Reproductive Strategy of a Tropical Pioneer Shrub, *Melastoma malabathricum* (Melastomataceae)

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Introduction

Many studies of excess flower production (the production of more flowers than fruits) have been conducted. Holtsford (1985) described five categories of hypotheses to explain this phenomenon: male function, pollinator attractiveness, reproductive assurance, resource boom, and selective fruiting.

The resource boom hypothesis assumes that the amount of resources that will be available for fruit production is not predictable at the flowering stage and that high fruit set occurs only when the resources for fruit production are sufficient. Previous studies of this hypothesis dealt with the unpredictability of supra-annual environmental fluctuations (Holtsford 1985; Eriksson 1987; Gorchov 1988; Vaughton 1991; Nishikawa 1998). However, in tropical regions, some pioneer plants reproduce continuously (Momose et al. 1998; Sakai et al. 1999), and they are considered to be affected by environmental fluctuations over much shorter time scales.

Previously, the resource boom hypothesis has been tested under artificial environmental control (Coulter 1979; Willson and Price 1980; Lee and Bazzaz 1982; Holtsford 1985; Eriksson 1987; Gorchov 1988; Vaughton 1991; Nishikawa 1998). As a new approach to testing this hypothesis, we measured fluctuations in the demand and supply of resources under natural conditions in a species that reproduces continuously and clarified how plants adapt to those fluctuations through increasing the number of reproductive organs and aborting these organs when resources are insufficient.

Methods

Study site and plant materials

The study was conducted in Lambir Hills National Park (4˚12′N, 114˚02′E; ca. 100 m a.s.l.), Sarawak, Malaysia. The climate is almost aseasonal (Kato et al. 1995).

The study species, *Melastoma malabathricum* L., is a pioneer shrub that is abundant along the edges between natural and artificial habitats (e.g. beside roads, Corner 1988). These plants reproduce almost continuously throughout the year, and reproductive organs at various stages, including young flower buds and mature fruits, are almost always found on a given individual.

Size and dry weight

To estimate the dry weight of the reproductive organs attached to plants, we determined relationships between their size and weight. To create these relationships, we harvested and measured 94 buds, 21 flowers, and 71 fruits (parameters: fresh weight, dry weight, length, and width). From these samples, we performed multiple regressions to analyze the relationships between dry weight (the explained variable) and length and width (independent variables) and between the water content in the reproductive organs (water weight) and their size (length and width).

Growth of reproductive organs

From 5 June until 24 July 2004, we measured the lengths and widths of marked reproductive organs every day without damaging the organs. In total, we measured the growth of 90 samples from six plants. The abortion rate of reproductive organs (the proportion of organs originally present on one day that were no longer present on the next day) was obtained from these samples. The size growth of the reproductive organs was transformed into a dry weight growth using the multiple regression equations for dry weight as a function of size. We calculated water weight similarly.

Monitoring the number of reproductive organs

We monitored fluctuations in the number of reproductive organs on each individual between consecutive days. The number of reproductive organs was counted daily in each of seven categories based on their reproductive stage: bud (young, intermediate, large), flower, and fruit (young, intermediate, and large). These stages were defined for the reproductive organs according to their sizes and colors.

Respiration and transpiration of reproductive organs

Diurnal changes in respiration and transpiration were measured every hour during the day and every 3 hours at night using an LI-6400 portable photosynthesis meter (LI-COR, Lincoln, Nebraska) with a model 6400-05 conifer chamber. In total, 56 samples (nine individuals) from seven reproductive stages were measured on nine individual plants. Under natural light, each sample was measured for only 1 day, and then its dry weight was determined.

Photosynthesis of leaves

Diurnal changes in leaf photosynthesis were measured using the LI-6400 meter under natural light conditions. After the measurements, the area of each leaf was measured, and the area of each leaf was calculated.

Meteorological data

Solar radiation was measured at 10-minute intervals using a Pyranometer (MS-801, EKO Seiki) at a fixed open site. The plants in our study were assumed to receive approximately the same amount of solar radiation as the sensor because they were located at the roadside. Rainfall was measured every hour using a tipping-bucket rain gauge that collected 0.5 mm per tip (No.34-T, OTA).

Analysis

Based on the assumption that carbohydrates and water were demanded by reproductive organs and that their supply fluctuated in the short term, we analyzed the responses of plants as a function of these fluctuations.

Demand for carbohydrates was expressed as the increase in dry weight (g), and carbohydrate consumption was expressed as the respiration per reproductive organ per day (g $C_6H_{12}O_6$ day^{-1}). Similarly, demand for water was expressed as the increase in water weight (g) and water consumption of the transpiration per reproductive organ per day (g H_2O day^{-1}). The average demands for carbohydrates and water at each stage were thus obtained. The number of reproductive organs counted at each reproductive stage on each day was multiplied by the carbohydrate and water demands for that stage to produce an estimated total demand for carbohydrates and water for nine plants each day.

The resource supply was determined from our photosynthetic measurements and meteorological data. The relationships between photosynthetic photon flux density (PPFD) and photosynthetic rate were estimated from the gross photosynthetic rate, the maximum gross photosynthetic rate, the respiration rate, and PPFD (μmol m^{-2} s^{-1}; Boote and Loomis 1991). The relationship between total radiation and PPFD at our study site was provided by Megumi Yamashita (Kinki Surveyor School, personal communication). The radiation measured on each day from 31 May to 17 July 2004 was transformed into PPFD based on this conversion factor. The daily total photosynthetic productivity (g cm^{-2} day^{-1}) was estimated for each day as a function of the calculated PPFD values. The daily total rainfall was also calculated.

The daily abortion rate of the population on the next day was compared with the carbohydrate demand on the current day divided by the total photosynthetic productivity during the previous 1, 3, or 5 days and with the demand for water on the current day divided by the total rainfall during the previous 5 days. Spearman's rank correlation coefficient was calculated for each of these comparisons.

Results

The demand for resources (carbohydrates and water) was greatest during the flower stage (Table 1). The photosynthetic rates of leaves and PPFD both varied during the day. Because stomatal conductance decreased after 1000, we obtained separate relationships between PPFD and photosynthetic rate before and after this time. Maximum gross photosynthetic rates of leaves before and after 1000 were 11.0 and 7.3 μmol CO_2 m^{-2} s^{-1}, respectively. The respiration rate was 0.80 μmol CO_2 m^{-2} s^{-1}. The leaf transpiration rate averaged 376 mg cm^{-2} day^{-1}, and the mean area of a single leaf was 19.7 cm^2.

The daily abortion rates on the next day were significantly correlated with the carbohydrate demand on the current day divided by the total photosynthetic production per unit leaf area during the previous 1, 3, or 5 days (Table 2). However, the daily abortion rates on the next day were not correlated with the water demand on the current day divided by the total rainfall during the previous 5 days. That is, the daily abortion rates were correlated with the available carbohydrate resources but not with the available water resource.

Discussion

The daily abortion rates were correlated with the carbohydrate demand divided by the total photosynthetic production per unit leaf area during the previous 1, 3, or 5 days. The abortion of reproductive organs in *M. malabathricum* thus appears to represent an adaptation to environmental fluctuations at shorter time scales than previously reported in other plants.

Even in the absence of seasonal environment limitations, tropical climax species tend to reproduce at intervals of 1 year or longer (Momose et al. 1998; Sakai et al. 1999). This suggests that they reserve resources, and that the higher their photosynthetic production, the more their resource reserves increase (Yoneda et al. 2002). In contrast, tropical pioneer shrubs such as *M. malabathricum* reproduce continuously. When photosynthetic production is low, they abort their reproductive organs. Such a reproductive strategy, which minimizes the resources reserved for reproduction, can be explained by the typically high mortality of tropical pioneer species (Clark and Clark 1992, Shimano 2000).

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Table 1. Demand for carbohydrate and water of reproductive organs in each stage.

Stage	Demand for carbohydrate (mg day^{-1})	Demand for water (g day^{-1})
Young bud	4.2	0.17
Intermediate bud	9.8	0.11
Large bud	16	0.56
Flower	23	2.0
Young-intermediate fruit	8.0	0.91
Large fruit	4.6	0.42

Table2. The carbohydrate demands of all individuals combined per the total photosynthetic productivity per leaf area during the previous one, three or five days were compared with abortion rates of reproductive organs by Spearman's rank correlation test. Also, the water demands of all individuals combined per the total rainfall for the previous five days were compared with abortion rates of reproductive organs.

	Demand per supply in carbohydrate			Demand per supply in water
	Previous day	1-3 days before	1-5 days before	1-5 days before
Abortion rates	0.547**	0.556**	0.568**	NS

**: $p < 0.01$, NS: $p > 0.05$