Research paper

No Effect of Host Tree Species on the Physiology of the Epiphytic Orchid *Bulbophyllum japonicum* in a Subtropical Rainforest in Northeastern Taiwan

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【Summary】

Chlorophyll concentrations, Crassulacean acid metabolism (CAM) acid fluctuations, and chlorophyll fluorescence parameters were measured in individuals of the epiphytic orchid *Bulbophyllum japonicum* growing on 3 different host tree species in a subtropical rainforest in northeastern Taiwan. No differences in any of the physiological measures were found. Thus, although the host tree species vary considerably in leaf morphology, bark characteristics, and elemental composition of stemflow water, such differences did not substantially impact the physiology of this epiphytic orchid. These results may reflect the slow growth rates and minimal nutrient requirements of this slow-growing, shade-adapted orchid. The findings of this study help explain the lack of host specificity in this epiphyte and perhaps in many other species.
Key words: Crassulacean acid metabolism, epiphyte, host specificity, orchid, subtropical rainforest.
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研究報告

台灣東北部亞熱帶雨林附生蘭科植物 (*Bulbophyllum japonicum*)之生理無宿主效應

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摘　要

　　本研究於台灣東北部亞熱帶雨林測量附生於三種不同宿主的日本捲瓣蘭(*Bulbophyllum japonicum*)之葉綠素濃度、景天酸代謝變動以及葉綠素螢光參數。所測量的項目在不同宿主的個體間皆無顯著差異，因此雖然這些宿主植物的葉形、樹皮特徵以及幹流水的營養組成有可觀的差異，這差異並未對此附生蘭的生理產生很大的影響。這樣的結果可能反應此生長緩慢、耐陰之蘭科植物其低生長速率以及低營養需求。本研究的發現有助於解釋此附生植物，可能也包括其它許多附生植物，缺乏宿主專一性的現象。

關鍵詞：景天酸代謝、附生植物、宿住專一性、蘭科、亞熱帶雨林。

INTRODUCTION

　　Epiphytic plants, especially those that do not accumulate humus, are completely dependent upon their host trees for physical support and the provision of elemental nutrients, although some nutrients may be obtained directly from the atmosphere or atmospheric particulates (Lüttge 1989, Benzing 1990). In most epiphytes, liquid water and the bulk of the elemental nutrients are supplied by rainwater in the form of stemflow or throughfall on the host tree. The pH and elemental composition of the latter sources of water are influenced by leachates from the leaves and bark of the tree (Tukey 1966, Comerford and White 1977, Herrmann et al. 2006). Thus, there is great potential for the host tree species to strongly influence the physiology, growth, and survival of its epiphytes. This influence can presumably result in host specificity in epiphytic taxa. Despite the potential importance of the host species, investigations of the effects of the host tree on the physiology of its resident epiphytes are surprisingly rare, although several studies have examined host effects on the growth of resident epiphytes. For example, greater growth of an epiphytic bromeliad and an epiphytic fern on preferred host tree species, relative to non-preferred host trees, was correlated with throughfall nutrient contents, light availability in the host canopy, and certain physical features of the stem bark (Schlesinger and Marks 1977, Callaway et al. 2002).

　　Although claims of host specificity among vascular epiphytes abound in the literature (Frei and Dodson 1972, García-Franco and Peters 1987, Catling and Lefkovitch 1989, ter Steege and Cornelissen 1989, Zimmerman and Olmsted 1992, Migenis and Ackerman 1993, Freiberg 1996, Zapfack et al. 1996, Díaz Santos 2000, Moran et al. 2003, Wolf and Flamenco-S 2003, Flores-Palacios and García-Franco 2004, Mehltreter et al. 2005), there are also a number of studies in which no evidence for host preferences was found (Zimmerman and Olmsted 1992, Migenis and Ackerman 1993, Hietz and Hietz-Seifert 1995, Nieder et al. 2000, González-Astorga et al. 2004, Kelly et al. 2004, Mehltreter et al. 2005, Cardelús et al. 2006, Cascante-Marín et al. 2006, Laube and Zotz 2006). In instances where a host preference has been reported, the following host features were cited as potential mechanisms underlying improved growth and survival of epiphytes on the host trees: throughfall chem-

istry (Frei and Dodson 1972, Schlesinger and Marks 1977, Callaway et al. 2002), light availability (Callaway et al. 2002), bark water retention (Castro Hernandez et al. 1999, Callaway et al. 2002, Mehltreter et al. 2005), bark stability (Schlesinger and Marks 1977, ter Steege and Cornelissen 1989, van Leerdam et al. 1990, Hietz and Hietz-Seifert 1995, Callaway et al. 2001, 2002), bark chemistry (Frei and Dodson 1972, van Leerdam et al. 1990, Hietz and Hietz-Seifert 1995, Castro Hernandez et al. 1999, Callaway et al. 2001), the quantity of suspended soil (Wolf 1994, Rudolph et al. 1998), the host tree growth rate (Wolf 1994, Merwin et al. 2003), the tree canopy structure (Garth 1964, van Leerdam et al. 1990, Rudolph et al. 1998), the presence of termite carton trails (Flores-Palacios and Ortiz-Pulido 2005), and a lack of non-vascular epiphytes such as lichens (Callaway et al. 2001). Despite numerous speculative comments about the importance of these host tree canopy biotic and abiotic factors to the physiology, growth, and survival of epiphytes, no studies could be located that examined the physiology of epiphytes on different hosts.

Bulbophyllum japonicum (Makino) Makino is an epiphytic orchid found in tropical and subtropical regions of Southeast Asia (Editorial Committee of the Flora of Taiwan 2000). Like most orchids, its velamentous roots adhere to the bark of the host tree, and are exposed to the atmosphere; accumulations of humus or debris are typically lacking (Benzing 1990). The thick leaves of this orchid exhibit the Crassulacean acid metabolism (CAM) photosynthetic pathway (see below) as do other species in this genus (Sayed 2001), in which water is conserved as a result of restriction of the stomatal opening at night, during which time CO_2 is absorbed, resulting in the nocturnal accumulation of malic acid in the leaf tissues (Kluge and Ting 1978, Lüt-

tge 1987). When this acid is decarboxylated during the day, the CO_2 released is reduced to carbohydrate using the typical Calvin-Benson cycle of photosynthesis. Thus, measures of the amount of acid accumulated at night provide a reliable indication of the amount of CO_2 absorbed by the plant at night, although some recycling of respiratory CO_2 often occurs (Martin 1996).

In the subtropical rainforests of Taiwan, *B. japonicum* is commonly found on a variety of host tree species. Thus, this epiphyte is ideal for investigating the influence of species of host trees on its physiology. Therefore, the goal of this study was to determine if differences in selected physiological features of this epiphytic orchid exist among individuals growing on 3 host tree species.

MATERIALS AND METHODS

Plants were studied *in situ* at the Fushan Experimental Forest (121°34′E, 24°46′N), a comparatively pristine tract of subtropical rainforest at an elevation of ~600 m located 40 km southeast of Taipei, Taiwan. For average climatic conditions at the Fushan site, see Martin et al. (2004). During the time of the study (8~11 January 2004), environmental conditions at the study site were an average daily temperature of 14.1℃, an average daily maximum temperature of 17.8℃, an average daily minimum temperature of 11.6℃, and an average daily relative humidity of 98.5%.

Individuals of *B. japonicum* used in this study were growing on the main stems and larger secondary or tertiary stems of several host tree species in a portion of the Fushan forest dissected by trails. This allowed easy access to the epiphytes. All orchids included in this study were growing at a height on the host of approximately 2~4 m. All plants were deeply shaded (see Fig. 1 for light levels
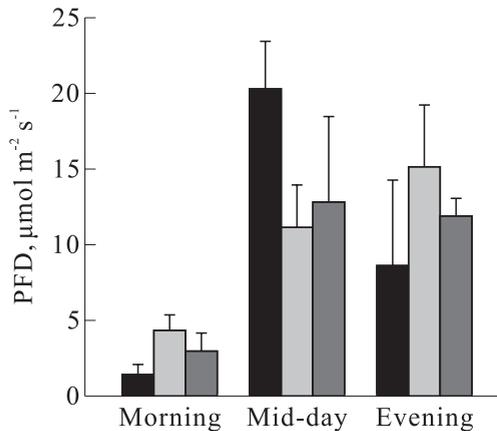
Fig. 1. Photosynthetic photon flux density (PPFD) at 3 times of day intercepted by the epiphytic orchid *Bulbophyllum japonicum* on 3 host tree species in a subtropical rainforest in northeastern Taiwan. The host species were *Engelhardia roxburghiana* (black bars), *Meliosma squamulata* (light-gray bars), and *Machilus zuihensis* (dark-gray bars). Data are presented as the mean and standard errors for six, five, and four trees per respective host species. None of the means at each time of measurement significantly differed (all $p > 0.05$).

Photosynthetic photon flux density (PPFD) levels intercepted by the orchids were measured with a LI-COR (Lincoln, NE, USA) LAI-190SB sensor and LI-185B light meter with the sensor held facing the sun and within several centimeters of the central portion of the epiphyte. PPFD was measured in the morning, midday, and in the late afternoon/ early evening.

Twice in a day, once in the early morning and once at midday, a leaf was removed from each orchid and transported back to the laboratory (about 5~10 min of transit time), where 3 disks (7 mm in diameter) were removed from the leaf, weighed, and placed in N, N-dimethylformamide (DMF) for 2 d at 5°C. After chlorophyll extraction (disks appeared colorless), the absorbance of the extract was determined using a Spectronic (Thermo Spectronic, Rochester, NY, USA) model 20D spectrophotometer. The wavelengths and equations used to determine the concentrations of chlorophylls a and b are given in Moran (1982).

Leaf fluorescence was also measured twice a day, at the same times as above, with a Walz (Effeltrich, Germany) PAM-2000 Portable Chlorophyll Fluorometer. The night before the measurements, the leaves to be measured after dawn were wrapped in aluminum foil to minimize their exposure to light in the morning. Shortly after dawn, F_v/F_m was measured in these leaves 2 min after detachment from each plant. During these 2 min, each leaf was exposed to an F_o lamp (6 µmol m^{-2} s^{-1}). Leaf temperatures at this time were 17~19°C. At midday, F_v/F_m was measured again after a 2-min F_o treatment (without an overnight dark period; these values obtained are not true measures of F_v/F_m). Using the same leaf, "light-adapted" fluorescence parameters were measured following a 3.5-min exposure of the detached leaf to 1000 µmol m^{-2} s^{-1} in the

intercepted by the plants). The velamentous roots of the epiphytes were exposed; no litter or humus appeared to have accumulated on or around the roots.

Three host tree species, *Engelhardia roxburghiana* Wall. (Juglandaceae), *Meliosma squamulata* Hance (Sabiaceae), and *Machilus zuihoensis* Hayata (Lauraceae) were selected for 2 reasons: 1) the abundance of individual trees hosting *B. japonicum*; and 2) accessibility of the epiphytic orchids in the tree canopy. Host trees were scattered throughout the study site. Exposure, tree age/height, and other ecological conditions were not controlled, yet appeared to vary only slightly among the 3 host species.

fluorometer leaf clip. Leaf temperatures for the mid-day measurements were 22~25℃. All calculated fluorescence values were taken from the instrument readout, except P and D, which were calculated from those values according to Demmig-Adams et al. (1996).

To estimate the degree of CAM, diurnal decreases in leaf acidity (equivalent to nocturnal increases) were measured in the orchids in the different host canopies. Leaves were removed shortly after dawn and in the late afternoon/early evening and frozen within 5~10 min in a laboratory freezer (-10℃). The next day, the leaves were weighed, thawed, ground in distilled water with a mortar and pestle, and the resultant slurry was titrated to pH 7.0 with 0.01 N NaOH.

All data were analyzed with 1- or 2-way analysis of variance (ANOVA) tests (Sokal and Rohlf 1981) using the statistical software package SigmaStat (SPSS, Chicago, IL,

USA). Means were considered to be equal if the resultant p values were > 0.05.

RESULTS AND DISCUSSION

Although highly variable, the PPFD levels received by individuals of $B. japonicum$ did not differ among the 3 host tree species (Fig. 1). Thus, any physiological differences among the orchids in the 3 different hosts should be attributable to other factors, most likely differences in the availability of essential elements in the stemflow water during precipitation events. Indeed, the concentration of several essential elements varied dramatically among the 3 host tree species in this study (Tables 1, 2). Despite this finding, no physiological parameters varied among the orchids on the 3 host species (Figs. 2~7).

All individuals of this epiphytic orchid exhibited CAM (Fig. 2), confirming previous

Table 1. Chemical characteristics (pH, conductivity, and concentrations of carbon and nitrogen) of stemflow water collected from 3 tree species in a subtropical rainforest in northeastern Taiwan. These species are common hosts of the epiphytic orchid *Bulbophyllum japonicum*. Stemflow was collected on 4 separate days between 22 and 29 August 2006 for 3 trees of each species. Other than the pH and conductivity data, all data are concentrations, in ppm, in stemflow water. IC, inorganic carbon. Values are presented as the mean (standard errors in parentheses) of the 12 samples per species. Means were compared for each chemical characteristic by analysis of variance (ANOVA). * Indicates a significant difference among the 3 means at $p \leq 0.05$; ** indicates a difference at $p \leq 0.01$; * indicates a difference at $p \leq 0.001$; ns indicates that the 3 means do not significantly differ (i.e., $p > 0.05$), while (ns) indicates that the means differ at $p \leq 0.10$ (yet > 0.05)**

Species	pH	Conductivity ($\mu s\ cm^{-1}$)	Total IC (ppm)	Total C (ppm)	Total N (ppm)	NH_4^+ (ppm)	NO_3^- (ppm)
Engelhardia roxburghiana	6.18 (0.09)	30.97 (8.59)	0.61 (0.14)	27.41 (5.23)	0.69 (0.15)	0.82 (0.61)	0.06 (0.02)
Machilus zuihensis	6.29 (0.10)	21.28 (3.52)	1.23 (0.76)	34.90 (5.11)	0.67 (0.12)	0.14 (0.03)	0.05 (0.01)
Meliosma squamulata	6.22 (0.17)	73.09 (16.90)	2.43 (1.27)	25.74 (3.78)	1.11 (0.17)	0.20 (0.06)	0.07 (0.02)
ANOVA results	ns	***	(ns)	ns	(ns)	ns	ns

Table 2. Chemical characteristics (concentrations of various macro- and micronutrients) of stemflow water collected from 3 tree species in a subtropical rainforest in northeastern Taiwan. These species are common hosts of the epiphytic orchid *Bulbophyllum japonicum*. Stemflow was collected on 4 separate days between 22 and 29 August 2006 for 3 trees of each species. All data are concentrations, in ppm, in the stemflow water. The values are presented as the mean (standard errors in parentheses) of the 12 samples per species. Means were compared for each chemical characteristic by analysis of variance (ANOVA). * Indicates a significant difference among the 3 means at $p \leq 0.05$; ** indicates a difference at $p \leq 0.01$; * indicates a difference at $p \leq 0.001$; ns indicates that the 3 means do not significantly differ (i.e., $p > 0.05$), while (ns) indicates that the means differ at $p \leq 0.10$ (yet > 0.05)**

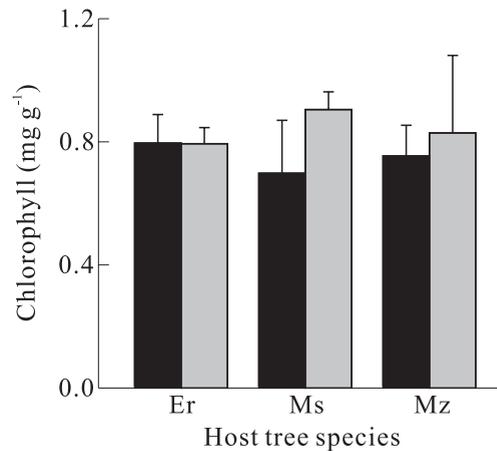| Species	Al (ppm)	Ca (ppm)	Cl (ppm)	Fe (ppm)	K (ppm)	Mg (ppm)	Mn (ppm)	Na (ppm)	PO_4^{-3} (ppm)	SO_4^{-2} (ppm)
Engelhardia roxburghiana	0.09 (0.03)	3.16 (1.00)	2.07 (0.86)	0.07 (0.03)	3.17 (0.68)	0.88 (0.24)	0.04 (0.02)	1.71 (0.58)	0.38 (0.08)	3.15 (0.95)
Machilus zuihensis	0.10 (0.02)	1.16 (0.19)	1.00 (0.22)	0.03 (0.01)	2.57 (0.42)	0.53 (0.06)	0.01 (0.00)	0.67 (0.13)	0.37 (0.09)	2.08 (0.39)
Meliosma squamulata	0.29 (0.05)	5.50 (2.00)	6.13 (1.21)	0.09 (0.01)	3.73 (1.50)	1.98 (0.73)	0.04 (0.01)	1.73 (0.27)	0.25 (0.04)	5.12 (1.17)
ANOVA results	**	*	***	**	ns	*	***	(ns)	ns	(ns)

reports of CAM in this genus (Sayed 2001). The degree of CAM, measured as diurnal decreases in tissue acidity, did not significantly differ among individuals in the canopies of the 3 host tree species. Furthermore, leaf chlorophyll concentrations (on both an area and weight basis) and *a*/*b* ratios were similar among the orchids growing in the canopies of the 3 host tree species (Fig. 3). Finally, no significant differences were found in any of the several fluorescence parameters measured *in situ* in the 3 groups of *B. japonicum* (Figs. 5~7). Values of F_v/F_m near 0.8 (Fig. 5), regardless of whether they were measured before sunrise or in the middle of the day following a brief period of darkness, indicate that these orchids were not excessively stressed; this was shown in many past studies to reflect no or low stress (Björkman and Demmig 1987, Demmig-Adams et al. 2006). The low values measured at midday for Fv'/Fm' and P (Fig. 6) indicate that very small amounts of the light energy absorbed were utilized by these plants for photochemistry. Likewise, the amount of absorbed light energy that was dissipated nonphotochemically by these orchids (D; Fig. 6) was exceptionally high. These findings most likely reflect the extreme shade-adapted nature of the photosynthetic apparatus in this epiphytic orchid. When subjected to 1000 μmol m^{-2} s^{-1} during the midday fluorescence measurements, most of this light energy was far in excess of that which could be productively utilized, and thus a large proportion of the absorbed light energy was dissipated nonphotochemically (Fig. 6). These results are not surprising when considering the PFD levels intercepted by these plants at midday (see Fig. 1). A number of other CAM epiphytes are also well-adapted to the low light levels found within the canopies of their host trees (Winter et al. 1986, Martin 1994).
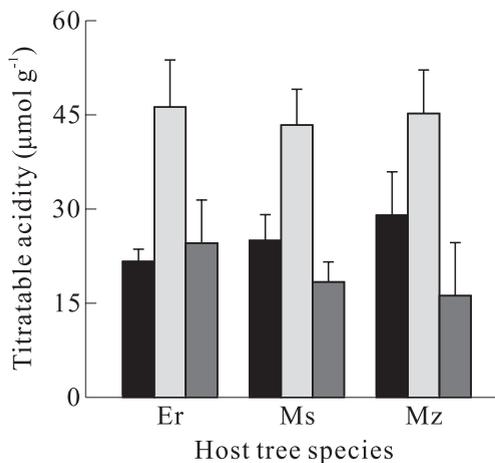
Fig. 2. Early evening (black bars), early morning (light-gray bars), and daytime decreases in (dark-gray bars) acidity (on a fresh mass basis) of leaves of the epiphytic orchid *Bulbophyllum japonicum* on 3 host tree species in a subtropical rainforest in northeastern Taiwan. The host species were *Engelhardia roxburghiana* (Er), *Meliosma squamulata* (Ms), and *Machilus zuihensis* (Mz). Data are presented as the mean and standard errors for 6 (Er), 5 (Ms), and 4 (Mz) trees per respective host species. For all three host species, leaf acidity in the morning was significantly greater than that in the evening (*p* < 0.001), yet daytime decreases in acidity did not vary among the host species (*p* > 0.05).

Fig. 3. Leaf chlorophyll concentrations (on a dry mass basis), in the morning (black bars) and at noon (light-gray bars), of leaves of the epiphytic orchid *Bulbophyllum japonicum* on 3 host tree species in a subtropical rainforest in northeastern Taiwan. The host species were *Engelhardia roxburghiana* (Er), *Meliosma squamulata* (Ms), and *Machilus zuihensis* (Mz). Data are presented as the mean and standard errors for 6 (Er), 5 (Ms), and 4 (Mz) trees per respective host species. None of the means at each time of measurement significantly differed (*p* > 0.05).

In conclusion, no substantial physiological differences were found *in situ* among *B. japonicum* individuals growing in the canopies of 3 different host tree species, despite rather large differences in the leaf morphology and stemflow chemistry among these trees. The fluorescence data indicated that all individuals, regardless of host tree species, were healthy and unstressed. Thus, it is reasonable to assume that individuals of this orchid are capable of obtaining all needed essential elements from their hosts over time, despite dif-

ferences in availability during any single precipitation event. In addition, demand for such nutrients may be low in such slowly growing epiphytic CAM plants (Martin et al. 1981, Zotz 1995, Schmidt and Zotz 2002).

The lack of host specificity in *B. japonicum* is not surprising given its physiological similarity among different host tree species. Because many epiphytic taxa are most likely shade-adapted and slow-growing, host specificity may be less frequent than commonly thought among such organisms. Further work is needed to verify this prediction.
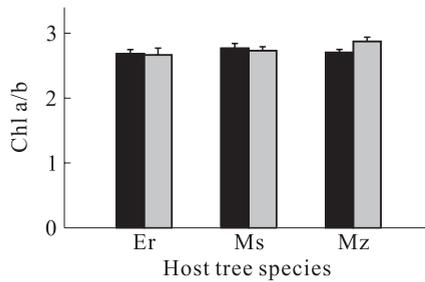
Fig. 4. Leaf chlorophyll (Chl) a/b ratios, in the morning (black bars) and at noon (light-gray bars), in leaves of the epiphytic orchid *Bulbophyllum japonicum* on 3 host tree species in a subtropical rainforest in northeastern Taiwan. The host species were *Engelhardia roxburghiana* (Er), *Meliosma squamulata* (Ms), and *Machilus zuihensis* (Mz). Data are presented as the mean and standard errors for 6 (Er), 5 (Ms), and 4 (Mz) trees per respective host species. None of the means at each time of measurement significantly differed ($p >$ 0.05).
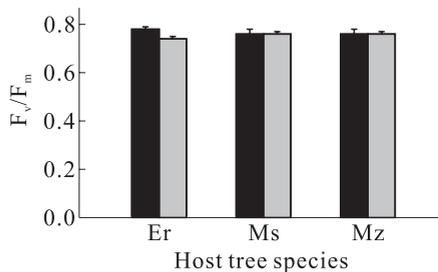
Fig. 5. Intrinsic efficiency of energy conversion in photosystem II (F_v/F_m) early in the morning (black bars) and at noon (light-gray bars) of leaves of the epiphytic orchid *Bulbophyllum japonicum* on 3 host tree species in a subtropical rainforest in northeastern Taiwan. The host species were *Engelhardia roxburghiana* (Er), *Meliosma squamulata* (Ms), and *Machilus zuihensis* (Mz). Data are presented as the mean and standard errors for 6 (Er), 5 (Ms), and 4 (Mz) trees per respective host species. None of the means at each time of measurement significantly differed ($p >$ 0.05).
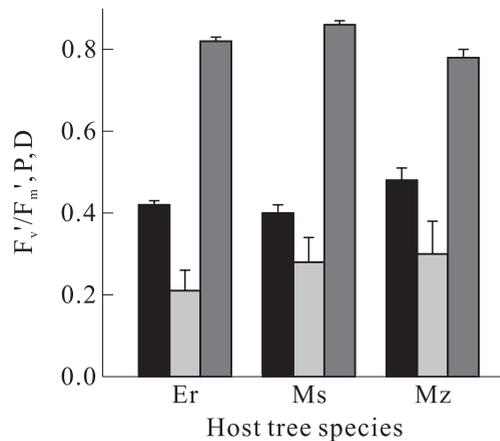
Fig. 6. Actual efficiency of energy conversion in photosystem II (F_v'/F_m'; black bars), energy dissipation in photosystem II via photochemistry (P; light-gray bars), and energy dissipation via nonphotochemical thermal means (D; dark-gray bars) at midday of leaves of the epiphytic orchid *Bulbophyllum japonicum* on 3 host tree species in a subtropical rainforest in northeastern Taiwan. The host species were *Engelhardia roxburghiana* (Er), *Meliosma squamulata* (Ms), and *Machilus zuihensis* (Mz). Data are presented as the mean and standard errors for 6 (Er), 5 (Ms), and 4 (Mz) trees per respective host species. None of the means at each time of measurement significantly differed ($p >$ 0.05).

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