BIODIVERSITAS
Volume 26, Number 7, July 2025
Pages: 3246-3251

ISSN: 1412-033X
E-ISSN: 2085-4722
DOI: 10.13057/biodiv/d260716

Flowering, fruit set and breeding systems of *Habenaria janellehayneana* and *H. rhodocheila* in Phu Hin Rong Kla National Park, Thailand

THEERA THUMMAVONSA[1,2], CHUTHAPOND MUSIMUN[1], SANTI WATTHANA[1], NOODUAN MUANGSAN[1,♥]
[1]School of Biology, Institute of Science, Suranaree University of Technology. 111 Maha Witthayalai Road, Suranari, Mueang Nakhon Ratchasima, Nakhon Ratchasima 30000, Thailand. Tel./fax.: +66-44-223000, ♥email: nooduan@g.sut.ac.th
[2]Department of Biology, Faculty of Science and Technology, Nakhon Ratchasima Rajabhat University. 340 Suranarai Road, Nai Mueang, Mueang Nakhon Ratchasima, Nakhon Ratchasima Province 30000, Thailand

Manuscript received: 13 December 2024. Revision accepted: 25 June 2025.

Abstract. *Thummavonsa T, Musimun C, Watthana S, Muangsan N. 2025. Flowering, fruit set and breeding systems of Habenaria janellehayneana and H. rhodocheila in Phu Hin Rong Kla National Park, Thailand. Biodiversitas 26: 3246-3251.* Reproductive biology studies are important information for orchids conservation in natural habitats, especially ones which have high potential for economic use. Over-collection is a main threat of orchid species with economic value. Moreover, the reduction of the habitat and climate change may result in population decline or extinction. Fruit set data is a preliminary evaluating the population survival, valuable for population conservation. This study aimed to examine flowering, natural fruit set and breeding systems of *Habenaria janellehayneana* and *H. rhodocheila*, attractive terrestrial orchids for pot plants, in Phu Hin Rong Kla National Park, Phitsanulok Province, Northern Thailand to collect basic information for in situ conservation. Two studied plots, 50x50 m plots of each species, were established to investigate the flowering and fruit set. Three experiments of hand-pollination, untouched, self- and cross-pollination were performed to compare with natural pollination to determine the breeding systems. Leaf length and shoot length showed no correlation with fruit set ($r<0.5$), while the number of flowers per inflorescence was slightly correlated ($r=0.6$). This result indicates that plant size is not a factor for fruit production, but the number of flowers per inflorescence is likely to be the factor to attract the pollinator. Natural fruit set is notably high in both species as they are nectar-rewarding species. Both species exhibited genetically self-incompatibility and non-autogamous but required pollinators for successful reproduction. *Habenaria janellehayneana* is firstly reported on its breeding system and fruit set, exhibiting as the main traits of the genus *Habenaria*. Moderately high number of fruit set in both species indicated that no pollinator scarcity. Maintaining the ecosystem of their habitat is necessary for conserve these orchid populations.

Keywords: Breeding systems, fruit and seed production, *Habenaria*, in situ conservation, terrestrial orchid

INTRODUCTION

Habenaria is one of the large terrestrial orchid genera with 898 species, belonging to the subfamily Orchidoideae of Orchidaceae family (POWO 2024). The genus is well-represented in Thailand, comprising 45 species primarily distributed across the northern and northeastern regions of the country (Kurzweil 2011). Many of them serves as ornamental pot plants as well as being traditional used to address various health conditions such as cough, asthma, kidney disorder, hernia, haematuria, and sexual dysfunction (Tinoammini et al. 2024). *Habenaria rhodocheila* Hance is a terrestrial orchid with showy flowers and varying floral colors, from pink, red to yellow (Kurzweil 2011). *Habenaria janellehayneana* Choltco, B.Moloney & Yong Gee, an endemic species closely related to *H. rhodocheila,* was first described in 2017 from Thailand and is exclusively found in Phitsanulok Province, Northern Thailand (Choltco et al. 2017). This species also exhibits significant potential as an ornamental potted plant. Based on its morphological characteristic, *H. janellehayneana* is included in the *H. rhodocheila* group. Although there is no report on in situ population conservation status of both species, the attractive orchids are to be demanded due to their colorful flowers. Moreover, habitat degradation and unsustainable harvesting for commercial purposes have led to significant declines in natural orchid populations by humans (Phelps and Webb 2015; Hinsley et al. 2018).

The understanding of reproductive biology, including the study of flowering phenology, fruit settings, and breeding systems, is essential for the conservation of natural plant populations, particularly in species that process complex reproductive strategies, such as orchids (Phillips et al. 2020). Many orchids face reproductive challenges due to low fruit production or specific pollinator requirements, which make them vulnerable in fragmented or changing habitats (Tremblay et al. 2005). This understanding of the reproductive mechanisms is crucial for effective conservation management, as it will provide strategies to enhance reproductive success and population viability. Without such knowledge, conservation may fail to address the key factors that limit population persistence, especially under rapid environmental alterations. Consequently, research into reproductive biology, including breeding systems and fruit set, is urgently needed to guide effective conservation, particularly in biodiversity hotspots (Phillips et al. 2020).

Breeding systems of Orchidaceae are mainly dependent on pollinators and self-compatibility (Ackerman et al. 2023). Most *Habenaria* species are self-compatible but rely on pollinators for successful reproduction (Pedron et al. 2012b; Chen et al. 2021a; Zhang et al. 2021). Main pollinators for *Habenaria* are primarily Lepidoptera, including various species of moths and butterflies, which facilitate cross-pollination (Zhang and Gao 2017). These pollination systems are often highly specialized, with adaptations that match floral morphology with the behaviors and physiological traits of their respective pollinators. However, reproductive strategies may vary within the genus and its reproductive success vary from species to species (Zhang and Gao 2021). For example, *H. malintana* (Blanco) Merr. is an exception because it reproduces through agamospermy and achieves 100% fruit set without pollinator involvement (Zhang and Gao 2018). Such variation in reproductive modes highlights the importance of understanding species-specific breeding systems to inform conservation strategies, as species dependent on pollinators may be more vulnerable to changes in pollinator populations or habitat disturbances (Pedron et al. 2012b; Chen et al. 2021a). Moreover, the breeding system type can be different among the population, as reported in *Phaius tankervilleae* (Banks) Blume (Gandawidjaja and Arditti 1982). *Habenaria rhodocheila*, orange form, has been reported from China as self-compatibility orchid pollinated by butterfly (Zhang and Gao 2021). It produces rather highly fruit set due to being reward species, i.e., species which provides nectar for pollinators (Chen et al. 2021b; Zhang et al. 2021). However, there is no information about reproductive of *H. janellehayneana*.

Basic information in nature is needed for conservation, particularly in local conserved areas where the natural habitat of orchid populations is. Understanding their reproductive success is crucial need. The main goals of this research were to investigate the reproductive traits, including flowering, fruit and seed set and breeding systems, of highly horticulturally potential *Habenaria*, *H. janellehayneana* and *H. rhodocheila* in particular natural habitat in Thailand. The results from this research study will provide basic information used for suitable orchid conservation in the local conserved areas.

MATERIALS AND METHODS

Study area

This study was conducted at Phu Hin Rong Kla National Park in Phitsanulok Province of Northern Thailand, during mid of August to the end of October 2019. The vegetation at the study site of both species is lower montane forest. Populations of *H. rhodocheila* and *H. janellehayneana* were studied at a 50x50 m sampling plot with 2 plots for each species: plot 1: *H. janellehayneana* in Mhundaeng waterfall (1,196 m asl), plot 2: *H. janellehayneana* in Romklaoparadorn waterfall (1,239 m asl), plot 3: *H. rhodocheila* in Lanhinpum (1,310 m asl), and plot 4: *H. rhodocheila* in Lanhintaek (1,104 m asl) (Figure 1). There was not a sympatric population in both species despite the habitat of both orchids is lower montane forest. In this study, *H. janellehayneana* was found only by stream banks, and *H. rhodocheila* was found on scrub forest on sandstone bedrock with moisture ground, but both species are dormant during dry season (November-May) (Figure 2).

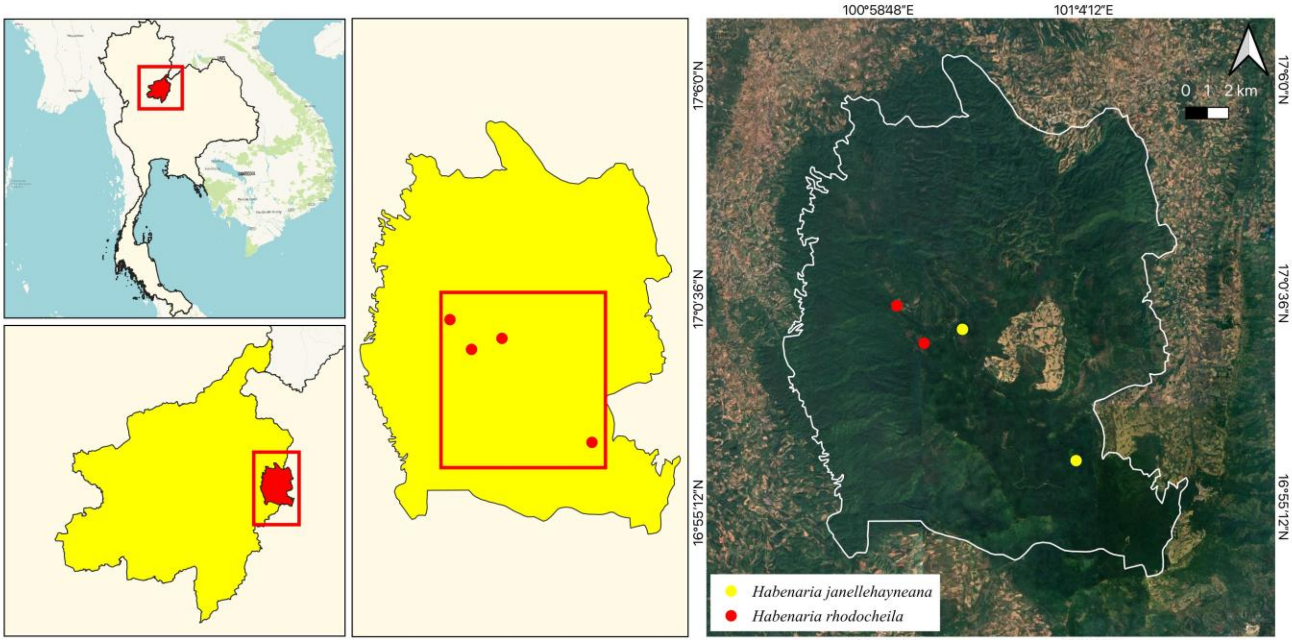

Figure 1. Location of Phu Hin Rong Kla National Park, Northern Thailand, indicating the studied plots of *Habenaria janellehayneana* and *Habenaria rhodocheila*

Figure 2. A. *Habenaria janellehayneana,* B. *Habenaria rhodocheila* in natural habitat (photos by S. Thongmueng)

Research procedure

Flowering and fruit set

For each species, data was collected from two plots. In the second week of August, we started to tag the orchid inflorescences. Then the number of fruits of both species were noted in the mid of October 2019, when the flowers of both species completely withered. In both *H. janellehayneana* and *H. rhodocheila*, the length of the longest leaf, shoot length, and the number of flowers per inflorescence were measured. To determine the fruit set, 50 flowers of each species were tagged across the plots and their fruits developed under natural conditions. Seeds from mature, dehisced capsules were collected and dried in silica gel. Seed counts per capsule were determined by using a low-power binocular microscope. From these seed counts, the average number of seeds per capsule as well as fertile, defined by rounded embryo visibility and sterile seeds, without embryo, per capsule was calculated.

Breeding system

The experiment on breeding systems of both species were performed at the same time of flowering of which flowering and fruit set studies. To investigate the breeding systems of *H. janellehayneana* and *H. rhodocheila*, we carried out three pollination treatments to compare with natural pollination. For each species, inflorescences from five individual plants were bagged with fine nylon mesh (0.5×0.5 mm) before the flowers opened. Once the flowers had fully opened, twelve flowers on each inflorescence were assigned to one of the following treatments: i) left untouched to test for spontaneous self-pollination, ii) hand self-pollinated, or iii) hand cross-pollinated using pollinia from a plant at least 10 meters away. After the treatments, the flowers were re-bagged and monitored for fruit development over four weeks. As a comparison, natural pollination was assessed by tagging 30 flowers per species in the field.

Fertile seeds and inbreeding depression

Three mature capsules from each pollination treatments (see above) were collected to evaluate % fertile seeds, with distinct large embryos. All seeds from each capsule were placed on a Petri dish and counted under a Stereo Microscope (Xenon XTD-217). The inbreeding depression index was calculated following Tao et al. (2018) as follows:

δ = 1- (proportion of well-developed seeds after self-pollination/proportion of well-developed seeds after cross-pollination).

Data analysis

To categorize the breeding system, percentage fruit-set for each treatment was calculated using the Self-Incompatibility Index (ISI) and Auto-Fertility Index (AFI) in order (Rodger and Ellis 2016). Using the program SPSS for Windows 22, Pearson's correlation coefficient was calculated to test correlations between leaf length and inflorescence length, and number of flowers per inflorescence. Analysis of Variance (ANOVA) was performed with SPSS V23.0 statistical package (SPSS Inc. Chicago, USA), and the means were compared by Duncan's multiple range test ($P \leq 0.05$).

RESULTS AND DISCUSSION

Floral features and flowering phenology

Habenaria janellehayneana produced a single racemose inflorescence on terminal shoot. The flowers are zygomorphic, with an inferior cylindrical ovary, pinkish sepals and petals. Labellum 2.7-2.9 cm long and 2.1-2.5 cm broad, bright pink with 3-lobbed, the mid-lobe is emarginate. Spur is cylindrical and slender, 5.1-5.5 cm long. The stigmas are 2 arms, convergent at the apical part. *Habenaria rhodocheila* has an overall feature similar to *H. janellehayneana*, but it differs in having greenish or cream sepals and petals, and orange labellum, spur and stigma arms, including a little smaller floral size. Additionally, its stigma arms are divergent at the apical part (Figure 2).

The flowering period of both orchid species occurs in the rainy season, *H. janellehayneana* from late July to September and *H. rhodocheila* from mid-July to September. *Habenaria janellehayneana* individuals reached the average height shoot length and leaf length almost 16 cm and 19 cm, respectively. The number of flowers per inflorescence ranged from 1 to 11. For *H. rhodocheila* the average height shoot length and leaf length were almost 19.8 cm and 15 cm, respectively, while the number of flowers per inflorescence ranged from 1 to 15 (Table 1).

Fruit set and seed set

Overall, the average fruit set at each plot varied from 1-15 fruits. The percentage of natural fruit set of *H. janellehayneana* was between 41.43-48.95% while *H. rhodocheila* was between 53.55-71.87%. There is neither correlation between the leaf length nor inflorescences length and fruit set (r<0.5). The number of flowers in an inflorescence showed slightly correlated with fruit set (r=0.6). In *H. janellehayneana*, the proportion of fertile seeds (with embryos) was significantly higher under natural pollination conditions (92.30%) compared to self-pollination (59.39%) and cross-pollination (64.53%) treatments ($p<0.05$). Similarly, *H. rhodocheila* exhibited significant differences ($p<0.05$) in fertile seed proportions, with 74.30% fertility in natural pollination, 67.45% in self-pollination, and 80.44% in cross-pollination (Table 2).

Breeding systems and inbreeding depression

No fruit set was observed in untouched, bagged flowers of both *H. janellehayneana* and *H. rhodocheila*. In contrast, all manually self-pollinated flowers achieved 100% fruit set in both species. The indices of Self-Incompatibility (ISI) and Auto-Fertility (AFI) were 1 and 0, respectively, for both species, indicating that they are genetically self-compatible but non-autogamous. No fruit developed in the no-pollination experiment indicated that both orchid species need insects for pollination. The total seed development varied significantly between hand self-pollination, hand cross-pollination, and natural pollination treatments ($p<0.05$). The inbreeding depression index of *H. janellehayneana* and *H. rhodocheila* were 0.08 and 0.16, respectively.

Discussion

Habenaria janellehayneana and *H. rhodocheila* are deciduous terrestrial or lithophytic orchids, producing leaves and inflorescence shoots above the ground during rainy season. Both species produce flowers in the same period, the flowers were produced in the late rainy season and their mature capsules broke before dry season. For *H. rhodocheila*, the flowering is different by each population, may be caused by the variation of environment and genetic backgrounds (Chen et al. 2021b; Zhang et al. 2021). The flower span in population is 29±3 days and an individual flower is 7±1.5 days (Zhang et al. 2021). There is no observation of individual and population flower span in *H. janellehayneana* in this study.

Table 1. Shoot length (including inflorescence length), leaf length, number of flowers per an inflorescence and % fruit set in four studied plots

Species	Plot	Shoot length (cm) mean±se (min-max)	Leaf length (cm) mean±se (min-max)	Number of flowers/inflorescence mean±se (min-max)	% Fruit set
H. janellehayneana	1	6.49±0.18^{b} (1.10-16.00) *N: 212	10.77±0.17^{a} (5.80-19.00) *N: 212	3.80±0.23^{b} (1.00-11.00) **N: 115	41.43±3.98^{b} **N: 115
	2	4.41±0.36^{c} (0.60-13.90) *N: 54	7.78±0.37^{c} (2.60-14.10) *N: 212	3.13±0.41^{b} (1.00-10.00) **N: 30	48.95±7.10^{b} **N: 30
H. rhodocheila	3	7.83±0.24^{a} (0.50-19.80) *N: 263	9.39±0.15^{b} (0.40-14.50) *N: 212	5.37±0.25^{a} (1.00-15.00) **N: 179	53.55±3.13^{b} **N: 179
	4	2.79±0.25^{d} (0.70-10.50) *N: 75	7.91±0.28^{c} (3.10-15.00) *N: 212	3.61±0.41^{b} (1.00-9.00) **N: 23	71.87±6.67^{a} **N: 23

Note: *N is number of reproductive and vegetative plants at each plot, **N is number of reproductive plants at each plot. Values followed by different letters within a column are significantly different at P<0.05 according to DMRT

Table 2. Type of pollination, fruit set, and seeds per capsule of *Habenaria janellehayneana* and *H. rhodocheila*

Species	Type of pollination (N)	Fruit set (%)	Total seeds (Mean±SD)	Fertile seeds (%) Mean (min-max±SD)
H. janellehayneana	Untouched (12)	0	0	0
	Self-pollination (12)	100	25,338±2,552^{a}	59.39±4.48^{b} (55.99-64.46)
	Cross-pollination (12)	100	9,432±1,048^{c}	64.53±0.84^{b} (63.57-65.11)
	Natural pollination (30)	50	13,287±1,949^{b}	92.30±0.48^{a} (92.00-92.56)
H. rhodocheila	Untouched (12)	0	0	0
	Self-pollination (12)	100	16,755±1,199^{b}	67.45±3.62^{b} (64.33-71.43)
	Cross-pollination (12)	100	23,463±4,494^{a}	80.44±0.29^{ab} (80.19-80.76)
	Natural pollination (30)	53.33	22,591±2,437^{ab}	74.30±1.16^{b} (72.97-75.11)

Note: Values followed by different letters within a column are significantly different at P<0.05 according to DMRT

According to Neiland and Wilcock (1998), nectar-rewarding orchid species generally exhibit higher fruit set rates compared to non-rewarding species. Similarly, *H. rhodocheila* and *H. janellehayneana*, both nectar-rewarding orchids, showed natural fruit set rates between 41.43% and 71.87% (Table 1). Other natural populations of *H. rhodocheila* revealed fruit set between 83.33-100% (Chen et al. 2021b; Zhang et al. 2021). The different reproductive success, based on fruit set, has shown different in populations of *H. rhodocheila*, that may be depended by number of pollinators. However, a number of factors, including the rewarding nectar, conspicuous bright flowers, and the dependable frequency and fidelity of the pollinators, may contribute to the relatively high fruit set in *H. rhodocheila* (Chen et al. 2021b). Other *Habenaria* species also have high fruit set such as *H. aitchisonii* Rchb.f. (86.5% fruit set) and *H. fordii* Rolfe (79.40-89.76% fruit set) (Zhang and Gao 2017; Xiong et al. 2019). Contrary, *H. malintana* exhibited as obligate agamospermy with 100% fruit set without pollination (Zhang and Gao 2018). Moreover, the distribution patterns of the terrestrial orchid species may be resulted by their fruit set. Srimuang et al. (2010) reported that the number of fruit sets of the narrowly distributed species of the orchid genus *Sirindhornia* was lower than the widely distributed species. Our result showed that the fruit set of narrowly distributed species, *H. janellehayneana* and wide distribution species, *H. rhodocheila*, did not differ. This may be due to the high abundance of pollinators present in the habitats of both species. Similarly, it has been shown that fruit success in tropical orchids is often linked to pollinator availability and efficiency (Reyes et al. 2021).

Fruit set is a useful parameter for determining the reproductive success of Orchidaceae (Tremblay et al. 2005; Zhang and Gao 2021). The fruit set of both species was relatively high, like other rewarded *Habenaria* species (Xiong et al. 2019). Although there are moderate and high number of fruit set (more than 50%) and embryonic seeds (59.39-92.30%) in both species, the germination and survival rate of seedlings were lower than 20% for in vitro experiment (Thummavongsa et al. 2022, et al. 2024). The breeding system traits of the orchid can also affect fruit and seed number. Travers et al. (2018) reported that *Platanthera praeclara* Sheviak & M.L.Bowles produced smaller amount seed number and embryo development in self-pollination comparing with cross-pollination. Our data of these *Habenaria* species did not exhibit the same. Self-pollination tended to have lower fertile seeds than cross-pollination in *H. janellehayneana*. Contrary to *H. rhodocheila*, the fertile seeds production from different breeding systems were not different.

Self-compatibility breeding systems seem to be the main trait in *Habenaria* (Zhang and Gao 2018; Chen et al. 2021a; Zhang et al. 2021). In this study, the breeding systems of *H. janellehayneana* and *H. rhodocheila* were genetically self-compatible, non-autogamous species and no apomixis occurs, like other orchid species in the genus *Habenaria* such as *H. gourlieana* Gillies ex Lindl., *H. hieronymi* Kraenzl., *H. limprichtii* Schltr., *H. montevidensis* Spreng., *H. parviflora* Lindl., *H. petelotii* Gagnep. and *H. rupicola* Barb.Rodr. (Tremblay et al. 2005; Zhang and Gao 2021). However, some species of *Habenaria* are autogamous species such as *H. malintana* (Zhang and Gao 2018).

In this study there was no data on pollination of both species. Recent study on pollination of *H. rhodocheila* reported that two diurnal swallowtail butterflies, *Papilio helenus* Linnaeus, 1758 and *P. nephelus* Boisduval, 1836 (Papilionidae) were effective pollinator in China (Chen et al. 2021b; Zhang et al. 2021). While *P. memnon* Linnaeus, 1758 was observed as pollinia remover on *H. rhodocheila* in Northern Thailand. (Williams and Watthana 2011). There is no information about pollination of *H. janellehayneana.* However, their floral characteristic is classed as rewarding species due to producing nectar inside their labellum spur including the bright colors such as pink, promoting the traditional pyschophily, butterfly pollinated flower (Balducci et al. 2019).

In terms of breeding system and genetic diversity, our findings are similar to those of Chen et al. (2021b), reported an inbreeding depression index at 0.22 in a southern China population of *H. rhodocheila,* while our results were at 0.16, much lower than that reported for *H. limprichtii* (Chen et al. 2021b). The index value for *H. janellehayneana* was 0.08, lower than *H. rhodocheila*. These low values suggest that self-pollination may occur and could serve as an adaptive strategy in response to limited pollinator availability. Such patterns may also reflect purging of deleterious alleles over time. However, in the long term, this may reduce genetic variation within populations and limit their evolutionary potential (Charlesworth and Willis 2009).

In conclusion, *H. janellehayneana* and *H. rhodocheila* populations in Phu Hin Rong Kla National Park exhibit non-spontaneous autogamy but being a self-compatibility. Their natural fruit set depends on pollination, with rather high fruit set, due to rewarding species and no showing 100% fruit set, autogamy. From our results it is interpreted that the population of both *Habenaria* species and populations have rather highly reproductive success. However, long term monitoring on fruit set should be performed to reflect the survival of each population including other subpopulation in this naturally conserved area. Our study revealed some autecology, especially reproductive success, estimated by fruit set, of commercial potential terrestrial orchid in natural habitat. Based on this basic information of this study, the maintenance of ecosystem is obviously important including the pollinators conservation. The survey on natural fruit set in the natural habitat is the quick assessment of population survival status, could be applied for other local conserved areas. Further study on survival rate including population dynamic shall be fulfilled basic knowledge for proper conservation of both species in this conserved area.

ACKNOWLEDEMENTS

This work was financially supported by National Science and Technology Development Agency (NSTDA), Ministry of Science and Technology (MOST), and Biodiversity-Based Economy Development Office (BEDO), Thailand. We would like to thank Sarawut Thongmueng for plant photographs and Edward Frank Gosser for English editing. A permit for this research was provided by the Department of National Parks, Wildlife and Plant Conservation of Thailand (Permit numbers: 0907.4/5517). Theera Thummavongsa: experimental work, data collection, data analysis, and writing the first draft of the manuscript. Chuthapond Musimun: experimental work, methodology assistance, data collection. Santi Watthana: study design, result interpretation and revision of the manuscript. Nooduan Muangsan: study design, writing, and manuscript revision. Santi Watthana and N. Muangsan contributed equally to this work.

REFERENCES

Ackerman JD, Phillips RD, Tremblay RL, Karremans A, Reiter N, Peter CI, Bogarín D, Pérez-Escobar OA, Liu H. 2023. Beyond the various contrivances by which orchids are pollinated: Global patterns in orchid pollination biology. Bot J Linn Soc 202 (3): 295-324. DOI: 10.1093/botlinnean/boac082.

Balducci MG, van der Niet T, Johnson SD. 2019. Butterfly pollination of *Bonatea cassidea* (Orchidaceae): Solving a puzzle from the Darwin era. S Afr J Bot 123: 308-316. DOI: 10.1016/j.sajb.2019.03.030.

Charlesworth D, Willis JH. 2009. The genetics of inbreeding depression. Nat Rev Genet 10 (11): 783-796. DOI: 10.1038/nrg2664.

Chen M, Zhang G, Luo Y, Chen X, Liu Z. 2021a. Pollination biology and reproductive ecology of *Habenaria* species in China. Plant Divers 43 (5): 333-345. DOI: 10.1002/ece3.7242.

Chen XH, Tan SL, Liang YL, Huang L, Xiao HW, Luo HL, Xiong DJ, Yang BY, Ren ZX. 2021b. The pollination of *Habenaria rhodocheila* (Orchidaceae) in South China: When butterflies take sides. Ecol Evol 11 (6): 2849-2861. DOI: 10.1002/ece3.7242.

Choltco TC, Moloney B, Yong G. 2017. A new *Habenaria* from Northern Thailand (Subfamily: Orchidoideae Tribe: Orchideae Subtribe: Orchidinae). Orchideen J 4 (5): 1-4.

Gandawidjaja D, Arditti J. 1982. Post-pollination phenomena in orchid flowers. XI. Autogamy in *Phajus tankervilliae* (Aiton) Blume, Orchidaceae. American Journal of Botany 69(3): 335-338. DOI: 10.1002/j.1537-2197.1982.tb13265.x.

Hinsley A, Boer HJ, Fay MF, Gale SW, Gardiner LM, Gunasekara RS, Kumar P, Masters S, Metusala D, Roberts DL, Veldman S, Wong S, Phelps J. 2018. A review of the trade in orchids and its implications for conservation. Bot J Linn Soc 186 (4): 435-455. DOI: 10.1093/botlinnean/box083.

Kurzweil H. 2011. *Habenaria* Willd. In: Santisuk T, Larsen K (eds). Flora of Thailand. The Forest Herbarium, Department of National Parks, Wildlife and Plant Conservation, Bangkok, Thailand.

Neiland MR, Wilcock CC. 1998. Fruit set, nectar reward, and rarity in the Orchidaceae. Am J Bot 85 (12): 1657. DOI: 10.2307/2446499.

Pedron M, Buzatto CR, Singer RB, Batista JAN, Moser A. 2012a. Pollination biology of four sympatric species of *Habenaria* (Orchidaceae: Orchidinae) from southern Brazil. Bot J Linn Soc 170: 141-156. DOI: 10.1111/j.1095-8339.2012.01285.x.

Pedron M, Galetto L, Singer RB. 2012b. Pollination biology of *Habenaria jaguariahyvae* and *Habenaria bractescens* (Orchidaceae) in south-eastern Brazil. Plant Species Biol 27 (2): 93-101.

Phelps J, Webb EL. 2015. Invisible wildlife trades: Southeast Asia's undocumented illegal trade in wild ornamental plants. Biol Conserv 186: 296-305. DOI: 10.1016/j.biocon.2015.03.030.

Phillips RD, Reiter N, Pealall R. 2020. Orchid conservation: From theory to practice. Ann Bot 126: 345-362. DOI: 10.1093/aob/mcaa093.

POWO. 2024. Plants of the World Online. Royal Botanic Gardens, Kew. https://powo.science.kew.org/.

Reyes H, Draper D, Marques I. 2021. Pollination in the rainforest: Scarce visitors and low effective pollinators limit the fruiting success of tropical orchids. Insects 12 (10): 856. DOI: 10.3390/insects12100856.

Rodger JG, Ellis AG. 2016. Distinct effects of pollinator dependence and self-incompatibility on pollen limitation in South African biodiversity hotspots. Biol Lett 12: 253. DOI: 10.1098/rsbl.2016.0253.

Srimuang K, Watthana S, Pedersen HÆ, Rangsayatorn N, Eungwanichayapant PD. 2010. Flowering phenology, floral display, and reproductive success in the genus *Sirindhornia* (Orchidaceae): A comparative study of three pollinator-rewarding species. Ann Bot Fenn 47: 439-448. DOI: 10.5735/085.047.0603.

Tao Z, Ren, Z-X, Bernhardt P, Huan L, Li H-D, Wang H. 2018. Nocturnal hawkmoth and noctuid moth pollination of *Habenaria limprichtii* (Orchidaceae) in sub-alpine meadows of the Yulong Snow Mountain (Yunnan, China). Bot J Linn Soc 187 (3): 483-489. DOI: 10.1093/botlinnean/boy023/5037747.

Thummavongsa T, Musimun C, Watthana S, Gale S, Choeyklin R, Wiriyathanawudhiwong N, Muangsan N. 2024. Enhancing germination of *Habenaria janellehayneana* (Orchidaceae): Insight from asymbiotic and symbiotic methods. Plants Ornam J 14 (1): 11-23.

Thummavongsa T, Watthana, S, Musimun C, Muangsan N. 2022. Asymbiotic germination of *Habenaria rhodocheila* Hance on different culture media and impact of plant growth regulators. Asia Pac J Sci Technol 27 (5): 1-9. DOI: 10.14456/apst.2022.82.

Tinoammini N, Aazhivaendhan G, Rajasekar C, Siva G, Senthil KT, Muthukumar M. 2024. Medicinal Orchids of genus *Habenaria*. In: Husen A, Pant M (eds). Exploring Medicinal Orchids. CRC press, Boca Raton. DOI: 10.1201/9781003436638-10.

Travers SE, Anderson K, Vitt P, Harris MO. 2018. Breeding system and inbreeding depression in the rare orchid, *Platanthera praeclara*, in a fragmented grassland landscape. Botany 96 (3): 151-159. DOI: 10.1139/cjb-2017-0104.

Tremblay RL, Ackerman JD, Zimmerman JK, Calvo RN. 2005. Variation in sexual reproduction in orchids and its evolutionary consequences: A spasmodic journey to diversification. Biol J Linn Soc 84 (1): 1-54. DOI: 10.1111/j.1095-8312.2004.00400.x.

Williams C, Watthana S. 2011. The pollination of *Habenaria rhodocheila*: A study trip to the forests of Northern Thailand to see the habitats of *H. lindleyana, H. lucida* and *H. limprichtii*. Orchid Rev 119: 206-213.

Xiong YZ, Jia LB, Liu CQ, Huang SQ. 2019. Effective pollinia transfer by settling moths' legs in an orchid *Habenaria aitchisonii*. J Syst Evol 58: 174-181. DOI: 10.1111/jse.12485.

Zhang W, Gao J. 2021. A comparative study on the reproductive success of two rewarding *Habenaria* species (Orchidaceae) occurring in roadside verge habitats. BMC Plant Biol 21 (1): 187. DOI: 10.1186/s12870-021-02968-w.

Zhang WL, Gao JY. 2017. Multiple factors contribute to reproductive isolation between two co-existing *Habenaria* species (Orchidaceae). Plos One 12: e0188594. DOI: 10.1371/journal.pone.0188594.

Zhang WL, Gao JY. 2018. High fruit sets in a reward less orchid: A case study of obligate agamospermy in *Habenaria*. Aust J Bot 66 (2): 144-151. DOI: 10.1071/BT17182.

Zhang Z, Cui X, Zhou J, Huang C, Deng J, Tang X, Luo S. 2021. Pollination of the Orchid *Habenaria rhodocheila* by the swallowtail butterfly *Papilio helenus* in Subtropical Evergreen broad-leaved forests in Southern China. Flora 274: 151736. DOI: 10.1016/j.flora.2020.151736.