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Domestication of cardamom (*Elettaria cardamomum*) in Western Ghats, India: divergence in productive traits and a shift in major pollinators

Giby Kuriakose, Palatty Allesh Sinu and K. R. Shivanna*

Ashoka Trust for Research in Ecology and the Environment, 659, 5th 'A' Main, Hebbal, Bangalore 560 024, India

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• *Background and Aims Elettaria cardamomum*, a highly priced spice, is native to the Western Ghats of South India. Wild populations still occur in isolated patches in their natural habitats; however, much of today's commercial product comes from cultivated sources. There is no information on domestication-related traits of this species; the main objective of this study was to compare wild and cultivated populations of cardamom in terms of vegetative and reproductive features in order to identify domestication syndromes and to examine whether the two populations have developed reproductive barriers.

• *Methods* Two wild populations and five cultivated plantations were used for the present study. Vegetative and floral traits, flowering phenology, pollination biology and breeding systems of wild and cultivated populations were compared. Effective pollinators amongst floral visitors were identified by confirming pollen transfer as well as by fruit set following their visit to virgin flowers. Manual pollinations were carried out in order to study the breeding systems of the two populations and reproductive barriers, if any, between them.

• *Key Results* Several productive traits including the number of branches, number of inflorescences, and total number of flowers per clump, number of flowers that open each day, the duration of flowering, the length of the flower and the amount of nectar per flower are significantly greater in cultivated cardamom. The principal pollinators in wild cardamom are solitary bees, *Megachile* sp. and two species of *Amegilla*, whereas those in cultivated cardamom are the social bees *Apis dorsata*, *A. cerana* and *Trigona iridipennis*. Both the wild and cultivated populations are self-compatible and there are no reproductive barriers between the two populations.

• *Conclusions* Domestication in cardamom has brought about significant changes in vegetative and reproductive traits and a shift in effective pollinators from native solitary bees to social bees. The shift in pollinators seems to be due to the availability of a large number of flowers for prolonged periods in cultivated cardamom that can attract and sustain social bees, rather than due to co-evolution of the flower and the pollinator.

Key words: *Elettaria cardamomum*, wild cardamom, domestication, *Amegilla* sp., *Apis cerana*, *Apis dorsata*, *Megachile* sp., pollination efficiency, solitary bees, social bees.

INTRODUCTION

Domestication of plants has resulted in a wide range of morphological and physiological traits, referred to as the domestication syndrome, that distinguish domesticated crops from their wild ancestors. Extensive studies have been carried out on evolutionary relationships of domestication in several major crop species and their progenitors (Fuller, 2007; Pickersgill, 2007), and this has facilitated efficient exploitation of genetic resources of wild relatives (Hajjar and Hodgkin, 2007; Vaughan *et al.*, 2007). Wild populations of several domesticated species, such as *Elettaria cardamomum*, *Piper nigram*, *Piper longum*, *Myristica* spp. and *Zingiber officinale*, occur in their natural habitats in the Western Ghats of India. So far there have been no studies to understand domestication-related traits in these species.

Elettaria cardamomum (Zingiberaceae) is a highly priced spice, growing in mid-elevations (600–1300 m a.s.l.) in wet, evergreen forests of the Western Ghats. Use of cardamom fruits for medicinal and culinary purposes dates back to the second century BC. *Elettaria cardamomum* is native to the southern part of the Western Ghats and wild populations are confined to small, isolated pockets, spatially separated from cultivars by over 40 km. Cardamom is cultivated extensively in the hills of the Western Ghats of the Southern States: Kerala, Karnataka and Tamil Nadu. The area under cultivation is around 80 000 ha. No information on the reproductive biology of wild populations of cardamom appears to have been published; however, studies on pollination biology of cultivated cardamom (Belavadi *et al.*, 1997; Sinu and Shivanna, 2007) conducted in a few localities in the Western Ghats have reported that social bees, *Apis dorsata*, *A. cerana* and *Trigona iridipennis* are the pollinators. The first two harvest pollen as well as nectar whilst *T. iridipennis* harvests only pollen. As the corolla tube, where the nectar is located, is longer than the probosis of the bees, they can harvest only a part of the nectar available (Belvadi *et al.*, 1997). Amongst the three pollinators, the principal pollinators vary in different localities and also within the flowering season (Sinu and Shivanna, 2007). Here, a study is made of the reproductive biology of cardamom in two wild and five cultivated populations distributed over about 500 km along the Western Ghats. As domestication generally modifies productive traits that eventually lead to reproductive isolation, the focus of this study was to compare wild and cultivated populations in relation to flowering phenology, vegetative and floral features, and the breeding system in order to identify domestication-related

* For correspondence. E-mail: shivanna@atree.org

traits, and in order to study reproductive barriers, if any, between wild and cultivated populations. Effective pollinators in wild and cultivated populations were also studied to check whether domestication has resulted in any shift in pollinators.

MATERIALS AND METHODS

Study area

Two wild populations of *Elettaria cardamomum* (Table 1, Fig. 1), which are separated from each other by about 10 km aerial distance, and five cultivated cardamom plantations were used for the present study. Wild populations are located near tribal settlements at the Pooyamkutty–Idamalayar valley of the Ernakulam district. The density of plants in wild populations is generally low (about 30 clumps per 500 m^2), and they are often subjected to ecological disturbances such as damage from elephant herds, fallen trees/branches and forest fires. The density of plants in cultivated plantations is 108 clumps per 500 m^2. Four of the cultivated populations are located in different parts of Kerala state, the centre of origin of cardamom, which produces more than 70 % of its commercial product, and one in Karnataka state (Fig. 1). 'Njellani', a high-yielding variety that covers about 90 % of the cardamom-growing area in Kerala, and another variety, 'Mudigere-1' were used in the present study (Table 1).

Elettaria cardamomum is a large, perennial, herbaceous, rhizomatous monocot. The rhizome bears many leafy shoots, 4–5 m tall. Leaves are alternate, sessile, linear-lanceolate, and 30–90 cm long. The flowers are borne on long racemose panicles that originate from the rhizome. The most conspicuous part of the flower is the whitish lip/labellum located at the tip of the corolla tube. It has violet nectar guides leading to the corolla tube. The single fertile stamen bears bi-lobed anthers. The pistil is trilocular and each locule bears over 20 ovules with axile placentation. The style is filiform and terminates with a laterally compressed, cup-shaped stigma located slightly above the anther. The inner surface of the stigmatic cup is receptive and is lined with a viscous exudate. Several varieties of cardamom, developed largely through clonal selection, have been released commercially (Madhusoodanan *et al.*, 2002).

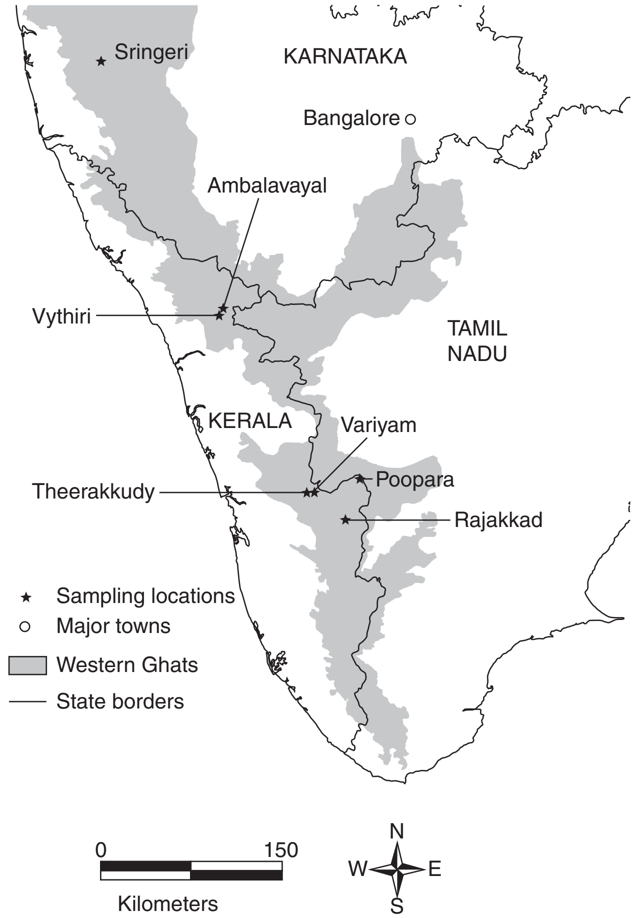

FIG. 1. Map showing study locations in Western Ghats, India.

Methods

Flowering phenology was studied throughout the flowering period (March–November, 2007 and 2008) through weekly field visits. During each visit the proportion of clumps that were in flower (all clumps from wild populations, 100 randomly tagged clumps from cultivated populations) were recorded (Dafni *et al.*, 2005). Since co-flowering species are likely to compete with cardamom for pollinators, other plant species that flowered along with cardamom were also recorded during each field visit. In order to study floral phenology such as flower opening (anthesis), anther dehiscence and floral senescence, the flower buds that would open the next morning ($n = 70$ and 110 for wild and cultivated populations, respectively) were tagged. The tagged flowers were monitored at 30 min intervals the next day from 0430 h until their senescence. Morphological details of wild and cultivated populations were compared by measuring vegetative and floral features with digital callipers. Earlier studies on nectar

TABLE 1. *Details of wild and cultivated populations used for the study*

Location	Latitude and longitude	Elevation (m)	Area of the population/ plantation (acres)	Ecological features	Population/variety
Theerakkudy	10°13′3·53″N, 76°47′58·81″E	655	~ 25	Undisturbed evergreen forest	Wild
Variyam	10°13′30·53″N, 76°51′21·63″E	1200	~10	Undisturbed evergreen forest	Wild
Rajakkad	10°1′08·84″N, 77°05′17·18″E	1097	33	Disturbed evergreen forest	Cultivated/'Njellani'
Poopara	10°08′21·40″N, 77°13′37·60″E	1626	50	Disturbed evergreen forest	Cultivated/'Njellani'
Vythiri	11°31′53·48″N, 76°03′17·2″E	869	44	Disturbed evergreen forest	Cultivated/'Njellani'
Ambalavayal	11°35′19·31″N, 76°10′06·54″E	770	3	Areca nut and coconut plantation	Cultivated/'Njellani'
Sringeri	13°29·332′N, 75°11·89′E	626	5	Areca nut plantation	Cultivated/'Mudigere-1'

secretion (G. Kuriakose *et al.*, unpubl. res.) showed that the maximum amount of nectar accumulates in the corolla tube by 1200 h; nectar volume was therefore compared in the wild and cultivated populations at 1200 h. For this, flower buds were bagged the evening prior to their opening in order to prevent insect visits, and buds were excised on the day of opening at 1200 h. The amount of nectar was estimated by using microcapillary tubes (5 μL; Drummond microcaps) and the concentration of sugar was estimtaed by using a portable refractometer (Model ABT-32, VEE GEE Scientific, Kirkland, WA, USA).

Flower visitors and pollinators were studied from observation locations selected randomly each day. Ten flowers of a clump, which were clearly visible from the observation location, were selected to study flower visitors. The frequency of visits and mode of foraging were recorded for each visitor. Observations on insect visits were made for a total of 88 h on 15 clumps for cultivars and 56 h on ten clumps for wild populations. Floral visitors were recorded as morphospecies and identified later. Effective pollinators were identified by confirming pollen transfer to the stigma as well as by fruit set following their visits to virgin flowers (sample numbers are given in Table 5). In order to study the pollination efficiency of each visitor, mature buds were bagged on the day prior to their opening and the next morning the bags were removed and the buds were kept under observation for floral visitors. Flowers were bagged after the visit of an insect. Pistils were excised from some of the flowers after 1800 h and their stigmas were observed under a stereomicroscope for the presence of pollen grains. The remaining flowers were left on the plant in order to record fruit set.

To assess pollination efficiency under open field conditions, flowers were randomly excised from different clumps after 1600 h, when the insect visits had ceased, and their stigmas observed under a stereomicroscope for pollen deposition. To study fruit set under open field conditions, flowers were randomly selected and marked with a tag; mature fruits were harvested and the number of seeds in each fruit was counted.

Manual pollinations were carried out in order to study the breeding system of both wild and cultivated cardamom. Both cross- (pollen from another clump) and self-pollinations (pollen from the same flower or another flower of the same inflorescence) were carried out. Some of the pollinated flowers ($n = 6–10$ for each treatment) were excised 24 h after pollination and used to study pollen germination and pollen-tube growth in the pistil using the aniline blue fluorescence method (Shivanna and Rangaswamy, 1992); the remaining flowers were left on the plants to record fruit set ($n = 40$ for wild populations and $n = 50$ for cultivars). Mature fruits were harvested and the number of seeds in each fruit were counted. In order to investigate probable autogamy, flower buds were bagged before anthesis ($n = 30$) and were left on the plant to record fruit set. Reproductive barriers between wild and cultivated populations were studied by carrying out reciprocal manual pollinations between wild and cultivated populations. Flowers from the plants used as the pollen source were excised in the early morning and were implanted in open agar plates. They were transported the same day to the other location(s) in order to carry out the reciprocal cross-pollinations; this transportation of pollen took 6–8 h, and pollen viability is not affected for up to 24 h (G. Kuriakose *et al.*, unpubl. res.). Pollinated flowers were bagged and kept under observation in order to record fruit set.

Statistical analyses

The Kruskal–Wallis test was used to compare the differences in vegetative and reproductive features, pollination efficiency and fruit set in flowers visited by different insects. The Mann–Whitney *U*-test was used to compare the differences in seed counts of self- and cross-pollinated flowers. All statistical analyses were carried out using the STATISTICA software (StatSoft, Inc.).

RESULTS

In wild populations, flowering was initiated in mid-April and continued up to mid-September with a peak in June–July. Flowering of many other forest species, such as *Vitex altissima*, *Terminalia paniculata*, *Terminalia travencorica*, *Drypetes* sp., *Schefflera stellata* (trees), *Psychotria thwaitesii*, *P. globicephala*, *Pavetta hispidula*, *P. indica* (shrubs), *Ophiorhiza* spp. and *Impatiens* sp. (herbs), was synchronized with the flowering of wild cardamom during the early flowering period. In the cultivars, flowering started by mid-March, soon after the summer rains, and extended until November. The peak of flowering in cultivated plantations was mid-May to August, which coincides with the peak of the monsoons. Many tree species, *Terminalia paniculata*, *Schefflera stellata*, *Meliosma pinnata*, *Mesua ferrea* and *Erythrina indica* flowered along with cardamom during April–May in the plantations located within evergreen forest mosaics (Table 1).

The number/length of all vegetative features was significantly higher in the cultivars when compared to wild cardamom (Table 2, Fig. 2A, B). Inflorescences in the wild populations spread horizontally on the ground and tended to become covered with leaf litter, resulting in the production of non-chlorophyllous fruits. The average number of flowers produced per clump (calculated using the data in Table 2) was estimated to be 2573 in wild cardamom, and 6751 in 'Mudigere-1' and 20 359 in 'Njellani'. As the wild populations were not managed, many herbs and grasses grew around the clumps and covered the inflorescences. Several floral traits such as the length of the flower, labellum, corolla tube, amount of nectar and concentration of sugar in the nectar were significantly greater in cultivated cardamom (Table 3).

Floral phenology was similar in both wild and cultivated cardamom. Flowers started opening by 0430 h and were fully open by 0530 h. Anthers dehisced between 0630 h and 0730 h. Flowers remained fresh until the end of the day and had started senescence by 1900–2030 h. The first sign of senescence was the initiation of bending of the anther–stigma column towards the labellum followed by closing of the petals. Eventually, the anther–stigma column touched the labellum, which curled inwards and wilted.

Pollinators and their efficiency

Details of pollinators and their frequency of visits in wild and cultivated cardamom are presented in Table 4. The

TABLE 2. *Comparison of some morphological features of wild and cultivated cardamom; values are means ± s.d.*

Character	Cultivated			Kruskal–Wallis
	'Njellani' (*n*)	'Mudigere-1' (*n*)	Wild (*n*)	
Number of leafy shoots per clump	53·34 ± 14·98 (50)	39·12 ± 5·82 (25)	14·75 ± 5·72 (44)	88·75***
Number of inflorescences per clump	60·85 ± 19·78 (80)	35·48 ± 4·38 (25)	14·84 ± 5·54 (44)	81·64***
Length of inflorescence (cm)	113·43 ± 25·15 (40)	70·69 ± 8·07 (35)	38·91 ± 10·52 (44)	77·29***
Number of cincinni† per inflorescence	26·83 ± 6·03 (40)	21·77 ± 2·59 (35)	18·09 ± 4·62 (44)	44·49***
Number of flowers produced per cincinni†	12·47 ± 5·1 (100)	8·74 ± 0·92 (50)	9·58 ± 3·21 (100)	1·93 ns
Number of flowers per clump at a given day in the peak flowering period	45·18 ± 20·94 (80)	(not available)	10·71 ± 3·26 (55)	61·5*** ‡

† A group of flowers that develop in successive nodes on the main axis of the inflorescence.
*** $P < 0{\cdot}00005$; ns, not significant.
‡ Mann–Whitney *U*-test.

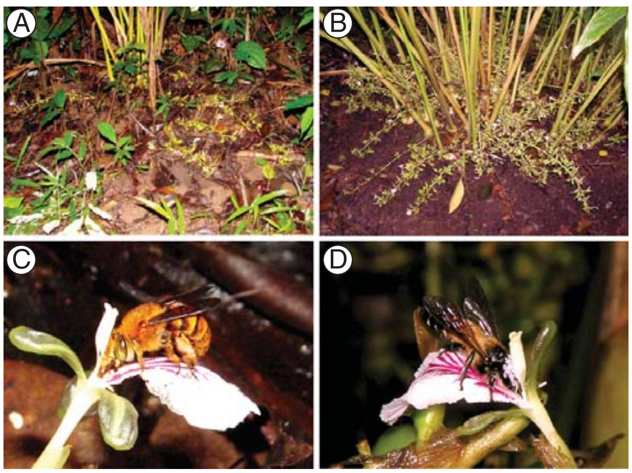

FIG. 2. (A) Basal part of a clump in a wild population. (B) Cultivated cardamom 'Njellani': the number of leafy shoots and inflorescences is much greater in comparison to (A). (C) One of the major pollinators, *Megachila* sp., harvesting nectar from a wild cardamom flower. (D) *Apis dorsata*, one of the major pollinators of cultivated cardamom, harvesting nectar; the pollen load on the forehead is clear.

principal pollinators of wild and cultivated populations tended to be mutually exclusive. While solitary bees were the exclusive visitors to wild populations, social bees were the dominant visitors to cultivated cardamom. In wild populations, *Megachile* sp. (Fig. 2C) and two species of *Amegilla* were the major pollinators. In addition, three species of butterflies (nectar foragers) and one species of syrphid fly (pollen forager) visited the flowers; however, they did not come in contact with the anthers and the stigma during foraging. Social bees (*Apis dorsata*, *A. cerana* and *Trigona iridipennis*) were found foraging the flowers of co-flowering plant species in the forests of wild populations; however, except for *A. cerana*, which visited cardamom flowers at very low frequency (Table 4), no other social bees visited wild cardamom. Even after flowering of other forest species ceased, social bees did not visit the flowers of wild cardamom either in the peak or late flowering periods.

Five species of bees, *A. dorsata* (Fig. 2D), *A. cerana*, *T. iridipennis*, *Amegilla* sp. 3 and *Xylocopa* sp., and two species of birds, *Nectarinia asiatica* (Purple Sunbird) and *Arachnothera longirostra* (Little Spiderhunter), were effective pollinators of cultivated cardamom (Table 4). However only two, *A. cerana* and *A. dorsata*, were the dominant visitors; the frequency of visits of other pollinators was very low and thus their role in pollination was minimal. During late flowering, there was no activity of *A. dorsata* in cultivated cardamom; this coincided with the maximum activity of *A. cerana*. Five species of butterflies (nectar foragers), one species of syrphid fly and a halictid bee (pollen foragers) visited cultivated cardamom flowers but none of them played any role in pollination.

The pollination success of different floral visitors of wild and cultivated cardamom is summarized in Table 5. Pollination efficiency and fruit set were comparable for all of the three effective pollinators of wild cardamom, and differences were not statistically significant. In cultivated cardamom, the pollination efficiency of the two bird species (Purple Sunbird and Little Spiderhunter) was very low when compared to bee visitors, and the differences were highly significant (Kruskal–Wallis: $H_{(4,195)} = 28{\cdot}40563$, $P < 0{\cdot}001$). On the basis of fruit set, *A. dorsata* was the most efficient pollinator (84 %).

Breeding system

Both self- and cross-pollinated pistils in wild as well as cultivated cardamom showed good pollen germination and pollen tubes reached the base of the style in 24 h. No significant differences in fruit set and seed count between self- and cross-pollinated flowers in wild and cultivated types were recorded (Table 6); thus, both wild and cultivated populations are self-compatible. Limited autogamy was observed in wild populations but none in cultivated populations (Table 6).

Reproductive barriers between wild and cultivated cardamom

There was no reproductive barrier between wild and cultivated populations. The extent of fruit and seed set in reciprocal crosses between wild and cultivated populations (Table 6) was comparable to the controls (wild × wild and cultivated × cultivated), and were not significantly different.

DISCUSSION

Domestication generally leads to changes in many productive traits in crop species when compared to their wild progenitors (Colunga-GarcíaMarín *et al.*, 1996; Colunga-GarcíaMarín and

TABLE 3. *Length (cm) of floral parts of wild and cultivated cardamom, and nectar volume and sugar concentration*

	Wild ($n = 22$)	Cultivated: 'Njellani' ($n = 25$)	Cultivated: 'Mudigere1' ($n = 30$)	Kruskal–Wallis test
Whole flower	4·45 ± 0·22	4·65 ± 0·18	4·31 ± 0·20	26·4**
Bract	1·84 ± 0·15	1·94 ± 0·14	1·82 ± 0·09	8·88*
Sepal	1·33 ± 0·09	1·58 ± 0·25	1·46 ± 0·09	21·95**
Lip/labellum	2·07 ± 0·43	2·30 ± 0·11	2·3 ± 0·14	12·85**
Petal	1·18 ± 0·06	1·20 ± 0·08	1·19 ± 0·06	1·31 ns
Anther	5·48 ± 0·48	5·92 ± 0·24	5·44 ± 0·17	27·35**
Stamen	8·50 ± 0·44	8·72 ± 0·41	8·66 ± 0·14	4·97 ns
Corolla tube	2·2 ± 0·09	2·29 ± 0·14	2·19 ± 0·03	14·654**
Stigma	0·85 ± 0·09	0·87 ± 0·05	0·82 ± 0·04	13·25**
Style	2·89 ± 0·13	2·75 ± 0·10	2·77 ± 0·05	20·62**
Pistil	3·27 ± 0·12	3·37 ± 0·13	3·73 ± 0·10	53·20**
Ovary	0·34 ± 0·03	0·34 ± 0·04	0·34 ± 0·05	0·58 ns
Nectary	0·32 ± 0·03	0·32 ± 0·02	0·33 ± 0·04	0·32 ns
Nectar volume (μL)	3·5 ± 1·04	5·2 ± 0·86	5·2 ± 0·8	42·3**
Sugar concentration in nectar (%)	31·75 ± 0·42	36·33 ± 2·34	(not available)	2* †

* $P < 0{\cdot}05$; ** $P < 0{\cdot}005$; ns, not significant.
† Mann–Whitney *U*-test.

TABLE 4. *Frequency of visits of pollinators (mean per flower h^{-1}) in wild and cultivated cardamom ('Njellani') during the various flowering periods*

Flower visitor	Wild: Early ($n = 20$)	Wild: Peak ($n = 30$)	Wild: Late ($n = 20$)	Cultivated: Early ($n = 20$)	Cultivated: Peak ($n = 70$)	Cultivated: Late ($n = 20$)
Megachile	1·8	3·2	1·5			
Amegilla sp1	0·6	2·9	0·7			
Amegilla sp2	0·4		0·3			
A. cerana	0·3			2·4	2·1	3·9
A. dorsata				0·2	1·8	
Amegilla sp3					0·1	0·04
Xylocopa verticalis †					0·1	
Trigona iridipennis				0·2	0·01	0·03
Nectarinia asiatica (Purple Sunbird) †					0·03	
Arcachnothera longirostra (Little Spiderhunter) †				Not available		

† Recorded only at the Ambalawayal plantation.

TABLE 5. *Pollination efficiency of each pollinator and resulting fruit set in wild and cultivated cardamom ('Njellani')*

Visitors	Wild: % of pollinated flowers (n)	Wild: % of fruit developed (n)	Cultivated: % of pollinated flowers (n)	Cultivated: % of fruit developed (n)
Megachile spp.	94·0 (38)	73·7 (41)		
Amegilla sp1	83·4 (60)	69·3 (36)		
Amegilla sp2	82·6 (58)	61·8 (37)		
A. cerana			77·6 (58)	56·7 (30)
A. dorsata			na	84 (25)
Amegilla sp3			77 (38)	64·7 (17)
Xylocopa verticalis			65 (56)	60 (20)
Nectarinia asiatica (Purple Sunbird)			26 (28)	na
Arcachnothera longirostra (Little Spiderhunter)			22 (10)	na
Open pollination		67·9 (78)		73 (100)

na, data not available.

May-Pat, 1997; Casas *et al.*, 1999, 2007). Spontaneously occurring mutations in productive traits provide genetic variations that have been selected by farmers during domestication (Bai and Lindhout, 2007). Continued divergence in reproductive traits eventually leads to reproductive isolation between the wild and cultivated populations (de Nettancourt, 2001;

TABLE 6. *Details of fruit and seed set for different pollination treatments in wild and cultivated cardamom; mean ± s.d.*

Population type	Mode of pollination	% fruit set (n)	Number of seeds (n)
Wild	Cross-	80 (35)*	16·70 ± 5·62
	Self -	74·3 (35)*	18·28 ± 5·50
	Autogamy	6·7 (30)	0·63 ± 2·12
	Wild × cultivated	82·14 (28)*	16·2 ± 3·93
Cultivated	Cross-	78 (50)	11·82 ± 6·58
	Self-	70 (50)	10·76 ± 5·8
	Autogamy	0 (30)	
	Cultivated × wild	80·77 (26)*	13·33 ± 3·53

* Number of flowers that could be scored for fruit and seed set: the remaining flowers (i.e. difference from the *n* given in the Methods) could not be located again because of disturbances by animals and/or damage by infection.

see also Widmer *et al.*, 2009). In *E. cardamomum*, domestication has increased the number of branches and the number of inflorescences per clump, which have resulted in a significant increase in the total number of flowers per clump. The number of flowers that open on a given day and the duration of the flowering are also markedly higher/longer in cultivated varieties than in wild cardamom. These features have obviously resulted in a significant increase in fruit yield in the cultivars.

The present study has shown that many of the changes in productive traits in domesticated cardamom have played a major role in bringing about a shift in principal pollinators. Wild populations depend largely on solitary bees, while the cultivated plantations depend on social bees for pollination services. *Megachile* sp. and two species of *Amegilla* are the principal (and efficient) pollinators of wild cardamom; neither of these species has previously been reported to be a major pollinator of cardamom. We never observed *A. dorsata*, one of the effective pollinators of cultivated cardamom, visiting wild cardamom. *Apis cerana* visited flowers of wild cardamom very rarely, and then only during the early flowering; thus, its contribution to the pollination of wild cardamom was negligible. Although social bee species visited the flowers of many other co-flowering forest species in large numbers during the early cardamom flowering season, they were not regular visitors of wild cardamom flowers. Even after flowering of other forest species ceased, *A. cerana*, *A. dorsata* and *T. iridipennis* were not attracted to the floral resources offered by the wild cardamom. Pollination efficiency of wild cardamom under field conditions was quite high and was comparable to that of cultivated cardamom; thus the native wild bee community provided adequate pollination services without the intervention of social bees (see also Kremen *et al.*, 2002).

In cultivated cardamom, the principle pollinators were the social bees *A. cerana* and *A. dorsata*. Although a few other species visited flowers of cultivated cardamom, their frequency was very low (see Table 4), and thus their contribution to pollination success was limited. Earlier studies have also recorded only social bees as effective pollinators of cultivated cardamom in the Indian subcontinent (Belavadi *et al.*, 1997; Klein *et al.*, 2007; Sinu and Shivanna, 2007). The present study, however, has established the role of another social bee, *Xylocopa verticalis*, and two bird species (Purple Sunbird and Little Spiderhunter) as pollinators of cultivated cardamom, although to a limited extent. To our knowledge, there are no previous reports of changes in principal pollinators following domestication (Arias-Coyotl *et al.*, 2006; Oaxaca-Villa *et al.*, 2006; Casas *et al.*, 2007).

The replacement by social bees as the principal pollinators in cultivated cardamom, compared with solitary bees in wild cardamom, has occurred without there being a change in basic floral architecture. This shift appears to be the result of the enormous increase in the population size of cultivated cardamom, with a higher density of plants and the availability of significantly greater numbers of flowers over a longer period. These features markedly increase the visibility of flowers and help to attract and sustain social bees. The native solitary bees have been significantly reduced in cultivated cardamom plantations, either due to competition from social bees or because of the high level management in the plantations.

In many species domestication has resulted in a change from self-incompatibility to self-compatibility (see de Nettancourt, 2001), for example, in *Polaskia chichipe*, a columnar cactus, domestication has increased the extent of self-compatibility (Otero-Arnaiz *et al.*, 2003); self-pollination in wild populations was successful only in 12 % of flowers, while in *in-situ* managed and cultivated populations it increased to 22–27 %. However, in cardamom domestication has not modified the breeding system: both wild and cultivated populations are self-compatible. This may be an adaptation to achieve satisfactory fruit and seed set in spite of prevailing geitonogamy. The pollinators tend to move from one flower to the next in the same clump and bring about geitonogamy. Cross-pollination takes place only when they visit flowers of another clump. Thus the number of flowers that get cross-pollinated, and hence set fruits, would be significantly limited if the species were to be self-incompatible.

The wild and cultivated populations have not developed reproductive barriers, as revealed through the results of controlled pollinations. However, there is no pollen flow between the two populations due to spatial isolation. Even in the absence of spatial isolation, pollen flow between wild and cultivated cardamom is unlikely since the principle pollinators of the two populations are different. Unlike many other species that have been domesticated for many centuries, domestication of cardamom is comparatively recent and is only about 200 years old (Anon., 2008). It appears that this limited period of domestication may not have been sufficient to develop reproductive barriers between the wild and cultivated populations. The results of this study highlight the need for similar research on many other domesticated crop species and their progenitors in the Western Ghats in order to have a better understanding on the domestication syndrome.

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