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from the deeper layers of soil and is influenced by better root penetrability. The same inference is reflected from the studies of several scientists¹⁰⁻¹⁵. Selection for root traits is arduous conventionally since it needs destructive sampling of the plants. As the expression of root characters is below the ground, the selection may not be much easier than that of the other characters which are above-ground level. Breeding varieties for improved roots is difficult because root traits are quantitative and have low heritability. Molecular markers can be used to identify linkage to quantitative trait loci (QTL) for rooting ability and these can be selected more easily in a breeding programme than the traits themselves¹⁶. Tagging of markers like BH14 and RM201 for traits conferring drought resistance, especially root-related traits helps in generating tools for marker-assisted selection, which in turn helps in accelerating crop improvement.

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Breeding systems and pollination modes of understory shrubs in a medium elevation wet evergreen forest, southern Western Ghats, India

M. Soubadra Devy¹ and Priya Davidar^{2,*}

¹Ashoka Trust for Research in Ecology and the Environment (ATREE), Hebbal, Bangalore 560 024, India

²Salim Ali School of Ecology and Environmental Sciences, Pondicherry University, Kalapet, Pondicherry 605 014, India

This study on the reproductive biology and pollination modes of 22 species of understory shrubs in 11 families was conducted in a medium elevation wet evergreen forest in the southern Western Ghats of India from 1994 to 1997. We evaluated whether this assemblage was predominantly outcrossing as in other tropical forests, and whether mating systems are related to pollination mode. We assessed whether species were hermaphrodites, dioecious or monoecious. We assessed the breeding systems of each species with hand self-pollinations. About 55% of the species produced small white and inconspicuous flowers. The majority of the flowers opened at dawn and was visited by diurnal pollinators. The proportion of dioecious and monoecious species was lower than for other tropical forests. Among the hermaphrodites, the majority had mixed mating systems. Therefore the overall levels of obligate outcrossers (37%) were low compared with other tropical forests. We recognized 7 pollination modes: social bees, solitary bees, diverse insects, flies, sunbird, sphingid moth and *Xylocopa* sp. Among these the social bees, flies and diverse insects visited more species than the other groups. Species pollinated by flies and diverse insects tended to be significantly more outcrossing than those pollinated by bees and other solitary pollinators.

Keywords: Breeding systems, India, pollination mode, shrubs, Western Ghats.

INFORMATION on the sexual and breeding systems of tropical plants is important for understanding speciation processes in tropical forests and for the conservation of tropical biodiversity¹⁻⁵. Data on the sexual and breeding

*For correspondence. (e-mail: pdavidar@yahoo.com)

systems of plants in different tropical forests is required in order to understand the selection pressures underlying the evolution of sexual and mating systems²⁻⁷. Sexual systems describe whether a plant is a hermaphrodite, monoecious or dioecious, whereas breeding or mating system assesses whether a hermaphroditic species is self-compatible or self-incompatible.

Studies have suggested that the levels of monoecy and dioecy in plant species are similar across Neotropical lowland forests⁸, but higher in Neotropical montane forests⁷. Species with unisexual flowers and hermaphrodites with self-incompatible flowers rely on pollen vectors to set seed. Hence these species tend to be predominantly outcrossing. Studies have shown that a large majority of plants in tropical forests are obligate outcrossers³⁻⁵, and therefore loss of pollinators could result in reproductive failure. Pollinators have differential effects on pollen flow. Long distance pollinators would move pollen across larger distances than territorial pollinators. Therefore understanding the reproductive systems of tropical plants and their pollination mode is important for the management of tropical biodiversity.

The relationship between pollination mode, species adapted for pollination by a particular pollinator group, and mating systems of the plants need further investigation. Bawa⁸ noted an association between dioecy and insect pollination. Levri⁹ has shown that the ecological factors such as time of pollination could affect the mating system of a plant, and Sobrevila and Arroyo⁷ suggested that pollinator reliability could select for self-compatibility in species in montane habitats where pollinators are scarce and inactive.

In this study conducted between 1994 and 1997 in a mid-elevation wet evergreen forest in the southern Western Ghats, India, we assessed the pollination mode and reproductive systems of 22 species of understory shrubs belonging to 11 families. We assessed whether species are predominantly outcrossing as in other tropical forests, and whether mating systems are related to ecological factors such as pollination mode.

The study site, Kakachi is a mid-elevation wet evergreen forest located at lat. 8°32'N and long. 77°23'E and altitude 1250 m amsl in the Kalakad–Mundanthurai Tiger Reserve of the Agastiyamalai range, southern Western Ghats. This region represents the southernmost limit of the evergreen forest continuum of the Western Ghats and is recognized as a center of plant diversity and endemism¹⁰.

Kakachi receives rainfall from the SW and the NE monsoon winds. The average annual rainfall is between 1500 mm and 3400 mm (BBTC rain gauge, Nalmukku, about 2 km from study site). The peak rainfall is during the NE monsoon. There are two dry seasons, a long dry season from March to May and short spell in September–October.

The forest type at Kakachi has been classified as the *Cullenia–Mesua–Palaquium* series¹¹. More than 50 species

of shrubs have been recorded from this site^{12,13}. The dominant families were Rubiaceae, Acanthaceae and Euphorbiaceae. Large stretches are dominated by species of the *Strobilanthes* complex, a monocarpic group.

Twenty two common understory shrub species that flowered during the study period 1994–1997 were chosen for the study and tagged. Species with sparse flowering, or where only a few individuals flowered, were excluded.

Flowers were classified based on their length as small (<10 mm), medium (10 to 20 mm) and large (>20 mm). The shape and colour of flowers were noted and length measured. Their sexual system, whether hermaphroditic, monoecious or dioecious, was determined by dissecting flowers from different individuals of each species. Time of anthesis was recorded by marking mature buds and observing the time at which the buds open.

Observations on flower visitors were made through the day and sometimes at dusk, and casual observations on the pollinators visiting the flowers were also recorded. Only those species coming in contact with the anthers and stigma were recorded as pollinators. Common visitors were identified by sight and unfamiliar visitors were collected for later identification. Plant species were assigned to particular pollination mode based on major flower visitors and floral characters.

More than 5 plants per species were selected for the hand pollination experiments and for assessments of natural fruit set. In the case of rare species or species that flowered rarely, <3 plants were used for the study. More than 30 flowers were selected per plant.

Autogamy was tested by hand pollination with pollen from the same flower. A branch in each plant was bagged in the evening and all the open flowers were hand pollinated the next morning. For species exhibiting nocturnal or crepuscular anthesis, hand pollination was carried out in the evening. The flowers were individually tagged and were re-bagged and fruit set was scored at fortnightly intervals. Species were classified as self-incompatible if <10% of the flowers hand pollinated with self pollen set fruit, partially compatible if 10 but 33% and as self-compatible or autogamous if > 33% set fruit. Natural fruit set under open pollination was determined by tagging flower buds and recording fruit set at maturity.

Due to small sample sizes for each category of breeding systems, we classified species that were self-compatible as inbreeding and the others as predominantly outcrossing. We assessed whether breeding systems tended to be associated with particular pollination mode compared with inbreeding species.

A total of 22 species were monitored in the study area. About 55% (12 species) of plants produced small, white or dull coloured flowers, of which 4 belonged to the family Euphorbiaceae and the rest to other families (Table 1). Large and medium-sized flowers were produced predominantly by the Acanthaceae and Rubiaceae (Table 1). The flowers of 19 (86%) species opened at dawn and

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Table 1. Floral characteristics, sexual and mating systems and pollination modes of 22 species of understorey shrubs at Kakachi

Species	Family	Sexual system	% Fruit set (N) self-pollen	Breeding system	% Fruit set (N) natural	Flower size	Flower colour	Flower anthesis time	Pollination mode
<i>Agrostistachys indica</i> Dalze	Euphorbiaceae	D	0 (85)*		42 (54)	Small	White	Dawn	Social bees
<i>Ardisia paucifolia</i> Heyne ex. Roxb.	Myrsinaceae	H	1 (399)	SI	2 (331)	Medium	White	Dawn	Solitary bee
<i>Chassalia curviflora</i> (Wall. ex. Kurz) Thw.	Rubiaceae	H	9 (431)	SI	22 (403)	Medium	White	Dawn	Diverse insects
<i>Croton zeylanicus</i> Muell.-Arg.	Euphorbiaceae	M	0 (59)		50 (63)	Small	White	Dawn	Diverse insects
<i>Didyplosandra lurida</i> (Wight) Bremek.	Acanthaceae	H	51 (58)	SC	62 (82)	Large	Purple	Dawn	Sunbirds
<i>Diotocanthus grandis</i> (Bedd.) Benth. ex Clarke	Acanthaceae	H	26 (52)	PC	15 (124)	Large	Pink	Dawn	Diverse insects
<i>Erythroxylum obtusifolium</i> (Wight) Hook. f.	Erythroxylaceae	H	31 (61)	PC	64 (62)	Small	White	Morning	Xylocopa
<i>Euonymus crenulatus</i> Wall. ex. Wight & Arn.	Celastraceae	H	17 (437)	PC	41 (170)	Small	Maroon	Dawn	Social bees
<i>Goldfussia tristis</i> Wight	Acanthaceae	H	82 (89)	SC	76 (536)	Medium	White	Dawn	Social bees
<i>Lasianthus cinereus</i> Gamble	Rubiaceae	H	38 (83)	SC	78 (46)	Medium	White	Dawn	Social bees
<i>Leptacanthus rubicundus</i> Nees in Wall.	Acanthaceae	H	78 (90)	SC	70 (844)	Large	White	Dawn	Social bees
<i>Litsea</i> sp.	Lauraceae	D	0 (190)*		7 (230)	Medium	White	Dawn	Social bees
<i>Lycianthes laevis</i> (Dunal) Bitter	Solanaceae	H	22 (280)	PC	55 (156)	Small	White	Dawn	Xylocopa
<i>Micrococca beddomei</i> (Hook.f.) Prain	Euphorbiaceae	D	14 (70)*		38 (39)	Small	Dull	Dawn	Flies
<i>Microtropis stocksii</i> Gamble	Celastraceae	H	31 (61)	PC	64 (40)	Small	Maroon	Dawn	Flies
<i>Ophiorrhiza grandiflora</i> Wight	Rubiaceae	H	43 (158)	SC	88 (86)	Large	White	Evening	Sphingid moths
<i>Phyllanthus fimbriatus</i> (Wight) Muell.-Arg.	Euphorbiaceae	M	19 (103)		62 (51)	Small	Dull	Dawn	Flies
<i>Polygala arillata</i> Buch.-Ham. ex. D. Don	Polygalaceae	H	5 (218)	SI	27 (125)	Medium	Yellow	Afternoon	Xylocopa
<i>Psychotria anamallayana</i> Bedd.	Rubiaceae	H	4 (85)	SI	55 (137)	Small	White	Dawn	Diverse insects
<i>Saprosma corymbosum</i> Bedd.	Rubiaceae	H	23 (217)	PC	53 (385)	Small	White	Dawn	Flies
<i>Sarcandra chloranthoides</i> Gard.	Chloranthaceae	H	4 (391)	SI	32 (354)	Small	Dull	Dawn	Flies
<i>Symplocos wynadense</i> (Kuntze) Nootb.	Symplocaceae	H	15 (179)	PC	46 (63)	Small	White	Dawn	Diverse insects

*H, Hermaphrodite; M, Monoecious; D, Dioecious.

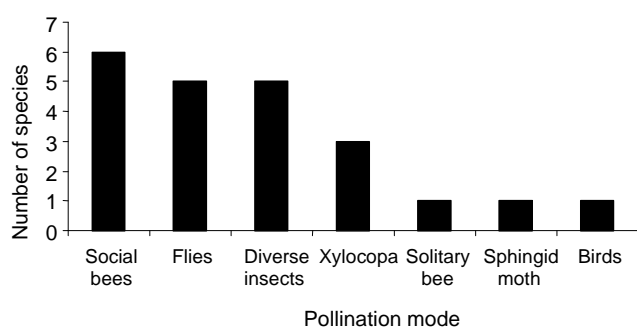


Figure 1. Number of species within each pollination mode at Kakachi.

were visited by diurnal pollinators. *Ophiorrhiza grandiflora* flowers visited by crepuscular sphingid moths opened in the evening and *Polygala arillata* flowers visited by *Xylocopa* bees opened in the afternoon (Table 1).

Of the 22 species, 17 were hermaphrodites, three were dioecious (14%) and two (9%) monoecious. Among the

hermaphrodites, 5 (29%) were self-compatible, 5 were self-incompatible (29%) and 7 (41%) were partially self-compatible (Table 1). If the self-incompatible species and dioecious species were combined, 37% of the species would be obligate outcrossers. This would increase to 45% if monoecious species were also included.

All species belonging to the Euphorbiaceae were either monoecious or dioecious. All the Acanthaceae were self-compatible whereas all three categories were represented among the Rubiaceae. This indicates that sexual and breeding systems could be a family level feature in certain cases.

We recognized 7 pollination modes among which social bees, flies and diverse insects were common pollinators in the study site (Figure 1).

Fruit set under natural conditions varied from 2% in *Ardisia pauciflora* to 88% in *Ophiorrhiza grandiflora*. Certain species such as *Diotocanthus grandis*, *Ardisia pauciflora* and *Litsea* had low levels of natural fruit set (Table 1).

Table 2. Relationship between breeding systems and pollination modes for 22 species of understorey shrubs at Kakachi ($G = 7.26$, $df = 1$, $p < 0.01$)

Pollination mode	Self-compatible	Partially compatible	Outcrossing
Flies	0	2	3
Social bees	3	1	2
Diverse insects	0	2	3
Solitary foragers	2	2	2

To increase sample sizes within the categories, we pooled pollination modes. Species pollinated by flies and diverse insects tended to be more outcrossing, so we pooled these two categories and compared them with those visited by social bees and other miscellaneous pollinators that tended to be more self-compatible. Species pollinated by flies and diverse insects tended to be significantly more outcrossing than those pollinated by bees and other solitary pollinators (Table 2: G test = 7.26, $df = 1$, $p < 0.01$).

We have assessed the sexual and breeding systems of 22 species of understorey shrubs in a medium elevation wet forest in the southern Western Ghats, out of a total of 59 species recorded in the study site^{12,13}. Our study shows that by comparison with other tropical forests the proportions of dioecious and self-incompatible species are lower. Dioecy is estimated to range from 16 to 25% for woody species^{6,8,14,15}, and the majority of hermaphrodites in low elevation tropical forests were found to be self-incompatible^{2-6,16}. This suggests that tropical plant species are mostly outcrossing. However, among the shrub assemblage studied at Kakachi, the overall outcrossing rate, including self-incompatible and dioecious species comprised about 36% and the majority of the hermaphrodites had mixed mating systems with partial self-compatibility.

Kakachi is a medium elevation site where most pollinators except for the eusocial *Apis* spp. are scarce. Species richness of butterflies was lower in Kakachi than for other lowland sites in the Western Ghats¹⁷. The small sunbird (*Nectarinia minima*), which is an important pollinator of certain group of plant species, is an altitudinal migrant and occurs only during summer months^{18,19}. The fruit bats, which are also known to be pollinators of many species, were very rare in the site^{20,21}. The mixed mating system among the understorey community could be a back up mechanism to compensate for the sporadic visits by many of the pollinators.

The social bees tend to form a high proportion of the visitors to the shrubs as for the canopy trees²². One unique feature of this shrub assemblage is the high proportion of the mass flowering monocarpic species belonging to the Acanthaceae. These species were *Didyplosandra lurida*, *Goldfussia tristis* and *Leptacanthus rubicundus*. These large synchronized floral displays attracted the social bees, which are important pollinators in this region^{22,23}. The social bees were drawn to understorey in great num-

ber only during the mass flowering of the Acanthaceae. The frequency of visits to the other understorey species such as *Euonymus crenulatus* and *Agrostistachys indica* Dalze was rare and erratic (Devy, personal observation).

Solitary foragers such as sunbirds, *Xylocopa* bees and sphingid moths also formed a significant proportion of the understorey pollinator assemblage. In other tropical forest sites the understorey assemblage consisted mostly of solitary trap lining foragers that followed a distinct route and visited few flowers per plant^{15,24-26}.

Pollinator foraging behaviour^{3,27} and their life history traits may be an important selective factor on the breeding systems of the tropical forest trees. Kress²⁸ observed that a greater proportion of hummingbird pollinated *Heliconia* spp. were self-compatible. He noted that outcrossing is ensured in *Heliconia*, because of low floral output and the tendency of traplining hummingbird species to visit just a few flowers. Therefore selection may not have favoured self-incompatibility. Species visited by diverse insects and flies tend to be more outcrossing than those visited by bees and more specialized visitor. The assemblage visited by flies and diverse insects produced inconspicuous small flowers with very little reward. Social bees and *Xylocopa* sp. because of their higher energetic demand trapline and visit many plants, in the process carrying lots of cross pollen. The flies and other small pollinators show low inter-plant movement and therefore may not transfer pollen as effectively to other plants, so obligate outcrossing mechanism could have evolved to counter clogging of stigma with self-pollen.

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