Selbyana 27(2): 165–174. 2006.

SUBSTRATE DIVERSITY, DEMOGRAPHY, AND FRUIT SET IN TWO POPULATIONS OF THE EPIPHYTE *POMATOCALPA SPICATUM* (ORCHIDACEAE) IN THAILAND

SANTI WATTHANA AND HENRIK ÆRENLUND PEDERSEN*

Botanical Garden & Museum, Natural History Museum of Denmark, University of Copenhagen,
Gothersgade 130, DK-1123 Copenhagen K, Denmark. Email: henrikp@snm.ku.dk

SOMRAN SUDDEE

Forest Herbarium (BKF), National Park, Wildlife and Plant Conservation Department, Chatuchak,
Bangkok 10900, Thailand.

ABSTRACT. The epiphytic orchid *Pomatocalpa spicatum* was studied with regard to substrate diversity, demography, and fruit set in two floristically and structurally different areas of lower tropical rain forest in southeastern Thailand. At both sites, the orchid was found to grow directly on the bark of the phorophytes, from near ground level to 2 to 3 m in height. The relative frequencies of *P. spicatum* on the four types of substrate (viz. tree trunk, branch, twig, and climber) differed markedly, however, between the two populations. We conclude that an apparently specific substrate requirement of this species at any one locality may reflect local forest structure rather than specific requirements on behalf of the orchid. Despite the large structural and floristic differences between the study sites, both the demographic patterns and the patterns of flowering and fruit set were remarkably similar. In comparison to published observations of other epiphytic orchids, including *P. naevatum,* small/young individuals were under-represented in both populations—possibly an effect of recent climatic fluctuations on a regional scale. The low relative fruit set in the populations (5.2% and 7.5%, respectively) suggests an allogamous breeding system. The Lorenz curves prepared for the two populations are very similar and document a disproportionately high female genetic contribution by relatively few individuals.

Key words: epiphytic orchid, *Pomatocalpa spicatum,* flowering, recruitment, breeding system, Lorenz curves, Thailand

INTRODUCTION

More than 70% of all orchid species are epiphytes (Kress 1986, Atwood 1986), and ca. 60% of all orchid genera contain epiphytic species (Atwood 1986). Up to now, the majority of biological and ecological studies of epiphytic orchids (and other epiphytes) have been conducted in the neotropics, while surprisingly little has been done in tropical Asia (Watson et al. 1987, van der Cingel 2001). Furthermore, most studies have been confined to a single locality, whereas comparative biological observations on two or more populations of the same species are few. In the present study, we compare two Thai populations of the epiphytic orchid *Pomatocalpa spicatum* Breda, mainly with regard to aspects of substrate preference, demography, and fruit set.

The biotope of epiphytes is a spatially heterogeneous, or patchy, environment. The partitioning of habitat is a product of the response of individual species to a range of environmental gradients, such as those of radiation and vapor pressure deficit (e.g., Dickinson et al. 1993). In addition, niche differentiation, ecological equivalency, and mass effect are important (Bennett 1986). The patchiness may exist at several hierarchical levels as indicated by habitat and phorophyte specificity, vertical stratification, and microsite preference (e.g., Johansson 1974, Benzing 1978, Kelly 1985, Bennett 1986, Santos 2000, Winkler & Hietz 2001). The phorophyte diversity of *Pomatocalpa spicatum* in Manusela National Park, Maluku, was studied by Mursidawati et al. (1999). They observed a particularly high frequency of this species on *Myristica succedanea* Blume (Myristicaceae) and *Syzygium* sp. (Myrtaceae). In the present study, we have disregarded the systematic identities of the phorophytes. Instead we have observed the distribution of *P. spicatum* among trunks, branches, twigs, and climbers at the two study sites. We particularly address the question whether the observed patterns are the result of specific microsite requirements, or if they vary with the spatial structure of the forest.

Understanding of the population dynamics of epiphytic orchids is crucial in connection with orchid conservation projects in humid tropical

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* Corresponding author.

forests. To achieve this knowledge, insights are needed with regard to individual, demographic, and environmental variation in time and space (Tremblay & Hutchings 2003). Thus far, however, few studies of these components have been conducted in the above context. In the present study, we have mapped the demographic composition of two population samples of *Pomatocalpa spicatum,* mainly to see if they exhibit the same pattern as generally reported for other epiphytic orchids (including *P. naevatum* J.J.Sm.). This pattern is one with a majority of small plants and a gradual decrease in frequency of larger individuals, reflecting high germination success and mortality rates of different life stages (e.g., Zotz 1998, Winkler & Hietz 2001, Watthana 2005).

Sexual reproduction, usually mediated by an insect vector, is necessary for the long-term survival of most orchid populations. The orchid-pollinator relationship is highly asymmetrical, with the orchid usually relying far more on its pollinators than do the pollinators on the orchid. As a consequence, successful orchid conservation will require a case-by-case functional ecosystem approach (Roberts 2003). In the present study, we compare the magnitude and pattern of fruit set in population samples from two floristically dissimilar forests. Thus, we address the question of whether the patterns of fruit set in *Pomatocalpa spicatum* depend on the overall floristic composition of the forest (i.e., if the long-term survival of *P. spicatum* populations may be susceptible to effects of small-scale environmental changes on fecundity). Additionally, we briefly discuss the patterns of fruit set in a population genetics context.

MATERIAL AND METHODS

Pomatocalpa spicatum is an epiphyte distributed from India to the Philippines and Maluku. The plant, a short-stemmed monopodial herb with 3–10 (linear-) oblanceolate leathery leaves, produces roots from the nodes. In the monsoon areas, flowering usually takes place by the end of the rainy season. The unbranched (rarely slightly branched) inflorescences penetrate the leaf sheaths. They consist of a very short peduncle and usually a 1.0–5.5 cm long rachis with 10–60 condensed, synchronously open flowers. The flowers are relatively small (dorsal sepal 2.1–5.0 mm long) with subsimilar obovate-elliptic sepals and petals, which are yellow with purplish brown spots. The lip consists mainly of a pale bucket-shaped spur, the entrance of which is blocked by a versatile tongue-like structure rising from the distal part of the back wall. The flowers seem to fit the bee pollination syndrome of van der Pijl and Dodson (1966).

Pomatocalpa spicatum was studied from 30 March to 4 April 2004 at two sites in southeastern Thailand: in Khao Ang Ru Nai Wildlife Sanctuary (13°24′58.1″N, 101°57′04.3″E) and at Ban Thaew Khlong (12°28′50.8″N, 102°13′01.1″E) on the border of Khao Sabab National Park. Both localities, situated 100 km apart, consist of lower tropical rain forest (sensu Smitinand 1989) and are located on fairly flat ground below 200 m. The forest at Ban Thaew Khlong is a gallery forest with fewer distinct stories than the forest at Khao Ang Ru Nai.

At each study site, all individuals (except leafless seedlings) of *Pomatocalpa spicatum* in a rectangular plot of 5 × 50 m were sampled. The sampling was timed to take place shortly after flowering had ceased, so that both flowering and fruit set could be quantified.

A survey of all woody species growing in each plot was prepared. Based on this survey, Sørensen's (1948) presence community coefficient was calculated as: $IS_S = (c/½(A + B)) \times 100\%$, where c is the number of species common to both plots, while A and B are the total numbers of species recorded in the plots at Khao Ang Ru Nai and Ban Thaew Khlong, respectively. In comparison to Jaccard's original index of similarity $(IS_J = (c / (A + B - c)) \times 100\%)$, Sørensen's index expresses the actually measured coinciding species occurrences against the theoretically possible ones. As noted by Mueller-Dombois and Ellenberg (1974), this may be mathematically more satisfactory, as it includes a statistical probability term.

The overall spatial distribution of *Pomatocalpa spicatum* was observed. For each individual, we noted if the plant was growing on a trunk, on a first-order branch, on a twig (including branches of second order and above), or on a climber. A chi-square test was used to determine whether the substrate preference of the species differed between the two plots.

The length of the longest leaf of every individual was measured and used as a general size-indicator of the plants.

Each individual was classified as flowering or vegetative. The numbers of inflorescences in all flowering individuals were counted, and the length of every inflorescence was measured. In each plot, 23 inflorescences were collected and their individual numbers of flowers were established from the numbers of nodes. For each plot, the following ratio was calculated: total number of flowers per total length of inflorescences. Based on the ratio obtained for each plot, the size of every inflorescence could be converted from length to approximate number of flowers.

Throughout the rest of the study, these approximate numbers of flowers were treated as real counts.

Fruit set was determined as the number of fruits produced, and for each plot the relative fruit set was calculated. Additionally, the individuals from each plot were sorted in ascending order by the number of fruits they produced, and the cumulative percent of individuals was then plotted against that of the fruits to form a Lorenz curve (Weiner & Solbrig 1984, Calvo 1990). Another pair of Lorenz curves, based on flowering individuals only, was prepared for comparison.

Pearson's correlation coefficient was used to test for correlation between (1) the length of the longest leaf and the number of inflorescences per individual, (2) the length of the longest leaf and the number of flowers per individual, (3) the number of inflorescences and the number of fruits per flowering individual, (4) the number of inflorescences and the relative fruit set per flowering individual, (5) the number of flowers and the number of fruits per flowering individual, (6) the number of flowers and the relative fruit set per flowering individual, (7) the number of flowers and the number of fruits per inflorescence, (8) the number of flowers and the relative fruit set per inflorescence. All tests were performed in the program PractiStat (Ashcroft & Pereira 2003) and conducted separately on the two population samples.

RESULTS

The composition of the flora of woody plants in the two plots is shown in TABLE 1. The flora was slightly more diverse in the plot at Khao Ang Ru Nai (0.17 species/m^2) than in the plot at Ban Thaew Khlong (0.12 species/m^2). Furthermore, the floristic composition was very dissimilar between the two plots ($IS_S = 13.7\%$).

At Khao Ang Ru Nai, all individuals of *Pomatocalpa spicatum* ($N = 122$) were found 0.2–2.0 m above ground, while at Ban Thaew Khlong, they grew 0.4–3.0 m above ground ($N = 85$). The relative frequencies of *P. spicatum* on the four types of substrate were found to differ between the plots ($P < 0.001$). At Khao Ang Ru Nai ($N = 122$), 52% of the individuals were found on trunks, 19% on climbers, 16% on twigs, and 13% on first-order branches. At Ban Thaew Khlong ($N = 85$), on the other hand, 72% of the individuals were found on twigs, 21% on first-order branches, 6% on climbers, and 1% on trunks.

The density of flowers in inflorescences of *Pomatocalpa spicatum* ranged from 8.7–15.3 per cm ($\mu = 11.5$, $SD = 1.5$) at Khao Ang Ru Nai and from 6.7–12.7 per cm ($\mu = 9.3$, $SD = 1.7$) at Ban Thaew Khlong. In the plot at Khao Ang Ru Nai, 56 of the 122 individual orchid plants (45.9%) had flowered with a total of 119 inflorescences. Of the 4630 flowers, 243 were fruiting, corresponding to a relative fruit set of 5.2%. In the plot at Ban Thaew Khlong, 31 of the 85 individuals (36.5%) had flowered with a total of 61 inflorescences. Of the 2717 flowers, 204 were fruiting, corresponding to a relative fruit set of 7.5%.

Variation in the length of the longest leaf in all individuals, and in flowering individuals only, is summarized for each plot in TABLE 2. The relative distribution of individuals among size classes is shown in FIGURE 1. The variation in the number of inflorescences per flowering individual is summarized for each plot in TABLE 2, and the relative distribution of vegetative and flowering individuals among size classes is shown in FIGURE 2. The variation in the number of flowers per flowering individual and per inflorescence is summarized for each plot in TABLE 2.

The variation in the number of fruits per flowering individual and per inflorescence is summarized for each plot in TABLE 2. The relative contribution of individuals to the fruit pools of the two plots can be seen from the Lorenz curves (FIGURE 3).

Both the number of inflorescences and the number of flowers per individual universally were found to be positively correlated with the length of the longest leaf ($P < 0.001$ in all four tests). In addition, the number of fruits per individual universally was found to be positively correlated with both the number of inflorescences and the number of flowers per individual ($P < 0.001$ in all four tests). Similarly, the number of fruits per inflorescence was found to be positively correlated with the number of flowers per inflorescence ($P < 0.05$ for Khao Ang Ru Nai; $P < 0.001$ for Ban Thaew Khlong). On the other hand, no correlation could be confirmed between the relative fruit set and the number of inflorescences or flowers per individual, or the number of flowers per inflorescence ($P > 0.05$ in all six tests). For all the statistically significant correlations detected, the equations of the regression lines are given in TABLE 3.

For both plots, the distribution of fruiting and non-fruiting individuals in relation to the length of their longest leaves and their numbers of flowers is shown in FIGURE 4.

DISCUSSION

Substrate Diversity

Our finding at both sites of *Pomatocalpa spicatum* as a low-growing epiphyte is in agree-

TABLE 1. List of woody plants occurring in forest plots at Khao Ang Ru Nai (A) and Ban Thaew Khlong (B), southeastern Thailand. Specimens found (+), no specimens found (−).

Woody plants	Plant family	A	B
TREES			
Acronychia pedunculata (L.) Miq.	Rutaceae	+	−
Archidendron jiringa (Jack) I.C.Nielsen	Leguminosae	−	+
Dalbergia cochinchinensis Pierre	Leguminosae	+	−
Diospyros rubra Lecomte	Ebenaceae	+	−
Diospyros transitoria Bakh.	Ebenaceae	+	−
Diospyros variegata Kurz	Ebenaceae	+	+
Diospyros venosa Wall. ex A.DC.	Ebenaceae	+	−
Ficus sp.	Moraceae	−	+
Hevea brasiliensis (Willd. ex A.Juss.) Müll.Arg.	Euphorbiaceae	−	+
Hydnocarpus ilicifolia King	Flacourtiaceae	+	−
Irvingia malayana Oliv. ex A.W.Benn.	Irvingiaceae	+	−
Lagerstroemia calyculata Kurz	Lythraceae	+	−
Mallotus peltatus Müll.Arg.	Euphorbiaceae	−	+
Peltophorum dasyrachis (Miq.) Kurz	Leguminosae	+	+
Pterocymbium tinctorium (Blanco) Merr.	Sterculiaceae	−	+
Pterospermum diversifolium Blume	Sterculiaceae	−	+
Shorea henryana Pierre	Dipterocarpaceae	+	−
Sterculia sp.	Sterculiaceae	−	+
Vatica harmandiana Pierre	Dipterocarpaceae	+	−
Xerospermum noronhianum (Blume) Blume	Sapindaceae	−	+
SHRUBS			
Acronychia pedunculata (L.) Miq.	Rutaceae	+	−
Aglaia tomentosa Teijsm. & Binn.	Meliaceae	+	−
Ardisia helferiana Kurz	Myrsinaceae	+	−
Atalantia monophylla (DC.) Corrêa	Rutaceae	+	−
Callicarpa poilanei Dop	Lamiaceae	+	−
Champereia manillana (Blume) Merr.	Opilaceae	+	−
Cladogynos orientalis Zipp. ex Span.	Euphorbiaceae	+	−
Croton roxburghii N.P.Balakr.	Euphorbiaceae	+	−
Dehaasia suborbicularis (Lecomte) Kosterm.	Lauraceae	+	−
Diospyros venosa Wall. ex A.DC.	Ebenaceae	−	+
Erismanthus sinensis Oliv.	Euphoribaceae	+	+
Fagerlindia armigera (K.Schum.) Tirveng.	Rubiaceae	+	−
Garcinia vilersiana Pierre	Clusiaceae	−	+
Irvingia malayana Oliv. ex A.W.Benn.	Irvingiaceae	+	−
Lasianthus inodorus Blume	Rubiaceae	+	−
Melodorum fruticosum Lour.	Annonaceae	+	−
Memecylon plebejum Kurz	Melastomataceae	−	+
Memecylon scutellatum Naudin	Melastomataceae	+	−
Memecylon sp. [not *M. plebejum* or *M. scutellatum*]	Melastomataceae	+	−
Micromelum minutum (Forst.) Wight & Arn.	Rutaceae	−	+
Millettia leucantha Kurz	Leguminosae	+	−
Murraya paniculata (L.) Jack	Rutaceae	−	+
Neolitsea reticulata Kosterm.	Lauraceae	+	−
Sampantaea amentiflora (AiryShaw) AiryShaw	Euphorbiaceae	+	−
Sandoricum koetjape (Burm. f.) Merr.	Meliaceae	−	+
Semecarpus cochinchinensis Engl.	Anacardiaceae	−	+
Schefflera sp.	Araliaceae	−	+
Shorea henryana Pierre	Dipterocarpaceae	+	−
Streblus taxoides (Heyne) Kurz	Moraceae	+	−
Walsura robusta Roxb.	Meliaceae	+	−
CLIMBERS			
Acacia comosa Gagnep.	Leguminosae	−	+
Ancistrocladus tectorius (Lour.) Merr.	Ancistrocladaceae	+	−
Bauhinia bracteata (Graham ex Benth.) Baker	Leguminosae	−	+
Calamus sp.	Arecaceae	+	−
Celastrus paniculatus Willd.	Celastraceae	−	+

TABLE 1. Continued.

Woody plants	Plant family	A	B
Derris sp. 1	Leguminosae	+	−
Derris sp. 2	Leguminosae	−	+
Gotomia floribunda (Roxb.) Lam.	Combretaceae	−	+
Jasminum coarctatum Roxb.	Oleaceae	−	+
Lygodium salicifolium C.Presl	Schizaeceae	+	−
Mucuna sp.	Leguminosae	−	+
Myxopyrum smilacifolium (Wall.) Blume	Oleaceae	+	+
Poikilospermum suaveolens Merr.	Cecropiaceae	−	+
Rauwenhoffia siamensis Scheff.	Annonaceae	+	+
Strychnos axillaris Colebr.	Loganiaceae	+	−
Tetrastigma sp.	Vitaceae	−	+
Thunbergia laurifolia Lindl.	Acanthaceae	−	+
Ventilago denticulata Willd.	Rhamnaceae	+	−

ment with observations from Java (Comber 1990) and Maluku (Mursidawati et al. 1999). The restriction of *P. spicatum* to substrates from near ground level to a few meters in height may reflect a requirement for elevated radiation levels, but also a lack of ability to cope with the severe evapotranspirational demands in the upper parts of the forest canopy.

In Manusela National Park, Maluku, Mursidawati et al. (1999) found *Pomatocalpa spicatum* to be an epiphyte growing primarily on the lower and main tree trunk (73.4% of the "clumps" recorded); only 20.0% were found in the inner third and 6.6% in the middle third of the tree canopy, while no plants were found in the outer third of the canopy (tree zones according to Johansson 1974). In our study, however, the distribution of *P. spicatum* individuals among trunks, first-order branches, twigs, and climbers differed between the two study populations. In the somewhat "scrubby" forest at Ban Thaew Khlong, only 1% of the orchids were found on tree trunks. This seems to indicate that the relative importance of substrate types depends strongly on forest structure (cf. also the very low floristic similarity between the two study plots; TABLE 1; $IS_S = 13.7\%$).

Contrary to the conclusion reached by Mursidawati et al. (1999), based on observations from a single locality, not only tree trunks, but also branches, twigs, and climbers can provide suitable substrates for establishment and growth of *Pomatocalpa spicatum.* An apparently specific substrate requirement at any one locality may reflect local forest structure rather than specific requirements on behalf of the orchid. Thus *P. spicatum* may be considered a generalist as far as substrate requirements are concerned. In ac-

TABLE 2. Summary of variation in the parameters examined. For each parameter, the values are indicated as (minimum–) $\mu-SD$–$\mu+SD$ (–maximum), followed by the coefficient of variation. The $\mu-SD$ value, however, has been ignored in cases where it was found to be lower than the minimum value observed.

	Khao Ang Ru Nai		Ban Thaew Khlong	
Parameters	Values	Coefficient of variation %	Values	Coefficient of variation %
Length of longest leaf (cm); all individuals	(0.8–)4.9–15.5(–25.2)	52	(1.6–)5.2–16.6(–27.2)	52
Length of longest leaf (cm); flowering individuals	(7.8–)10.8–17.8(–25.2)	25	(9.6–)12.4–20.5(–27.2)	25
Inflorescences per flowering individual (No.)	1–3(–5)	61	1–3(–4)	55
Flowers per flowering individual (No.)	9–173(–333)	109	13–162(–308)	85
Flowers per inflorescence (No.)	(6–)17–58(–95)	55	(13–)19–65(–104)	55
Fruits per flowering individual (No.)	0–11(–28)	157	(0–)1–12(–19)	89
Fruits per inflorescence (No.)	0–5(–19)	173	0–7(–15)	117

TABLE 3. Equations for linear regression lines representing positive correlations detected in population samples of *Pomatocalpa spicatum* at Khao Ang Ru Nai (A) and Ban Thaew Khlong (B), southeastern Thailand.

		Regression line	
Abscissa (x)	Ordinate (y)	A	B
Length of longest leaf (cm)	Inflorescences per individual (No.)	$y = -0.85 + 0.18x$	$y = -0.82 + 0.14x$
Length of longest leaf (cm)	Flowers per individual (No.)	$y = -56.10 + 9.31x$	$y = -52.15 + 7.72x$
Inflorescences per individual (No.)	Fruits per individual (No.)	$y = -0.68 + 2.36x$	$y = -0.35 + 3.54x$
Flowers per individual (No.)	Fruits per individual (No.)	$y = 1.29 + 0.04x$	$y = 1.20 + 0.06x$
Flowers per inflorescence (No.)	Fruits per inflorescence (No.)	$y = 0.73 + 0.03x$	$y = -0.63 + 0.09x$

cordance with Mursidawati et al. (1999), however, we usually found this species growing directly on the bark, apparently avoiding major humus deposits.

Demography

The relative distribution of individuals among size classes was very similar in the two population samples (FIGURE 1), and the populations also exhibited similar patterns of flowering and fruit set (FIGURES 2, 4). We do not know of any recent disturbances that might have interfered with sexual reproduction or seedling establish-

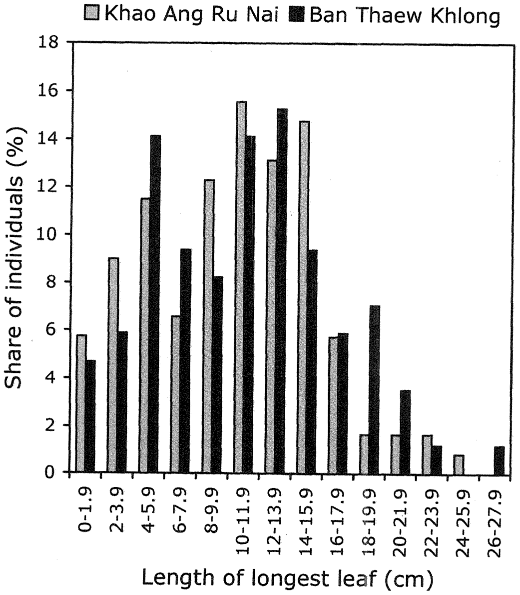

FIGURE 1. Relative distribution of individuals of *Pomatocalpa spicatum* among size classes (length of the longest leaf) at Khao Ang Ru Nai ($N = 122$) and Ban Thaew Khlong ($N = 85$).

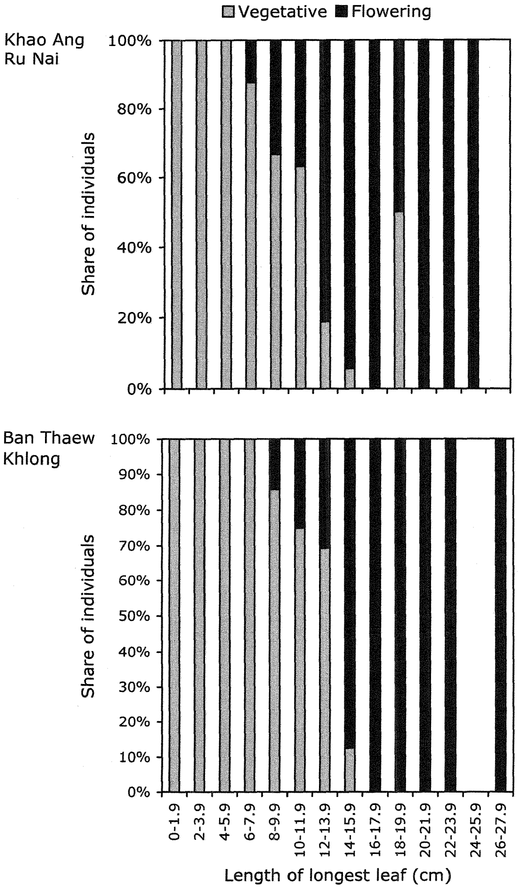

FIGURE 2. Relative distribution of vegetative and flowering individuals of *Pomatocalpa spicatum* among size classes at Khao Ang Ru Nai ($N = 122$) and Ban Thaew Khlong ($N = 85$).

ment at the two sites. Surprisingly the plants with maximum leaf lengths of ca. 10–14 cm were recorded as more frequent than were individuals of smaller size (FIGURE 1). A majority of small plants and a gradual decrease in frequency of larger individuals would have been expected, in accordance with observations of other epiphytic orchids (Zotz 1998, Winkler & Hietz 2001, Watthana 2005). The pattern observed in the present study suggests low recent recruitment, as plant size tends to be strongly correlated with age in this short-stemmed monopodial species. Since the overall demographic pattern is similar in both populations (FIGURE 1), it is tempting to ascribe the underrepresentation of small/young individuals to effects of recent climatic fluctuations on a regional scale. It is not possible, however, to test this hypothesis against climatic data from southeastern Thailand, as long as the growth rate of *Pomatocalpa spicatum* is unknown.

Breeding and Fruit Set

Next to nothing is known about the diversity of breeding systems in *Pomatocalpa.* In Australia, Jones (1981) observed a small bee (*Trigona* sp.) with the dark pollinarium of *P. macphersonii* (F.Muell.) T.E.Hunt attached to its head entering a flower of *Rhinerrhiza moorei* (Rchb.f.) M.A.Clements, B.Wallace & D.Jones. Since all species of *Pomatocalpa* have a similar flower morphology, the assumption, carefully made, is that *P. spicatum* also is pollinated by small bees. Whether *P. spicatum* produces nectar or acts by deceit is unknown, but (assuming self-compatibility) the very low relative fruit set (5.2% at Khao Ang Ru Nai; 7.5% at Ban Thaew Khlong) suggests deceit. Thus, in the review by Neiland and Wilcock (1998), the relative fruit set was found to be 0.0–43.0% (μ = 11.5%) in nectarless tropical orchids, but 17.8–41.0% (μ = 24.9%) in nectar-producing plants of this group.

The present study did not include direct observations of the breeding system of *Pomatocalpa spicatum,* but the Lorenz curves based on flowering individuals (FIGURE 3B) are far more similar to the curves that Calvo (1990) provided for allogamous orchid species than to the curve that he provided for the autogamous *Oecoclades maculata* (Lindl.) Lindl. This suggests an insect-operated breeding system of relatively low efficiency (see also TABLE 2), but probably with a relatively high rate of outcrossing. The Lorenz curves were remarkably similar between the two population samples (FIGURE 3). Interestingly, when seen in conjunction with the very low floristic similarity between the two plots (IS_S = 13.7%), it suggests a generalist component in the breeding system of *P. spicatum.* It appears unlikely that fecundity in populations of this species would be very susceptible to small-scale environmental changes.

The low overall fruit set in both study populations reflects the situation in the majority of entomogamous orchids (see review by Neiland & Wilcock 1998). Also the high proportion of fruitless individuals (FIGURE 3B) is shared with many other orchid species (e.g., Janzen et al. 1980, Schemske 1980, Ackerman 1989, Gill 1989, Zimmerman & Aide 1989, Calvo 1990, Pedersen et al. 2005, Watthana 2005). These characteristics strongly suggest that annual fruit set in *Pomatocalpa spicatum* is pollination-limited.

A positive correlation was found in both populations between the number of fruits on the one hand and the number of flowers per individual or inflorescence or the number of inflorescences per individual, on the other (TABLE 3). This correlation demonstrates a selective pressure toward an increase of the number and size of inflorescences (i.e., a general increase of the floral display). Since the relative fruit set was found to be unaffected by changes in floral display, the natural selection driven by pollinators in *Pomatocalpa spicatum* cannot be very strong. Surprisingly, the synchronously flowering *P. spicatum* is similar in this respect to orchids with sequential floral display (e.g., Firmage & Cole 1988, Ackerman 1989, Montalvo & Ackerman 1987, Zimmerman & Aide 1989). In other orchids with synchronous floral display, the relative fruit set has been found to increase with inflorescence size (Schemske 1980, Inoue 1986, Murren & Ellison 1996).

As noticed by Calvo (1990), the potential for pollinator-mediated selection on floral display may be limited by the low overall pollination level and the usually loose response of pollinators to variation in the number and size of inflorescences. Furthermore, increased fruit set in orchids has been observed to result in reduced future growth and/or reproduction (e.g., Ackerman 1989, Snow & Whigham 1989, Zimmerman & Aide 1989, Ackerman & Montalvo 1990, Mattila & Kuitunen 2000, Meléndez-Ackerman et al. 2000, Primack 2002). This phenomenon seems to be most pronounced in epiphytic species (Roberts 2003). Thus the selection for increased floral display in *Pomatocalpa spicatum* may be counterbalanced by selection for a "sustainable" annual fruit set that maximizes the lifetime fruit production of the individual. Long-term observations of fruit set variation and its effect on the overall individual fitness are needed to explore this topic in detail (Nilsson 1992).

The remarkable similarity between the Lorenz

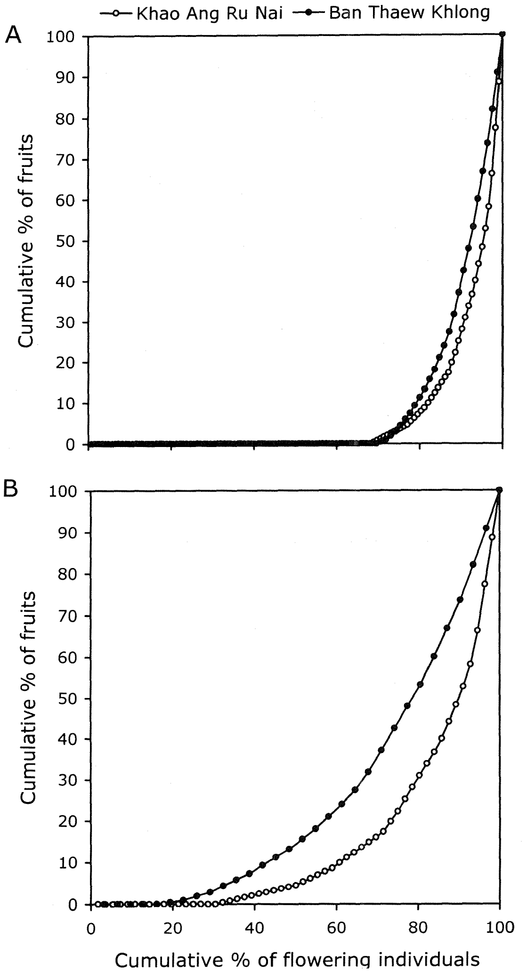

FIGURE 3. Lorenz curves for *Pomatocalpa spicatum* at Khao Ang Ru Nai and Ban Thaew Khlong (A: based on all individuals, B: based on flowering individuals only). A diagonal line from the lower left to the upper right corner would indicate equal contributions of individuals to the capsule pool, while curves deviating from this diagonal line indicate inequality.

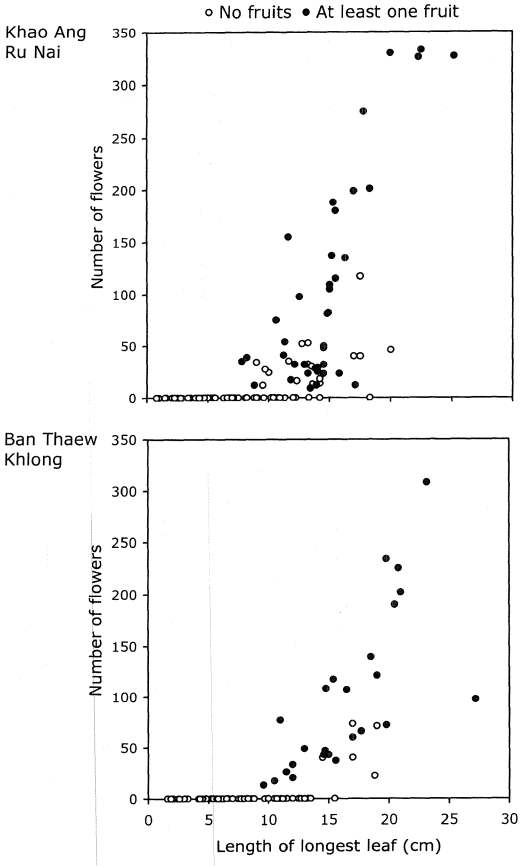

FIGURE 4. Distribution of fruiting and non-fruiting individuals of *Pomatocalpa spicatum* in relation to the length of their longest leaves and their numbers of flowers at Khao Ang Ru Nai and Ban Thaew Khlong.

curves based on all individuals from each of the two population samples (FIGURE 3A) relies partly on similar demographic patterns (FIGURE 1) combined with the positive correlation between plant size and flowering (FIGURE 2, TABLE 3). Thus, when only flowering individuals are examined, the slight difference between the two population samples becomes clearer (FIGURE 3B): the flowering individuals at Ban Thaew Khlong make a slightly more equal contribution to the fruit pool of the population than do those at Khao Ang Ru Nai. At the latter site, the distribution of fruits among individuals is characterized by being more skewed to the right, and with a higher maximum number of fruits per flowering individual (FIGURE 3B, TABLE 2). The same phenomenon can be deduced from the coefficient of variation (CV). Compared to Ban Thaew Khlong, the sample from Khao Ang Ru Nai has markedly higher CV values for the number of fruits per flowering individual and for the number of fruits per inflorescence (TABLE 2).

The unequal distribution of fruits among individuals within both study populations (FIGURE 3) accounts for differences in the female genetic contribution of progeny. Obviously, this might influence the future genetic composition of the populations through a disproportionately high female genetic contribution by relatively few individuals. An expected high rate of full sibness (resulting from one pollinarium fertilizing all ovules in an ovary) might well account for a correspondingly unequal male genetic contribution, but this remains to be studied. Based on current knowledge, effective population size usually is much smaller than absolute population size in *Pomatocalpa spicatum.*

ACKNOWLEDGMENTS

This study was supported financially by a grant from the DANIDA project, Capacity Building in the Field of Biodiversity, at the Queen Sirikit Botanic Garden. We are indebted to staff members of the Khao Ang Ru Nai Wildlife Sanctuary and the RFD Centennial Botanical Garden for assistance during fieldwork at Khao Ang Ru Nai. Finally, we thank Ingeborg Nielsen for technical assistance with illustrations and three anonymous reviewers for useful comments on the manuscript.

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