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Diversity Pays in Crop Pollination

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ABSTRACT

Pollination is an often overlooked but large cost factor in crop production. In spite of the high diversity of flowers, which requires an adequate diversity of pollinators, almost all animal pollination is simplistically ascribed to the manageable but often less efficient pollinator, the European honeybee, *Apis mellifera* L. In the case of poor pollination by honeybees, a number of costly techniques is applied to enforce fruit set—often with poor results. Finally, growers may resort to hand pollination, which greatly raises production costs. Knowledge of the appropriate pollinator is already available in many cases, however. This is demonstrated in this paper with examples spanning the whole range of pollination syndromes. To make this knowledge accessible, an expert-based Internet-accessible database is suggested.

POLLINATION is usually a critical step in crop production in temperate as well as in tropical regions, although some crops set fruit parthenocarpically [i.e., without pollination and thus without seed set, e.g., in banana, *Musa* spp., and pineapple, *Ananas comosus* (L.) Merr.] and although progress has been made with vegetative propagation via cell culture (e.g., orchids—*Phalaenopsis* spp., *Dendrobium* spp.) or cuttings. Fruit and seed set are especially dependent on successful pollination when the species under consideration cannot or must not be (automatically) selfed. This is true if the flowers have any adaptations for the avoidance of selfing: spatial (intrafloral herkogamy, monoecious or dioecious dichliny; Webb and Lloyd, 1986) or temporal (dichogamy: protandry, protogyny; Lloyd and Webb, 1986) separation of stigma and pollen presentation, or self incompatibility. It also applies if cross pollination is required, be it for breeding purposes or for hybrid seed production (positive heterosis, hybrid vigor). Wind pollinated staples like cereal grasses are left out of consideration in the following.

In spite of many published reports to the contrary, nearly all pollination in nature and agriculture is simplistically credited to the common European honeybee (Parker et al., 1987; Batra, 1995; Allen-Wardell et al., 1998; Kearns et al., 1998) in most parts of the world (see handbooks of, e.g., Crane and Walker, 1984; Free, 1993). In (sub-)tropical Asia, the Asiatic hive bee, *Apis cerana* (Fabricius), is also in use (Parker et al., 1987; Sihag and Mishra, 1995; Kevan, 1995). Although some people think that honeybees are responsible for about 80% of all insect pollination of crops (in the USA), others suggest that this estimate is unusually high; Buchmann and Nabhan (1996) state that honeybees are the dominant pollinators of only some 15% of the world's crops (all figures from Buchmann and Nabhan, 1996; Ingram et al., 1996).

Honeybees and certain stingless bees were brought into domestication long ago, but for their honey production rather than for any superior pollinating abilities; pollination of crops was not a consideration at that time (Batra, 1995). Although honeybees do pollinate certain crops (e.g., *Brassica* species), the reliance on a single agricultural pollinator—which simply cannot fulfil this excessive demand (see below)—is hard to understand considering the great diversity of flowers and the uniformity in size of the honeybee (which is required for the correct data transmission during dance communication, Waddington, 1989). It is, however, not only the inappropriate match between honeybees and the great diversity of flowers which often makes them inefficient pollinators, but also certain idiosyncrasies of honeybee behavior (Westerkamp, 1991) which lead to an “inherent inefficiency” (Ferrari, 1997), which is described below.

Solitary bees [the term *bee* refers to any member of the Apidae sensu Schwarz et al. (1996) or Apoidea sensu Michener et al., 1994] have a short, fixed flying season, which coincides with the flowering time of certain plants and thus may result in a mutual fit. Honeybee colonies, on the other hand, live year round, and are even “immortal.” They rely on many floral hosts for provisioning. The honeybees cannot specialize on particular species but must learn how to handle the actual flower. Thus they are able to learn to avoid flower-caused discomfort

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like becoming contaminated with pollen (the inevitable precondition for pollination, Westerkamp, 1996) while foraging for nectar (e.g., sideworking in apple; Degrandi-Hoffman et al., 1985) or discard the pollen (honeybees on sunflowers, *Helianthus* spp., Macfarlane, 1995a), or they avoid the “hook” of the explosive flower of alfalfa (*Medicago sativa* L.) which is essential for coming into contact with the stigma and pollen [see Alfalfa (*Medicago sativa* L., Fabaceae)]. The extreme division of labor, with its scout-based search for the most rewarding food sources, allows for an extreme constancy of foragers; thus, they may, for example, harvest pollen from dichogamous flowers (those with male and female functions separated in time) for days and consequently never contact a receptive stigma. Here, the usually highly esteemed floral constancy is deleterious for pollination. Because neither predilection for a certain forage and food plant nor the activity of the honeybees on the actual flower is constant from year to year (Ginsberg, 1979), flowers are unable to cope with this “predictably unpredictable” (Gould, 1986) behavior. Honeybee-adapted flowers in the strict sense do not exist (Westerkamp, 1991). Instead, honeybees often visit flowers and gain food from them without effectively triggering the pollination mechanisms while at the same time they discourage or displace native pollinators, both insects and vertebrates, from the flowers (Westerkamp, personal observation; Westrich, 1989; Sazima and Sazima, 1989; Paton, 1993; Richards, 1993; Kevan and Baker, 1998).

In North America, the problem of the supposed dependency on a single managed pollinator species (e.g., Richards, 1993) has become obvious mainly in two ways: the decline of the honeybee industry in the USA [some reasons for which are, e.g., the advance of African(ized) honeybees, pests like tracheal mites, *Acarapis woodii* (Rennie), or varroa mites, *Varroa jacobsonii* Oudemans; Parker et al., 1987; Richards, 1993; Watanabe, 1994; Buchmann and Nabhan, 1996; Allen-Wardell et al., 1998] and the demise of natural pollinator populations caused by pesticide application (Kevan and Plowright, 1995), habitat destruction, monocultures, etc.

The bias in favor of maladapted but manageable honeybees (Batra, 1995) has resulted in poor fruit and seed set in several crops which growers try to remedy by supplemental pollination, applying one of the following techniques, to name just a few: (i) hand pollination [see, e.g., Apple (*Malus domestica* Borkh., Rosaceae), Kiwifruit (*Actinidia deliciosa* (A. Chev.) C.F. Liang & A.R. Ferguson, Actinidiaceae), Vanilla (*Vanilla planifolia* Jacks., Orchidaceae), Cherimoya (*Annona cherimola* Mill., Annonaceae), Cacao (*Theobroma cacao* L.,

Sterculiaceae)] with brushes (Campbell and Phillips, 1994), bee-sticks (dead honeybees on a tooth pick, Williams, 1980), hand held pollen guns (Richardson and Anderson, 1996), or whole (male) flowers (Hopping, 1982a; González et al., 1998); (ii) spray pollination [see Kiwifruit (*Actinidia deliciosa* (A. Chev.) C.F. Liang & A.R. Ferguson, Actinidiaceae)] with pollen suspended in aqueous (which requires measures to cope with bursting or drying grains; Hopping and Simpson, 1982; Hopping, 1982b) or dry dusty (e.g., *Lycopodium* spores, talc; Faegri and Pijl, 1979; Speldewinde and Pereira, 1974) media, even from aircraft or by bombs (Hardon and Corley, 1976; Faegri and Pijl, 1979); and (iii) enpollination, i.e., artificial contamination of flower visitors (e.g., honeybees) with (precollected) compatible pollen at the hive exit (Free, 1993; Ferrari, 1997), for example with a pollen dispenser [see Apple (*Malus domestica* Borkh. Rosaceae)] or a pollination enhancer (a pollen transfer device, Hatjina et al., 1998, 1999).

The above-mentioned methods of artificial pollination all require previously hand-collected pollen, which makes them highly expensive.

Other supplemental pollination methods that growers have used are the following: (i) use of “electric bees” to simulate buzz-foraging [see Tomato (*Lycopersicon esculentum* Mill., Solanaceae)]; (ii) application of growth substances (Chareonboonsit et al., 1985) to promote fruit growth without pollination [see Tomato (*Lycopersicon esculentum* Mill., Solanaceae)]; (iii) application of growth inhibitors to produce shorter-tubed flowers (Free, 1993) to make nectar available to shorter-tongued bees like honeybees [see Red Clover (*Trifolium pratense* L., Fabaceae)]; (iv) placing of bouquets of flowers of a compatible cultivar amidst the flowers of the crop plant (Ferrari, 1997), as practiced since classical times, at least, in date palms (*Phoenix dactylifera* L.) and figs (Meeuse, 1961; Valdeyron and Lloyd, 1979) [see Fig (*Ficus carica* L., Moraceae)]; (v) grafting compatible cultivars onto existing trees (Ferrari, 1997); (vi) directing honeybees to target crops by applying chemical attractants (sugar water, scents including pheromones) to the crops and/or repellents to competing flowering species (Jay, 1986; Goodwin, 1997; Currie et al., 1992a,b); and (vii) inundation (“saturation,” Robinson et al., 1989) with honeybees in excess to overcome pollination deficiencies by providing, e.g., sufficient amounts of novices [see Apple (*Malus domestica* Borkh. Rosaceae) and Alfalfa (*Medicago sativa* L., Fabaceae)] or enhanced competition with subsequent intertree movement of the honeybees (Degrandi-Hoffman, 1987). Some examples are given in Table 1. Consequent overcrowding stresses, however, strongly debilitate the bee

Table 1. Numbers of bees per hectare (100 by 100 m²) used in flooding crops for improved pollination.

Crop	Units†/ha	Unit	Species	Source
Kiwifruit (<i>Actinidia chinensis</i>)	8	Colonies	<i>Apis mellifera</i>	Goodwin, 1997
Apples (<i>Malus</i> sp.)	2–6	Colonies	<i>Apis mellifera</i>	Robinson et al., 1989
Pears (<i>Pyrus communis</i>)	37	Colonies	<i>Bombus occidentalis</i>	Mayer and Lunden, 1997
Alfalfa (<i>Medicago sativa</i>)	20–25	Colonies	<i>Apis mellifera</i>	Robinson et al., 1989
Alfalfa (<i>Medicago sativa</i>)	124 000	Bees	<i>Megachile rotundata</i>	Strickler, 1997
Onions (<i>Allium</i> sp.)	10–30	Colonies	<i>Apis mellifera</i>	Macfarlane, 1995a
Blueberries (<i>Vaccinium</i> spp.)	up to 25	Colonies	<i>Apis mellifera</i>	Robinson et al., 1989
Tomatoes (<i>Lycopersicon</i> sp.)	10–15	Colonies	<i>Bombus terrestris</i>	Ravestijn & Sande, 1991

† Adjusted to 1 ha when originally given for another area unit.

misshapen fruits result (Free, 1993). To understand at least some of the problems encountered, it is best to follow the visit of a honeybee. Because of division of labor, foragers are usually interested only in nectar or only in pollen, and because apple blossoms are protogynous (Lloyd and Webb, 1986), pollen foragers only rarely come into contact with fertile stigmas—at least in the male phase. Newly recruited nectar foragers, on the other hand, become dusted with pollen when they first land on the clustering ring of stamens and make their way into the flower's depth for the nectar located between the stamens and the carpels. A honeybee soon learns to avoid this contamination with pollen by landing on the inner side of the petals and inserting its tongue between the staminal filaments (“sideworking,” Degrandi-Hoffman et al., 1985). This is especially simple for a honeybee to learn in cultivars like Delicious which have stamens in bundles with large interstices between them (Robinson, 1979). Once having learned this method, the honeybees rarely come into contact with pollen (and stigmas) again. So they are lost as potential pollinators. Even the pollen transfer by novices does not usually result in fertilization because of the fidelity of the honeybees to a certain plant, which is counterproductive given the self incompatibility encountered in these trees. Only rarely do the honeybees move between pollinizer (a pollen source for compatible grains) and fruit trees (Degrandi-Hoffman et al., 1984b). Most transfer of viable pollen may be achieved by intranidal contact between foragers working on different varieties of apples (“bee-to-bee” instead of “tree-to-tree,” Degrandi-Hoffman et al., 1984a, 1986) and is thus less efficient than direct pollination. To provide as many naive foragers as possible, (expensive) flooding of apple orchards with honeybees (Robinson, 1979) and frequent exchange of hives for new ones unfamiliar with apples are suggested. Recommendations for honeybees indicate two to six hives per hectare of apples—but about 600 blue orchard bees (*Osmia lignaria propinqua* Cresson; Torchio, 1987) or even as few as 80 female horn-faced mason bees (*O. cornifrons* Radoszkowski) suffice (Batra, 1994). In 1995, hornfaced mason bees pollinated more than 70% of the area devoted for apples in Japan (Sekita et al., 1996), the majority of which had been hand pollinated until quite recently—costly (about U.S. \$70 million, calculated from data in Maeta, 1990) and troublesome work (Maeta, 1990).

These bees, like other *Osmia* species, consistently land amidst the stamens and contact them, as well as the stigmas, during each visit (Bosch and Blas, 1994; Márquez et al., 1994). They even have the advantage that they carry pollen for homeward transport in a dry state in a ventral abdominal scopa where it can contact the stigmas even after having been stored away (Westerkamp, 1997). Honeybees, like many other bees, moisten pollen before storing it in their corbiculae, rendering it unavailable and largely nonfunctional for further pollinations (it is washed before being utilized in hand pollinations, Sasaki, 1985).

Besides the temporary measure of hand application of pollen to flowers (Maeta, 1990; Free, 1993) and spray pollination, honeybees are sometimes dusted with com-

patible pollen in a pollen dispenser (Free, 1993) as they leave the hive (enpollination) to contaminate them with hand-collected pollen from a compatible variety.

Alfalfa (*Medicago sativa* L., Fabaceae)

Alfalfa displays heads of small keel flowers (sensu Westerkamp, 1997). Strength is required to enter between the keel (which contains pollen and stigma) and the opposed flag when searching for the nectar produced at the base of the gynoeceum. When the keel is sufficiently depressed to give access for the bee's tongue, the central column of style and stamens, which was kept under high tension, is explosively released. In an all-or-nothing mechanism, the column strikes the underside of the bee's head, momentarily even trapping it, and receives and deposits pollen in the proboscis fossa (Westerkamp, personal observation).

Honeybees learning how to handle these flowers try to avoid this “hook” and soon become used to approaching the flowers from the side. Their sufficiently long tongue still gives them access to the nectar but they no longer trip the flower when sideworking. Without tripping, the stigmatic membrane that covers the stigmatic exudate and only rarely breaks passively (Kreitner and Sorensen, 1984) does not rupture and thus prevents selfing. As in apples (see above), “saturation” with 20 to 25 hives of honeybees per hectare is suggested for alfalfa pollination (Robinson et al., 1989). However, even with an exchange of colonies for a continuous supply of new, inexperienced foragers, the tripping rate remains low (Free, 1993).

In nature, alfalfa is visited and pollinated by a multitude of bees (e.g., Westrich, 1989) none of which is a specialized alfalfa pollinator. It was by chance that a successful candidate for alfalfa pollination was found outside the natural distributions of both the plant and the bee. In the 1930s, *Megachile rotundata* (Fabricius) (later on called the “alfalfa leafcutter bee”) accidentally came to North America. As this species did not encounter competitors and lives in dense aggregations, population sizes increased in western North America; as it proved to be a successful pollinator of alfalfa plantations, this bee was domesticated and became a great success (Dorn and Weber, 1988; Richards, 1993, 1996).

Only 2000 to 3000 females per hectare of *M. rotundata* are needed (Tasei and Delaude, 1984; Parker et al., 1987), as compared with the numbers of honeybees quoted above. Nevertheless, 50 000 plus (Richards, 1993) or even 100 000 leafcutter bees per hectare, which cost U.S. \$500 (Batra, 1994) are suggested (Peterson et al., 1992). Growers often inundate the fields with up to 124 000 leafcutter bees per hectare, although that greatly reduces the return of bee offspring and requires that owners purchase bees anew each year (Strickler, 1996, 1997). As a consequence, the costs for the bees constitute about a quarter of the price of alfalfa seed (Peterson et al., 1992).

Red Clover (*Trifolium pratense* L., Fabaceae)

Red clover also hides pollen and stigma within a keel which has to be removed for pollination. The keel blossom here is combined with a long tube which is formed

by a fusion of the bases of all petals and the nine lower stamens. Nectar is produced at the very base of this tube, and thus is only available to bees with a sufficiently long proboscis, e.g., long-tongued bumblebees [e.g., *Bombus hortorum* (L.); see Macfarlane, 1995a], but not to honeybees. Although this was known even to Darwin (e.g., Darwin, 1876), attempts were made to pollinate the flowers with honeybees. Because that failed, trials were made to breed shorter-tubed flowers as well as longer-tongued honeybees; also, growth inhibitors were applied to produce flowers accessible to honeybees (Free, 1993). However, suitable pollinators are found, not bred. Long-tongued bumblebees are still the best pollinators. As seed production of this forage legume has decreased within the European Community in parallel with losses of long-tongued bumblebee species, seed is procured from, e.g., New Zealand these days (Osborne et al., 1991). There, neither clover nor bumblebees are native. As proboscides of indigenous bees are too short to pollinate the clover introduced by 19th century settlers, long-tongued bumblebees were subsequently introduced from Europe (Donovan, 1990). Several bumblebee species (four species, at least, including *B. hortorum*; Donovan, 1980) have been successfully established since, and red clover seed can be re-imported into Europe (Osborne et al., 1991).

Tomato (*Lycopersicon esculentum* Mill., Solanaceae)

In tomato flowers, the anthers form a cone. They are connected laterally by interthecal hairs. Pollen is shed into this cone and may only escape by a common opening at the tip, which is partly occluded by the style. To release pollen, the cone has to be vibrated. Bees from most bee families employ this so-called buzz foraging (Buchmann, 1983; Westerkamp, 1987), and include, e.g., bumblebees, which vibrate their body by activity of the indirect flight muscles. This sonication is required even for self pollination. Honeybees, although producing tones of the same frequencies during dance communication, for unknown reasons do not use this behavior in flowers. So alternative means of pollination had to be found, especially for the year-round production of greenhouse-grown tomatoes.

Growers tried shaker tables as benches for tomato plants to force pollen mechanically from the anthers, or installed speakers blasting out high-energy sound waves for the acoustical production of the required sound pressure (DeTar et al., 1968; Buchmann and Nabhan, 1996). Finally, they relied on hand-held vibrators (electric bees) to sonicate pollen from the anthers. This was a labor-intensive and, therefore, expensive operation (Picken, 1984; Macfarlane, 1995a). In 1996, it would have cost some U.S. \$30 million alone for the 2000 ha under cultivation in the Netherlands (A. de Ruijter, 1996, lecture given at the 7th International Symposium on Pollination, Lethbridge, Canada). The application of hormones to increase the ovary without pollination seemed to offer an attractive alternative to the electric bee in view of the labor costs (Picken, 1984). However, the topical spraying of flowers with 4-CPA (4-chlorophenoxyacetic acid) for fruit set was also labor intensive and, moreover, resulted in low quality, puffy fruit (Asada and Ono, 1997).

Only after it had become possible to avoid bumblebee queen hibernation (Röseler, 1985) and thus to produce colonies year round, were bumblebees used commercially for tomato pollination. Hundreds of thousands of colonies of *Bombus terrestris* (L.) are reared and sold each year in Europe alone. They are placed in greenhouses for tomato pollination and replaced by new colonies as required (Ruijter, 1997; hives are added bi-weekly, Natupol, Koppert B.V., Berkel en Rodenrijs, the Netherlands). As tomato flowers do not provide nectar, sugar water has to be supplied for colony survival. As calculated by Ravestijn and Sande (1991), 10 to 15 colonies are required per hectare. In North America, *Bombus impatiens* (Cresson) and *B. occidentalis* (Greene) are successfully utilized in (greenhouse) pollination of tomatoes (Kevan et al., 1991; Kevan, 1999).

Fig (*Ficus carica* L., Moraceae)

In the figs, the tiny reduced flowers are hidden within urn-shaped inflorescences (syconia, the future figs) and thus accessible only to certain specialized pollinators (Berg, 1990). These have to squeeze themselves between the interlaced scales, which block the entry into the flower-containing chamber. They may lose wings and/or antennae or even get stuck in the "opening" (Valdeyron, 1984), but they may visit more than one syconium in sequence (Giberneau et al., 1996).

The common fig, *Ficus carica*, is (gyno-)dioecious, as are about 50% of the about 750 fig species (Berg, 1990). Functionally male trees ("caprifigs") are the source of pollen and pollinators, specific gall wasps (*Blastophaga psenes* L., Hymenoptera: Chalcidoidea: Agaonidae). They develop within the ovaries of the short-styled female flowers, the style length reflecting the length of the wasps' ovipositor. Instead of forming fruit, the female flowers of the male trees are usually transformed into pollinator-producing galls. Female trees possess long-styled flowers only and thus cannot serve for pollinator reproduction; they only form seeds and thus the edible figs. Scents from within the syconia (Hossaert-McKey et al., 1994) attract wasps to either male (wasp reproduction) or female (fig reproduction) inflorescences, mimicking each other (Grafen and Godfray, 1991) in a complicated phenological scheme (Kjellberg et al., 1987).

Forms exist that produce figs parthenocarpically, and this process may be fostered by the application of growth substances (Stenz, 1994a). The bulk of fig production, however, depends on pollination. This was well known to Theophrastus or Aristotle (Valdeyron and Lloyd, 1979). Caprifigs (source of pollen and pollinators) have been brought to receptive female trees manually ("caprification") since classical times, at least (Valdeyron and Lloyd, 1979), if male trees are absent from the neighborhood. Nevertheless, fig production in California failed at first because only female trees were planted (Free, 1993).

Pineapple Guava [*Acca sellowiana* (O. Berg) Burret, Myrtaceae]

The floral biology of the large flowers of the temperate South American pineapple guava remained an

enigma for many fruit growers until recently. This often resulted in ascribing the pollinating ability to honeybees (e.g., Schroeder, 1947; Free, 1993), but as *Apis* tend to act as pollen thieves (i.e., they collect pollen in a manner that precludes pollination; for definition, see Inouye, 1980), stocking orchards with them has little to recommend it (Macfarlane, 1995a).

Instead, large perching birds pollinate *Acca*. This plant, however, displays unusual ornithophilous flowers because they are devoid of nectar. Their conspicuousness is based on long, stiff red stamens topped and contrasted by yellow anthers. At a glance the white petals, sometimes with a pinkish or reddish hue, remind one of juicy berries. They are highly succulent and rolled up, and indeed have a sweet taste. Frugivorous birds, which perch on twigs next to the flowers, feed on these "berries." When they are sufficiently large, they may contact pollen and stigma and thus pollinate. That these berries are attractive to birds outside the native country is often observed (Westerkamp, personal observation) and of great value for trees cultivated as crops. In New Zealand, Stewart and Craig (1989) found that (likewise introduced) European blackbirds (*Turdus merula*, Turdidae) and Indian mynas (*Acridotheres tristis*, Sturnidae) are the most efficient cross pollinators. That *Acca* is bird pollinated, however, had been clear for more than a 100 yr (Müller, 1886) and has been confirmed repeatedly (e.g., Werner, 1919; Fisk and Steen, 1976; Macfarlane, 1995a).

Kiwifruit [*Actinidia deliciosa* (A. Chev.) C.F. Liang & A.R. Ferguson, Actinidiaceae]

The pollinator of the dioecious flowers of kiwifruit in nature is unknown. There are two competing concepts today. The observation that bumblebees successfully buzz-forage from these flowers (Corbet et al., 1988) led to a growing interest in these bees as pollinators, but the flowers are so large even in relation to bumblebee queens that the bees may forage for pollen with little contact to the stigma (Macfarlane, 1995a). So it is hypothesized that the flower might be *Xylocopa*-adapted in nature (Anders Nilsson, 1999, personal communication; see also King and Ferguson, 1994).

The plants under cultivation, however, are wind pollinated (anemophilous; data from Craig and Stewart, 1988 and personal observation)—although this is contradicted time and again (see, e.g., Gonzalez et al., 1998): kiwifruit pollen is aerodynamically very good as compared with, e.g., pine pollen (King and Ferguson, 1991), the flowers are shaped to direct an airstream flowing past them through the stigmas (which has the effect of maximizing pollen/stigma contact; King and Ferguson, 1991), and the stigma is large and multi-branched (and thus compares well with the feathery stigma of other typical anemophilous plants, e.g., grasses). In orchards, however, the plants first are grown behind windbreaks or shelter belts to protect them and especially the fruit from wind damage (Jay and Jay, 1984). Secondly, very few males are interplanted since too much female production space is sacrificed if males occupy more than

10% of the area (Free, 1993). Consequently, poor pollination results.

Different measures have been taken to improve pollination. Mostly, honeybees (and nowadays, buzz-foraging bumblebees) are in use; they are also impeded (by the shade) or even excluded by the dense shelter belts (Hopping and Jerram, 1980). As the flowers do not provide nectar, bees can only forage for pollen, which is present in male and female morphs; in the latter, however, the grains are empty (Schmid, 1978). As honeybees show a tendency to be largely specific to flowers of one sex even on consecutive days (fidelity), they should be considered detrimental because they serve only to remove pollen from the orchard (Craig and Stewart, 1988). To avoid drift of honeybees to nectar sources outside the orchards, sugar syrup has to be added to the colonies. Considering stocking rates of up to 800 colonies per km² (Goodwin, 1997), this requires the employment of temporary staff and even resulted in a bottling plant which produces the syrup during the pollination season (Goodwin, 1997).

Supplemental pollination is also tried by spraying, either in aqueous solutions (which require additives to impede bursting and precocious drying of pollen grains; Hopping and Simpson, 1982) or in dry state (King and Ferguson, 1991). Hand pollination, however, is considered superior (Costa et al., 1993; González et al., 1998), although it requires some 100 man hours (Costa et al., 1993) and 5.9 kg of kiwifruit pollen (mechanically collected at a rate of 70–140 g/h; King and Ferguson, 1991) per ha.

Free admission of wind, at least at the time of flowering, and a sufficient number of male plants in the right place may be a more cost-effective solution to kiwifruit pollination. At the same time, it may help to favor one of the two competing concepts.

Tropical

Vanilla (*Vanilla planifolia* Jacks., Orchidaceae)

As is usual for most orchids, flowers and pollinators, and thus pollination events are rare in nature. On the other hand, more than 80% of vanilla is produced outside its native area (Mexico: 6% of 1997 production only) on islands in the Indian Ocean, mainly Indonesia and Madagascar (FAOSTAT, 1998), and thus outside the geographical range (Neotropics) of its pollinators (large euglossine bees, e.g., *Eulaema polychroma*, *E. speciosa*, *E. cingulata*, *E. nigrita*; Roubik, 1995b). For these two reasons, pollination has been done by hand since 1841 in plantations (Franke, 1997), even in its natural area. Anther and stigma are pressed together causing self pollination (Proctor et al., 1996) and sterile seeds (Free, 1993). Trained personnel can pollinate 1000 to 2000 flowers per day (Free, 1993). Hand pollination is said to represent 40% of the total cost of vanilla production (Crane and Walker, 1984). Growing the plants in their home range and a concomitant fostering of the pollinators should reduce pollination and thus production costs.

Passionfruit, *Granadilla*, *Maracujá* (*Passiflora* L. spp., *Passifloraceae*)

Passiflora comprises more than 500 species. About 50 of them are used for fruit and 20 are under cultivation (Stenz, 1994b), not only in the native Neotropics but also in all countries with a sufficiently warm climate. Passionflowers show an enormous wealth of forms—diameters range from less than 1 cm to 17 cm, and blossoms may attain 18 cm in length (Endress, 1994). Floral syndromes span a similar diversity, from bee- to bird- to bat-pollinated species (Vogel, 1990). The crops (mainly *P. edulis* Sims), however, are usually pollinated by large bees (*Xylocopa*, *Centris*, *Epicharis*, *Eulaema*, *Bombus*, *Ptiloglossa*; Janzen, 1968; Corbet and Willmer, 1980; Gottsberger et al., 1988; Sazima and Sazima, 1989; Roubik, 1995b; Koschnitzke and Sazima, 1997; García and Hoc, 1998). Carpenter bees (*Xylocopini*) of the right size are found in many of the countries in which *Passiflora* is cultivated (Mardan et al., 1991; Macfarlane, 1995b). Hand pollination, however, is largely used for passion fruit production (Faegri and Pijl, 1979; Macfarlane, 1995b; Vanderplank, 1991). Field workers are said to pollinate about 600 flowers per hour with a 60 to 70% success rate (Vanderplank, 1991). Honeybees (*Apis* spp.) and stingless bees (*Trigona* sp.) only steal pollen and/or nectar; they can deplete pollen before the appropriate bees can make a visit (Mardan et al., 1991) or even drive them away (Sazima and Sazima, 1989). They are too small to transfer pollen regularly. Only bees large enough to fit in between the perch formed by the corona and the roof (first formed by the anthers and then by the stigmas) while making their round in the flowers, are potential pollinators, as was revealed as early as 1793 by Sprengel. Provision of wooden logs for carpenter bee nesting should suffice to provide the right number of pollinators where these bees occur (Mardan et al., 1991).

Pineapple [*Ananas comosus* (L.) Merr., *Bromeliaceae*]

Pineapple may serve as a Neotropical example of flowers pollinated by hovering birds (hummingbirds), although the crop is produced parthenocarpically. Its cultivars are self incompatible, forming fruits without seeds. Different cultivars can be crossed and then form seeds (Leal, 1989). Seed set is only required for breeding purposes. The presence of seeds lowers the economic value of the fruit. Thus, the importation of hummingbirds into Hawaii, a major pineapple-growing area, is strictly forbidden in an attempt to avoid any pollination (Free, 1993).

Banana, Manila Hemp (*Musa* spp., *Musa textilis* Née, *Musaceae*)

Although diploid wild bananas are still pollinated by their usual bat pollinators (Nur, 1976; Dobat and Peikert-Holle, 1985), cultivars producing edible fruit are usually triploid hybrids of *Musa acuminata* Colla and *Musa balbisiana* Colla (both originating from southeast

Asia, Vandermeer, 1983), which no longer need pollinators. They are propagated by cuttings and form fruits parthenocarpically. Nectar, however, is produced so abundantly at night (Vandermeer, 1983), that *Musa* ranks as an important honey source (Crane and Walker, 1984). And although flower visitors cannot influence fruit set because the plants are usually male-sterile, visits by bats are disliked in plantations because their claw marks might turn the future fruits unattractive for the consumer. Bats and bat roosts have thus been intentionally destroyed to impede visits (Jiménez, 1973; Stephens and Tyson, 1975; Felten, 1980).

Musa textilis, Manila hemp, is cultivated because of its fibers and has comparable chiropterophilous flower and inflorescence characteristics (Faegri and Pijl, 1979; Dobat and Peikert-Holle, 1985; Roubik, 1995b). It still sets fruit and seed in nature. Some wild bananas with flowers on erect inflorescences with pink bracts and with nectar production primarily in the daytime were found being pollinated by nectarivorous nectariniid birds (Nur, 1976; Itino et al., 1991).

Durian (*Durio zibethinus* Murray, *Bombacaceae*)

The cauliflorous durian opens its large (entrance diameter 2.5–3 cm, Dobat and Peikert-Holle, 1985) protogynous flowers during late afternoon. Anther dehiscence follows stigma maturation with a lag time of 1 to 3 h. Open flowers emanate a strong stench (reminiscent of sour milk, human feces, etc.; Dobat and Peikert-Holle, 1985). The nectaries on the inner side of the calyx produce large amounts of watery nectar during a single night (e.g., 0.63 mL, Gould, 1978; Appanah, 1990). Durians are obviously pollinated by bats, e.g., *Eonycteris spelaea* (Soepadmo and Eow, 1976; Gould, 1978; Faegri and Pijl, 1979; Dobat and Peikert-Holle, 1985), although doubts are expressed because honeybees and certain night-flying insects have been observed as visitors (Free, 1993).

There is variability in the amount of self incompatibility among different clones. Some durian clones on plantations can be totally self incompatible with no fruit at all, or partially self incompatible, or even self compatible as was observed with trees in Darwin, Australia (Lim and Luders, 1998). To enhance fruit yield and to lower costs polyclonal plantings and a better promotion of pollinating bats are recommended (especially sleeping caves; e.g., Vogel and Westerkamp, 1991).

Cherimoya (*Annona cherimola* Mill., *Annonaceae*)

The Neotropical *Annona cherimola*, the cherimoya, *A. squamosa* L., the sugar apple, *A. reticulata* L., the custard apple and other *Annonaceae*, principally of the genera *Annona* and *Rollinia*, with edible and very much appreciated fruits, show pollination processes that rely on the activity of beetles. Very often, this fact is largely or completely misunderstood or neglected, with negative consequences for crop production. For example, in the U.S. Agriculture Handbook (McGregor, 1976), the high costs of hand pollination of cherimoya, e.g., in California, are considered and the need for basic polli-

nation studies in the homeland of this species is suggested. The most curious suggestion by McGregor (1976), an apiculturist, was "saturation pollination" with honeybees (see also Introduction and Table 1), based on the simple fact that this procedure "has proven feasible on some other crops." In his book, Free (1993) misinterprets the pollination biology of the Annonaceae. In the recent FAO textbook *Pollination of Cultivated Plants in the Tropics* it is stated that "visitors and pollinators have seldom been observed but include beetles, especially the dynastine scarab, *Cyclocephala*" (Roubik, 1995b).

The accumulated knowledge on Annonaceae pollination, however, should be considered more adequately. Honeybees cannot be potential pollinators because bees are completely unable to enter the floral chamber of the protogynous Annonaceae flowers during receptivity of the stigmas. All these species possess relatively small flowers and small floral chambers. It has long been known that small, flat nitidulid species are the effective pollinators of these Annonaceae to which they are attracted by fruity odors, and not dynastid scarabs like *Cyclocephala* (see Wester, 1910; Gottsberger, 1977, 1985, 1989; Webber, 1981).

Sugar apple and cherimoya, even planted outside their natural range, are visited there also by nitidulid beetles which are principally responsible for fruit set (Israel: Gazit et al., 1982, Florida: Nadel and Pena, 1994).

The nitidulid beetles develop on rotting fruits (see Gottsberger, 1970). Therefore, it would be relatively easy to augment their populations in plantations of *Annona* and *Rollinia* by simply offering breeding sites. This would economize costs, because growers suggest (Campbell and Phillips, 1994; Richardson and Anderson, 1996) and rely on hand pollination, which requires as many as 100 working days per hectare (Ahmed, 1936; Schroeder, 1971; Gazit et al., 1982).

Oil Palm (*Elaeis guineensis* Jacq., Arcaceae)

The monoecious oil palm, with its male and female inflorescences flowering at different times and thus dependent on cross pollination (Hardon and Corley, 1976; Syed, 1979; Uhl and Dransfield, 1987), was erroneously thought to be wind pollinated until quite recently (see Syed, 1979). Fruit set had never been a problem in its home region (West Africa). Set was poor, however, in Malaysia and Indonesia where the bulk of today's (1997) palm oil is produced (FAOSTAT, 1998). So assisted pollination was needed (Greathead, 1983) and was accomplished by people blowing hand-collected pollen mixed with talc or another diluent onto the receptive female flowers (e.g., Speldewinde and Pereira, 1974; Hardon and Corley, 1976).

An intense search for the actual pollinator revealed certain Curculionidae-Derelomini (Coleoptera), which had been recognized as pollinators as early as 1910 by A. Chevalier (Greathead, 1983). These beetles breed in spent male inflorescences, attracted by a specific aniseed-like scent (estragole = 4-allylanisole; Hussein et

al., 1991). At certain times, when stigmas are receptive, they are attracted to the female inflorescences by short pulses of a similar but sharper and more penetrating scent. Since these offer nothing (deceit pollination; Proctor et al., 1996), the weevils soon return to the male inflorescences. They feed (on the filament tubes of spent florets), mate, and oviposit here. Because the larvae feed and develop only on the decomposing flowers (Chee and Chiu, 1998), they cause no harm.

After a careful quarantine and a study of its potential to become a pest of non-target plants, the species *Elaeiodobius kamerunicus* (Faust) was introduced into Malaysia with impressive success (Syed et al., 1982); the industry saved some estimated U.S. \$60 million per year because of avoided hand pollination alone. Together with an increased yield, the annual savings were said to amount to U.S. \$100 million (Hussein et al., 1991; U.S. \$115 million, Greathead, 1983).

Papaya (*Carica papaya* L., Caricaceae)

The dioecious (or at least gynodioecious) papaya has night-blooming flowers, which release a strong sweet perfume especially noticeable in the evening. Male flowers are produced in abundance; they are tubular and produce nectar around the (usually; hermaphroditic flowers may occur) rudimentary pistil, which is out of reach of bees because of the long tube. Female flowers are tubeless and nectarless. Their large stylar lobes are said to mimic the corolla lobes of the male flowers. The pollinators are hawkmoth (Sphingidae), which also visit the nectarless female flowers. Parthenocarpy is said to occur (Baker, 1976; Bawa, 1983). Good conditions for the hawkmoth pollinators must be ensured for successful pollination.

Cacao (*Theobroma cacao* L., Sterculiaceae)

Cacao flowers are fly pollinated, midges of the Ceratopogonidae and Cecidomyiidae being the main groups of pollinators (Young, 1986). Nowadays, it is accepted that in this case, honeybees cannot play a role in pollination (Free, 1993). Other bees (e.g., *Trigona jaty* Smith) function as pollen thieves, which glean pollen from the freshly opened flowers thus diminishing the likelihood of successful pollination by the actual pollinators. This is especially true if flowers of this understory tree are in full sunlight (Young, 1985). Cacao flowers need pollen vectors because the stigmas are surrounded by a fence of staminodes and the anthers are hidden inside cave-shaped petal hoods; thus, anthers and stigmas are widely separated within the flower (e.g., Kaufmann, 1975). Moreover, the flowers are often self incompatible (Pandey, 1960). It is not known for what reason (Young, 1986) the pollinating midges first search between the stigmas and the closely fitting staminodes (thus delivering pollen), and then in the petal hood (taking up new pollen) of these faintly scented flowers (Young et al., 1984; major fragrance constituent is 1-pentadecene; Erickson et al., 1987). When hand pollinated (up to 250 flowers per worker per day; Soria, 1981), the trees are said to mature a larger number of fruits than when these

are left to natural pollinators (Young, 1986; Franke, 1994). Usually, less than 5% of the flowers are pollinated; an even smaller fraction (0.5–2%) leads to the final crop (Alvim, 1984).

For their reproduction, the pollinating Ceratopogonidae need water to provide the bacteria which nourish their larvae (Soria, 1981), a fact which became especially apparent when pollinators were missing during longer dry spells or after the eradication (for malaria vector control) of phytotelmata (plant-held pools of water, as in the base of leaves of bromeliads, usually growing as epiphytes on shade trees). These water reservoirs serve for raising disease-carrying mosquitoes (*Anopheles*) (Pittendrigh, 1948), as well as cacao-pollinating Ceratopogonidae (Fish and Soria, 1978; Frank, 1983). Piles of banana trunk sections or cocoa husks may also serve as (water-holding) breeding sites for the pollinating midges (Young, 1986).

REASONS

From the case histories given above, certain generalizations may be drawn as to the reasons behind the pollination problems.

The idea that “**pollen gatherers are reported to be better pollinators** than nectar gatherers since they have greater stigma contact” (Goodwin, 1997) is based on a sound observation and an over generalization. When honeybees forage for nectar on alfalfa [see Alfalfa (*Medicago sativa* L., Fabaceae)], for example, they may reach nectar without tripping while sideworking the flower. However, if honeybees are forced to collect pollen from these flowers, they have to trip them in order to get access to the pollen grains hidden in the keel. The all-or-nothing spring mechanism results in a rupture of the stigmatic membrane, and thus pollination occurs. Considering the legitimate pollinators, however, most flowers (including alfalfa) are nectar flowers (Westerkamp, 1997). They hide nectar at some depth. Visitors are contaminated with pollen while searching for nectar, and thus can pollinate the next flower of the same species. When visiting these very same flowers for pollen, bees often do not even contact the stigma (and thus are deleterious pollen thieves). And even if they contact the stigma, this often does not result in pollination because donating and receptive phases are separated in time in many plant species to avoid clogging and/or selfing (Lloyd and Webb, 1986).

Considering the high diversity in floral form and width, the **reliance on a single (standard) bee species** as the only pollinator is unsound. This uniformity in size is part of honeybee biology because it is a precondition to avoid misinformation during dance communication (Waddington, 1989).

Moreover, it is not only the missing appropriate match but also especially the **missing know-how** in flower handling, which results in the malfunction of the honeybee at certain flowers. As its colonies live year round, they must not show any adaptations to particular flower species (which evolved adapted to pollination by short-lived solitary bee species) because they have to cope

with whatever flowers are available. Some floral mechanisms are too complicated to be learned by honeybees (e.g., certain fabaceous keel flowers; Westerkamp, 1993; Teppner, 1988). On the other hand, behaviors are learned which serve the honeybees to get their share in the most efficient, easy, and energy-saving way, but do not result in pollination [see Apple *Malus domestica* Borkh. Rosaceae), Alfalfa *Medicago sativa* L., Fabaceae), and Kiwifruit (*Actinidia deliciosa* (A. Chev.) C.F. Liang & A.R. Ferguson, Actinidiaceae)].

The **year-round demand by customers** for certain crops [e.g., tomatoes; see Tomato (*Lycopersicon esculentum* Mill., Solanaceae)] confronts biology with a serious problem. Temperate flowers (and thus fruit) as well as temperate bees are highly seasonal and short lived. Their synchronicity led to certain partnerships between a flower species and a pollinator, giving handling efficiency, pollination reliability, and exclusivity of attractants. In greenhouses with climate control, crops can be grown year round. Animal life cycles are more difficult to influence: for example, year-round rearing of bumblebees only became possible after queen hibernation could be bypassed by a two-fold CO₂ narcosis (Röseler, 1985).

Growing of **alien crops** is often unsuccessful if they rely on highly specialized pollinators, which have not been brought along to the new fields [e.g., vanilla, see Vanilla (*Vanilla planifolia* Jacks., Orchidaceae)]. Only after subsequent importation of the specialists (e.g., *Elaeidobius kamerunicus* to Malaysia for *Elaeis guineensis* Jacq.; *Bombus hortorum* to New Zealand for *Trifolium pratense*) do these crops flourish in their new environments.

Honeybees and stingless bees were domesticated for maximum **honey production**, not for any superiority in pollination (Batra, 1995). There have been trials to select for pollination-related characters (Free, 1993; Hellmich et al., 1985), but with limited success. In fact, they are often extremely poor pollinators of certain crops. Growers, however, preferred poor pollinators to no pollinators at all when these are missing for whatever reason.

Today's methods of crop production often also destroy the surrounding natural ecosystem, such as pesticides killing off the animals that would pollinate the crop plant. Pollination requirements are not considered before growing the crop: Who pollinates? What does this pollinating organism need to make its living? Therefore, expensive hand pollination must be applied.

Pollinators are rare or extirpated and substitutes are not available. Possible reasons are the nesting or food habitat is missing, crop fields are too large (e.g., up to 600 km² for alfalfa seed in California; Motter, 1981) to allow influx of pollinators from the fringes, the blooming season of the crop is too short to allow establishment of pollinator populations, temperatures during the flowering season do not match those required by the pollinators (Corbet et al., 1995), and overuse of pesticides which also kills alternative forage along field margins.

The **restriction to a single pollinator species** is unwise, especially when it is provided with the idiosyncrasies of

the honeybee (Westerkamp, 1991) and its susceptibility to pest organisms (varroa mites, etc.).

SOLUTIONS

As the previous sections have indicated, the high diversity of crop-flower species requires an adequate diversity of pollinators which goes far beyond bees (see also, e.g., Roubik, 1995a). Nevertheless, solitary bees are the most essential group of pollinators. This fact is beginning to be appreciated also in applied research (surveys of Parker et al., 1987; Torchio, 1987; Kevan et al., 1990; Richards, 1993; Batra, 1995; Cane, 1997). As soon as crop pollination systems are working and management of a certain bee species functions, these bees are tried on different crops and they often perform poorly, as demonstrated, for example, in the use of (non-buzzing) *Megachile rotundata* in (buzz-pollinated) cranberries, *Vaccinium macrocarpon* Aiton (MacKenzie and Javorek, 1997).

Solitary bees are more or less specialized for the flowers they visit, a fact, which may pose problems but also offers opportunities. Usually (and luckily) these specializations are not too narrow as guilds are involved on either side, i.e., a bee species is not dependent on a single flower species and a flower is visited by a range of similar bees which may all contribute to pollination. Specialized bees have relatively short adult life spans and often show behavioral and morphological traits that fit them to their host plants. Therefore, they are efficient pollinators and become “immune to the siren songs of plant species which flower contemporaneously” (Parker et al., 1987). The solitary bees’ adult life span is synchronized with the host plants’ flowering. So, when the host is an economic plant and the flowering is intense enough to allow for successful reproduction of the bees, it is not necessary for man to take care of them (as is necessary when using honeybees), and this greatly reduces costs (Parker et al., 1987). On the other hand, these bees do not produce honey, so beekeeping with them does not provide a supplementary income (Parker et al., 1987) via honey. If they, however, produce a surplus of bees, the growers can sell these extra bees as well as nesting substrate needed to propagate the bees.

The simplest way in which a crop grower can save extraordinarily high pollination costs is to use knowledge already published. As some of the above examples have shown, much knowledge is available, and has been so in part for centuries. The only requirement is to find and critically read and interpret the relevant publications.

If basic knowledge is missing, research has to be done. The very first step is to try to understand floral function. Often, a detailed study of functional morphology by an experienced observer alone may suffice to characterize the floral syndrome of the flower and to suggest which organism might be the sought pollinator if biotic pollination prevails (Vogel, 1954, 1990; Faegri and Pijl, 1979). If no actual visitor fits the flower, a search should be started preferentially in the natural range of the crop plant.

As far as generalized pollinators are concerned (e.g., *Xylocopa* bees), crop cultivation outside the home range of the plant does not usually pose a problem—at least in pollination. If, however, suitable pollinators are missing in a new area, the difficult question arises about whether or not to import the pollinator. In some cases, importation has been highly successful and has not harmed the native biota of the new range as far as can be assessed up to now (e.g., *Elaeidobius kamerunicus*). There are problems, however, with imported pollinators, which often diminish or even wipe out native pollinators: (i) European and (especially) African honeybees (*Apis mellifera*) in the New World (Kevan and Baker, 1998), Australia (Paton, 1993), and New Zealand; (ii) European bumblebees (especially *Bombus terrestris*) in Israel (Dafni and Shmida, 1996; Dafni, 1998), Japan (Asada and Ono, 1996), and New Zealand; and (iii) worldwide monocultures of European *Megachile rotundata*. So, this adulteration of flora and fauna should be avoided by any means.

If we are to have natural pollinators at our disposal, their needs have to be respected. Environmental conditions must be offered (Banaszak, 1992; Matheson et al., 1996; Jones and Munn, 1998) that allow for their survival and reproduction. This will have considerable effects on growing methods (e.g., extent of continuous areas covered by crops versus refuge areas for pollinators, etc.).

CONCLUSIONS

Pollination is an often overlooked but major cost factor in crop production. The knowledge required for appropriate pollination is frequently already available as shown in the examples cited in the previous chapters. It has only to be found in the voluminous and, if ancient, often non-English literature. This wealth of experience has to be used and, where appropriate, extended. To make it accessible, a body of experts should input their knowledge into an Internet-based data bank, including an evaluation of existing literature, rather than just providing lists of references that are often already available to the authors. This would also help to overcome the problem of non-English languages. Apparent gaps must be identified and ranked as to their priority, and then be filled. As ill-judged pollination modes result in unnecessary expense whenever a crop is grown and for every grower on every field in every season anew, a single investment into filling the gaps of knowledge is obviously cheaper.

On the other hand, teaching programs have to be set up at all levels of education so that the available knowledge reaches those who require it in the fields and plantations. The main problem remains ignorance, or even worse, superficial knowledge. Information on pollination primarily involves understanding floral functioning, and not just proficiency in apiculture. This is the knowledge to be spread among pollination advisers in the end—and that means spreading it first among higher levels like supra-regional and regional agricultural organizations and the respective political entities on the one

side and among the scientific agricultural community (universities, etc.) on the other side.

Money can be saved by knowing the most appropriate methods of pollination and by applying them. In the best case, pollination is cost free. A more ecologically based method is usually the most economical way in pollination.

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