, *Melitta* and *Eucera* are among the genera that forage on lucerne, but the leaf-cutters (*Megachile*) are outstanding. In Canada, for instance, a single nesting female of *Megachile perihirta* may in her life-time pollinate 15,000 lucerne flowers, which would yield 2 lb (1 kg) of seed (ref. 66). The foraging season of this bee is rather late for lucerne, and there is no question of any evolutionary relationship, since lucerne is of European or Asiatic origin and this leaf-cutter bee is North American.

Various attempts at rearing different *Megachile* bees in bulk for pollinating lucerne were not altogether successful, until *Megachile rotundata* appeared on the scene. This leaf-cutter bee, which is a native of Asia, was inadvertently introduced to North America in the 1930s;

it was recorded in Virginia in 1937. It is a very adaptable bee and reached the other side of the continent by 1954. Studies of the bee's life cycle in Pacific coast States (ref. 182) showed that it does not excavate its own nesting holes, but utilises various abandoned tunnels $\frac{3}{16}$ inch (5mm) in diameter (refs. 176, 181).

These results led to experiments in which the bees accepted as nesting tunnels paper straws, corrugated paper, holes bored in wood, and so on, that were provided for them (e.g. refs. 91, 176, 181). The next development was to prepare large-scale batches of nesting tunnels in a form suitable for transport. Cartons of wide paper drinking straws (cut to half-length) are suitable for commercial use, also blocks of wood in which several thousand parallel holes are drilled—often by stacking flat boards with parallel semicircular grooves so that each pair of adjacent boards provides a row of circular tunnels (ref. 70). Similar sheets of expanded polystyrene have also been tried out.

The blocks of nests containing prepupae are overwintered in large cold-rooms (refs. 90, 192); by raising the temperature at the right time (ref. 180) the date of emergence of the adult bees can be controlled so that the bees are active when the lucerne is in bloom.

Further north, in Western Canada, the bees would not survive the winter in natural conditions, and this is a help in controlling indigenous parasites and predators. The indigenous leaf-cutter bee *Megachile relativa*, on the other hand, cannot be separated from its parasites in this way because the conditions necessary for their survival are too similar to those that suit the bee (ref. 69). Some of the parasites of *Megachile rotundata*, that overwinter with it, are easily trapped by fitting a light source above a dish of water. The parasites emerge and fly slightly earlier than the bees (refs. 69, 88); they are attracted to the light and, after flying around it, drop into the water and drown.

ARTIFICIAL BEE BEDS

There is another efficient lucerne pollinator which, like *Megachile rotundata*, nests gregariously and is therefore amenable to bulk rearing. This is the alkali bee *Nomia melanderi*, which nests in soil that is sufficiently alkaline and sufficiently moist, in western coastal regions of North America (refs. 89, 162, 177, 179). Artificial "bee beds" can be created in suitable areas by introducing cores of soil containing prepupae, and keeping the soil suitably irrigated and controlling its temperature by heating cables (refs. 50, 175, 178). A pit is dug out, lined with polythene sheeting, and filled with soil above a bottom layer of gravel and sand. Water is provided by pipes that lead down to the gravel layer. If necessary sodium or potassium salt is mixed with the top layer of soil to draw water upwards and to provide a firm surface which is sufficiently impermeable to water (refs. 23, 175, 177). With such a "bee bed" built on the edge of a lucerne plot in Oregon, burrows were established within two years at a density around 2500 per square yard (ref. 175), about 8 times the highest natural density. As with *Megachile*, the spring emergence of adult *Nomia* bees can be made to coincide with the flowering of lucerne, by temperature regulation. The female bees are attracted by the presence of other females in the vicinity—hence the gregarious nesting. A "bee bed" 8 × 15 yards (metres) should pollinate 40 acres (16 ha) of lucerne (ref. 177).

The success with large-scale commercial rearing of *Megachile rotundata* and *Nomia melanderi* in North America has led other countries, many of which have problems with lucerne pollination, to consider importing these bees (e.g. New Zealand, ref. 133). It has also encouraged many countries besides the U.S. and Canada to search for other bees that might be of economic value as pollinators. The successful use of squash bees (*Peponapis* and *Xenoglossa*) for pollinating cucurbits lies outside the scope of this survey on seed production (refs. 116, 117). Researches in progress suggest that species of *Osmia*, *Xylocopa* and *Anthophora* may prove suitable for commercial rearing as pollinators. Possibilities are wide—the motto among the research workers concerned might almost be: "Give us a crop and we will find a bee to pollinate it."

OTHER CROPS AND HONEYBEES

The honeybee is the most efficient general-purpose insect pollinator of all, and it can conveniently be moved in large numbers from crop to crop. If it were as efficient at pollinating lucerne and red clover as it is at pollinating many other crops, a large amount of the research work mentioned earlier would have been unnecessary. Nevertheless, the value of the honeybee is not to be ignored, even for lucerne and red clover. Summarised results for both crops (ref. 47) show that plants in cages which excluded bees set virtually no seed; plants in the open set variable amounts (the number of wild pollinators varied greatly in different series of experiments); plants caged *with* honeybees usually gave even higher yields.

For a wide variety of crops honeybees are efficient pollinators, and provided they are present in sufficient numbers, pollination need not be a limiting factor to the seed yield obtained. In general, these crops can be maximally pollinated by taking colonies of honeybees to the fields—unless there are already sufficient within reach. Some representative examples are given here.

OILSEED CROPS

Sunflower (*Helianthus annuus*) has been widely grown as an oilseed crop for many years. Its enormous flower head may contain florets at various stages of development: unopened florets in the centre, round these a circle of florets at the male stage, then circles at the female stage, and withered florets on the outside. Florets at the male stage contain most nectar; bees stand on the female circle while collecting it, thus pollinating and cross-pollinating the florets with the pollen on their bodies (ref. 45). Measurements in Bulgaria showed that 97 per cent of the visiting insects were honeybees: without them, the plants gave only 2–3 per cent of full seeds; with them, the yield was 82–91 per cent. In Rumania, provided plants were open to insect pollination, manual pollination gave no additional advantage (ref. 166). In three years of experiments, seed production was increased 21–27 per cent by placing honeybee colonies on the crop, about 1 per hectare or 2·4 acres (ref. 31). Twice this density is, however, recommended (ref. 30), and the colonies should be taken to the crop as soon as 3–5 per cent of the plants are in flower.

Much attention has been paid to sunflower cultivation in the Soviet Union, where honeybees have been found to constitute 98–100 per cent of the insects pollinating it (ref. 99). The weight of kernels from 100 seeds was 5·7 g after honeybee pollination and only 0·5 g after self-pollination (ref. 98).

In the United States and Canada, interest has recently been directed to the cultivation of safflower (*Carthamus tintorius*). Here again, honeybees are the predominant insect visitor, and plants from which insects were excluded yielded only half as much seed as those open to insects (refs. 15, 40).

Niger (*Guizotia abyssinica*) is another crop whose yield has been increased by honeybee pollination, in India (ref. 12) and U.S.S.R. (ref. 17).

Seed yields from rape (*Brassica napus* var. *oleifera*) have been appreciably increased in various parts of Europe by bringing honeybee colonies to the plots (e.g. refs. 92, 115, 157, 158). This has not happened everywhere (e.g. refs. 28, 48), and the local population of wild bees—or the amount of shade on the crop—can be a determining factor. A formula for assessing the economic value of honeybees for seed production in rape has been worked out (refs. 187, 188). Bees on rape (e.g. refs. 125, 183), like those working lucerne (e.g. refs. 7, 85, 184), are especially likely to suffer damage through careless or indiscriminate pest control practices, and much work has been done to minimise this danger (ref. 86). Loss of bees by poisoning is, however, outside the scope of this paper.

Seed crops from other brassicas may be increased greatly by using honeybees. Yields from mustard (*Brassica alba*) have been improved by 66 per cent in Czechoslovakia (ref. 92) and by 100 per cent in England (ref. 49). In the Ukraine the seed yield from cabbage went up by 300 per cent, and that from radish by 22 per cent (ref. 159). In New Zealand, honeybee pollination of chou moellier (*Brassica oleraceae*) has been studied in relation to pest control, with a fairly satisfactory outcome (ref. 135).

VEGETABLE SEED CROPS

Experiments suggest that taking honeybee colonies to carrot seed fields may be well worth while (ref. 64). Flowers of carrot (*Daucus carota*) are pollinated by flies and wild bees as well as by honeybees (ref. 142). A yield 15·3 times as great was obtained from plants accessible to insects as from plants covered with muslin (ref. 141). Honeybees are efficient pollinators of carrot flowers, and their scarcity on the flowers in some circumstances has been attributed to competition from lucerne flowering at the same time (refs. 20, 43).

Seed production in sugar beet is not dependent on bees (ref. 47), but there is some evidence that honeybees can increase the yield (refs. 55, 118).

Onion seed production has received increased attention recently, and the value of honeybees is well established (refs. 79, 103, 122, 190, 191). Wild bees and flies are the other important pollinators; insect visitation is linked up with the daily cycle of sugar concentration in the nectar (ref. 103).

FIBRE CROPS

It has been shown repeatedly that honeybees are among the most important pollinators of cotton (*Gossypium*), improving both quantity and quality of the crop (e.g. refs. 94, 143, 148, 168, also 47 for a general discussion). Honeybees have also been instrumental in producing new hybrid varieties. There are complications with cotton because the floral nectaries are often less readily visited by bees than the extrafloral ones—which have nothing to do with pollination. Of the 38 publications on cotton referred to in *Pollination of seed crops* (ref. 34), 21 are from the U.S.S.R., 11 from the U.S.A., and others from India, Albania, Bulgaria and Chad. Cotton is, however, not grown in Britain, so a detailed discussion is not given here.

Honeybees are of less use to flax (*Linum*) (ref. 47); increases in both quality and quantity of seeds have nevertheless been recorded when honeybees foraged on the plants (refs. 59a, 108).

LAVENDER

The interrelation between lavender and foraging insects is unusual. The plant most grown for its aromatic oil nowadays is a sterile hybrid between *Lavandula latifolia* and *L. vera*, known in French as lavandin. Bees collect the nectar, but not the pollen (which is sterile), and pollination is not involved. An extended study was initiated in the south of France after growers had complained about the presence of bees on the flowers when pickers were working among them. The researches showed that removal of nectar from lavandin by bees stimulates oil production in the plants, increasing the yield by 16–20 per cent (refs. 9, 10, 11).

OTHER CROPS

The indispensability of honeybees for seed production in a number of other crops has been demonstrated. White clover (*Trifolium repens*) is one (e.g. refs. 42, 97, 131)—except where there are ample populations of wild bees. Crimson clover (*T. incarnatum*) is another (e.g. refs. 13, 54); also crown vetch, *Coronilla varia* (ref. 6); milk vetch, *Astragalus sinicus* (ref. 53); and sainfoin, *Onobrychis sativa* (ref. 41).

Beans (*Vicia faba* and *Phaseolus* spp.) present a similar problem to red clover in that bumble bees pierce the corolla to reach the nectar, and honeybees can then forage without pollinating the flower. In New Zealand this has been overcome (and the set of pods doubled) by replacing the colonies of honeybees every 7–14 days with fresh ones; it took the newcomers some time to learn the easier method of working the flowers, and meanwhile pollination was accomplished (ref. 27). In one experiment (ref. 167) honeybees were themselves observed to pierce the corolla. Extrafloral nectaries can also attract non-pollinating foragers (ref. 44). There are many problems with beans (refs. 34, 47). Pollination is often a limiting factor in bean production, and in general it seems to be beneficial to put honeybee colonies into the fields at the rate of 1 colony per acre (ref. 167).

In general much less work has been done on the pollination of tropical crops than on those grown in the temperate zones. There is no doubt that yields of *some* could be improved by increased pollination, whether by honeybees or other species. The great need is for more information on specific crops; several reviews summarise the knowledge so far available (refs. 29, 33, 38).

CONCLUSION

This review is concerned with ways in which bees of various kinds can be useful to the human effort of seed crop production. At one end of the scale we have to deal with the intimate relationships between an individual bee and a single flower or floret (refs. 144, 145). The bee is anatomically equipped to carry out the micromanipulations by which pollen is moved from one flower to another. The bee also has instincts that make her perform certain actions which bring about this transfer of pollen—the transfer is usually a side-effect of the bee's search for food. The shape and contour of a flower, as well as its colour and scent, are important in attracting a bee to visit it. If she is to be a useful pollinator she must subsequently visit other flowers of the same species, and she will do this only if each provides her with an acceptable reward. So she must be able to reach the nectar, and this must be sweet enough to compete successfully with other sources of nectar within her flight range.

The bee may be an even better pollinator if she is collecting pollen, and she is likely to do this only if her colony requires it (which the beekeeper may be able to arrange, by ensuring that the colony has plenty of larvae that need feeding). If the bee encounters an unacceptable hindrance when collecting the pollen—as with lucerne—she will easily be attracted away to other sources. The foraging bee is less likely to visit (and pollinate) plants if the flowers move about too much in the wind—hence the importance of shelter belts. If the temperature is too low she cannot fly far from the hive, or she may not be able to fly at all. Pollination is essentially an environmental problem.

At the other end of the scale this review has been concerned with the work of humans, scientists and growers, in many parts of the world. The research work touched on has almost all been carried out within the past fifteen years, and it represents only 20–25 per cent of the output during the period (ref. 34). An impressive amount of research on bees is thus being done in order to solve problems that face crop growers in connection with new crops, or with demands for better yields from existing crops. Bees that are especially efficient pollinators of a certain crop are being sought out. Crops are being bred for bees, and bees for crops. The honeybee is still the most efficient general-purpose pollinator, and ideas for using it have been stimulated by the "competition" from the wild-bee research. New methods of using honeybees—for instance in expendable cartons—are being tried out. The approach is much more active and dynamic than a generation ago.

Research work is continuing unabated in many countries and much of it has practical applications elsewhere. Countries which have not contributed at all to the cost of a particular piece of research can thus benefit from it. The cost of keeping up to date with information about researches done in other countries is only a fraction of one per cent of the cost of doing similar work at home. The widest possible knowledge of relevant research work on crop pollination can prove a very profitable investment for those designing experiments that *must* be done on the spot, within any particular country—and certainly for the growers themselves.

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