

## BEE POLLINATION AND FRUIT SET OF *COFFEA ARABICA* AND *C. CANEPHORA* (RUBIACEAE)<sup>1</sup>

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Self-sterile *Coffea canephora* and self-fertile *C. arabica* are important cash crops in many tropical countries. We examined the relative importance of insect, wind, and spontaneous self-pollination and the degree of self-fertility of these two coffee species in 24 agroforestry coffee fields in Indonesia. In both species, open pollination and cross pollination by hand led to the highest fruit set. Wind pollination (including self-pollination) led to 16% lower fruit set than open pollination in *C. canephora* and to 12.3% lower fruit set in *C. arabica*. Self-pollinated flowers and unmanipulated controls achieved an extremely low fruit set of 10% or less in the self-sterile species, and of 60% and 48%, respectively in the self-fertile species. These results constitute experimental evidence that cross pollination by bees causes a significant increase in fruit set of not only the self-sterile, but also the self-fertile coffee species. The practical implication is that coffee yield may be improved by managing fields for increased flower visitation by bees.

**Key words:** agroforestry; *Coffea*; Indonesia; plant–pollinator interactions; Rubiaceae; Sulawesi; sustainable agriculture.

Fruit set of most plants depends on successful pollination by wind or animals, but herbivory, nutrient availability, and microclimatic conditions may also be important (Eriksson and Ehrlén, 1992; Turnbull, Crawley, and Rees, 2000). Bawa (1990) estimated that 89–99% of all flowering plant species in tropical lowland rainforest are pollinated by animals, and bees are the most important pollinators (Roubik, 1995; Renner, 1998). Further, one-third of the total human diet in tropical countries is derived from insect-pollinated plants (Crane and Walker, 1983), and even in Europe, many crops depend on insect, especially bee, pollination (Corbet, Williams, and Osborne, 1991; Delaplane and Mayer, 2000). However, only a few crops are totally dependent on animal pollination and only few clear examples of low crop yield resulting from pollinator limitation have been described (Richards, 2001). Despite their role as dominant pollen vectors, studies specific to bees in tropical Asia are rare, in contrast to the neotropics (Bawa et al., 1985; Roubik, 1993). In this paper, we experimentally examined the pollination systems of the lowland coffee (*Coffea canephora* Pierre ex Froehner, syn. *Coffea robusta*) and the highland coffee (*Coffea arabica* L.) and additionally observed the community of flower-visiting bees in 24 Indonesian coffee fields. We focussed on the following questions: (1) What is the relative importance of cross pollination and self-pollination for fruit set in the two coffee species? (2) Does wind pollination lead to pollen limitation in comparison with pollination

by insects? (3) Do the flower-visiting bee communities differ between the two coffee species?

To our knowledge, this is the first comparative study of pollination mechanism and the relative importance of wild bee communities for pollination and fruit set of *C. canephora* and *C. arabica*.

### MATERIALS AND METHODS

**Study species**—The lowland coffee (*Coffea canephora*, syn. *Coffea robusta*) and the highland coffee (*Coffea arabica*) are two widespread species. *Coffea canephora*, a self-sterile, diploid species, is reported to be primarily wind pollinated, but is also expected to benefit from bees for effective outcrossing and fruit set (Le Pelley, 1973; Crane and Walker, 1983; Willmer and Stone, 1989). *Coffea canephora* prefers low-altitude habitats, growing in sites where the more widespread *Coffea arabica* will not thrive. *Coffea arabica* is reported as a self-fertile, tetraploid species (Crane and Walker, 1983; Reddy, Raju, and Dharmaraj, 1988; Smith et al., 1992; Free, 1993). However, Raw and Free (1977) showed that caged honey bees (*Apis mellifera* L.) may almost double the yield of mature fruits in comparison to spontaneous self-pollination, and fruit retention also seems to be enhanced by outcrossing (Reddy, Raju, and Dharmaraj, 1988; Free, 1993; Roubik, 2002). Coffee is frequently visited by bees during flowering (McDonald, 1930; Nogueira-Neto, Carvalho, and Antunes, 1959; Raw and Free, 1977; Willmer and Stone, 1989; Klein et al., 2002).

**Flower morphology**—Flower morphology is similar in both species, although the flowers of *C. canephora* are bigger and there are more flowers in the axils of leaves, on average 8–20 flowers per axil for *C. canephora* and 2–12 for *C. arabica* (personal observation; Free, 1993). The flowers of both species have a five-segmented calyx and five white petals, the lower half of which are fused into a cylindrical, elongated corolla tube. There are five stamens with long anthers and short filaments inserted into the corolla, a long thin style with a two-branched stigma, and an inferior ovary of two chambers each containing one ovule. The stigma is receptive when a flower opens at dawn and the anthers dehisce soon afterwards. The disc surrounding the base of the style secretes nectar (Free, 1993).

**Study area**—The study was conducted from November 2000 to March 2001 in Central Sulawesi (Indonesia), at the margin of the Lore-Lindu National Park, 100 km northeast from the city of Palu, in the villages of Wuasa, Watumaeta, Alitupu, and Kaduwaa (1000–1200 m above sea level). We chose 24 different agroforestry coffee fields, which differed with respect to shade

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and vegetation. While *C. arabica* grew in all 24 fields, *C. canephora* was planted in only 15 fields.

**Pollination experiments and fruit set**—To examine the reproductive systems of *C. canephora* and *C. arabica*, we carried out six pollination experiments on open and bagged branches bearing dense and mature flower buds. For each of the six treatments we selected six different branches on each of four different coffee shrubs and replicated this in all 24 fields (96 branches for each of the six experimental treatments resulting in altogether 576 branches) for *C. arabica* and in 15 fields (60 branches for each treatment resulting in altogether 360 branches) for *C. canephora*. The six pollination treatments were as follows: (1) open pollination, in which all insects had access to flowers (insect pollination), but wind pollination was also possible; (2) wind pollination and spontaneous selfing were possible, insects were excluded by coarse mesh gauze; (3) cross pollination (between-plant pollination), hand pollination with pollen of several other plants; (4) self-pollination (within-plant pollination), hand pollination with pollen of the same plant, but from other flowers; (5) self-pollination, hand pollination with pollen of the same flower; (6) control (no pollination by external vectors), bagged flowers. Pollination by insects and wind was excluded, thereby testing for possible spontaneous self-pollination (autogamy). To manipulate wind pollination we bagged branches with cotton mesh gauze with 0.8–1.0 mm openings. For hand-pollination experiments very fine nylon mesh gauze (10  $\mu$ m) was used to avoid wind pollination, following Willmer and Stone (1989). We put sticky glue on the branch beneath the bagged flowers to eliminate crawling insects, especially ants. The bags were put in place 1–6 d before flowering. Flower numbers of the observed bagged and open branches were counted. One mesh bag included 6–12 flowers for *C. arabica* and 10–21 flowers for *C. canephora*. Thus we sampled about 864 flowers in each of the six pollination experiments for *C. arabica* (on average nine flowers on each of four branches selected in each of the 24 fields) and about 900 flowers in each of the six pollination experiments for *C. canephora* (on average 15 flowers on each of four branches selected in each of the 15 fields). Coffee started flowering usually 3–4 d after substantial rainfall and synchronously (all branches had open flowers at the same time) within individual plants. The flowering period finished after 3 d in *C. canephora*, whereas *C. arabica* had flowering periods of up to 7 d. In the hand-pollination experiments, pollen was transferred to stigmas with a brush on the first day of flower opening. Five weeks after the end of the flowering period, bags were removed from flowers and the number of green fruits per branch were counted for each treatment.

**Flower-visiting bees**—Abundance and species richness of flower visitors to the coffee bushes were observed from the end of December 2000 to the beginning of January 2001, in which period a substantial flush of flowers occurred. We observed flower visitors in each coffee field three times at three sequent days for 25 min on sunny days between 0900 and 1400. Only flower-visiting bees are included in this study, because other insects, such as butterflies and beetles, were extremely rare. After each 25-min observation period, bees were caught by sweep netting for another 5 min, for species identification in the laboratory. Social bees were identified with the help of a collection from Dr. Gard Otis, University of Guelph, Guelph, Ontario, Canada. Solitary bees were identified by Dr. Donald B. Baker, Hope Entomological Collections, Oxford University Museum of Natural History, Oxford, UK.

**Statistical analysis**—Statistical analysis of the data was performed using Statgraphics Plus 3.0 (Manugistics, 1997). When necessary, logarithmic or square-root-transformed variables were used to achieve a normal distribution. To compare the fruit set we used a multifactor analyses of variance with three variables (coffee fields, each coffee shrub observed, and the six pollination treatments). Fruit set did not differ between coffee fields ( $F = 0.98$ ,  $P = 0.478$  for *C. canephora*;  $F = 0.72$ ,  $P = 0.827$  for *C. arabica*) or coffee shrubs ( $F = 0.76$ ,  $P = 0.511$  for *C. canephora*;  $F = 0.37$ ,  $P = 0.773$  for *C. arabica*) but between pollination treatments. Therefore, only effects of pollination treatments are shown in the results section. We used the Scheffé test to separate significantly different groups (Sokal and Rohlf, 1995). To compare the means of species and individual numbers between *C. canephora* and *C. arabica* we

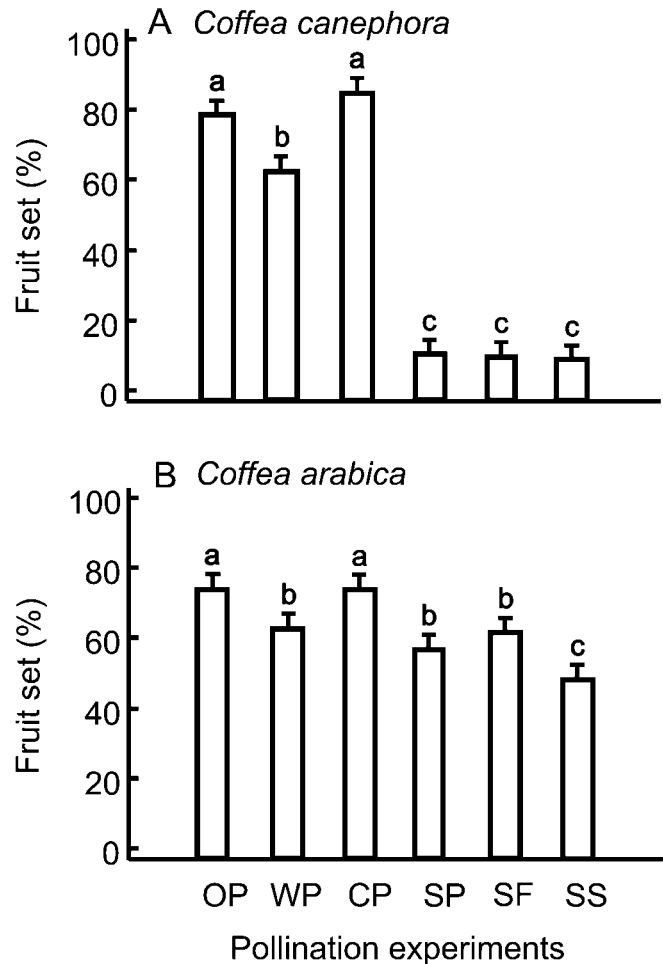


Fig. 1. Fruit set of *C. canephora* and *C. arabica* after different pollination treatments. Arithmetic means and pooled standard deviations are given. Different letters show significant differences between experiments. (A) Fruit set of *C. canephora*:  $df = 359$ ,  $F = 205.06$ ,  $P < 0.001$ ,  $N = 360$  branches in 15 sites (means + 1 SE). (B) Fruit set of *C. arabica*:  $df = 575$ ,  $F = 18.39$ ,  $P < 0.001$ ,  $N = 576$  branches in 24 sites (means + 1 SE). OP, open pollination (insects and wind); WP, wind pollination; CP, cross pollination (between-plant); SP, self-pollination (within-plant); SF, self-pollination (within-flower); SS, spontaneous selfing (control).

used the paired  $t$  test. To estimate the total bee species richness for each coffee field, we used the estimator ACE (abundance-based coverage estimator of species richness) with Estimate S, Version 5 (Colwell, 1997), which allows calculating species saturation curves in dependence on sample size.

## RESULTS

***Coffea canephora***—Fruit set for *C. canephora* was 78.1% in open pollination and 83.8% when flowers were hand pollinated with pollen of another plant (Fig. 1). There were no significant differences between hand pollination with pollen of another plant and open pollination, but wind pollination plus autogamy resulted in a significantly reduced 62.3% fruit set. Accordingly, bee pollination caused a 15.8% increase in fruit set, compared to wind pollination plus autogamy. Geitonogamous (within-plant) pollination resulted in 10.9% fruit set, autogamous (manual within-flower) pollination in 8.9% fruit set, and the control (insect and wind pollination excluded, so only autogamy was possible) in 8.7% fruit set. The latter three treat-

ments showed no significant differences. Cross pollination by hand resulted in a 75.2% higher fruit set than in the control, and open pollination in a 69.4% higher fruit set than the control (Fig. 1A).

***Coffea arabica***—The self-fertile *C. arabica* showed 75.2% fruit set in open pollination and 75% in manually cross-pollinated flowers (Fig. 1B). Wind pollination plus autogamy resulted in a significantly lower fruit set of 62.9%, so bee pollination accounted for a 12.3% increase in fruit set. Geitonogamy resulted in 57.5%, and manual pollination within flowers in 62.4% fruit set. Within these three treatments no significant differences were found, but fruit set of the control (autogamy, 47.9%) was significantly lower than all other treatments in *C. arabica*. We found 27% more fruit set in open pollination or cross pollination by hand as compared to the control (Fig. 1B). The comparison of both figures shows that differences between wind pollination (plus autogamy) and the control (autogamy) is much higher in *C. canephora* (53.6%) than in *C. arabica* (16%).

**Flower visitation**—We found 33 species and 2269 individuals of bees visiting *C. canephora* flowers within a 1125-min observation time (96.8% species saturation according to the ACE method; Colwell, 1997) and 29 species and 2038 individuals of flower-visiting bees in *C. arabica* within the 1800-min observation time (96.4% species saturation) (Appendix). Flowers of *C. canephora* were visited by significantly higher numbers of bee species than those of *C. arabica* in the 15 coffee fields where both species could be observed ( $T = -3.202$ ,  $P = 0.006$ ,  $N = 15$ ), and the number of bee individuals was also significantly higher in *C. canephora* ( $T = -3.418$ ,  $P = 0.004$ ,  $N = 15$ ). Total bee communities visiting the two coffee species differed of additional four solitary bee species observed at *C. canephora*, but not at *C. arabica* [*Amegilla* sp., *Chalicodoma* (*Callomegachile*) *incisum*, and two unidentified Halictidae], even though we sampled bees on *C. arabica* in nine additional fields. All other bee species were found on both coffee species. The same social bee species were found at *C. canephora* and *C. arabica* (Appendix). We found 231 more bee individuals in *C. canephora*, although we sampled in only 15 coffee fields, in comparison to the 24 coffee fields sampled for *C. arabica* (Appendix).

## DISCUSSION

The main finding of our study is that both coffee species profit from cross pollination by bees. Using an experimental approach on a large spatial scale we could quantify the relative contribution of bees and wind as pollen vectors as well as differences between self- and cross-pollinated plants. Fruit set of *C. canephora* was significantly more improved by cross pollination than fruit set of *C. arabica*, which showed a high degree of self-compatibility. The fruit set of *C. canephora* and *C. arabica*, following cross pollination by hand and by open pollination (insect and wind pollination), was significantly higher than fruit set of wind or manually self-pollinated flowers.

*Coffea canephora* is generally assumed to be a self-sterile wind-pollinated plant (Free, 1993), although indirect evidence of enhanced fruit set due to insect pollination exists (Le Pelley, 1973; Crane and Walker, 1983). A related study of Willmer and Stone (1989) confirm the self-sterility of *C. canephora* but

found a much lower importance of wind pollination. A possible reason could be the different weather conditions. In our study period the weather was unusually dry during the flowering time, which should enhance possible wind pollination. Although *C. arabica* is reported as a self-fertile species (Free, 1993), an increase of fruit set through cross pollination took place. The fact that some flowers produced fruits even in the absence of any external pollen vector (the control treatment) indicates that *C. arabica* may be amphicarpic, i.e., that some flowers need cross pollination, whereas others develop fruits even after spontaneous self-pollination (see Roubik, 1995; Raw and Free, 1977). Several authors have shown that cross pollination on *C. arabica* increases the amount of fruit set. The differences between cross pollination and spontaneous selfing differed in these studies: Taschdjian (1932) found a 54% higher fruit set in cross-pollinated *C. arabica*, Krug and Costa (1947) 10%, Carvalho and Krug (1949) 4%, and Reddy, Raju, and Dharmaraj (1988) a 17% higher fruit set compared to spontaneously self-pollinated flowers, so cross pollination appears to be generally important in *C. arabica*. However, these results are only based on hand-pollination experiments with bagged flowers or caged coffee plants and are not related to the effect of naturally occurring pollinator communities. In two studies, caged coffee shrubs with honey bees had a 52% higher fruit set than the control without caged honey bees (Nogueira-Neto, Carvalho, and Antunes, 1959; Raw and Free, 1977), and open-pollinated shrubs can lead to even higher fruit set (Raw and Free, 1977). The importance of the naturally occurring bee community for pollination of *C. arabica* has been shown in a recent study by Roubik (2002) in Panama, but it has not been shown before (Nogueira-Neto, Carvalho, and Antunes, 1959; Roubik, 2002).

We found a high diversity of flower-visiting bee species, with 33 species in *C. canephora* and 29 species in *C. arabica*. In Jamaica Raw and Free (1977) observed only four bee species visiting the flowers of *C. arabica*. In a recent study by Roubik (in press) in Panama, 22 flower-visiting bee species were observed on *C. arabica*. For *C. canephora* four bee genera, *Apis*, *Trigona*, *Creightonella*, and *Amegilla*, are described as frequent flower visitors in Papua New Guinea (Willmer and Stone, 1989). We also found these four genera, but also several other genera in Indonesia. Species richness and abundance of flower-visiting bees were higher in *C. canephora* than in *C. arabica*, which may be explained by differences in the floral biology. Both species have flowers with a strong smell, but in *C. canephora*, the flowers are much bigger and coffee shrubs produce more flowers. The high diversity of flower-visiting bees on coffee in our study compared to other studies may be explained by the absence of introduced honey bees, which are the dominant flower visitors on coffee in most other tropical regions (Roubik, 2002).

In general, self-sterile species benefit much more from cross pollination, especially by pollinating animals, than self-fertile species (Burd, 1994; Larson, Barrett, and Barrett, 2000). However, our results show that even fruit set of a self-fertile crop species can be improved by cross pollination. When we consider the potential increase of coffee harvest by improved management of pollinators, we have to take into account that optimal pollination of all flowers of a shrub may result in nutrient limitation within 1 yr or in the following year (Zimmerman and Pyke, 1988; Cambell and Halama, 1993). Cross-pollinated flowers per branch may receive more than their share of the plants resources, giving a higher fruit set per flow-

er than could be achieved if all the flowers per plant had been manually cross-pollinated. Second, fruit set in one pollination episode, or even in one year may be higher or lower than in further years (Zimmerman and Pyke, 1988). To show the full lifetime reproductive success of a specific plant, pollination experiments would have to be done with a whole plant over several pollination episodes, but this is rarely possible. Additionally, the high fruit set of open-pollinated flowers in our study suggests that at least within-year resource redistribution to the hand-pollinated branches did not play a significant role.

The self-sterility of *C. canephora* could be a result of genetically induced self-incompatibility, prezygotic self-incompatibility or of inbreeding depression after self-pollination. Genetical self-incompatibility seems unlikely, because this would lead to even lower fruit set upon selfing (generally to <5%, G. Ostermeijer, personal communication, 2002, Institute for Biodiversity and Ecosystem Dynamics, University of Amsterdam) and would also give a lower fruit set after cross pollination because of incompatibility of some donors. Therefore prezygotic self-incompatibility or strong inbreeding depression appears to be more likely.

In conclusion, the results indicate that both coffee species, although they differ in pollination biology, significantly profit from pollination through natural pollinators. This is of economic importance, and coffee farmers should therefore consider enhancement of bee populations as part of their coffee field management. This could be done by a reduced use of pesticides, by providing nesting sites for solitary bees, and by improving pollen and nectar availability for bees. Nesting sites could be improved by establishing earth banks for ground-nesting bees (Willmer and Stone 1989) and by preserving old shadow trees for bees using wood as nesting sites. Also trap-nests of reed internodes can provide nesting sites for several solitary bees (Tscharnke, Gathmann, and Steffan-Dewenter, 1998; Klein et al., 2002). Raw and Free (1977) suggested that coffee farmers should keep honey bee colonies in their fields during the flowering period to obtain greater yields. Other studies indicate that solitary bees are the more effective pollinators (Willmer and Stone, 1989; Klein et al., 2002). If solitary bees are the better pollinators, the introduction of honey bees should be considered carefully, because the introduction of social bees, at least of non-native honey bees, should lead to a decline of solitary bees. We suggest the improvement of coffee fields be achieved with more nesting sites for solitary bees, more open ground for ground-nesting bees, and old or dead trees for bees that use as nesting sites.

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APPENDIX. Flower-visiting bee species of *Coffea canephora* and *C. arabica*. Values are numbers of individuals seen within the observation time (1125 min for *C. canephora*, 1800 min for *C. arabica*).

| Flower-visiting bees                                 | No. <i>C. canephora</i> individuals | No. <i>C. arabica</i> individuals |
|--|-------------------------------------|-----------------------------------|
| <b>Social bees</b>                                   |                                     |                                   |
| <i>Apis cerana</i>                                   | 156                                 | 269                               |
| <i>Apis dorsata</i>                                  | 271                                 | 229                               |
| <i>Apis nigrocincta binghami</i>                     | 404                                 | 343                               |
| <i>Trigona (Heterotrigona) sp. 1</i>                 | 83                                  | 19                                |
| <i>Trigona (Heterotrigona) sp. 2</i>                 | 198                                 | 154                               |
| <i>Trigona (Lepidotrigona) terminata</i>             | 224                                 | 106                               |
| <i>Trigona</i> spp.                                  | 27                                  | 23                                |
| Total  | 1363                                | 1143                              |
| <b>Solitary bees</b>                                 |                                     |                                   |
| <i>Amegilla</i> sp. aff. <i>samarensis</i>           | 17                                  | 20                                |
| <i>Amegilla</i> sp. <i>zonata</i> -group             | 15                                  | —                                 |
| <i>Amegilla whiteheadi</i>                           | 47                                  | 37                                |
| <i>Chalicodoma (Callomegachile) terminale</i>        | 8                                   | 5                                 |
| <i>Chalicodoma (Callomegachile) incisum</i>          | 10                                  | —                                 |
| <i>Chalicodoma (Eumegachinana) tub. tuberculatum</i> | 35                                  | 28                                |
| <i>Ceratina (Ceratinidia) rugifrons</i>              | 20                                  | 26                                |
| <i>Coelioxys smithii</i>                             | 13                                  | 5                                 |
| <i>Creightonella frontalis atrata</i>                | 115                                 | 101                               |
| Halictidae 9   | 51                                  | —                                 |
| Halictidae 18  | 7                                   | —                                 |
| Halictidae 21  | 38                                  | 72                                |
| Halictidae 22  | 61                                  | 74                                |
| <i>Heriades</i> sp. 1                                | 161                                 | 113                               |
| <i>Heriades</i> sp. 2                                | 50                                  | 47                                |
| <i>Lipotriches</i> sp.                               | 13                                  | 67                                |
| <i>Megachile</i> sp. aff. <i>bakeri</i>              | 18                                  | 17                                |
| <i>Nomia (Thoraconomia) thoracica</i>                | 56                                  | 105                               |
| <i>Paracella</i> sp. 1                               | 27                                  | 21                                |
| <i>Paracella</i> sp. 2                               | 35                                  | 10                                |
| <i>Patellapis (Pachyhalictus) sp.</i>                | 3                                   | 15                                |
| <i>Thyreus nitidus quartinae</i>                     | 9                                   | 10                                |
| <i>Torridapis ducalis</i>                            | 17                                  | 24                                |
| <i>Xylocopa (Koptortosoma) aestuans</i>              | 22                                  | 33                                |
| <i>Xylocopa (Zonohirsuta) dejeanii</i>               | 45                                  | 53                                |
| <i>Xylocopa (Koptortosoma) smithii</i>               | 13                                  | 12                                |
| Total  | 906                                 | 895                               |