Reproductive Phenology and Influencing Factors of Macrosolen in Xishuangbanna: Postprint

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Abstract

Mistletoe plants serve as important keystone species and keystone food resources in ecosystems. As a mistletoe species, the reproductive phenology of Scurrula not only influences its own reproductive fitness but also affects animals that depend on it for food resources. To investigate the reproductive phenological characteristics of Scurrula and their influencing factors, and to explore the interactive relationships between Scurrula and its host plants and seed dispersers, this study focused on Scurrula distributed in the Xishuangbanna region. Through regular observations of the reproductive phenology of Scurrula and its host plant Schima, measurements of their biological characteristics and environmental factors such as temperature and humidity, the reproductive phenological characteristics of Scurrula were analyzed at both individual and population levels, as well as the effects of host plants and temperature and humidity conditions on its reproductive phenology. The results indicated that: (1) The flowering phenology of Scurrula exhibits a concentrated mass-flowering pattern; the flowering and fruiting periods of the entire population lasted approximately 20 d and 72 d, respectively, with both periods showing high synchrony indices. The quantity and rate of fruit consumption by animals reached maximum in mid-June, subsequently declining; (2) The onset of flowering in Scurrula was highly correlated with that of Schima, with the flowering and fruiting periods substantially overlapping with the reproductive phenology of Schima; (3) The number of individuals flowering and fruiting each month was not significantly correlated with the mean temperature and relative humidity of the same month or the previous month. Overall, the reproductive phenological characteristics of mistletoe plants may be subject to multiple influencing factors, and a comprehensive understanding of the reproductive phenology of hemiparasitic plants requires consideration of the synergistic effects of various biotic and abiotic factors.

Full Text

Reproductive Phenological Characteristics and Impact Factors of *Macrosolen cochinchinensis* in Xishuangbanna

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Abstract: Mistletoes play a crucial role in ecosystems as keystone species and critical food resources for many animals. As a hemiparasitic mistletoe, the reproductive phenology of *Macrosolen cochinchinensis* not only affects its own reproductive fitness but also influences animal species that depend on it for food resources. To understand the reproductive phenological characteristics of this species and their influencing factors, and to explore the interactions between host plants and seed dispersers, we conducted a study on *M. cochinchinensis* in Xishuangbanna. We regularly monitored the reproductive phenology of both *M. cochinchinensis* and its host plant *Schima superba*, measured their biological characteristics, and recorded environmental factors such as temperature and humidity. We analyzed the reproductive phenological patterns at both individual and population levels, and examined how host plants and environmental factors affect mistletoe phenology. The results showed that: (1) The flowering phenology of *M. cochinchinensis* follows a mass-flowering pattern, with population-level flowering and fruiting durations of approximately 20 days and 72 days, respectively. Both flowering and fruiting periods exhibited high synchrony indices, with fruit consumption by birds peaking in mid-June before gradually declining. (2) The first flowering date of *M. cochinchinensis* was highly correlated with that of *S. superba*, and their reproductive periods substantially overlapped. (3) The number of flowering and fruit-ripening individuals per month showed no significant correlation with average temperature or relative humidity during the same or previous month. In conclusion, mistletoe reproductive phenology appears to be influenced by multiple factors, and a comprehensive understanding of hemiparasitic plant phenology requires consideration of both biotic and abiotic factors.

Keywords: flowering phenology, synchrony, seed dispersal, host plants, mistletoe

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Seasonal and periodic reproductive phenological events represent important components of plant life histories, influencing not only pollination and seed dispersal but also affecting animals that rely on these plants for resources. Plant reproductive phenology can be quantitatively described using multiple parameters including onset, duration, and synchrony. While flowering phenology typically focuses on the anthesis stage when plants achieve reproductive capacity, fruiting phenology encompasses fruit appearance, growth, maturation, and seed dispersal. In addition to phylogenetic influences, plant reproductive timing is shaped by various biotic factors (such as co-occurring plants, pollinators, and seed dispersers) and abiotic factors (including temperature, photoperiod, and precipitation). Furthermore, intrinsic biological characteristics affect flowering phenology and reproductive fitness, with larger individuals generally flowering earlier and longer than smaller ones, though often with lower synchrony.

Mistletoes are hemiparasitic evergreen shrubs capable of photosynthesis that interact extensively with host plants, pollinators, and seed dispersers through their unique life form and history. They infect host branches through specialized attachment organs called haustoria, absorbing water and nutrients from host xylem to meet their developmental needs. Research indicates that when host and parasite reproductive phenology overlap partially, infected hosts attract more pollinators and seed dispersers than uninfected conspecifics. Seed dispersal is critical for mistletoe survival, with most species relying on birds that ingest fruits and subsequently deposit sticky seeds onto host branches through regurgitation or defecation, enabling germination and establishment. During mistletoe reproductive periods, bird abundance and richness increase significantly in infected forest areas, suggesting a diffuse coevolutionary relationship.

While studies on mistletoe reproductive phenology have been conducted in urban and semi-desert shrub ecosystems, research in tropical rainforest ecosystems remains lacking. It remains unclear whether tropical mistletoe phenology is similarly influenced by host plant phenology and species identity, intrinsic biological traits, and climatic factors. This study focuses on *Macrosolen cochinchinensis* (Loranthaceae) in Xishuangbanna to address two questions: (1) What are the reproductive phenological characteristics of *M. cochinchinensis*? (2) How do biotic factors (host phenology, biological characteristics) and abiotic factors (temperature and humidity) influence its reproductive phenology? We aim to enhance understanding of host-mistletoe-seed disperser interactions and provide baseline data for forest management of hemiparasitic plants under global climate change.

1.1 Phenological Observations

The study was conducted in the tropical rainforest of Xishuangbanna National Nature Reserve-Menglun Sector (101°07' -101°09' E, 21°58' -21°59' N). This region represents the northern tropical zone with a tropical monsoon climate, featuring an average annual temperature of approximately 22°C and annual precipitation of 1500 mm. Based on precipitation patterns, the year is divided into three seasons: rainy season (mid-May to late October), fog-cool season (late October to mid-March), and dry season (mid-March to mid-May). We selected 24 healthy, reproductive *M. cochinchinensis* individuals parasitizing eight *S. superba* host trees. *M. cochinchinensis* is distributed primarily in southwestern and southeastern China, occurring in primary and secondary forests on tall trees and in heavily disturbed habitats, with seed dispersal mainly by small birds such as flowerpeckers (Dicaeidae). Binoculars were used to assist phenological observations.

Based on preliminary observations since 2017, *M. cochinchinensis* reproductive periods concentrate from March to August each year. To capture complete phenological data, we conducted weekly observations from February to September 2018, recording four phenological parameters: first and last flowering dates, and initial and final fruiting dates (with initial fruit ripening recorded only for mistletoe and fruit appearance recorded for the host). Phenological events were converted to Julian days (days since January 1) for calculation convenience. Observation criteria were defined as: first flowering date when the first flower appeared on an individual (if flowering was observed during an interval, flower color was used to determine onset); last flowering date as the final observation of flowers on branches. To quantify fruit consumption dynamics, we constructed 1.5 m × 1.5 m fruit peel collection frames using 5 mm mesh netting and PVC pipes, placing them beneath four spatially isolated mistletoe individuals to ensure peels originated from single plants. Collections were made weekly, with foraging rate calculated as peels collected divided by days between collections, expressed as mean ± standard error.

1.2 Phenological Parameter Calculations

First flowering and fruit ripening dates were recorded according to observation criteria. Flowering and fruiting durations were calculated as intervals between onset and end dates. Asynchrony at individual and population levels was quantified using Augspurger' s (1983) synchrony index formulas, where Xi represents phenological synchrony between a given individual and all other conspecifics (Formula 1), and Z represents the mean synchrony index across all individuals (Formula 2). Both Xi and Z range from 0 (no overlap) to 1 (complete overlap).

1.3 Biological Characteristics and Temperature-Humidity Measurements

Biological measurements included host DBH, crown width, mistletoe parasitism height, and crown width. Host DBH was measured at 1.3 m using diameter tape, while tree height and parasitism height were measured with a rangefinder. Crown widths were estimated for both host and parasite. Temperature and humidity were recorded every 90 minutes using ibutton DS1923 data loggers (Shanghai Wodisen Electronics Technology Co., Ltd.).

1.4 Data Analysis

Normality was tested using Shapiro-Wilk tests. Since some variables remained non-normal after transformation, we used Spearman correlation analysis to examine relationships among the four phenological parameters of *M. cochinchinensis* and between these parameters and biological characteristics (parasite crown width, parasitism height), host characteristics (host crown width, host height), and temperature-humidity variables. When correlations between biological characteristics and phenological parameters, or between monthly flowering/fruiting individuals and temperature/humidity, were significant, regression analysis was subsequently performed.

2.1 Reproductive Phenological Characteristics of *M. cochinchinensis*

Flowering phenology: *M. cochinchinensis* in the study area began flowering in late March to early April, peaking in mid-April, with the entire population entering the final flowering stage in late April. Flowering duration ranged from 10 to 31 days, averaging approximately 20 days, representing a unimodal mass-flowering pattern with a right-skewed curve. Earlier-flowering individuals had longer flowering periods ($r = -0.864$, $P < 0.001$). The population' s mean first flowering dates differed by about 6 days, with a maximum difference of 20 days [Figure 1: see original paper], and the flowering synchrony index was 0.79.

Fruiting phenology: Fruits first appeared in mid-to-late April, turning from green to orange in mid-to-late May before gradually maturing. The population reached final fruiting stage in early August, with fruiting duration ranging from 63 to 97 days and averaging 72 days. The fruiting pattern was plateau-shaped, with ripe fruits present on all individuals for an extended period. Similar to flowering, earlier fruit maturation correlated with longer fruiting duration ($r = -0.777$, $P < 0.001$), while later fruit maturation correlated with higher synchrony ($r = 0.815$, $P < 0.001$). Mean first fruit ripening dates differed by about 7 days, with a maximum difference of 27 days [Figure 1: see original paper]. Fruiting synchrony ($Z = 0.88$) was higher than flowering synchrony, though individual-level synchrony between flowering and fruiting was not significantly correlated ($r = 0.115$, $P = 0.699$).

Fruit consumption by birds began in late May, peaking in mid-June (96.3 ± 18.6 peels), then declining. Foraging rate followed the same trend, with the population entering final fruiting stage in mid-to-late July [Figure 2: see original paper].

2.2 Host Phenology Effects on *M. cochinchinensis* Reproduction

The host plant *S. superba* began flowering in late March for a few individuals, with most entering first flowering in mid-April, peaking in early May, and reaching final flowering in late May. Flowering duration ranged from 21 to 50 days, averaging 30 days. Fruit set began in mid-May, with the population reaching final fruiting in early August and an average fruiting period of 85 days. *M. cochinchinensis* began flowering about one week before its host, with first flowering dates highly correlated ($P < 0.001$). The mistletoe' s average flowering duration was about 10 days shorter than the host' s, while fruiting periods substantially overlapped [Figure 3: see original paper].

2.3 Effects of Host and Parasite Biological Characteristics

Host biological effects: Host crown width correlated significantly with tree height ($r = 0.556$, $P < 0.05$) but not with mistletoe phenological parameters. Mistletoe parasitism height occurred above mid-canopy and increased with host height ($r = 0.627$, $P < 0.05$). Host height significantly correlated with mistletoe first flowering date and flowering duration, with taller hosts associated with earlier flowering and shorter flowering periods . Regression analysis confirmed host height significantly affected flowering duration ($R^2 = 0.281$, $P < 0.05$).

Parasite biological effects: Higher parasitism height correlated with smaller crown width and earlier fruit maturation, as well as shorter flowering and fruiting durations, though these relationships were not statistically significant .

2.4 Temperature and Humidity Effects on *M. cochinchinensis* Phenology

During the observation period, mean monthly temperature was 21.4°C, while mean relative humidity increased steadily from 51.86% to 97.19% with the onset of the rainy season [Figure 4: see original paper]. Flowering was largely completed before the rainy season, while fruiting synchronized with it. However, the number of monthly flowering and fruit-ripening individuals showed no significant correlation with mean temperature or relative humidity during the same or previous month.

3.1 Reproductive Phenological Characteristics of *M. cochinchinensis*

Plant reproductive phenology is influenced by various biotic and abiotic factors, and for hemiparasites that absorb water and nutrients from hosts while interacting with pollinators and seed dispersers, these influences are particularly complex. *M. cochinchinensis* exhibits mass-flowering phenology with high synchrony, a pattern consistent with other Loranthaceae species. High flowering synchrony is thought to attract more pollinators, though complete synchrony is impossible due to environmental and genetic variation. The transition from flowering to fruit maturation is gradual, so fruiting phenology is constrained by first flowering date and duration. Earlier-flowering individuals had earlier fruit maturation, and fruiting synchrony increased with later fruit maturation, a pattern confirmed in other vertebrate-dispersed plants. Contrary to previous studies showing fruiting synchrony lower than flowering synchrony, our study found higher fruiting synchrony with a weak positive correlation between them ($r = 0.115$, $P = 0.699$).

Larger-crowned mistletoes produced more fruits, and higher fruit production generally leads to greater removal. By late July, only large-crowned individuals retained fruits, resulting in decreased foraging quantity and rate, similar to patterns observed in *Phoradendron californicum*. Since bird foraging behavior and rapid mistletoe seed germination mean that peeled fruit numbers represent maximum potential seed dispersal, larger fruit crops increase dispersal probability.

3.2 Host Phenology Effects on *M. cochinchinensis* Reproduction

When hosts accumulate sufficient resources for their own reproduction, infected mistletoes tend to flower concurrently. We found significant correlation between first flowering dates of *S. superba* and *M. cochinchinensis*, with substantial temporal overlap in reproductive periods. However, studies on desert mistletoe (*Phoradendron californicum*) found inconsistent phenological sequences with its five host species. Although *M. cochinchinensis* flowered before its host, *S. superba* is hermaphroditic and insect-pollinated, not relying on birds for seed dispersal, suggesting its phenology may not significantly enhance mistletoe pollination or dispersal. Therefore, temporal overlap alone does not indicate host phenology as the sole determinant of mistletoe reproductive timing.

3.3 Effects of Biological Characteristics on Reproductive Phenology

M. cochinchinensis flowering duration was affected by host height, possibly because host height influenced parasitism height, which indirectly affected flowering duration. Higher parasitism height correlated with later first flowering, likely because flowering occurred before the rainy season when water and nutrients must be transported from host roots through xylem to the canopy. Studies on herbaceous plants similarly show taller species flower later than shorter ones.

Plant size affects reproductive phenology, with larger *M. cochinchinensis* individuals flowering earlier and longer. Similar patterns in *Lotus corniculatus* show plant size correlates with earlier flowering and longer duration. In wild nutmeg, larger individuals have longer flowering periods and lower synchrony. Thus, plant size influences flowering phenology, which in turn affects reproductive fitness.

3.4 Temperature and Humidity Effects on Reproductive Phenology

Tropical plant flowering and fruiting concentrate in the wet season, with flowering species numbers positively correlated with monthly precipitation. The substantial overlap between *S. superba* and *M. cochinchinensis* phenology may be climate-mediated. Our study found *M. cochinchinensis* reproductive phenology concentrated in the rainy season, with fruiting duration correlating with relative humidity, consistent with African mistletoe studies showing peak fruiting in wet seasons. However, monthly flowering and fruiting individual numbers were not significantly correlated with temperature or humidity. Additionally, during peel collection, immature fruit numbers showed opposite trends to consumed peels due to high precipitation.

Our study has limitations. First, low understory visibility in tropical rainforests constrained sample size. Second, high parasitism height and host growth sometimes obscured branches, potentially affecting phenological event detection. Third, aggregated mistletoe distribution and variable infection densities per host, combined with limited host numbers, prevented analysis of phenological variation among mistletoes on single hosts.

Surveys of mistletoe-host networks in Xishuangbanna reveal *M. cochinchinensis* infects 46 host species, and parasite phenology varies with host identity. Future research should examine phenology of single parasite species across multiple hosts, considering event duration and intensity, and conduct long-term observations across habitats and climates for more mistletoe species. With global warming increasing extreme climate events and advancing first flowering dates while reducing synchrony, and given variable phenological responses across regions and species, long-term monitoring is needed for bird-dispersed hemiparasites. Additionally, climate warming effects on biological traits, pollinator abundance, and seed disperser interactions must be examined to comprehensively reveal phenological patterns, influencing factors, and climate change responses.

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Note: Figure translations are in progress. See original paper for figures.