

ORIGINAL ARTICLE

Variations in the reproductive cycle of Bornean montane tree species along elevational gradients on ultrabasic and non-ultrabasic soils

Yuki Tsujii^{1,2,3,4}  | Shoko Sakai¹  | Masayuki Ushio^{1,5,6}  | Shin-ichiro Aiba⁷  | Kanehiro Kitayama⁸ ¹Center for Ecological Research, Kyoto University, Otsu, Japan²Faculty of Science, Kyushu University, Fukuoka, Japan³School of Natural Sciences, Macquarie University, Sydney, New South Wales, Australia⁴Hawkesbury Institute for the Environment, Western Sydney University, Penrith, New South Wales, Australia⁵Hakubi Center, Kyoto University, Kyoto, Japan⁶Department of Ocean Science, The Hong Kong University of Science and Technology, Kowloon, Hong Kong SAR⁷Faculty of Environmental Earth Science, Hokkaido University, Sapporo, Japan⁸Graduate School of Agriculture, Kyoto University, Kyoto, Japan**Correspondence**

Yuki Tsujii, Center for Ecological Research, Kyoto University, 509-3 Hirano 2-Chome, Otsu, Shiga 520-2113, Japan.

Email: tsujii.yuki.251@m.kyushu-u.ac.jp**Funding information**

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Associate Editor: Ferry Slik**Handling Editor:** Donald Franklin**Abstract**

Although lowland tree species in the ever-wet regions of Southeast Asia are characterized by the supra-annual cycle of reproduction, the reproductive phenology of montane tree species remains poorly understood. In this study, we investigated the reproductive phenology of montane tree species using litter samples that were collected every 2 weeks from six rainforest sites, consisting of three elevations (1700, 2700, and 3100 m), on Mount Kinabalu, Borneo. At each elevation, one site was on infertile ultrabasic soil and one was on relatively fertile non-ultrabasic soil. We used a composite sample from 10 or 20 litter traps per site and sorted it by species. Therefore, the obtained data captured reproductive phenology in the population of each species rather than in an individual tree. Ten-year time series of flower and fruit litterfall were obtained for 30 and 39 tree species, respectively. Fourier analysis was used to identify the dominant cycle of each time series. The most abundant cycle across species was supra-annual, followed by sub-annual, and annual cycles. Many species at higher elevations showed supra-annual cycles of flower litterfall, whereas species in the 1700 m sites often showed annual or sub-annual cycles regardless of soil types. No systematic differences were found among sites for fruit litterfall. Mechanisms underlying these elevational patterns in reproductive cycle remain unclear but may include more severe El Niño droughts, lower primary productivity, lower soil fertility, and the absence of some sub-annually or annually reproducing families at higher elevations.

KEYWORDS

alpine, altitude, El Niño Southern Oscillation, general flowering, masting, Mount Kinabalu, nutrient limitation, phosphorus deficiency

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1 | INTRODUCTION

The reproductive phenology of tropical rainforest trees is characterized by considerable variations in cycle length, ranging from sub-annual (several times per year) to supra-annual cycles (once per several years; Gentry, 1974; Newstrom et al., 1994; Sakai & Kitajima, 2019; van Schaik et al., 1993). Trees in the ever-wet regions of Southeast Asia, including Borneo and the Malay Peninsula, often exhibit supra-annual cycles of flowering and fruiting at irregular time intervals (Appanah, 1985; Medway, 1972; Sakai, 2001). In contrast, annual cycles are predominant in parts of Thailand (Kurten et al., 2017) and the Philippines (Hamann, 2004), South Asia (Ashton, 1988), Africa (Adamescu et al., 2018), Australia (Boulter et al., 2006), and America (Morellato et al., 2013; Newstrom et al., 1994; Norden et al., 2007). The supra-annual cycles of reproduction in the ever-wet regions of Southeast Asia are thought to be associated with the lack of well-defined annual rainfall patterns (Sakai, 2001), whereas the annual cycles of reproduction in other regions may be triggered by regular dry seasons (Adamescu et al., 2018; Janzen, 1967; van Schaik et al., 1993). Within each region, the reproductive cycles of tropical rainforest trees vary with the local climate (Numata et al., 2003) and soil type (Cannon et al., 2007; Janzen, 1974); this variation is poorly understood in part because of a lack of long-term monitoring across a wide range of elevations (i.e. from lowland to alpine zones), with associated variations in climate and soil fertility.

In the ever-wet regions of Southeast Asia, long-term monitoring studies have been performed in the lowland dipterocarp forests which are well known for supra-annual cycles of reproduction with synchronized flowering of many species at irregular time intervals, called general flowering (GF) (Appanah, 1985). Several hypotheses to explain GF have been proposed, including the ultimate (i.e. evolutionary forces) and proximate mechanisms (i.e. climatic controls and physiological constraints). Evolutionary forces in the synchronization of flowering and fruiting include the promotion of pollination via intra- and interspecific synchronization (Sakai et al., 1999) and avoidance of seed predation via predator satiation (Curran & Leighton, 2000; Janzen, 1971). It has been suggested that climatic cues, such as low air temperatures (Ashton et al., 1988; Wycherley, 1973) and droughts (Medway, 1972; Sakai et al., 2006) and their synergisms (Chen et al., 2018; Satake et al., 2019; Ushio et al., 2020) with El Niño Southern Oscillation (ENSO) (Ashton et al., 1988; Yasuda et al., 1999), might upregulate the expression of flowering-related genes (Kobayashi et al., 2013; Yeoh et al., 2017).

It has been also suggested that the reproductive cycles of dominant tree species vary among dipterocarp forests with different climatic conditions and soil types. For example, Numata et al. (2003) found that the dominant species of dipterocarp forests in the Malay Peninsula generally had peak GF after an unusually low rainfall during December–February, whereas those in the central and southern parts often had second GF peaks following unusually low rainfall during June–August. Considering the effect of soil fertility, Janzen (1974) indicated that trees on infertile soils had longer time intervals between reproductions than those on fertile soils. Cannon

et al. (2007) reported that tree species in a montane dipterocarp forest (at 700–1100 m a.s.l.) did not show GF but reproduced more frequently than those in lowland dipterocarp forests. This suggests that the evolutionary mechanisms underlying reproductive phenology may be different between montane and lowland dipterocarp forests.

It remains uncertain whether this knowledge from dipterocarp forests applies across montane forests because tree community composition, climatic conditions, and soil fertility vary with elevation in montane forests. In the case of Borneo, which hosts a variety of forest types across a wide range of elevations (up to >4000 m), Dipterocarpaceae are absent above ca. 1600 m, and Fagaceae, Myrtaceae, and Podocarpaceae are predominant at higher elevations (Kitayama, 1992; Slik et al., 2009). More severe El Niño droughts have been reported in the alpine zone (3270 m) than in the upper and lower montane zones (2650 and 1560 m, respectively) on Mount Kinabalu (Kitayama et al., 2014), where the availability of soil nutrients such as phosphorus (P) and nitrogen (N) was lower at higher elevations (Kitayama & Aiba, 2002; Kitayama et al., 1998).

The present study aimed to understand the variations in the reproductive cycle of montane tree species in the ever-wet regions of Southeast Asia. Our investigation was conducted on Mount Kinabalu, Borneo (6°05'N, 116°33'E, 4095 m). This mountain is the highest between the Himalayas and New Guinea and has exceptionally high plant species diversity, with variations in the composition of tree species across elevations and soil types (Aiba & Kitayama, 1999). The mountain is unique also because mature primary forests are preserved from lowland to treeline zones (ca. at 3700 m; Kitayama, 1992), making it an ideal model system for studying the ecology of tropical rainforests in Southeast Asia. The reproductive phenology of montane tree species was examined using litter samples collected every 2 weeks over 10 years from six montane rainforest sites, ranging from lower montane (at 1700 m a.s.l.) to alpine zones (at 3100 m a.s.l.). These sites were selected based on the earlier reports on influences of elevation, soil type, and their interaction on forest properties (Aiba & Kitayama, 1999; Kitayama & Aiba, 2002). We examined the cycles of the reproductive litterfall of dominant tree species in the selected sites.

2 | METHODS

2.1 | Study sites

The six study sites included three elevations (1700, 2700, and 3100 m a.s.l.) on the southern slope of Mount Kinabalu. At each elevation, one site was on ultrabasic soils (i.e. soils derived from ultrabasic rocks), which are characterized by nutrient deficiencies, such as P, and potassium (Proctor, 1999). Another was on non-ultrabasic soils (including soils derived from granite or sedimentary rocks). Non-ultrabasic soils were underlain by sedimentary rocks at 1700 and 2700 m and by granite at 3100 m. Comparisons between the ultrabasic and non-ultrabasic sites allowed us to examine the influence of soil P limitation on plant performance, because the concentrations

of total and soluble soil P were consistently lower at the ultrabasic sites (Table 1). Indeed, mean leaf N:P ratios of dominant tree species were higher at the ultrabasic sites than at the non-ultrabasic sites (data from Tsujii et al. (2020) and unpublished; Table 1). The values at the ultrabasic sites were much higher than the P limitation threshold (>16–20; Güsewell, 2004; Redfield, 1958), indicating a strong limitation of P relative to N.

The climate is humid tropical (Table 1), with droughts in El Niño years (Kitayama et al., 2014). Detailed climate data can be found in Ushio (2020) and Kitayama et al. (2021). Our monitoring period included two El Niño episodes (1997–1998 and 2002–2003). The 1997–1998 El Niño was one of the strongest ENSO events on record and included a severe dry period with a much greater potential evapotranspiration than total rainfall during December 1997–May 1998 (Kitayama et al., 2014; Figure S1). Therefore, we focused on the influence of the 1997–1998 El Niño drought on reproductive phenology. Air temperature and photosynthetically active radiation showed significant annual and half-year cycles at the 1700 and 3100m sites, respectively (Kitayama et al., 2021), but not at the cloud-laden 2700m sites. A spectrum convergent-cross mapping analysis suggested that air temperature was a dominant driver of the annual cycles of leaf litterfall at the 1700 and 3100m sites, except

the non-ultrabasic 1700m site (Kitayama et al., 2021), during our monitoring period. In contrast, a Fourier analysis showed the significant supra-annual cycles of reproductive litterfall (flowers and fruits combined), ranging from 15 to >48 months, with no consistent patterns across elevations and soil types (Kitayama et al., 2021).

2.2 | Data collection

Reproductive phenology was examined using litter samples collected every 2 weeks between February 1996 and March 2006 during earlier studies (Kitayama et al., 2015, 2021). Twenty, ten, and ten litter traps (0.5 m² area) were placed 1 m aboveground at 10 m intervals at 1700, 2700, and 3100m sites, respectively. After drying at 70°C, the samples from the 10 or 20 traps were combined per sampling date and stored in the laboratory at the Kinabalu Park Headquarters. Therefore, there was only a single composite sample per site at each sampling date. Reproductive litter in the combined sample was sorted by species and weighed after being grouped into two categories: flower and fruit. Flowers were defined as inflorescences with flower buds, petals, stigmas, and stamens. The remaining reproductive organs, including immature and mature fruit, were

TABLE 1 Description of six rainforest sites on Mount Kinabalu.

Site name	U1700	N1700	U2700	N2700	U3100	N3100
Rock substrate	Ultrabasic	Sedimentary	Ultrabasic	Sedimentary	Ultrabasic	Granite
Exact elevation (m)	1860	1560	2700	2590	3050	3080
MAT (°C)	17.1	18.7	12.5	13.1	10.6	10.4
MAP (mm year ⁻¹)	2714	2714	2085	2085	3285	3285
Total soil P (µg g ⁻¹)	35.3	123.0	114.4	248.1	53.2	247.9
Soluble soil P (µg g ⁻¹)	0.84	2.70	1.89	20.93	0.80	6.23
PUE (g g ⁻¹)	5159	3025	4785	2230	6326	2478
Reproductive litter (g m ⁻² year ⁻¹)	24.3	40.0	11.7	38.1	11.5	29.1
Proportion of reproductive litter per total litterfall (%)	3.9	5.3	2	6.9	6.7	4.4
Canopy height (m)	22.6	30	14.2	20.6	6.1	15
Number of sampled species for flower/male-cone litter (coverage rate)	9 (21%, 66.9%)	10 (8%, 56.1%)	8 (28%, 70%)	7 (30%, 75.1%)	3 (18%, 90.7%)	6 (24%, 38.1%)
Number of sampled species for fruit/seed-cone litter (coverage rate)	11 (26%, 70.6%)	19 (14%, 32.3%)	9 (31%, 86.1%)	9 (39%, 84.2%)	7 (44%, 99.9%)	8 (32%, 72.5%)
Leaf N:P	30.5	20.6	23.0	18.0	28.9	20.9

Note: The site name is expressed as the combination of common elevations with soil types, that is U and N for ultrabasic and non-ultrabasic soils, respectively. Total soil P represents the concentration of total soil P (in 30 cm deep topsoil) (cited from Kitayama et al. (2000)). Soil soluble P represents the concentration of P extracted with hydrochloric-ammonium fluoride solution (in 15 cm deep topsoil; cited from Kitayama and Aiba (2002)). Rock substrate, elevation, mean annual air temperature (MAT), and precipitation (MAP) and canopy height were cited from Kitayama and Aiba (2002). MAP was observed at 1560, 2700, and 3270 m, for 1700 m, 2700 m, and 3100 m sites, respectively. The P-use efficiency of net primary production (PUE; calculated as the inverse of P concentration in the litter), annual productivity of reproductive litter, and its relative proportion in total litterfall were cited from Kitayama et al. (2015). The coverage rates were calculated in two manners: (1) the percentage of the number of sampled species per the total number of species recorded in each site (with >4.8 cm at the diameter of breast height; the first value in parentheses), and (2) basal-area basis (the second value in parentheses). The total number of species was based on the tree census data from Aiba et al. (2015). The relative basal area data of each species were cited from Aiba et al. (2002).

included in the fruit category. Among the conifers, male cones always had pollen scales, whereas the developmental stages of seed cones were not easily identifiable. Male-cone and seed-cone litter were grouped with flower and fruit litter, respectively. Hereafter, these groups will be referred as 'flower/male-cone' and 'fruit/seed-cone' litters, respectively. Exceptionally, the flowers of *Lithocarpus* and *Quercus* at the 1700m non-ultrabasic site and the flowers and fruits of *Syzygium* at 1700m sites were sorted by genus because of the lack of species identification references. In total, 43 and 63 time series (as the combination of site and species, including 30 and 39 species) were obtained for flower/male-cone and fruit/seed-cone litterfall, respectively.

2.3 | Data analyses

A Fourier analysis with significance testing was performed to estimate the cycle length of reproductive litterfall (following the R code from Bush et al., 2017). Although Fourier analysis requires a consecutive time series, our time series contained missing values. Therefore, after a maximum of three consecutive missing values were linearly interpolated, we extracted the longest consecutive subset. This time series still covered >7.5 years of the monitoring period (February 1996–October 2003) and was longer than the shortest period required to detect significant annual cycles of flowering and fruiting (>6 years; Bush et al., 2017); however, Bush et al. (2017) also suggested that >20 years of time series may be required for species with irregular reproductive phenology. Fourier analysis also requires the time series to be stationary. Six and fifteen of the 43 and 63 time series of flower/male-cone and fruit/seed-cone litterfall, respectively, did not meet this requirement (Augmented Dickey-Fuller [ADF] test $p > .05$, when the alternative hypothesis is stationary). Therefore, after excluding the non-stationarity time series, Fourier analysis was performed for 37 and 48 time series (including 27 and 37 species) of flower/male-cone and fruit/seed-cone litterfall, respectively. The lag orders in the ADF test were determined based on the Akaike information criterion using the CADFtest package (Lupi, 2009).

Each time series was decomposed into a series of sine waves after smoothing by the Daniell kernel method. The R code of Bush et al. (2017) adjusts the width of the Daniell kernel and develops a smoothed spectral estimate with 0.1 bandwidth when the frequency of time series is 12 data points per year. The 0.1 bandwidth is a resolution sufficient to identify the peaks of flowering and fruiting for the time series with the frequency of 12 per year (Bush et al., 2017) and corresponds to ca. 0.2 bandwidth in our time series with the frequency of 26 per year. The 95% confidence intervals of the dominant peak were calculated on the assumption that spectral estimates approximate a chi-square distribution. The null continuum of the spectrum rather than the average spectrum (i.e. white noise spectrum) was used as a null hypothesis to avoid false positive results (Bush et al., 2017). The dominant cycle was defined as significant cycle when the lower confidence intervals of the dominant cycle were

greater than the null continuum of the spectrum. The null continuum of the spectrum was made by applying the Daniell kernel to give a bandwidth similar to 2.0. The 2.0 bandwidth corresponds to the 1.0 bandwidth in the R code of Bush et al. (2017). The annual cycle was defined as 44–60 weeks (12 ± 2 months), and the cycles shorter or longer than this definition were categorized as sub- and supra-annual cycles (<44 and 61–200 weeks), respectively. Fourier analysis may return false-positive results when the data contain noise, or the identified dominant cycles are longer than half of the times series (Bush et al., 2017). Therefore, we categorized cycles longer than 200 weeks as non-convergent cycles. The results of the Fourier analyses included many insignificant and non-convergent cycles; hence, we did not perform post hoc statistical tests but discussed patterns among the sites, families, mycorrhizal types, and fruit types. Because DNA data were not available for our study species, we developed a phylogenetic tree at the family level with the APG-III classification data from plants (Zanne et al., 2014), using Phylomatic software (version 3; Webb & Donoghue, 2005) and the ape package (Paradis et al., 2004). Mycorrhizal types were categorized using genus-level data from Soudzilovskaia et al. (2020). Fruit-type data were cited from Tsujii and Kitayama (2018) with slight modification (see Table S1).

Wavelet analysis was performed to supplement the Fourier analysis. The temporal changes in reproductive cycles were visualized using Waveletcomp package of R (Röesch & Schmidbauer, 2018). We used Morlet wavelet as a mother wavelet. Wavelet analysis was performed for all the time series of reproductive litterfall, including the non-stationary time series. All statistical analyses were performed using R version 3.6.3 (R Core Team, 2020).

3 | RESULTS

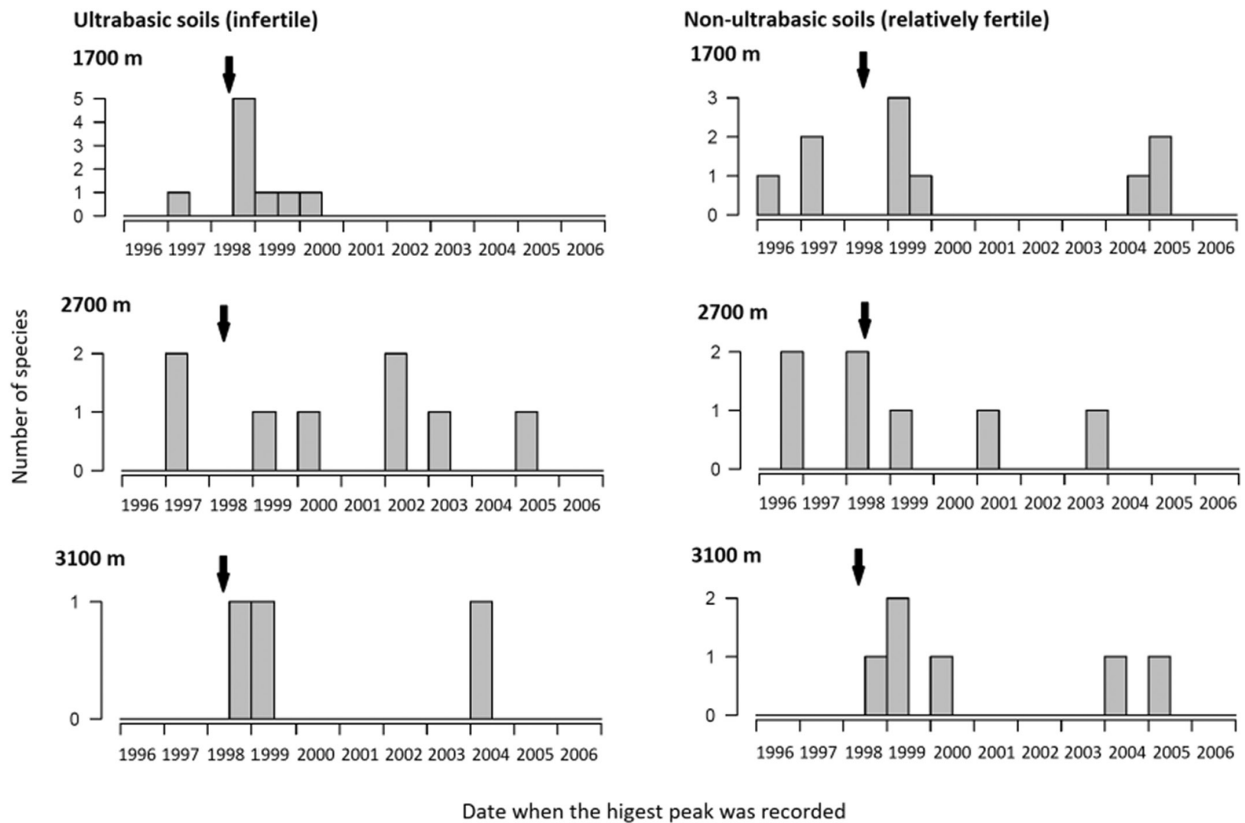
3.1 | Data quality

A major challenge in the present study was to identify the species in litter samples because some samples decomposed or were in fragments after remaining in litter traps for 2 weeks. We identified species in $81\% \pm 15\%$ (mean \pm SD) of the total litter sample weight per site. Our dataset covered $21\% \pm 8\%$ and $31\% \pm 10\%$ (mean \pm SD) of the total numbers of species recorded at each site (with >5 cm of the diameter at breast height), with $66\% \pm 18\%$ and $74\% \pm 23\%$ (mean \pm SD) on basal-area basis, for flower/male-cone and fruit/seed-cone litterfall, respectively (Table 1).

3.2 | Influence of the 1997–1998 El Niño drought

Inter-annual fluctuations in reproductive litterfall were found across species (Figures S2 and S3). Figure 1 plots the dates when each species exhibited the highest peak of reproductive litterfall during the monitoring period; 37% of 43 time series recorded the highest peaks of flower/male-cone litterfall between the second

(a) Flower/male-cone litterfall



(b) Fruit/seed-cone litterfall

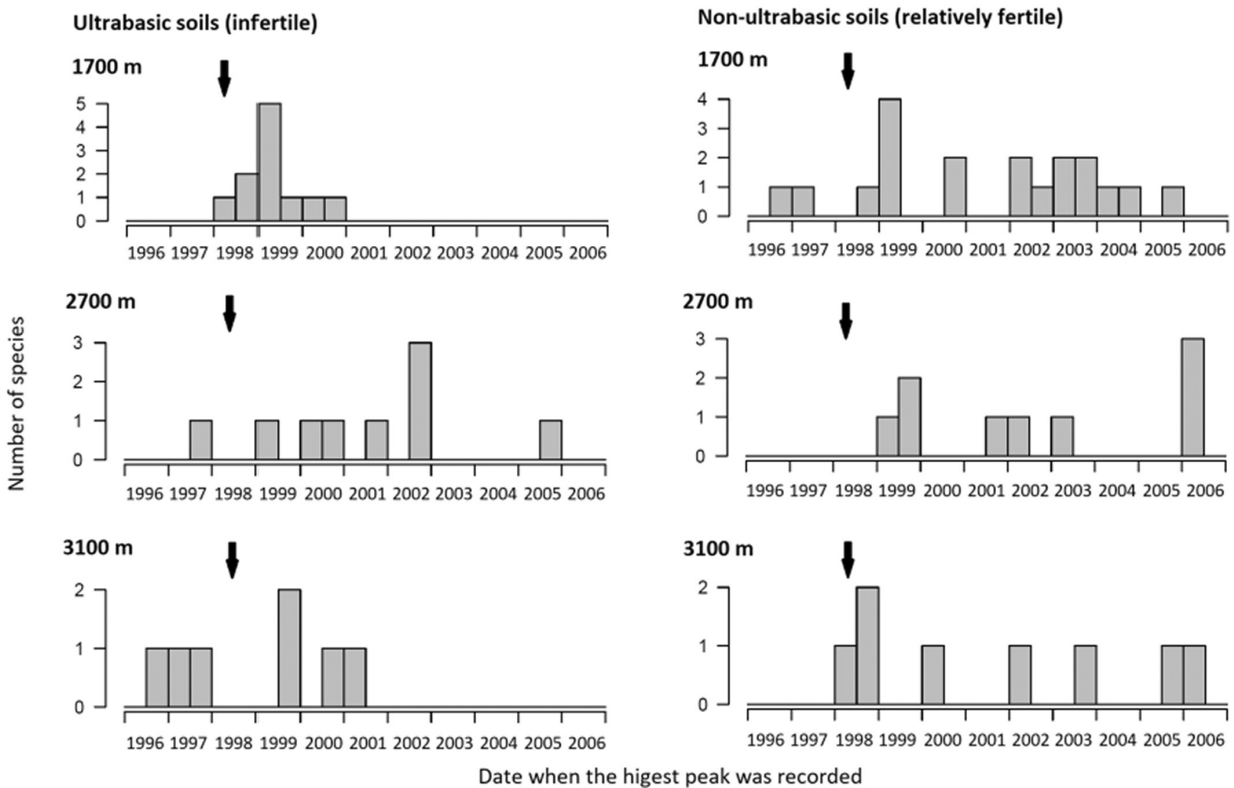


FIGURE 1 Frequency histograms of the dates when each species exhibited the highest peaks of (a) flower/male-cone and (b) fruit/seed-cone litterfall in six Bornean montane rainforest sites. The arrows indicate the end of the 1997–1998 El Niño drought (i.e. May 1998).

half of 1998 and the first half of 1999 (i.e. after the 1997–1998 El Niño drought). This trend was pronounced at the 1700 and 3100m sites but not at the 2700m sites. Similar trends were observed for fruit/seed-cone litterfall; that is, 25% of 63 time series recorded the highest peaks between the second half of 1998 and the first half of 1999.

3.3 | Reproductive cycle

The cycle length of flower/male-cone litterfall varied among species from 8 to >200 weeks (Table S1), with 22% exhibiting sub-annual cycles, 22% annual cycles, 46% supra-annual cycles, and 11% non-convergent cycles, respectively. Sub-annual and annual cycles were predominant at 1700m, whereas supra-annual cycles were predominant at higher elevations (Figure 2a). This pattern was common for trees in both soil types. The cycle length of fruit/seed-cone litterfall ranged from 7 to >200 weeks, with 21% exhibiting sub-annual cycles, 10% annual cycles, 50% supra-annual cycles, and 19% non-convergent cycles, respectively. No apparent differences were found among sites (Figure 2b). Significant cycles were detected only for four and seven time series of flower/male-cone and fruit/seed-cone litterfall, respectively (Table S1).

Reproductive cycles also varied among families. For example, Myrtaceae often showed supra-annual cycles of flower litterfall across sites. In contrast, Podocarpaceae showed different cycles at different elevations for male-cone litterfall, from sub-annual or annual cycles at 1700 and 2700m sites to supra-annual cycles at 3100m sites (Figure 3a); this reflected the pattern within *Phyllocladus hypophyllus* (Table S1). For fruit/seed-cone litterfall, no apparent differences were found among families (Figure 3b). No apparent differences were found among mycorrhizal types (Figure S4) or fruit types (Figure S5).

Wavelet analysis returned similar results to the Fourier analysis. Exceptionally, the seed-cone litterfall of *Dacrycarpus kinabaluensis* exhibited a half-year cycle in addition to the annual cycle that was detected by the Fourier analysis (Figure S6 and also see Figure S7 for other species).

4 | DISCUSSION

4.1 | General patterns across Bornean montane rainforests

In the ever-wet regions of the Southeast Asian tropics, flowering after El Niño droughts has been reported for many lowland tree species from different families (Appanah, 1985; Medway, 1972; Sakai, 2001). Similarly, peaks of flower/male-cone litterfall were recorded after the 1997–1998 El Niño drought for many species at the 1700m and 3100m sites. In addition to our study sites, Kudo and Suzuki (2004) reported that some dominant species, including *Leptospermum recurvum* and *Rhododendron buxifolium* (Ericaceae), at 3900–3950m had a flowering peak after the 1997–1998 El Niño drought on the same mountain. Exceptionally, flowering peaks were unrelated to the 1997–1998 El Niño for the species at the 2700m sites; however, it should be noted that seed-cone/fruit litterfall peaked at the beginning of 2006, following a drought in March 2005 (see Figure S1) at the 2700m non-ultrabasic site.

We used Fourier analysis to quantify the cycle length of reproductive litterfall. Across our study sites, 46% and 50% of 37 and 48 stationary time series had supra-annual cycles of flower/male-cone and fruit/seed-cone litterfall, respectively. This result contrasts with a previous study applying Fourier analysis to time series data from African tropical trees, which showed that supra-annual cycles accounted for only 25% and 35% of the time series for flowering and fruiting, respectively (Adamescu et al., 2018). Adamescu et al. (2018) reported that 46% and 42% of the time series had annual cycles, respectively. The different reproductive cycles between Borneo and Africa might be explained by climatic seasonality. Adamescu et al. (2018) proposed that annual seasonality of rainfall is related to the dominance of the annual cycles of reproduction across African tropical forests. In contrast, the annual seasonality of rainfall does not follow a well-defined pattern across our study sites (Kitayama et al., 2021). However, we cannot rule out the possibility that differences between the data collection methodology of Adamescu et al. (2018) and that used in the present study (i.e. visual monitoring and sampling by litter traps, respectively) might have caused

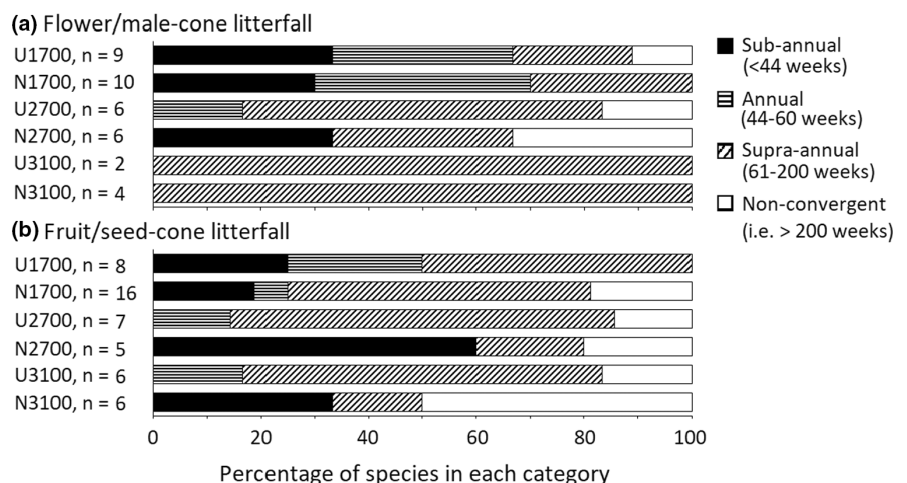
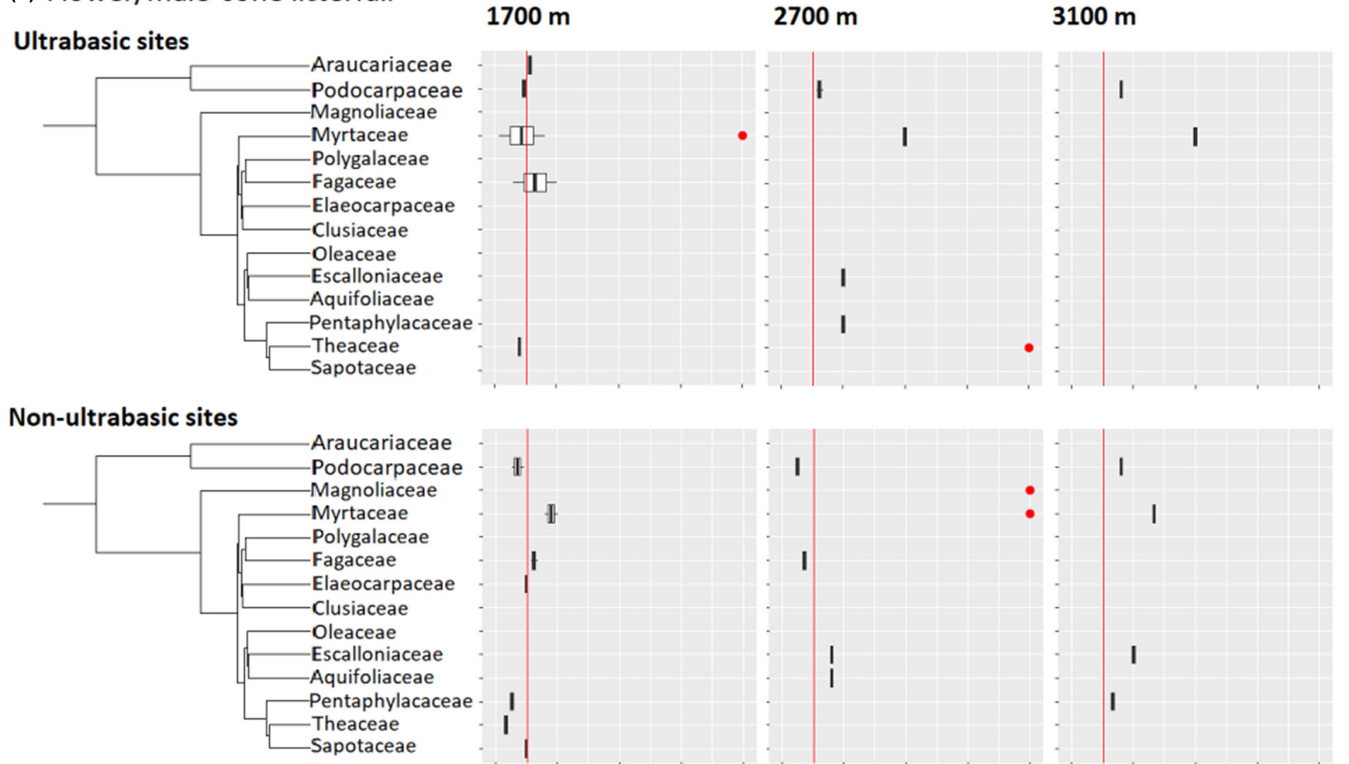


FIGURE 2 Relative proportions of the dominant cycles of (a) flower/male-cone and (b) fruit/female-cone litterfall for 27 and 37 tree species, respectively, from six Bornean montane rainforest sites. The site name is expressed as the combination of common elevations with soil types, that is, U and N for ultrabasic and non-ultrabasic soils, respectively. *n* represents the number of species.

(a) Flower/male-cone litterfall



(b) Fruit/seed-cone litterfall

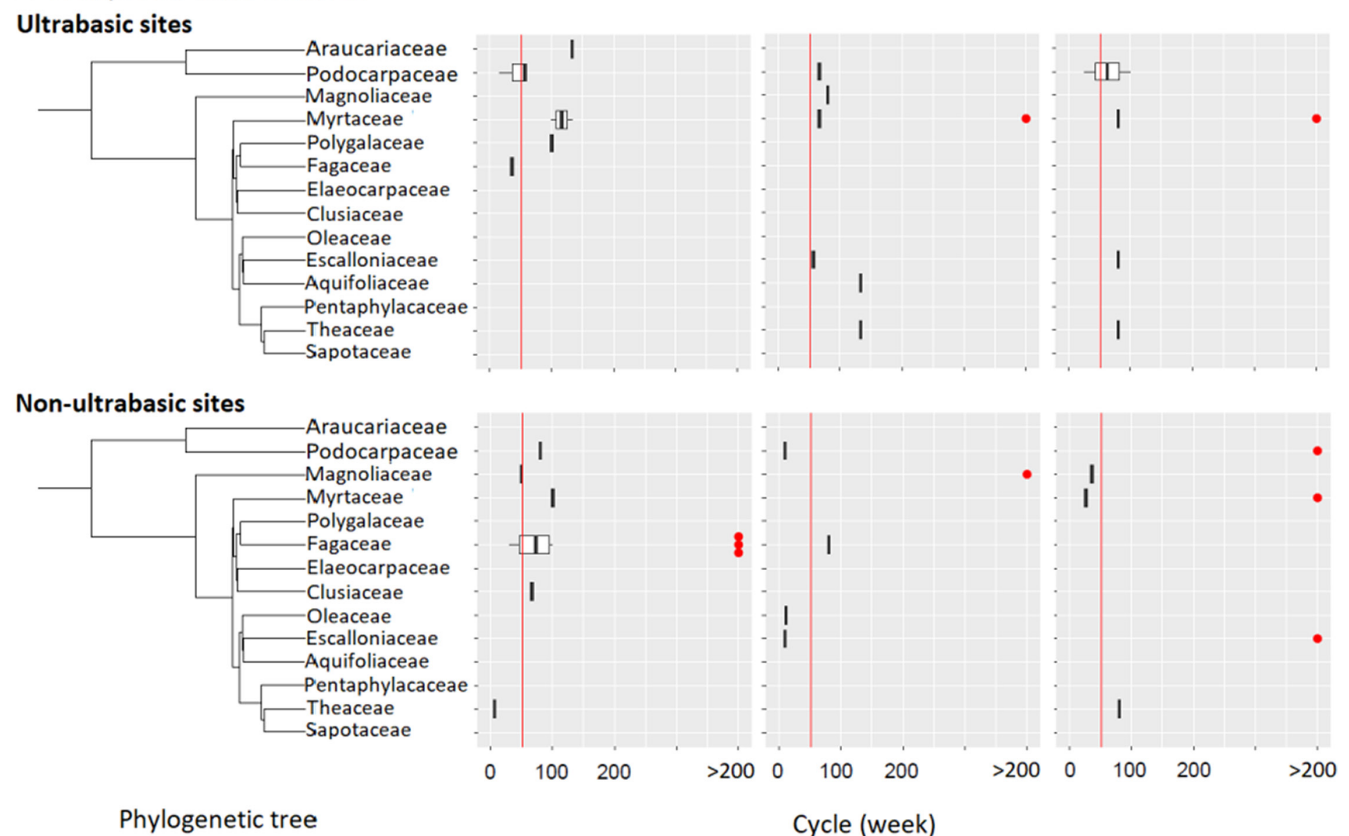


FIGURE 3 Box plots showing the cycle lengths of (a) flower/male-cone and (b) fruit/seed-cone litterfall for 14 families in six Bornean montane rainforest sites. The central boxes show the interquartile ranges and medians. The whiskers extend 1.5 times the interquartile or to the most extreme value. The vertical red lines represent 1 year cycle (i.e. 52 weeks). Red circles represent the data points of the species with a non-convergent cycle (i.e. >200 weeks).

the discrepancy. In the present study, less numbers of species were identified for flower/male-cone litter than fruit/seed-cone litter. This implies that flowers and male cones often decomposed before they fell to the litter trap and fruits and seed cones were dispersed more widely. Thus, our dataset captured the reproductive behaviors of the limited subsets of the entire forest communities.

4.2 | Elevational patterns of the reproductive cycle

Many species at the 2700 and 3100m sites exhibited supra-annual cycles of flower/male-cone litterfall, whereas the 1700m species often exhibited sub-annual and annual cycles. Significant cycles of flower/male-cone litterfall were detected only for four species, presumably reflecting weak seasonality and/or irregular cycles of flowering or male-cone production in Bornean montane species. The mechanisms underlying these elevational patterns remain unclear but probably involve multiple factors. In terms of climate, the 1997–1998 El Niño drought was the most severe at the 3100m sites (Kitayama et al., 2014), whereas significant annual cycles of potential evapotranspiration and saturation deficit were found only at 1700m sites (Kitayama et al., 2021). Lower primary productivity (Kitayama & Aiba, 2002) and lower soil fertility (Kitayama & Aiba, 2002; Kitayama et al., 1998) under cooler climates may slow down the accumulation of resources for reproduction at higher elevations. Plant–animal interactions should be also taken into account because the species diversity of small mammals may decrease from the lower montane forests (at ca. 1400m) to the forests at higher elevations (Nor, 2001).

Fruit/seed-cone litterfall did not show clear elevational patterns. This may be due to abortion or intraspecific variation in fruit development. In the Fagaceae, fertilization can be delayed by up to >1 year after pollination (Sogo & Tobe, 2006). Some fruits may remain on trees for longer and disperse slowly (Babweteera et al., 2018), making the identification of cyclicity difficult.

4.3 | Soil type, phylogeny, mycorrhizal association, and fruit types

We expected that trees on infertile ultrabasic soils would have longer reproductive cycles than those on relatively fertile non-ultrabasic soils, because longer time intervals may be required to accumulate enough resources under stronger nutrient limitation (Janzen, 1974). However, we did not find apparent differences between the reproductive cycles of trees growing on different soil types at the same elevations. This might be explained by efficient P utilization and acquisition, which may shorten the time required to accumulate resources. Among our study sites, it was reported that P concentration in reproductive organs decreased with soil P deficiency (Kitayama et al., 2015; Tsujii & Kitayama, 2018). This may reduce the P requirement per reproduction. In addition, special root traits, such as high phosphatase activities (Kitayama, 2013; Ushio et al., 2015), large surface areas per root biomass (Ushio et al., 2015), and high

exudation rates of organic acids (Aoki et al., 2012), may enhance the uptake rates of P from soil. Similar reproductive cycles between different soil types may also be associated with lower productivity of reproductive litter in the ultrabasic sites than in non-ultrabasic sites at the same elevation (Kitayama et al., 2015; Table 1), pointing to the possibility that trees maintain the frequency of reproduction in exchange for fewer reproductive organs per event. However, this suggestion is not fully supported because the relative proportion of reproductive organs per total litterfall was independent of soil P availability (Table 1).

Phylogenetic conservatism is another key aspect of the reproductive phenology of tropical trees (Bawa et al., 2003; Wright & Calderón, 1995). In the present study, the Myrtaceae showed supra-annual cycles of flowering across sites (Figure 3a), although this family includes capsulate and fleshy-fruited genera with different P demands for fruiting (Tsujii & Kitayama, 2018). Elevational variation in reproductive phenology was associated with taxa composition. Some families with an annual reproductive cycle, such as the Araucariaceae and Sapotaceae, were absent at higher elevations. The cycle length of the male-cone production of the Podocarpaceae varied along elevational gradients, with longer cycles at higher elevations (Figure 3a), primarily due to a considerable variation within *Phyllocladus hypophyllus*. Mycorrhizal association, a trait strongly constrained by phylogeny, has also been suggested to affect the reproductive cycle because masting species are often ectomycorrhizal (Newbery, 2005). However, this hypothesis was not tested because our dataset consisted mostly of arbuscular mycorrhizal species. The differences among fruit types were also unclear.

5 | CONCLUSIONS

The present study is currently the most comprehensive survey of the reproductive phenology of Bornean montane tree species across a wide range of elevations in two soil types. Our long-term monitoring data revealed that Bornean montane species have three characteristic reproductive phenologies. The first is reproduction in response to El Niño droughts, which indicates that ENSO affects reproductive phenology as is the case with the lowland dipterocarp forests. The second is the dominance of the supra-annual reproductive cycle at higher elevations, which may be attributed to lower primary productivity and soil fertility, and the absence of some sub-annually and annually reproducing families. The third is the sub-annual and annual cycles of reproduction for the lower montane species (i.e. species in the 1700m sites), which possibly reflects the sub-annual or annual seasonality of some climatic factors that include photosynthetically active radiation, air temperature, potential evapotranspiration, and saturation deficit.

AUTHOR CONTRIBUTIONS

Y.T., S.S., M.U., and K.K. conceived the ideas and designed methodology; K.K. and S.A. conducted the litter sampling; Y.T. collected the data using the litter samples; Y.T. analyzed the data, with

contributions from M.U.; Y.T. and K.K. wrote the first draft; all authors were involved in final writing.

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CONFLICT OF INTEREST

No potential conflict of interest was reported by the authors.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in the Dryad Digital Repository: <https://doi.org/10.5061/dryad.ffbg79czz> (Tsuji et al., 2022).

ORCID

Yuki Tsujii  <https://orcid.org/0000-0003-3646-8142>

Shoko Sakai  <https://orcid.org/0000-0002-4267-8405>

Masayuki Ushio  <https://orcid.org/0000-0003-4831-7181>

Shin-ichiro Aiba  <https://orcid.org/0000-0002-3844-0138>

Kanehiro Kitayama  <https://orcid.org/0000-0002-6863-7118>

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