Mating system and seedling growth of five tropical tree species

Sistema reprodutivo e crescimento de mudas de cinco espécies arbóreas tropicais

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Resumo

Um estudo foi feito para determinar o sistema reprodutivo de três espécies arbóreas tropicais entomófilas e duas espécies ornitófilas através de cruzamentos controlados e seu impacto sobre a germinação das sementes. As espécies selecionadas foram *Bombax ceiba*, *Erythrina stricta* (ambas ornitófilas), *Lagerstroemia speciosa*, *Mesua ferrea* e *Schima wallichii* (todas entomófilas). O índice do valor de auto-incompatibilidade (ISI) para as distintas espécies foi de 0,00 para *B. ceiba*, 0,04 para *E. stricta*, 0,62 para *L. speciosa*, 0,60 para *M. ferrea* e 0,48 para *S. wallichii*. Os resultados revelaram que *B. ceiba* e *E. stricta* são espécies auto-incompatíveis, enquanto *L. speciosa*, *M. ferrea* e *S. wallichii* são parcialmente auto-incompatíveis. As sementes produzidas por polinização controlada resultaram em maior germinação de sementes seguidas das sementes desenvolvidas por polinização aberta em todas as espécies estudadas.

Palavras-chave: Sistema reprodutivo, auto-fecundação, fecundação cruzada, fertilização floral, depressão de endogamia.

Abstract

This study was conducted to estimate breeding system through controlled crosses and its impact on seed germination percentage of three entomophilous and two ornithophilous tropical woody taxa. The taxa selected were *Bombax ceiba*, *Erythrina stricta* (both ornithophilous), *Lagerstroemia speciosa*, *Mesua ferrea* and *Schima wallichii* (all entomophilous). The index of self incompatibility (ISI) value for different species was 0.00 for *B. ceiba*, 0.04 for *E. stricta*, 0.62 for *L. speciosa*, 0.60 for *M. ferrea* and 0.48 for *S. wallichii*. The results revealed that *B. ceiba* and *E. stricta* are self incompatible species whereas *L. speciosa*, *M. ferrea* and *S. wallichii* are partially self incompatible. The seeds produced from controlled cross-pollination proclaimed highest seed germination followed by the seeds developed through open pollination in all the study species.

Keywords: Breeding system, selfing, outcrossing, flower fertilization, inbreeding depression.

INTRODUCTION

High species richness with low population density is one of the characteristic features of tropical forests (APPANAH, 1981; BAWA et al., 1985). The mating system of tropical tree species of different tropical regions of the world have been studied by several workers (BAWA, 1974; Bawa et al., 1985; BULLOCK, 1985; O'MALLEY; BAWA, 1987; MURAWSKI; HAMRICK, 1991, 1992; SARAIVA et al., 1996; MOMOSE et al., 1998; OLIVEIRA; GIBBS, 2000; GOODWILLIE, 2000; RIBEIRO; LOVATO, 2004; KRISHNAMURTHY et al., 1997; NAGARAJAN et al., 1997; TANDON et al., 2001, 2003; RAO; RAJU, 2002, FERRER et al., 2009). The study of the behaviour of plant mating system is important for acquiring knowledge about the tree inheritance patterns, and for subsequent tree improvement and breeding programmes. Knowledge of the mating system and structure of genetic populations of species are important for managing breeding populations and for designing efficient genetic conservation strategies. The mechanism of pollination among the higher plant groups is highly significant in respect of biological studies in ecology, co-evolution, variation and speciation, classical and applied genetics and plant breeding. Variability is controlled by the breeding system of which pollination mechanism forms an integral component. The principal aim of this study is to acquire detailed knowledge about the breeding system through controlled crosses and germination competence of seeds developed by selfed and cross-pollinated crosses of five important tropical tree species, viz. *Bombax ceiba* Linn., *Erythrina stricta* Roxb., *Lagerstroemia speciosa* (L.) Pers., *Mesua ferrea* Linn. and *Schima wallichii* (DC.) Korth. All the study species are economically important as (1) *Bombax ceiba* (family Bombacaceae): flower bud used as vegetable, presence of floss surrounding the

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seeds, which is used for making pillows, cushions, wood used in construction of boats, boatyards and canoe and also in matchwood and plywood industry. Seeds yield edible oil. The bark, gum and roots are medicinally useful (JAIN et al., 2009). (2) *Erythrina stricta* (family Papilionaceae): used medicinally for the treatment of rheumatism, jaundice, bronchitis, fever, skin eruption and wound. Leaves extract contain anti-inflammatory activity (KIRTHIKAR; BASU, 1987). (3) *Lagerstroemia speciosa* (family Lythraceae): The leaves are medicinally useful that contain antidiabetic, antiobesity and antioxidant activity. Wood is used for construction, boat-building, carts and other timber purposes (SUZUKI et al., 1999; KLEIN et al., 2007). (4) *Mesua ferrea* (family Guttiferae): Highly medicinal plant known as Cobras Saffron and iron wood tree. Its flower contains several pharmacological activities viz. antiasthmatic, anti-inflammatory, estrogenic and progestational, antispasmodic, antimicrobial and anthelmintic, anticancerous, antioxidant and immunomodulatory (MEHERJI et al., 1978; CHAHAR et al., 2012). (5) *Schima wallichii* (family Theaceae): a commercial timber tree. Bark contains alkaloid that is used as fish poison and also used for dying. Corollas of the flower are used to treat uterine disorders and hysteria (TAMRAKAR, 1992; LI-ZHEN; LI, 1997). The knowledge about the biology of reproductive systems of the selected five aforesaid tree species is skimpy except for the few studies done by Raju et al. (2005), Khanduri et al. (2013), Khanduri (2014) and Khanduri et al. (2015). Though the taxonomic, ethnobotanical, medicinal and pharmacological extent of the studied tree species were worked by You et al. (2003) for *Bombax ceiba*, Subhashini et al. (2011) for *Erythrina stricta*, Chanda et al. (2013) for *Mesua ferrea*, MISHRA et al. (1990) for *Lagerstroemia speciosa* and Li-Zhen and Li, (1997) for *Schima wallichii*, the detailed breeding systems of all the selected species have been ignored repulsively so far. The seed production for these tree species, especially fruitification is less than 50 per cent (in case of *Bombax ceiba* and *Erythrina stricta*) and below 70 per cent (in case of *Mesua ferrea*, *Lagerstroemia speciosa* and *Schima wallichii*), which also follows temporal pattern of production (KHANDURI et al., 2015). The present study of controlled crosses would augment fruitification potential in all the five investigated tropical tree species.

MATERIAL AND METHODS

Study area

The study was undertaken in the year 2010 and 2011 in a semi-deciduous natural forest at Bethlehem Vengthlang in the district Aizawl, Mizoram, the north eastern hill region (NEH) of India (N 23° 43' 47.5" E 92° 43' 53.5"; 900 m asl.). The forest of Bethlehem Vengthlang is dominated by *Anthocephalos cadamba* (Roxb.) Bosser, *Gmelina arborea* Roxb., *Schima wallichii*, *Erythrina stricta* in association with *Lagerstroemia speciosa*, *Mesua ferrea*, *Bombax ceiba* and *Castenopsis* spp.

Mating system

The assessment of breeding system involved six trees in each species during the flowering time in the year 2010 for *Lagerstroemia speciosa*, *Mesua ferrea* and *Schima wallichii* and in the year 2011 for *Erythrina stricta* and *Bombax ceiba*. For this purpose the following treatments were performed: (i) natural pollination, in which flowers were not manipulated and left uncovered during the entire flowering season; (ii) spontaneous self-pollination, in which buds were bagged by fine net throughout the flowering period; (iii) hand self-pollination, in which bagged flowers were hand pollinated with their own pollen; (iv) inter flower hand self-pollination (geitonogamy), in which emasculated isolated flowers were hand pollinated with the pollen of other flowers of the same tree; (v) hand cross-pollination, in which emasculated bagged flowers were pollinated with pollen from other trees (pollen were collected and mixed from five different trees selected randomly in a population at least 250 meters apart and applied by a brush to the stigma of selected flowers); and (vi) apomixis, in which anthers and stigma of buds were clipped. All the aforesaid six treatments were done in each individual selected for every species in a population (6 x 5 = 30 individuals). Each treatment was conducted on six inflorescences in each tree with a total of thirty six inflorescences per tree for all six treatments. Fruit-set was calculated by dividing the average number of fruits per inflorescence by the average number of flowers per inflorescence at pollination for each treatment. Fruits developed from each treatment were harvested at maturity. The seed-set percentage was calculated by dividing the average number of seeds per fruit/pod by the average number of ovules per flower for each spe-

cies in every treatment. The ovule number in all the five species has been determined (KHANDURI et al., 2015). To compare fruit-set among hand-selfed and hand crossed treatments, and among open pollinated and hand-crossed treatments, Chi-square analysis was performed (ZAR 1999) to know the pattern of variability between these treatments. An indirect measure of self-incompatibility was obtained by dividing the average fruit set after hand self-pollination by the average fruit set after hand cross-pollination (ZAPATA; ARROYO, 1978; Lloyd; Schoen, 1992). According to Zapata and Arroyo (1978), the resultant value of index reflects the possibilities as: (i) >1 = self compatible; (ii) >0.2 and <1 = partially self incompatible; (iii) <0.2 = Mostly self incompatible; and (iv) 0.0 = completely self incompatible.

For each species, inbreeding depression was calculated for fruit-set, seed-set and seed germination, using the formula; $\delta = 1 - W_s/W_o$ Where δ = inbreeding depression, W_s = the performance of progeny resulted from self-pollination and W_o = the performance of progeny estimated from cross-pollination (LANDE; SCHEMSKE, 1985). A threshold value for inbreeding depression of $\delta = 0.5$, indicates that the selfing is favoured below the value, and above which outcrossing is supported (LANDE; SCHEMSKE, 1985).

Seed germination

Fruit/pod setting and development on each treatment was recorded at fortnightly interval in case of *B. ceiba* and *E. stricta*, whereas after one month interval in *M. ferrea*, *L. speciosa* and *S. wallichii*. This was done because the fruit development period of later three species is 6, 9 and 9 months, respectively. Fruits were harvested at maturity and the seeds were collected manually. Twenty fruits of each treatment from all the six trees were collected for size measurement and the physical features of the fruits/pods/capsules (length, diameter (cm) and weight in g.) and seeds (length/length $\times$ width (mm), number of seeds per fruit/pod/ capsule and 100 seed weight in g.). The germination tests of the seeds developed from self, cross and open pollinated flowers of all species were conducted under laboratory conditions at room temperatures ($18.0 \pm 1.25^\circ\text{C}$). Thirty seeds of each treatment of each species were taken for germinations tests. Three replicates of each treatment were made and the seeds were placed in the Petri-dishes (10 seeds in each Petri-dish). Petri-dishes with Whatman blotting paper was used as germination media. The germination tests of the seeds were done without any treatment. Running tap water was used to moisten the Whatman paper on Petri dishes so that the germination percentage would be at par to the natural conditions.

RESULTS AND DISCUSSION

The results of the controlled pollination have been summarized in Table 1. Flowers used to test for apomixis did not set fruit. There was significant differences between hand-selfed and hand-crossed treatments in all five species ($\chi^2 = 28.42$, $p < 0.0001$ for *B. ceiba*, $\chi^2 = 25.25$, $p < 0.0001$ for *E. stricta*, $\chi^2 = 17.54$, $p < 0.0001$ for *L. speciosa*, $\chi^2 = 18.24$, $p < 0.0001$ for *M. ferrea* and $\chi^2 = 20.12$, $p < 0.0001$ for *S. wallichii*). The differences between the open pollinated and hand cross treatments was also significant for the studied species ($\chi^2 = 14.82$, $p < 0.001$, $\chi^2 = 8.24$, $p < 0.005$, $\chi^2 = 7.62$, $p < 0.006$, $\chi^2 = 10.12$, $p < 0.001$, $\chi^2 = 10.74$, $p < 0.001$, respectively for *B. ceiba*, *E. stricta*, *L. speciosa*, *M. ferrea* and *S. wallichii*). The index of self incompatibility (ISI) value for different species was 0.00 for *B. ceiba* (constituting completely self incompatible), 0.04 for *E. stricta* (Mostly self incompatible), 0.62 for *L. speciosa* (partially self incompatible), 0.60 for *M. ferrea* (partially self incompatible) and 0.48 for *S. wallichii* (partially self incompatible). The results pertaining to inbreeding depression showed that among the partially self incompatible species *L. speciosa* and *M. ferrea* supporting selfing whereas *S. wallichii* favoured slightly outcrossing (Table 2).

There was a significant ($p < 0.0001$) variation in morphological features of fruits and seeds developed from self and cross-pollinated flowers of all five species. The morphological variation in fruits and seeds, and seed germination percentage following self, open and cross-pollination has been presented in Table 3. The variation is nearly two fold in each morphological traits, viz. size and weight of fruits and seeds. Highest seed germination of 92% was found in cross-pollinated seeds of *E. stricta*, which was only 24% in self pollinated seeds. The partially self compatible species, i.e. *S. wallichii*, *M. ferrea*, and *L. speciosa* also proclaimed the similar trend, however, the value of germina-

tion percentage in cross-pollinated seeds was 72.48, 66.84 and 64.92%, respectively. The maximum seed germination following open pollination was recorded as 87.27% for *E. stricta*, followed by 66.66% for *S. wallichii*, 63.4% for *B. ceiba*, 60.54% for *M. ferrea* and 53.3% for *L. speciosa* (Table 3).

Table 1. Mating system studies in five tropical trees in a natural population at Bethlehem Vengthlang.

Tabela 1. Sistema reprodutivo em cinco espécies arbóreas tropicais numa população em Bethlehem Vengthlang.

Treatments	% fruit set	% seed set
<i>Bombax ceiba</i>		
Apomixis	0.00	0.00
spontaneous self-pollination	0.00	0.00
Natural pollination	51.64±4.95	71.4±4.16
Hand self-pollination	00	00
Geitonogamy (by hand)	3.8±0.92	40.6±2.56
Hand cross-pollination	70.6±5.24	82.6±4.98
<i>Erythrina stricta</i>		
Apomixis	0.00	0.00
spontaneous self-pollination	0.00	0.00
Natural pollination	40.24±3.42	72.6±6.82
Hand self-pollination	1.6±0.56	16.4±1.88
Geitonogamy (by hand)	2.4±1.74	58.6±2.62
Hand cross-pollination	42.8±4.76	70.6±3.68
<i>Lagerstroemia speciosa</i>		
Apomixis	0.00	0.00
spontaneous self-pollination	6.4±1.14	21.4±2.72
Natural pollination	72.8±6.64	76.4±8.54
Hand self-pollination	46.6±4.56	48.2±4.46
Geitonogamy (by hand)	66.4±5.74	72.8±7.56
Hand cross-pollination	74.6±8.62	86.4±7.84
<i>Mesua ferrea</i>		
Apomixis	0.00	0.00
spontaneous self-pollination	4.5±0.98	12.2±2.12
Natural pollination	73.9±2.90	82.4±10.28
Hand self-pollination	48.4±5.42	52.8±2.94
Geitonogamy (by hand)	70.4±6.32	78.4±9.58
Hand cross-pollination	80.6±7.84	90.4±9.12
<i>Schima wallichii</i>		
Apomixis	0.00	0.00
spontaneous self-pollination	8.8±1.24	24.6±2.432
Natural pollination	68.2±5.84	58.8±8.32
Hand self-pollination	36.4±3.26	33.8±3.42
Geitonogamy (by hand)	60.42±4.42	50.4±3.46
Hand cross-pollination	76.4±5.86	70.2±7.24

Table 2. Inbreeding depression of self- and cross-sired progeny of five tropical trees.

Tabela 2. Depressão de endogamia de progênie obtida por auto-fecundação e fecundação cruzada em cinco espécies arbóreas tropicais.

Name of species	Inbreeding depression (δ)			
	Fruit set	Seed set	Seed germination	Average
<i>Bombax ceiba</i>	1.0	1.0	1.0	1.0
<i>Erythrina stricta</i>	0.96	0.77	0.74	0.82
<i>Lagerstroemia speciosa</i>	0.38	0.44	0.34	0.39
<i>Mesua ferrea</i>	0.40	0.41	0.30	0.37
<i>Schima wallichii</i>	0.52	0.52	0.52	0.52

Table 3. Variation in seed germination and physical characteristics of fruit/pods and seeds developed following self, open and cross pollinated flowers.

Tabela 3. Variação na germinação de sementes e características físicas dos frutos/vagens obtidos depois de auto-polinização, polinização aberta e polinização cruzada.

Variables	Size (length/ Diameter) of fruit/pod (cm)	Size of seed (mm) Length/length × Width (mm)	Weight of fruit (g)	No. of seeds per capsule/ fruit	100 seed weight (g)	Seed Germination (%)
<i>Bombax ceiba</i>						
Self pollinated						
Open pollinated	16.4±0.62	8.2±0.20	18.8±0.86	284±21.05	2.14±0.16	63.4±2.46
Cross pollinated	16.8±0.34	8.4±0.20	19.2±0.56	306±23.56	2.60±0.16	66.40±2.10
<i>Erythrina stricta</i>						
Self pollinated	8.76±2.78	10.0±0.36	1.40±0.38	0.55±0.15	18.20±4.60	24.26±1.62
Open pollinated	10.89±2.44	12.5±0.28	2.67±0.56	2.45±0.55	27.0±2.48	87.27±4.56
Cross pollinated	11.52±1.84	18.4±0.42	2.98±0.64	2.90±0.48	29.45±2.56	92.56±4.86
<i>Lagerstroemia speciosa</i>						
Self pollinated	1.10±0.20	9.42±2.00 x2.35±0.36	0.54±0.18	52.50±17.44	0.25±0.10	42.52±4.14
Open pollinated	1.19±0.27	9.83±2.20 x2.65±0.59	0.66±0.14	68.55±15.33	0.30±0.12	53.3±2.56
Cross pollinated	1.78±0.46	10.48±2.40 x3.20±0.52	0.96±0.18	84.62±18.34	0.48±0.38	64.92±3.58
<i>Mesua ferrea</i>						
Self pollinated	3.1±0.56	21.4±2.12	34.20±2.14	1-4	260	46.52±3.16
Open pollinated	3.6±0.46	27.6±2.76	36.10±3.14	1-4	350	60.54±2.16
Cross pollinated	4.1±0.52	30.2±2.64	39.48±2.48	1-4	412	66.84±4.16
<i>Schima wallichii</i>						
Self pollinated	1.10±0.24	6.4±1.24 x2.2±0.42	0.46±.16	9.10±2.48	0.16±0.07	34.80±3.45
Open pollinated	1.10±0.22	7.0±1.57 x2.6±0.58	0.56±.12	9.55±2.14	0.20±0.06	66.66±4.42
Cross pollinated	1.60±0.32	7.84±1.34 x2.9±0.42	0.88±.18	10.24±2.02	0.38±0.20	72.48±5.56

The mating system study of five different tree species revealed that the manipulated cross-pollination proclaimed high fruit and seed setting in all the species, however, the manipulated geitonogamous selfing also resulted high seed setting in *S. wallichii*, *M. ferrea*, and *L. speciosa* which indicates that in natural pollination the possibility of inter-flower selfing in these species within the population would be high. This would be due to three reasons that (i) the species are mostly bee pollinated (*Apis* bee and *Xylocopa* bee), (ii) prevailed dichogamy; slightly protandry (*S. wallichii*) and protogyny (*L. speciosa* and *M. ferrea*) and (iii) the species showed asynchronization in flowering among individuals within a population. The other two species, viz. *E. stricta* and *B. ceiba*, reveal high outcrossing with very low geitonogamy. Both species are ornithophilous and have shown high synchrony in flowering within population. Birds made frequent inter-tree movements in search of nectar and such foraging behaviour was considered to effect cross-pollination. Nevertheless, birds might also be responsible for inter-flower selfing by foraging nectar from different flowers on one individual tree. The experiment on controlled pollination in this study is supporting the level of viability and variability among the seeds developed from self and cross-pollination. Seed set from cross-pollination proclaimed maximum seed germination in all five species, whereas self pollinated seeds had lowest germination. Seed set from open pollination follows the middle range of germination, as there are always chances of mixed mating in open pollination.

The mating system of *B. ceiba* and *E. stricta* has been found to be self-incompatible whereas *L. speciosa*, *M. ferrea* and *S. wallichii* had indicated to be partially self-incompatible. Self-incompatibility is a well-defined phenomenon in woody species and a variety of studies has shown complete self-incompatibility in *Nothofagus menziesii* (GODLEY, 1979), *Eucalyptus morrisbyi* (POTTS; SAVVA, 1988), *Discaria toumatou* (WEBB, 1985), *Pseudowintera colorata* (LLOYD; WELLS, 1992), *Corokia cotoneaster* (WEBB, 1994) *Cordyline australis* (BEEVER; Parkes, 1996), *Metrosideros excelsa* (ADAMS et al., 1999), *Faidherbia albida* (GASSAMA-DIA et al., 2003), *Erythrina falcata* (ETCHEVERRY; ALE-MÁN, 2005), partial self-incompatibility in *Butea monosperma* (TANDON et al., 2003), *Tamarindus indica* (DIALLO et al., 2008) and *Flourensia cernua* (FERRER et al., 2009). Self-compatibility has also been reported for several *Eucalyptus* spp., viz., *E. regnans*, *E. grandis*, and *E. cladocalyx* (POTTS; SAVVA, 1988; ELLIS; SEDGLEY, 1992) and *Balanites aegyptiaca* (NDOYE et al., 2004). Relatively low

fruit setting is common in self-incompatible species (SUTHERLAND, 1986; LARSON; BARRETT, 2000); when quantitative variation in the strength of self-incompatible (variation among plants from being partially self-incompatible to self-compatible) occurs, the species are referred to as partially self-incompatible or pseudo-self-compatible or pseudo self-fertile (LEVIN, 1996).

CONCLUSIONS

The study revealed that all the analysed species exhibited either partial or complete self-incompatible mating system. *B. ceiba* and *E. stricta* maintained very low levels of inbreeding which would allow populations of both species to increase reproductive output to reconcile high regeneration potential. *L. speciosa* and *M. ferrea* had partially self-incompatible mating system with a value of inbreeding depression below 0.5 that favoured selfing. This indicates that both species have chances of poor reproductive survival through regeneration in natural population. The inbreeding depression value of *S. wallichii* is above 0.5, supporting outcrossing, and the species would be capable to maintain new population at the time of colonization through better survival of in-growth.

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Recebido em 01/04/2015

Aceito para publicação em 17/12/2015