Oviposition site preference of the bamboo gall maker, *Aiolomorphus rhopaloides* (Hymenoptera: Eurytomidae), on bamboo in terms of plant-vigor hypothesis

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Abstract

Oviposition site preference of the bamboo gall maker, *Aiolomorphus rhopaloides* Walker, was investigated in a bamboo stand in terms of plant-vigor hypothesis. Galls in branches were distributed contagiously due to the difference in branch length. More galls were found on longer branches. Survival rates within galls, nitrogen content and gall size did not differ with branch-length class, suggesting that oviposition preference on longer branches is not attributed to better progeny fitness. The phenology of the buds where females oviposit and the greater number of buds on longer branches might contribute to female oviposition site preference.

Key words: *Aiolomorphus rhopaloides*; bamboo; gall maker; oviposition site preference; *Phyllostachys heterocycla*

INTRODUCTION

Female gall insects lay their eggs in plant tissues, and galls are formed by the stimulus caused by oviposition stimuli and/or the result of larval feeding (Price et al., 1987). Because the larvae of gall insects cannot exit the host gall during their development, the eventual performance can be more affected by the host conditions than the performance of free-living insects. In other words, the oviposition sites may be very important for gall insects, and the distribution of galls may affect the performance in subsequent developmental stages.

Price et al. (1995) emphasized the importance of a link between oviposition preference and offspring performance in population studies, especially of gall-forming sawflies. Price (1991) proposed a plant-vigor hypothesis in which female galling insects select relatively large modules on which the larvae survive better; plant individuals from nutrient-rich environments are used more frequently than plant individuals from low-resource habitats. However, Rehill and Schultz (2001) tested the plant-vigor hypothesis by determining the distribution of galls formed on leaves of witch hazel, *Hamamelis virginiana*, by the aphid, *Hormaphis*

hamamelidis, and demonstrated that the average number of galls per leaf was not related to the mean leaf size, contrary to the preference prediction of the plant-vigor hypothesis.

The bamboo gall maker, *Aiolomorphus rhopaloides* Walker (Hymenoptera: Eurytomidae), causes galls on two species of bamboo, *Phyllostachys heterocycla* Matsumura and *P. bambusoides* Siebold and Zuccarini (Monocotyledoneae: Gramineae) in Japan (Takahashi and Mizuta, 1971; Kobayashi, 1994; Yukawa and Masuda, 1996). This species of gall maker is univoltine; adult females emerge from galls from mid-April to early May (Shibata, 2001; Shibata and Ito, 2005) and oviposit in the young buds of bamboo branchlets, which develop into unitary galls (length: 20–30 mm, width: 2–4 mm) (Takahashi and Mizuta, 1971). Outbreaks of *A. rhopaloides* occasionally occur in stands of *P. heterocycla* in west Japan (Kobayashi, 1994). This study examines how *A. rhopaloides* oviposits in a bamboo stand in terms of the plant-vigor hypothesis. On the basis of the distribution of galls, survival rates within galls and gall size in terms of performance are evaluated with branch length, bud nitrogen levels, and bud length as proximate factors.

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MATERIALS AND METHODS

Study stand. This study was conducted in a stand of *P. heterocyclus* with an area of ca. 400 m² in Nagoya City, central Japan. Mean diameter at breast height (dbh) and height were 4.5 ± 0.8 cm (mean $\pm$ SD) and 7.2 ± 0.9 m, respectively.

Methods. In mid-March 1999, five bamboo culms were cut at random just before gall-maker emergence. All branches were clipped from each culm after measuring the height of the base of each branch from the ground. After the branch lengths were measured and the number of galls on each branch was counted, the galls were collected and put in individual test tubes (diameter: 1 cm, length: 7 cm) kept outdoors at ambient temperatures. Emerged gall makers were counted every 2–3 d until mid-July. After the emergence of the *A. rhopaloides* females, the diameter of the central part of each gall from which *A. rhopaloides* emerged was measured using vernier calipers.

To determine the relationship between branch length and bud number, five bamboo culms were cut in late May 1998 and 10 branches were cut from each of the five culms at random. After measuring the branch length, the number of buds on each branch was counted.

To evaluate the nutritional conditions of the bamboo buds, eight bamboo culms were selected and eight branches of each culm were cut on 13 May and 1 July 1998. After measuring each branch length, each bud on each branch was put in an envelope and then dried (80°C for 3 d). The total nitrogen content in each bud was determined using a C-N analyzer (MT-1600, Yanako, Tokyo, Japan).

Statistical analyses. Statistical analyses were performed using the SPSS computer program (Norussis, 1993). Three-way ANOVA was used to detect significant differences in gall numbers on branches per 10-cm branch length (transformed to $\log[x+1]$) among culms, among height classes and among branch length classes. Differences in branch number (transformed to $\log[x+1]$), in branch length and in number of young buds (transformed to $\log[x+1]$) among height classes were detected by one-way ANOVA with Tukey's HSD multiple test. One-way ANOVA with Tukey's HSD multiple test was used to determine differences in gall numbers per 10-cm branch length (transformed to $\log[x+1]$), in percentages of buds observed with

galls (transformed to arcsine) and in survival rates (transformed to arcsine) among branch-length classes. The *F*-test was used to determine differences in bud length and in nitrogen content (transformed to arcsine) between dates. The Pearson correlation coefficient (r^2) was applied to the relationships between branch length and bud length, between branch length and nitrogen content, and between branch length and gall size. The spatial distribution pattern of galls on each branch was analyzed using Morisita's I_δ index (Morisita, 1959).

RESULTS

Bamboo module structure and vertical distribution of galls

Significant differences were detected in the mean number of branches for height classes ($F=4.71$, $df=7$, $p=0.01$). There were more branches at heights of 2–7 m than <2 m and >7 m (Fig. 1a). The mean branch length differed significantly among height classes ($F=37.15$, $df=7$, $p<0.001$). Branches were longer at heights of 2–5 m than at <2 m and at >5 m (Fig. 1b). Branch length and bud number formed an exponential curve (x : branch length, y : bud number, $n=50$, $y=5.89x^{0.0281}$, $r^2=0.779$) and the mean bud number per branch estimated from this relationship differed significantly among height classes ($F=36.93$, $df=7$, $p<0.001$). There were more buds at heights of 2–6 m than at <2 m and at >6 m (Fig. 1c). There was a significant difference in the number of galls per 10-cm branch length among height classes ($F=2.49$, $df=7$, $p=0.019$) with more galls at heights of 2–8 m than at <2 m and at >8 m (Fig. 1d). Three-way ANOVA on the mean number of galls showed significant interactions between culm and height, and between height and branch length, but not between culm and branch length (Table 1). This suggests that branch length on which galls are abundant is similar in every culm. Consequently, I combined data on branch length for all culms.

Gall spatial distribution pattern

The index of spatial distribution, I_δ , was 2.36 ($F=919.2$, $p<0.001$), indicating that bamboo galls are contagiously distributed on the bamboo branches.

Fig. 1. Mean number of branches (a), mean branch length (b), mean number of buds (c), and mean number of galls per 10-cm branch length (d) at each bamboo height. Horizontal lines show +SE. Different letters show significant differences ($p < 0.05$).

Table 1. Three-way ANOVA of mean number of galls per 10-cm branch length for culm, height class and branch length class

Source	df	Mean square	<i>F</i>	<i>p</i>
Culm	4	0.940	88.962	<0.001
Height	7	0.013	1.261	0.273
Branch length	7	0.023	2.163	0.039
Culm×Height	20	0.029	2.708	<0.001
Culm×Branch length	24	0.009	0.845	0.675
Height×Branch length	25	0.018	1.699	0.026
Culm×Height×Branch length	15	0.011	0.999	0.458
Error	170	0.011		
Total	276			

Number of galls per 10-cm branch length in branch-length class

The mean number of galls per 10-cm branch length differed significantly among branch-length classes and increased as branch length increased ($F=14.62$, $df=7$, $p<0.001$) (Fig. 2a).

Percentage of galled buds for branch length

There was a significant difference in the proportion of galled buds among branch length classes with more galled buds at lengths of 40–60 cm ($F=2.45$, $df=7$, $p=0.019$) (Fig. 2b).

Survival rate in branch-length class

The survival rate was not significantly different among branch-length classes ($F=0.46$, $df=7$, $p=0.861$) (Fig. 2c).

Bud elongation

A significant difference in bud length was detected between 13 May (2.70 ± 0.47 cm) and 1 July (2.97 ± 0.09 cm) ($F=21.01$, $df=1$, $p<0.001$). Significant correlations were detected between branch length and bud length on 13 May and on 1 July (13 May: $n=64$, $r^2=0.233$, $p<0.001$, 1 July: $n=64$, $r^2=0.115$, $p<0.05$) (Fig. 3a). However, bud length tended to be constant on 1 July (Fig. 3a).

Bud nutrition

On 13 May and 1 July, there was a significant difference in bud nitrogen content (13 May: $3.25 \pm 0.50\%$, 1 July: $2.35 \pm 0.49\%$) ($F=196.35$, $df=1$, $p<0.001$). No significant correlations were found between branch length and nitrogen content on 13 May and on 1 July (13 May: $n=120$, $r^2=0.001$, $p>0.05$, 1 July: $n=124$, $r^2=0.052$,

Fig. 2. Mean number of galls per 10-cm branch length (a), mean percentage of buds with gall (b), and mean survival rate within galls (c) in each branch-length class. Vertical lines show $\pm$ SE. Different letters show significant differences ($p < 0.05$). $p > 0.05$) (Fig. 3b).

Relationship between branch length and gall size

There was no significant correlation between branch length and gall size ($n=21$, $r^2=0.027$, $p > 0.05$) (Fig. 4).

DISCUSSION

There was a significant difference in the number of bamboo galls on culms. This could be due to asynchronism of adult emergence of *A. rhopaloides* and bud-burst of branches where females lay eggs (Shibata, 2003).

Spatial distribution is an important aspect of the

Fig. 4. Relationship between branch length and gall size. Data are based on galls from which *A. rhopaloides* emerged.

Fig. 3. Relationships between branch length and bud length (a), and between branch length and nitrogen content (b). Left: 13 May, right: 1 July.

population structure and is determined by the intrinsic properties of the species and its habitat (Iwao, 1970). The spatial distribution of insects is not usually random, but is often contagious due to the uneven quality of habitats (Kuno, 1986). In this study, more bamboo galls were formed on longer branches, explaining that the galls are distributed contagiously. Kuno (1986) pointed out that oviposition behavior also contributes to contagious distribution.

More galls are found on longer branches in other galling insects such as sawflies (e.g., Price, 1991; Price and Ohgushi, 1995) and cynipid wasps (e.g. Caouette and Price, 1989; Pires and Price, 2000; Ito and Hijii, 2001) as presented in this study, suggesting the possibility that the module size plays some part in oviposition site preference by female *A. rhopaloides* and that they utilize larger branches more frequently. However, there was no significant difference in the survival rates of *A. rhopaloides* among branch-length classes like in *Andricus moriokae* (Hymenoptera: Cynipidae) (Ito and Hijii, 2004). This is different from the sawflies, where survival rates increased with branch length (e.g., Price, 1991; Price and Ohgushi, 1995). Thus, the selection of longer branches for oviposition does not cause better offspring survival in *A. rhopaloides*.

For gall insects, reproductive success and larval survival depend on successful oviposition in plant tissue that is suitable for production of nutritious galls (Abrahamson and Weis, 1987). On 13 May when the bud elongated and female *A. rhopaloides* oviposited (Shibata, 2001), no significant relationship was found between the branch length and nitrogen content, suggesting that longer branches do not have a higher nutritional content than shorter ones. On 1 July when the larvae of *A. rhopaloides* were developed in the galls (Shibata and Ito, 2005), there was no significant relationship between the branch length and nitrogen content. Thus, the selection of buds on longer branches for oviposition cannot be an adaptive consequence, at least, to increase the offspring survival.

Gall size varies with the gall position on the host plant (Sitch et al., 1988; Ngakan and Yukawa, 1997). The size of the bamboo gall can be a good predictor for potential fecundity because potential fecundity is positively correlated with gall diameter (Shibata, 2002), suggesting that production of

larger females from larger galls might improve fitness. However, galls on longer branches were not significantly larger than galls on the shorter branches, suggesting that oviposition on longer branches might not increase the progeny number, or fitness of offspring.

Thus, the preference of female *A. rhopaloides* for longer branches as an oviposition sites might not increase fitness. Inbar et al. (2001) emphasized that experiments on growth, chemical defense and nutrition of plants might be needed as evidence for the plant-vigor hypothesis. I did not study chemical defense by the bamboo bud against oviposition, and more field experiments on this are needed.

There are two possible reasons why female *A. rhopaloides* might prefer longer branches for oviposition. There was a positive correlation between branch length and bud length on 13 May, but bud length tended to be constant on 1 July. This indicates that bud elongation was more advanced on larger branches than on shorter branches. Shibata (2001) found that *A. rhopaloides* emerging from galls from mid-April to early May when bamboo buds elongate and the phenology of bamboo might be important for the population dynamics of this insect as a bottom-up effect. *A. rhopaloides* is pro-ovigenic; emerging females have ca. 80 eggs in their ovaries, suggesting that they can oviposit soon after emergence (Shibata, 2002). It is possible that females oviposit on longer branches because bud elongation and oviposition coincide on longer branches. Thus, the difference in branch phenology in relation to length might affect oviposition site preference.

In this study, the percentage of buds with galls in each branch-length class was nearly constant, suggesting that branch length does not affect the selection of branches when females search buds for oviposition. In addition, longer branches have more buds for oviposition. Thus, female adults might select branches based on the number of buds. In a bamboo stand, there are more branches and buds at heights from 2 to 5 m, so females oviposit on longer branches not because this increases offspring performance but simply because larger branches with more buds allow effective oviposition.

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