

Flowering phenology and seed production of three threatened tropical palms, *Johannesteijsmannia* spp. (Arecaceae)

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ABSTRACT. The reproductive behaviour and fruit production of three endangered species of *Johannesteijsmannia* H.E.Moore were studied for two years. Flowering occurred annually in *Johannesteijsmannia magnifica* J.Dransf. and sub-annually in *J. lanceolata* J.Dransf. and *J. perakensis* J.Dransf. The flowering of all species peaked from March to May and occurred during the wet seasons. High seed loss of 84–98% was recorded among the species. On average, *Johannesteijsmannia perakensis* produced the highest number of mature fruits per year (229) and *J. lanceolata* the lowest (69). This preliminary study provides vital information on species fecundity and demonstrates that each species, although within the same genus, has different flowering and fruiting behaviour.

Keywords. Climate, fruit set, Palmae, rare endemic, reproductive biology

Introduction

Climate factors may serve as a proximate cue for flowering in palms. In the Neotropics, there are numerous studies on the flowering of palms in response to climate factors, which mostly relate to rainfall and very few to both rainfall and temperature (Table 1). In some species, there seems to be a clear relationship between flowering and the dry or wet season (e.g. *Bactris constanciae* Barb.Rodr. and *Astrocaryum gynacanthum* Mart.) (Table 2). In others the relationship is less clear, especially in those that show aseasonal (almost continuous) or irregular flowering patterns, such as *Bactris major* Jacq. and *B. maraja* Mart. Many palms in Brazil and Panama have been reported to flower mainly during the wet season along with a few species that flower in between the dry and wet seasons (Table 2). On the other hand, most species studied in Mexico (11 species over nine years) and French Guiana (seven species over 22 months) have been reported to flower in the dry season (review by Henderson, 2002).

Similar studies of palms in the Paleotropics are scarce or anecdotal: 1) in Peninsular Malaysia, the one-year study by Fong (1978) merely stated that the peak flowering of an understorey palm, *Eugeissona tristis* Griff., occurred during the rainy season from April to August; 2) in Thailand the flowering of three species of *Licuala* Thunb. correlated differently with rainfall (Barfod et al., 2003): *Licuala spinosa* Wurm. flowered in the early rainy season, *L. peltata* Roxb. ex Buch.-Ham. at the end of the rainy season, and *L. distans* Ridl. in the early dry season; and 3) in Peninsular Malaysia, based on his own observations, Dransfield (1972) suggested that drought probably triggered gregarious flowering in *Johannesteijsmannia* H.E.Moore.

Johannesteijsmannia is a popular ornamental that is traded mainly in the southern parts of North America, Taiwan and Japan (P. Boyce, pers. comm.). Domestication of

Johannesteijsmannia began about 20 years ago in Sarawak, Malaysia (P. Boyce, pers. comm.) but reports exist of seeds still being collected in the wild by indigenous people for trading in Peninsular Malaysia (Chan & Saw, 2009; Tan & Chan, 2019). Although a recent survey among major suppliers and smallholders revealed that the demand for the palms seems to have declined (Tan & Chan, 2019), there are currently no data available on seed production in natural populations to be able to assess if this trade is sustainable.

Phenological studies and quantification of seed production are useful for estimating the reproductive capacity of a species and for conservation management (Morellato et al., 2016). Here, we 1) describe the phenology, 2) correlate climatic cues (temperature and rainfall) with flowering, and 3) provide preliminary data on the seed production of three endangered species of *Johannesteijsmannia* occurring in Peninsular Malaysia.

Materials and methods

Species description

The three species studied, *Johannesteijsmannia lanceolata* J.Dransf., *J. magnifica* J.Dransf. and *J. perakensis* J.Dransf. (Livistoninae, subfamily Coryphoideae) (Dransfield et al., 2008) are all endangered perennial palms in Malaysia (Chan et al., 2011). *Johannesteijsmannia lanceolata* and *J. magnifica* are acaulescent species growing up to 3 m tall, whereas *J. perakensis* has a trunk and reaches up to 5 m in height. Although all species are endemic to Peninsular Malaysia, they are abundant and form a dominant understorey vegetation in their restricted local niches. The inflorescences are axillary and, depending on species, have one to six orders of branching. The rachillae of *Johannesteijsmannia magnifica* and *J. perakensis* are comb-like whereas those of *J. lanceolata* are finger-like. The duration from the first appearance of an inflorescence bud to anthesis is about one month and flowering takes up to two weeks (Chan & Saw, 2011). Young fruits are cream to pinkish white at first and when the pericarp breaks up they turn orange-brown. Maturing fruits are light brown in *Johannesteijsmannia magnifica* and *J. lanceolata*, and dark brown in *J. perakensis*.

Study sites and meteorological data

Three study sites were selected: 1) the Angsi Forest Reserve (FR) for *Johannesteijsmannia lanceolata* in the state of Negeri Sembilan, 2) the Kledang-Saiong FR for *J. perakensis* in Perak, and 3) the Berembun FR for *J. magnifica* in Negeri Sembilan (Fig. 1). All of the populations studied occur at 120–350 m above sea level in evergreen tropical lowland dipterocarp forest. To minimise human disturbances at these sites, we placed warning signs that an experiment was in progress. We did not observe any direct or indirect signs of seed harvest activity at the study sites.

The Malaysian Meteorological Service Department supplied the rainfall and temperature data that were logged from November 2003 until January 2006 at the nearest weather stations in districts of Kuala Pilah (c. 22 km from the Angsi FR), Bukit Kledang (c. 12 km from the Kledang-Saiong FR study site) and Jelebu (c. 15 km from the Berembun FR). These data could not reflect the microclimates in the forests but served as the best estimates of weather conditions or seasonality at the study sites. In 2005, no rainfall data were available from the Jelebu station in September (for *Johannesteijsmannia magnifica*) and from the Kuala Pilah station in October (for *J. lanceolata*) (Fig. 2). Temperature data were also not available from the Kuala Pilah

Table 1. Studies on the phenology of palms in tropical climates (Santa Catarina is subtropical).

Reference	Study site	Annual rainfall, mm	Mean annual temperature, °C	Vegetation type	Study duration
Adler et al. (1998)	Chicha Island, Panama	Not reported	Not reported	Second-growth moist forest	44 months
De Steven et al. (1987)	Barro Colorado Island, Panama	1995–4633	Not reported	Semideciduous lowland forest	4 years
Fava et al. (2011)	Pantanal, Brazil	1080	27.6	Riparian forest	14 months
Henderson et al. (2000)	Central Amazon, Brazil	2186	Not reported	Lowland moist forest	40 months
Martén & Quesada (2001)	Heredia, Costa Rica	7000–8000	Not reported	Premontane rain forest	2 years
Nazareno & Reis (2012)	Santa Catarina, Southern Brazil	1500	17.1	Grassland	20 months
Rojas-Robles & Stiles (2009)	Colombian Andes, Colombia	1914	22.7	Premontane humid forest	4 years
Rosa et al. (2013)	Roraima, Brazilian Amazonia	1614	Not reported	Lowland savanna & semi-deciduous forest	2 years
Scariot et al. (1991)	Central Brazil	1566	21.7	Pasture & tropical latifoliate semideciduous forest	1 year

station in September 2004 and from April to August in 2005. A summary of the temperature and rainfall data during the study period from year 2004 to 2005 is shown in Table 3. The mean annual temperature for Kuala Pilah, Bukit Kledang and Jelebu was around 27°C. Bukit Kledang received the highest mean annual rainfall (2736 mm) whereas Jelebu received the lowest (1124 mm). We followed Numata et al. (2013) in defining a low temperature as a mean monthly minimum temperature (MT) < 20 °C, a drought as when the monthly rainfall was < 40 mm, and a prolonged drought as when there was no rainfall for > 30 days.

Phenology and fruit production

Thirty adult plants were tagged in each population of *Johannesteijsmannia lanceolata*, *J. magnifica* and *J. perakensis*. Flowering (from when the first flowers in an inflorescence open until all its flowers have opened) and fruiting (from the end of flowering until fruit maturity) were monitored monthly from February 2004 to January

Table 2. Literature review of flowering of palms in relation to climate. See Table 1 for the study sites using references. All species are understory except those marked (*) which are canopy species.

Species	Flowering season	Main flowering period	Reference
<i>Attalea attaleoides</i> (Barb.Rodr.) Wess.Boer	Aseasonal	Oct–Dec	Henderson et al. (2000)
<i>Attalea phalerata</i> Mart. ex Spreng	Aseasonal, mainly dry	Sep–Oct	Fava et al. (2011)
<i>Bactris major</i> Jacq.	Aseasonal, mainly wet	May–Aug	De Steven et al. (1987)
<i>Elaeis oleifera</i> (Kunth) Cortés	Aseasonal	Irregular	De Steven et al. (1987)
<i>Euterpe precatoria</i> Mart. *	Aseasonal	Irregular	Henderson et al. (2000)
<i>Geonoma deversa</i> (Poit.) Kunth	Aseasonal	Irregular	Henderson et al. (2000)
<i>Geonoma petiolata</i> H.E.Moore	Aseasonal, throughout the year	Unclear	Marten & Quesada (2001)
<i>Geonoma maxima</i> var. <i>maxima</i> (Poit.) Kunth	Aseasonal	Unclear	Henderson et al. (2000)
<i>Geonoma stricta</i> var. <i>stricta</i> (Poit.) Kunth	Aseasonal	Jan–Mar	Henderson et al. (2000)
<i>Oenocarpus bacaba</i> Mart. *	Aseasonal	Irregular	Henderson et al. (2000)
<i>Oenocarpus bataua</i> Mart. *	Aseasonal	Irregular	Henderson et al. (2000), Rojas-Robles & Stiles (2009)
<i>Synechanthus warscewiczianus</i> H.Wendl.	Aseasonal, mainly wet	May–Jul	De Steven et al. (1987)
<i>Astrocaryum sciophilum</i> (Miq.) Pulle	Dry	Sep	Henderson et al. (2000)
<i>Bactris constanciae</i> Barb.Rodr.	Dry	July	Henderson et al. (2000)
<i>Bactris elegans</i> Barb.Rodr. & Trail	Dry	July	Henderson et al. (2000)
<i>Bactris hirta</i> Mart.	Dry	July–Aug	Henderson et al. (2000)

Table 2. Continuation.

Species	Flowering season	Main flowering period	Reference
<i>Chamaedorea tepejilote</i> Liebm.	Dry	Dec–Jan	De Steven et al. (1987)
<i>Geonoma cuneata</i> H.Wendl. ex Spruce	Dry and wet interface	May–Jul	De Steven et al. (1987)
<i>Hyospathe elegans</i> Mart.	Dry	Aug–Oct	Henderson et al. (2000)
<i>Oenocarpus mapora</i> H.Karst. *	Dry and wet	Oct–Mar	De Steven et al. (1987)
<i>Socratea exorrhiza</i> (Mart.) H.Wendl. *	Dry and wet interface	Jun–Aug	De Steven et al. (1987)
<i>Bactris acanthocarpa</i> var. <i>exscapa</i> Barb.Rodr.	Irregular	Irregular	Henderson et al. (2000)
<i>Bactris maraja</i> Mart.	Irregular	Apr, Jun	Henderson et al. (2000)
<i>Bactris simplicifrons</i> Mart.	Irregular	Jan	Henderson et al. (2000)
<i>Geonoma interrupta</i> (Ruiz & Pav.) Mart.	Irregular, mainly wet	Aug–Dec	De Steven et al. (1987)
<i>Socratea exorrhiza</i> (Mart.) H.Wendl. *	Irregular, mainly dry	Sep–Oct	Henderson et al. (2000)
<i>Syagrus inajai</i> (Spruce) Becc. *	Irregular	Unclear	Henderson et al. (2000)
<i>Acrocomia aculeata</i> (Jacq.) Lodd. ex Mart. *	Wet	Oct–Nov	Scariot et al. (1991)
<i>Astrocaryum gynacanthum</i> Mart.	Wet	Dec–Mar	Henderson et al. (2000)
<i>Astrocaryum standleyanum</i> L.H.Bailey	Wet	Jul–Aug	De Steven et al. (1987)
<i>Attalea rostrata</i> Oerst. *	Wet	May–Sep	De Steven et al. (1987)
<i>Bactris acanthocarpa</i> var. <i>intermedia</i> A.J.Hend.	Wet	Irregular	Henderson et al. (2000)
<i>Bactris acanthocarpa</i> var. <i>trailiana</i> (Barb.Rodr.) A.J.Hend.	Wet	Apr–Jul	Henderson et al. (2000)
<i>Bactris barronis</i> L.H.Bailey	Wet	May–Jun	De Steven et al. (1987)

Table 2. Continuation.

Species	Flowering season	Main flowering period	Reference
<i>Bactris coloniata</i> L.H.Bailey	Wet	May–Jun	De Steven et al. (1987)
<i>Bactris gastoniana</i> Barb.Rodr.	Wet	May	Henderson et al. (2000)
<i>Bactris glaucescens</i> Drude	Wet	Oct–Nov	Fava et al. (2011)
<i>Bactris hirta</i> var. <i>pectinata</i> (Mart.) Govaerts	Wet	Dec–Feb	Henderson et al. (2000)
<i>Bactris killipii</i> Burret	Wet	Jan, Apr	Henderson et al. (2000)
<i>Bactris tomentosa</i> Mart.	Wet	Jan–Apr	Henderson et al. (2000)
<i>Butia eriospatha</i> (Mart. ex Drude) Beccarii *	Wet	Oct–Mar	Nazareno & Reis (2012)
<i>Cryosophila warscewiczii</i> (H.Wendl.) Bartlett	Wet	Jul–Sep	De Steven et al. (1987), Adler et al. (1998)
<i>Geonoma maxima</i> subsp. <i>spixiana</i> (Mart.) A.J.Hend.	Wet and dry interface	Jun–Aug	Henderson et al. (2000)
<i>Mauritia flexuosa</i> L.f. *	Wet and dry interface	Aug–Nov	Rosa et al. (2013)
<i>Oenocarpus minor</i> Mart.	Wet	Dec–Feb	Henderson et al. (2000)

2006. A semi-mature fruit has a soft endosperm whereas a mature fruit has a stony endosperm. For *Johannesteijsmannia lanceolata*, fruits of 2–3 cm diameter were considered semi-mature and those of > 3 cm diameter were regarded as mature. For *Johannesteijsmannia magnifica* and *J. perakensis*, semi-mature fruits were defined as fruits of 3–4 cm diameter and mature as those of > 4 cm diameter. The phenology for *Johannesteijsmannia magnifica* in May 2004 and for *J. perakensis* in January and July 2005 was not observed. For these months, flowering was inferred from the occurrence of old inflorescences or young infructescences in subsequent observations. Each month we counted the number of inflorescences in flower (flowering intensity) and the number of infructescences bearing mature fruits (fruits mature at the same time in an infructescence) in each population. For each species, the significance of correlation between the flowering frequency and the monthly rainfall or MT was tested using Spearman-rank tests in the R package (version 3.1.1). For each population, we also counted the number of inflorescences that failed to set fruit after flowering (terminated). We classified the phenology patterns according to Newstrom et al. (1994), i.e., sub-annual (flowering in more than one cycle per year) and annual (only one major cycle per year).

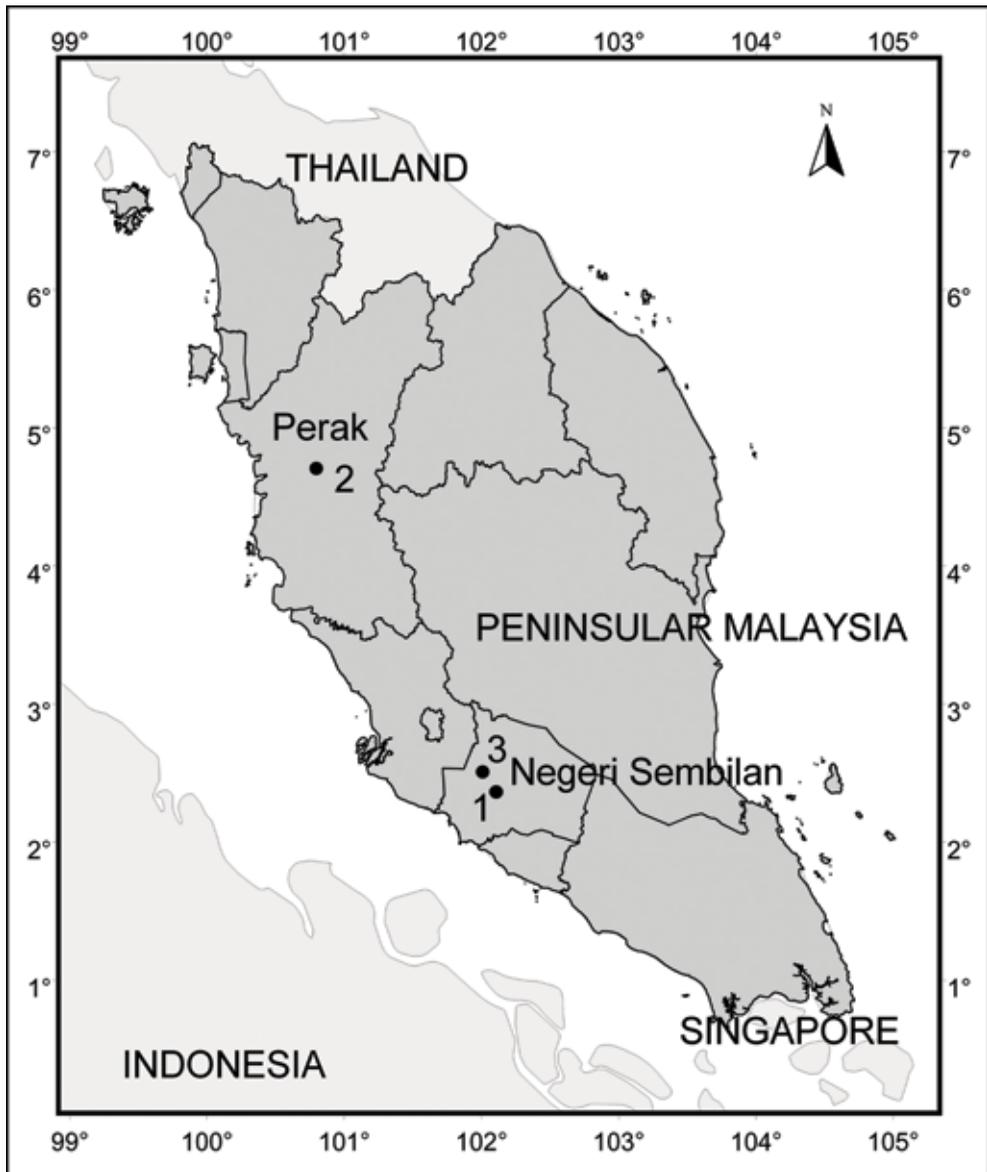


Fig. 1. Study sites in Peninsular Malaysia: (1) Angsi, (2) Kledang-Saiong and (3) Berembun Forest Reserves.

Respectively, 80, 90 and 54 infructescences of *Johannesteijsmannia lanceolata*, *J. perakensis* and *J. magnifica* were tagged and observed during the study period. We counted the number of infructescences with total seed abortion at an initial stage (fruits < 5 mm in diameter) and the number of semi-mature and mature fruits produced by 54, 62 and 49 infructescences of each species (N plant = 13, 18 and 19), respectively.

To estimate seed loss at different stages of fruit development, we subsampled 15, 21 and 6 infructescences of *Johannesteijsmannia lanceolata* (N plant = 10),

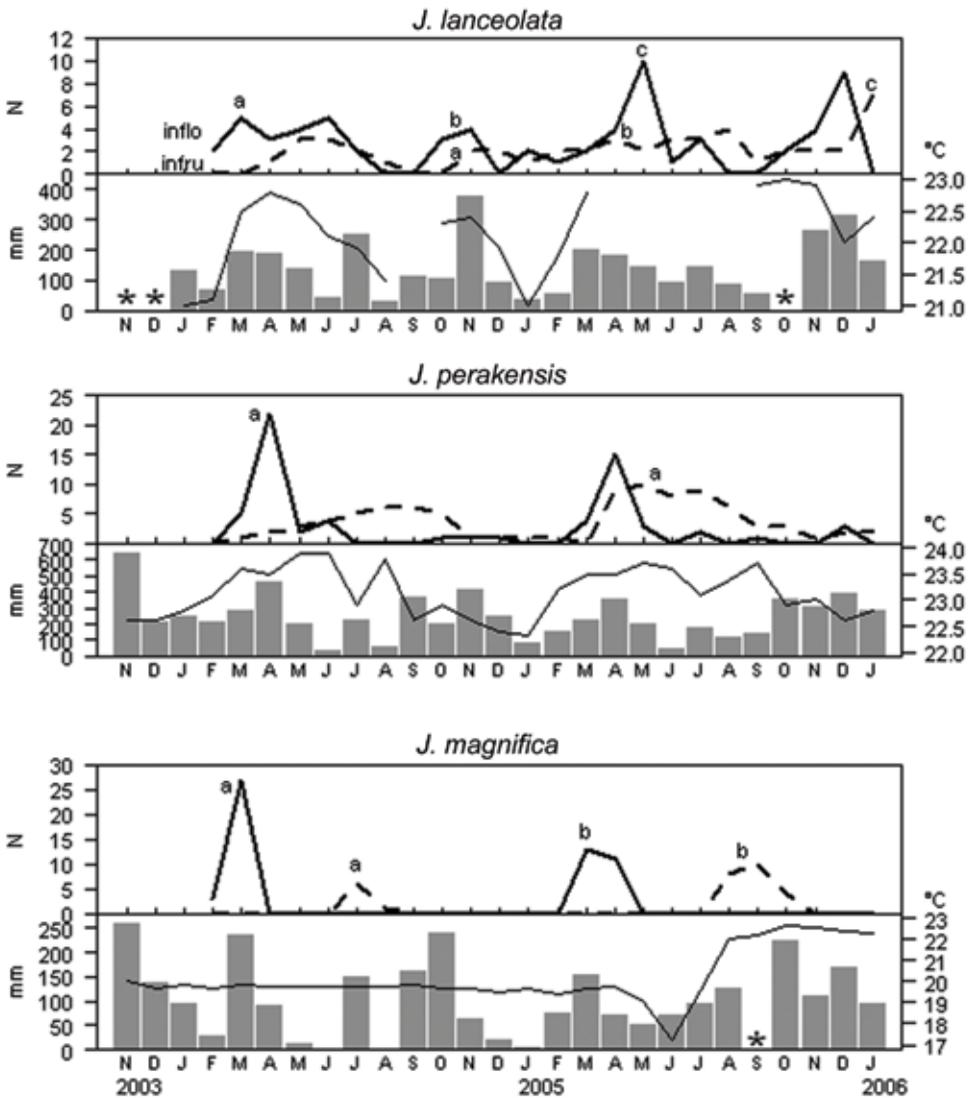


Fig. 2. Phenologies of *Johannesteijsmannia* species and their relationships with mean monthly minimum temperature and rainfall patterns from November 2003 to January 2006. Phenological observations started in February 2004. The upper half of the graph shows the number of inflorescence in flower (solid line) and the number of infructescence bearing mature fruits (dashed line). Flowering in season ‘a’ corresponded with fruiting in season ‘a’. The same applies to ‘b’ and ‘c’. X-axis is the month and year of observations. Bottom half of the graph: line represents mean monthly minimum temperature in degrees Celcius and the bar shows rainfall in millimetres, collected at the nearest weather stations. Broken lines and ‘*’ indicate no data.

J. magnifica (11) and *J. perakensis* (5) respectively, beginning from the young fruit stage (5–10 mm diameter) until fruit maturity. We did not count the initial fruit set (fruits < 5 mm diameter) to minimise injury to the fruits and as counting was

Table 3. Temperature (temp, in °C) and rainfall (in mm) data from January 2004 to December 2005, recorded from the weather stations nearest to the study sites.

	Kuala Pilah	Bukit Kledang	Jelebu
Mean annual temp	27.3	27.9	26.7
Mean monthly minimum temp	22.1	23.2	20.2
Mean monthly maximum temp	32.6	32.5	34.1
Mean monthly rainfall	143	228	98

impractical, particularly for *J. magnifica* and *J. perakensis*, because of their massive infructescences. We defined early, late and final seed loss respectively, as the loss of fruits from the stage of young to semi-mature, semi-mature to mature and young to mature. The seed loss includes the loss of fruits by predation in all stages. Fruit predation was indicated by fruits with bite marks or otherwise damaged before maturity.

Results

Flowering phenology

The three *Johannesteijsmannia* species were different in their flowering and fruiting behaviour (Fig. 2). Flowering was sub-annual in both populations of *Johannesteijsmannia lanceolata* and *J. perakensis*, and it appeared to be more seasonal in *J. perakensis*. In contrast, *Johannesteijsmannia magnifica* showed distinct annual flowering and fruiting. The flowering of all species studied peaked from March to May but the flowering intensities were not consistent between years. For *Johannesteijsmannia perakensis* and *J. magnifica* the intensities reduced in 2005 after prolific flowering in 2004, whereas *J. lanceolata* flowered more in 2005 than in 2004 (Fig. 2). Premature death of inflorescences before flowering was only recorded in *Johannesteijsmannia lanceolata* (two inflorescences or 3% of the total number). The reproductive biology of the three species is summarised and compared in Table 4.

In the population of *Johannesteijsmannia lanceolata*, 14 (47%) of the sampled individuals flowered during the study period (Table 4). These 14 palms flowered every year except for one single palm that flowered only in 2005. At the individual level, many palms flowered 3–4 times within two years, with non-flowering gaps usually of 1–3 months (e.g., Fig. 3). One palm could continuously produce up to seven inflorescences per year. Typically, only one inflorescence was at anthesis at a time. Flowering peaked in May 2005 when nine palms produced 10 inflorescences (Fig. 2). For *Johannesteijsmannia perakensis*, 18 palms (60%) flowered throughout the study period. Of these, 11 palms flowered in both years. A palm could produce up to six inflorescences per year and the inflorescences appeared sequentially, usually within the same month or one month apart. Flowering was sub-annual, with a prominent peak in April, followed by irregular, smaller peaks towards the end of the year. For

Table 4. The reproductive biology of *Johannesteijsmannia* species during the two-year study period. Inflo = inflorescence, infruc = infructescence, N = sample size.

	<i>J. lanceolata</i>	<i>J. perakensis</i>	<i>J. magnifica</i>
Population sample	30	30	30
Reproductive plants (N, %)	14, 47	18, 60	19, 63
Total N inflo	66	64	54
N inflo per plant per year (mean, max)	2, 7	2, 9	1, 5
Terminated inflo (N, %)	2, 3.0	3, 4.7	3, 5.6
Flowering behaviour	Sub-annual	Sub-annual	Annual
Peak flowering period	Mar–May & Nov–Dec	Mar–May	Feb–Apr
Total N infruc*	80	90	54
N infruc per plant per year (mean, max)	3, 6	3, 11	1, 5
Fruit maturity peak period	May–Aug, Jan	Apr–Sep	July–Oct
Fruit development until maturity (month, mode)	5–9, 8	11–16, 12	4–7, 4
Infruc with total initial seed abortion (%)	31.5	19.4	18.4
N semi-mature fruits per infruc (mean, range)	5, 0–21	22, 0–122	11, 0–50
N mature fruits per infruc (mean, range)	3, 0–16	7, 0–56	3, 0–30
N mature fruits per year (mean)	69	229	82
Mean size of mature fruit (cm ± sd, N)	4.1 ± 0.2, 21	4.6 ± 0.3, 129	4.2 ± 0.1, 49

* Number of infructescences observed in the population during the study period.

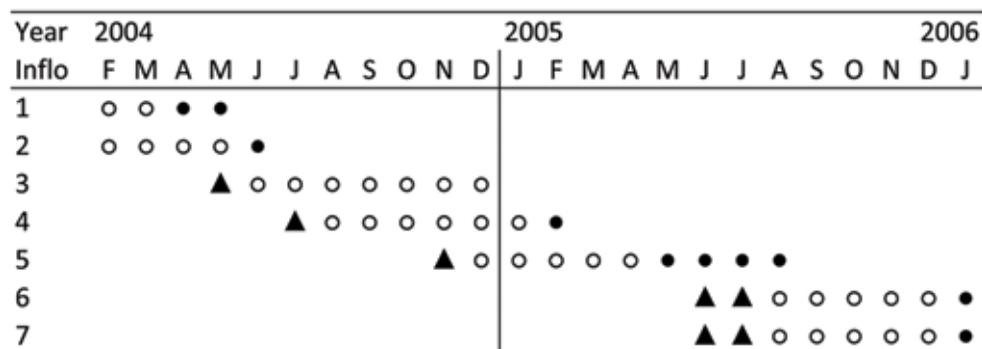


Fig. 3. Phenology of a selected individual of *Johannesteijsmannia lanceolata* during the study period. Legend: (▲) Floral phase from bud to flower, (○) young fruit, and (●) mature fruit.

Johannesteijsmannia magnifica, 19 palms (63%) flowered during the study period of which 10 flowered and fruited in both years. One of the palms produced five inflorescences that flowered within the same month. The species showed distinct annual flowering that occurred from February to April. In the population, flowering was gregarious, synchronous and lasted for two months.

Fruit production and seed loss

Fruits were continuously produced in the populations of *Johannesteijsmannia lanceolata* and *J. perakensis*. As a result, fruits in different stages of maturation were present throughout the study period. In *Johannesteijsmannia perakensis*, fruits were produced continuously within a plant as well. The population of *Johannesteijsmannia magnifica*, however, fruited only from April to October. The percentage of terminated inflorescence was low (3.0–5.6%) for all species (Table 4). Total seed abortion at the initial stage ranged from 18% to 32% and was highest in *Johannesteijsmannia lanceolata*. Mature fruits were found almost continuously in the populations of *Johannesteijsmannia lanceolata* and *J. perakensis* whereas those of *J. magnifica* were available only from July to October. Among the species, the duration of fruiting was shortest in *Johannesteijsmannia magnifica* and longest in *J. perakensis* (lasting up to 16 months) (Table 4). The population of *Johannesteijsmannia perakensis* produced the highest number of mature fruits per year (mean = 229) and that of *J. lanceolata* the lowest (mean = 69). In *Johannesteijsmannia lanceolata*, the highest number of mature fruits recorded was in June 2004 (i.e., 24), August 2005 (26) and January 2006 (32).

Fruit production and late seed loss varied from year to year among the species studied (Fig. 4 and 5). The populations of *Johannesteijsmannia perakensis* and *J. magnifica* produced more fruits in 2004 than in 2005, but seed loss was also higher in 2004. In *Johannesteijsmannia lanceolata*, we observed the opposite trend: in 2005 more fruits were produced with a lower seed loss. Among the species, we recorded the lowest total seed loss in *Johannesteijsmannia lanceolata* (47.3%) and the highest in *J. magnifica* (70.9%) (Fig. 5). In the subsample, the final seed loss in all species was more than 84%, caused mainly by seed loss in the early stages of fruit maturation (Table 5). Both *Johannesteijsmannia magnifica* and *J. perakensis* recorded extremely high overall seed loss, close to 98%.

In all species studied the fruit predation rate was unknown. In *Johannesteijsmannia perakensis*, a number of fruits were lost before maturity. Bite marks (probably by rodents) on the semi-mature and mature fruits indicated fruit predation. In several observations, mature fruits were found on the forest floor with the mesocarps chewed but the seeds left intact and undamaged and thus, were not considered to have been preyed upon. Fruit predation of *Johannesteijsmannia magnifica* mainly occurred from July to August. The predation rate of infructescences (i.e. number of infructescences having fruits preyed upon compared to the total number of observed infructescences) was estimated at 3.7% and 31% for *Johannesteijsmannia lanceolata* and *J. magnifica*, respectively.

Correlation between flowering and climate variables

For the three species, peak flowering appeared to coincide with months of high rainfall (Fig. 2). In the population of *Johannesteijsmannia lanceolata*, flowering occurred two to three months after a drop in the mean temperature (MT) and a low rainfall (< 90 mm) in February and August 2004 as well as in January 2005. This pattern is barely discernable in the populations of *Johannesteijsmannia perakensis* and *J. magnifica*. Only in *Johannesteijsmannia lanceolata* did we find a significant correlation between the monthly rainfall and flowering intensity ($r = 0.48$, $p < 0.05$, $N = 23$). No significant relationship was detected between MT and flowering intensity in any species.

For *Johannesteijsmannia lanceolata*, the flowering generally coincided with the rainy seasons, which occurred in March–May and November–December (Fig. 2). Droughts were experienced in August 2004 and January 2005 whereas the lowest MT (21.0 °C) was reached in January of both years. The absence of flowering in August–September coincided with drier months.

For *Johannesteijsmannia perakensis*, most flowering episodes coincided with high rainfall. There was only one drought event in June 2004 and no low temperatures were recorded during the study period. The lowest MTs occurred in December 2004 (22.4 °C) and January 2005 (22.3 °C). The flowering event in April 2005 was apparently related to low rainfall and low MT that occurred 2–3 months previously. However, this relationship was less pronounced for the flowering event in April 2004.

The distinct annual flowering of *Johannesteijsmannia magnifica* also coincided with high rainfall. Both flowering events in *Johannesteijsmannia magnifica* were preceded by low temperatures (≤ 19.7 °C) and drought in February 2004 and December–January 2005. Even though similar climatic conditions also occurred in May, June (with a prolonged drought) and August in 2004, no flowering occurred in the following months. Again, there was no flowering after the MT dropped to the lowest (17.2 °C) with little rainfall (70 mm) in June 2015. In summary, the population of *Johannesteijsmannia magnifica* experienced a stronger climate effect with prolonged periods of drought as well as low temperatures. Low temperature and prolonged drought did not occur at the study sites of *Johannesteijsmannia lanceolata* and *J. perakensis*.

Discussion

In this study, we have shown that reproductive phenology differs in the three *Johannesteijsmannia* species. Although flowering peaked during the same

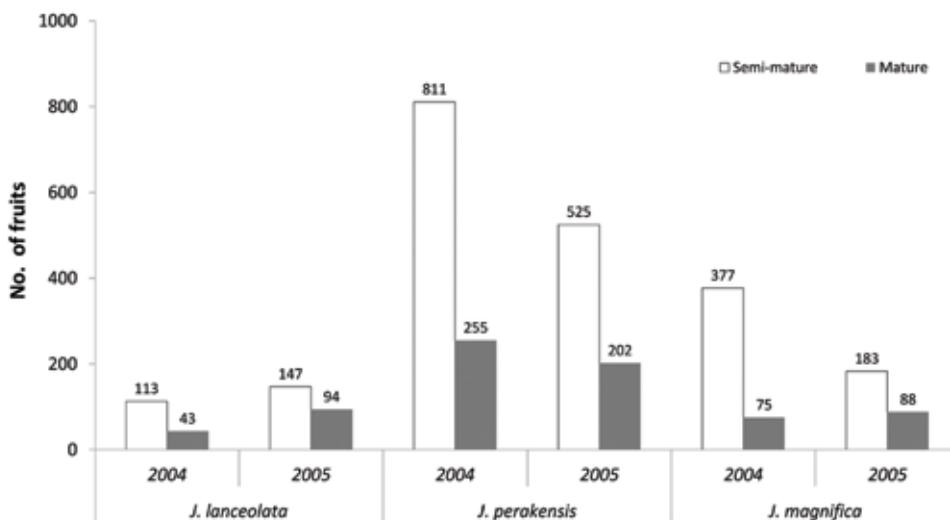


Fig. 4. Yearly fruit production by *Johannesteijsmannia* spp. Number of infructescences: 54 for *J. lanceolata*, 62 for *J. perakensis* and 49 for *J. magnifica*.

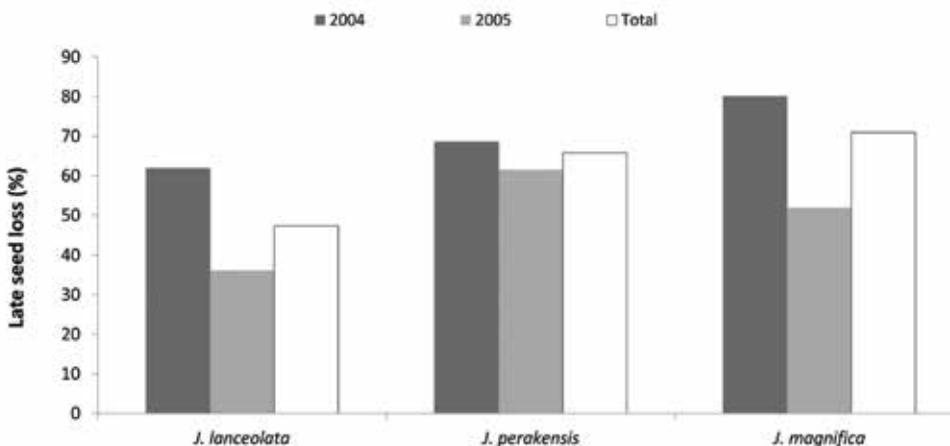


Fig. 5. Percentage of late seed loss from the semi-mature to mature stage, according to species and year. The total is the seed loss throughout the two years. Early seed loss from the young to the semi-mature stage was not recorded due to reasons stated in the Materials and methods section.

period, the flowering pattern was aberrant in *Johannesteijsmannia magnifica*. *Johannesteijsmannia altifrons* (Rchb.f. & Zoll.) H.E.Moore, which was not studied here, shows sub-annual flowering pattern. A population at the Jerangau FR in Terengganu was observed flowering in March 2010, January, July and December 2011, and March and Jun 2012 (W.S.Y. Yong, pers. comm.).

Table 5. Seed loss (mean % \pm sd) estimated from subsampling. The value for N young fruit per infructescence is given as a mean and the range (in brackets).

Seed loss	<i>J. lanceolata</i>	<i>J. perakensis</i>	<i>J. magnifica</i>
Early	62.6 \pm 37	80.5 \pm 19	85.2 \pm 17
Late	43.4 \pm 42	57.1 \pm 50	65.7 \pm 48
Final	84.4 \pm 22	97.9 \pm 5	97.8 \pm 4
N infructescence	15	6	21
N young fruit per infructescence	17 (1–94)	56 (9–130)	109 (10–200)

The studied species flowered in the wet seasons and, therefore, high rainfall could be a cue to fruiting, particularly in *Johannesteijsmannia lanceolata* and *J. perakensis*. In Sarawak (East Malaysia), cultivated plants of *Johannesteijsmannia altifrons* and *J. magnifica* flowered annually for about six months and flowering peaked during the onset of the rains (P. Boyce, pers. comm.). In *Johannesteijsmannia perakensis*, however, Dransfield (1972) observed that there was no obvious relationship between flowering and climatic pattern.

In *Johannesteijsmannia magnifica*, we suspect flowering is triggered by seasonal drought, as speculated by Dransfield (1972), and that the gregarious flowering of *J. magnifica* in May 1968 at Sungai Lalang FR, was probably triggered by the dry season that occurred from January to March of that year. However, *Johannesteijsmannia magnifica* did not flower when similar conditions occurred in May–June 2004 (this study). Similarly, general flowering in dipterocarp trees is highly associated with drought (Numata et al., 2013; Chen et al., 2017) but drought is not always followed by flowering (Numata et al., 2003). Other factors such as resource limitation, long photoperiod and solar radiation have been implicated (Appanah, 1993; Ichie et al., 2005; Sakai et al., 2006).

The drier conditions in Jelebu may affect water and soil nutrient uptake by *Johannesteijsmannia magnifica*. Resource limitation encountered by the population possibly determines its flowering frequency and may have played a significant role in determining the most advantageous timing for flowering. In the Kepong Botanical Gardens of the Forest Research Institute Malaysia (FRIM), where plants receive more sunlight, abundant rainfall and occasional applications of fertilisers, *Johannesteijsmannia magnifica* flowered sub-annually (pers. obs.). This study, however, was preliminary, and the study duration is insufficient to establish a consistent pattern. We therefore recommend more long-term studies on tropical palm communities in relation to flowering behaviour and climate factors.

Seed loss was high in the species studied and the percentage of early seed loss could even be higher since fruits less than 5 mm in diameter were not included in the study. In *Johannesteijsmannia lanceolata*, the mean number of fruits counted at the initial stage (1–2 mm diameter) for six infructescences was 230 (Chan, 2009), but in

this study the number was much lower when we started counting at the young fruit stage (Table 5). Factors that promote fruit abortion could be weather conditions, seed predation and resource limitation (Stephenson, 1981). Limited maternal resources, such as water deficit (Turc & Tardieu, 2018), may explain the great seed loss, especially in the population of *Johannesteijsmannia magnifica* that went through prolonged droughts. Seed loss also could be caused by some degree of inbreeding (Simiqueli et al., 2018) as the genus is hypothesised to be outcrossing based on genetic studies (Look, 2007) but is self-compatible based on floral biology (Chan & Saw, 2011).

The total late seed loss for the populations studied is considered to be high (Fig. 5). In *Johannesteijsmannia perakensis*, seed boring by beetles in some fruits (pers. obs.) could partly account for the seed loss. More research is required to determine whether such predation is significantly contributing to seed loss. In *Geonoma epetiolata* H.E. Moore, a rare understorey neotropical palm in Costa Rica, predation by weevils accounted for 6% of the total 67% seed loss that occurred during the early stages of fruit development (Martén & Quesada, 2001). In understorey palms, a great range of natural seed set (i.e. number of fruits per number of flowers) has been reported but most species have low seed set: 3% in *Geonoma* (Martén & Quesada, 2001), 6% in *Licuala* (Barfod et al., 2003), 9% in *Johannesteijsmannia* (Chan, 2009), 13–43% in *Chamaedorea* (Otero-Arnaiz & Oyama, 2001; Berry & Gorchov, 2004), 20% in *Eugeissona* (Fong, 1978), 21% in *Serenoa* (Carrington et al., 2003) and 80% in *Coccothrinax* (Rosa & Koptur, 2009).

Johannesteijsmannia lanceolata and *J. perakensis* are similar in their reproductive strategy. The populations carried fruits throughout the study period. This could be a way to reduce seedling competition by spreading out the seeds temporally and spatially. The continuous seed supply in the population of *Johannesteijsmannia lanceolata* may attract continuous predation, but the low number of seeds and the unpredictable location of fruiting individuals in the population may help to reduce predation rate. Piñero & Sarukhan (1982) suggested that this strategy would require predators to spend more time and energy searching for fruiting individuals. Searching for the limited fruits of *Johannesteijsmannia lanceolata* may not be a wise investment if there are alternative energy-rich food resources readily available in the forest. *Johannesteijsmannia perakensis* showed a similar strategy but the late seed loss was greater, probably because the predation rate increased when more fruits were available over a longer time period.

Johannesteijsmannia magnifica has a strikingly different reproductive strategy – every year the population flowered and fruited in synchrony. Synchronised flowering attracts more pollinators. It increases chances of pollination success and promotes outcrossing (Sakai, 2002). Indeed, more insects were observed visiting the inflorescences of *Johannesteijsmannia magnifica* compared to those of *J. lanceolata* (pers. obs.). This could be an effect of *Johannesteijsmannia magnifica* producing much more flowers than *J. lanceolata*. Yet, the population still suffered very high percentage of seed loss at the early stages of fruit development, possibly because of limitation in maternal resources.

This preliminary study also showed that among species, there were big differences in seed production and these data may suggest the need for a specific harvesting limit for each species. To assess the sustainability of seed harvesting for the ornamental trade however, we require further studies on the seed production pattern, harvesting practice and the proportion of seeds removed from each species.

Conclusions

We have shown that rainfall pattern may serve as a proximate cue to flowering and fruiting in the three species of *Johannesteijsmannia*. Our study also demonstrates that each species may require different conservation management due to different reproductive behaviour. Flowering was sub-annual in *Johannesteijsmannia lanceolata* and *J. perakensis* and annual in *J. magnifica*. However, longer term studies with microclimate data are needed to validate these results.

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