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Interactions between *Oncideres humeralis* Thomson (Coleoptera: Cerambycidae) and Melastomataceae: Host-Plant Selection and Patterns of Host Use in South-East Brazil

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Interações Entre *Oncideres humeralis* Thomson (Coleoptera: Cerambycidae) e Melastomataceae: Seleção das Plantas Hospedeiras e Padrões de Uso no Sudeste do Brasil

RESUMO - *Oncideres humeralis* Thomson (Cerambycidae) foi observado serrando o tronco principal de plantas da família Melastomataceae no sudeste do Brasil. Os principais objetivos deste trabalho identificar quais plantas hospedeiras *O. humeralis* seleciona no campo e quais as características das plantas preferidas. *O. humeralis* usou somente Melastomataceae como plantas hospedeiras, atacando quatro das 11 espécies presentes na área de estudo. Das quatro espécies atacadas, *Miconia sellowiana* Naudin e *M. jucunda* Triana, a espécie mais abundante e a maior, respectivamente, foram as preferidas. Quando as plantas eram altas, *O. humeralis* serrou o tronco em posições mais elevadas, indicando que as fêmeas selecionam plantas com diâmetro ótimo de tronco e ajustam o ponto para serrar em função da altura da hospedeira. As fêmeas também selecionaram plantas com maior número de ramos secundários. Estes resultados indicam que *O. humeralis* apresenta especificidade para determinadas espécies de Melastomataceae e que plantas hospedeiras são selecionadas pela sua abundância, tamanho ou número de ramos secundários.

PALAVRAS-CHAVE: Brocador, floema intra-xilemático, interação inseto-planta, *Miconia*

ABSTRACT - *Oncideres humeralis* Thomson (Cerambycidae) was observed girdling the main trunk of plants of the Melastomataceae family in south-eastern Brazil. The main objectives of this work were to identify which host plants *O. humeralis* selects in the field and which are the characteristics of the preferred plants. *O. humeralis* specifically used Melastomataceae as host plants, attacking only four of the 11 species present in the study area. From the four attacked species, *Miconia sellowiana* Naudin and *M. jucunda* Triana were the preferred owes; they are the most abundant and the largest species, respectively. When the plants were taller, *O. humeralis* girdled the trunk at higher positions, indicating that females select plants with optimum trunk diameter and adjust the point to girdle according to the host height. Females also selected plants with greater numbers of secondary branches. These results indicate that *O. humeralis* is specific to certain species of Melastomataceae, and that host plants are selected on the basis of their abundance, size or number of secondary branches.

KEY WORDS: Wood-borers, intra-xylematic phloem, insect-plant interaction, *Miconia*

Beetles of the family Cerambycidae constitute one of the major insect groups, with approximately 35,000 species (Lawrence 1982). Cerambycids diversified together with angiosperms (Farrell 1998), and are especially abundant and diverse in the tropics (Berkov & Tavakilian 1999, Berkov *et al*. 2000). Their larvae are woodborers and use dead or living trunks (Borror & DeLong 1964, Hanks *et al.* 1991). Among the species that use living tissues, there are those which bore the timber and those that girdle the trunk, boring them afterwards (Cannon & Robinson 1982, Edwards & Linit 1991, Rice 1995). Cerambycid beetles can be specialists associated with only one plant species (Papp & Samuelson 1981, Tavakilian *et al.* 1997, Berkov & Tavakilian 1999), use plant groups of the same genus or family (Hanks *et al.* 1991, 1993a,

1995, Berkov & Tavakilian 1999, Berkov 2002) or do not present any specificity (Solomon 1977, Rice 1985, Tavakilian *et al.* 1997).

Beetles of the genus *Oncideres* (Lamiinae) present the most specialized behaviour in host-plant use, in which the female uses its mandibles to girdle young plants or stems and prepares the oviposition site by perforating the bark and inserting the ovipositor (Rice 1989, Caraglio *et al.* 2001). *Oncideres humeralis* Thomson (Cerambycidae) uses several Melastomataceae species as host-plants. Females girdle the main living trunk of the trees with their mandibles, causing the loss of the canopy, and lay eggs in the bifurcation of secondary branches of the freshly killed host (Paulino Neto 2003).

Various shrubs of the Melastomataceae were observed without crowns due to the attack by *O. humeralis* in a semideciduous forest in the south-east of Brazil. The main questions addressed were: 1) Is *O. humeralis* a specialist associated with Melastomataceae? 2) Do these beetles have any preference for certain melastome species and for any specific host-plant size? 3) Does the number of secondary branches affect the plant choice by *O. humeralis*?

Material and Methods

Study Area. This study was conducted at the margins of a semideciduous forest, along two tracks: Mirante (400 m) and Paraíso III (~ 800 m), in Serra do Japi (23º11'S, 46º52'W), Jundiaí City, São Paulo State, from August 2000 to July 2002. The climate is seasonal, with hot, wet summers and cold, dry winters. The monthly average temperatures vary from 13.5ºC in July to 20.3ºC in January (Pinto 1992).

Host-Plant Selection. To determine whether *O. humeralis* uses only Melastomataceae or other plant families indiscriminately, direct observations of the beetles girdling and of the freshly girdled plants were made. These females and branches were collected for later identification. The trunks which were girdled by an unknown species (n = 29 individuals of *Miconia sellowiana* Naudin. and n = 12 individuals of *M. jucunda* Triana) were brought to the laboratory and individually kept in PVC tubes (150 cm x 10 cm) until emergence of the adults. For each plant species, the number of individuals and the cerambycid species that emerged were recorded. Larvae and adults that emerged and that were observed in the field were collected and identified.

To determine whether *O. humeralis* was only girdling particular species of Melastomataceae, we recorded the girdled plants found at a distance of up to 3 m in the direction of the forest interior (margins), the occurrence area of Melastomataceae. In addition, a census of all available non-girdled plants was also done in this area. Only not girdled plants with similar trunk diameter at 10 cm above ground (DAG) as the girdled plants were considered available. The frequency distribution of the plants of each family and individuals of each melastome species available and used were compared using G-test (Zar 1999). Manly's index (Krebs 1999) was used to assess which plant species *O. humeralis* prefers. The formula for Manly's index is:

$$\alpha_i = \frac{r_i}{n_i}\left[\frac{1}{\Sigma\,(r_j / n_j)}\right]$$

where a_i = Manly's index for plant species i; r_i, r_j = proportion of plant species i or j used and n_i, n_j = proportion of plant species i or j available. A preference reflects some deviation from random utilization of the plant species is indicated by values of $a_i > 1/m$ (m = total number of plant species). In contrast, avoidance is indicated by values of $a_i < 1/m$ (see Krebs 1999 for more details).

Plant Size and Number of Secondary Branches of the Hosts. To verify whether *O. humeralis* selects plants within an optimum size, we determined the size structure of the available and used Melastomataceae species by the beetle. The size structure was determined based on the trunk diameter at DAG, including trees that stood within 3 m distance from the forest edge, to its interior and considering as available only melastomes with a trunk diameter similar to the plants attacked by the beetle. The frequency distribution of the used and available trunk diameters was compared using the G-test (Zar 1999).

If *O. humeralis* uses an optimum trunk diameter, it is expected that beetles will girdle higher on trunks of larger trees where diameters are appropriate. This relationship was tested with linear regression, with DAG as the independent variable and the girdle height as the dependent variable.

O. humeralis females oviposit in the bifurcation of secondary branches of melastomes (Paulino Neto 2003). Hence, it is expected that females may choose among host-plants based on the number of secondary branches. To test this hypothesis, each girdled specimen of *M. sellowiana*, and the intact closest neighbour of the same species, with a similar trunk diameter, had their DAG measured and the number of secondary branches counted. *M. sellowiana* was used because it was the most abundant species, and was most frequently attacked by the beetle. The number of secondary branches of girdled and not girdled plants was compared using randomized-block ANCOVA (Zar 1999), in which the plants (two levels) were the fixed factor, blocks were the random factor and the plants' DAG was the covariate. All variations of means were computed as ± 1 SE.

Results

Host-Plant Selection. In total, of the 92 plants girdled by the cerambycid beetle, 85 (92%) were Melastomataceae and seven (8%) belonged to other families (Euphorbiaceae, Lauraceae, Fabaceae, Myrcinaceae, Myrtaceae and Rosaceae). The direct field observations and laboratory rearing showed that the main families used by the Cerambycidae were Melastomataceae and Myrtaceae (Table 1). Five *Oncideres* species were associated with various plant species belonging to diverse families, and *O. humeralis* was the most common. Nevertheless, *O. humeralis* used only Melastomataceae (Table 1). Other two *Oncideres* species (*O. cervina* Thomson

Table 1. Host-plants of various Cerambycidae species and frequencies with which they were reared from hosts or observed on hosts in the field.

Cerambycidae species	Habit[1]	Plant species	Plant family	Mode		Total
				Reared	Observed	
Oncideres humeralis Thomson	G	*Miconia sellowiana*	Melastomataceae	7	12	19
O. humeralis	G	*M. jucunda*	Melastomataceae	2	5	7
O. humeralis	G	*M. latecrenata*	Melastomataceae	--	3	3
O. humeralis	G	*L. scabra*	Melastomataceae	--	2	2
O. cervina Thomson	G	*Ocotea* sp.	Lauraceae	--	2	2
O. dejeani Thomson	G	*Croton urucurana*	Euphorbiaceae	--	6	6
O. impluviata Germar	G	*Inga* sp.	Fabaceae	--	2	2
O. impluviata	G	*Myrsina ferruginea*	Myrsinaceae	--	4	4
O. saga Dalman	G	*Psidium guajava*	Myrtaceae	--	2	2
O. saga	G	*Inga* sp.	Fabaceae	--	1	1
Psyllotoxus griseocinctus Thomson	G	*Psidium guajava*	Myrtaceae	--	12	12
P. griseocinctus	G	*Eugenia* sp.	Myrtaceae	--	2	2
P. griseocinctus	G	*Syzygium cuminii*	Myrtaceae	--	2	2
P. griseocinctus	G	*Prunus persica*	Rosaceae	--	1	1
Trestonia capreola Germar	NG	*Ocotea* sp.	Lauraceae	--	2	2
Temnopis megacephala Germar	NG	*Miconia sellowiana*	Melastomataceae	2	3	5

[1]Habit: G = girdlers, NG = non-girdlers

and *O. dejeani* Thomson) also used only one plant family as host-plant; *O. impluviata* Germ. and *O. saga* Dalm used two plant families (Table 1), sharing one plant species (*Inga* sp., Fabaceae). From the trunks of *M. sellowiana* collected seven individuals of *O. humeralis* and two individuals of *Temnopsis megacephala* (a secondary colonizer species) emerged. Two individuals of *O. humeralis* emerged from the trunks of *M. jucunda* collected. The remainder were observed girdling their host plants (Table 1).

There were 11 Melastomataceae species in the study area, but *O. humeralis* used only four species as host-plants: *M. sellowiana, M. jucunda, M. latecrenata* (DC.) Naudin and *Leandra scabra* DC. However, attack rates differed across tree species ($G = 23.3$; 3 df; $P < 0.001$), with beetles preferring *M. sellowiana* and particularly *M. jucunda* (Fig. 1), in spite of the fact that the latter is the least abundant species (Fig. 2).

Plant Size and Number of Secondary Branches of the Hosts. *O. humeralis* girdled plants with diameters from 1.1 cm to 6.6 cm at 10 cm above ground and from 1.0 cm to 3.0 cm at the girdle height, with the plants' height varying from 1.3 m to 5.2 m. The beetle girdled the largest trees of the four host-plant species (Fig. 2; $G_{M.\ sellowiana} = 129.8$; 5 df; $P < 0.001$; $G_{M.\ jucunda} = 21.04$; 5 df; $P < 0.001$; $G_{M.\ latecrenata} = 30.6$; 4 df; $P < 0.001$). The use pattern of *L. scabra* was similar to the three species, but statistical tests were not applied due to the low sample size for girdled plants (Fig. 2). *O. humeralis* did not girdle trees of the species *Leandra* sp. 1, *Leandra* sp. 2, *Leandra* sp. 3, *Leandra* sp. 4, *Miconia* sp. 1, *Miconia* sp. 2 and *Tibouchina* sp. 1. Avoidance of the *Leandra* species could be due to their small size (Fig. 3). However, *Miconia* sp.1, *Miconia* sp.2 and *Tibouchina* sp.1 distributed among the same classes of trunk diameter of the girdled plants (Figs. 2 and 3), but were not used by the beetle (Fig. 3).

Most of the melastome trunks attacked by *O. humeralis* females (84%) were girdled at heights less than 1.5 m from the ground. Taller host-plants were girdled at greater heights (Fig. 4; *M. sellowiana*: $r^2 = 0.45$; $F_{1, 120} = 99.8$; $P < 0.001$; *M. jucunda*: $r^2 = 0.48$; $F_{1, 25} = 23.2$; $P < 0.001$ and *M. latecrenata*: $r^2 = 0.71$; $F_{1, 18} = 44.6$; $P < 0.001$). Although this relationship was also evident for *L. scabra*, it was not significant (Fig. 4; $r^2 = 0.36$; $F_{1, 4} = 2.22$; $P = 0.210$).

Mi. sellowiana trees used by *O. humeralis* had a significantly greater number of secondary branches than trees that were not used (Table 2; girdled: 7.42 $\pm$ 2.74; not girdled: 3.84 1.38).

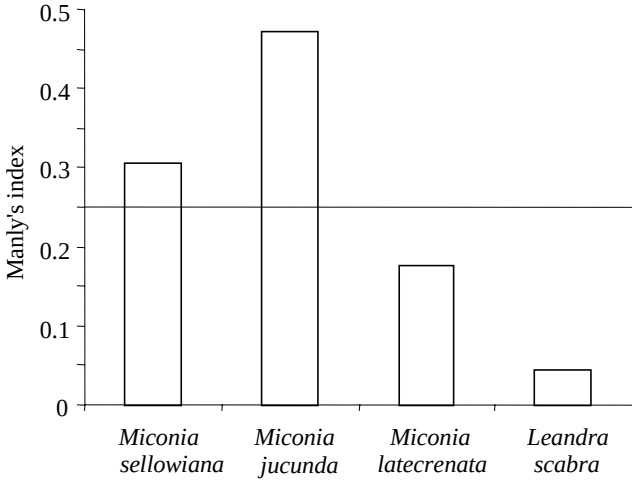

Figure 1. Manly's index of melastome species preference for *O. humeralis*. Values above and below 0.25 (1/total number of plant species) indicate a preference for and avoidance of plant species by the beetle, respectively. Available plants = 1458 plants, used = 175.

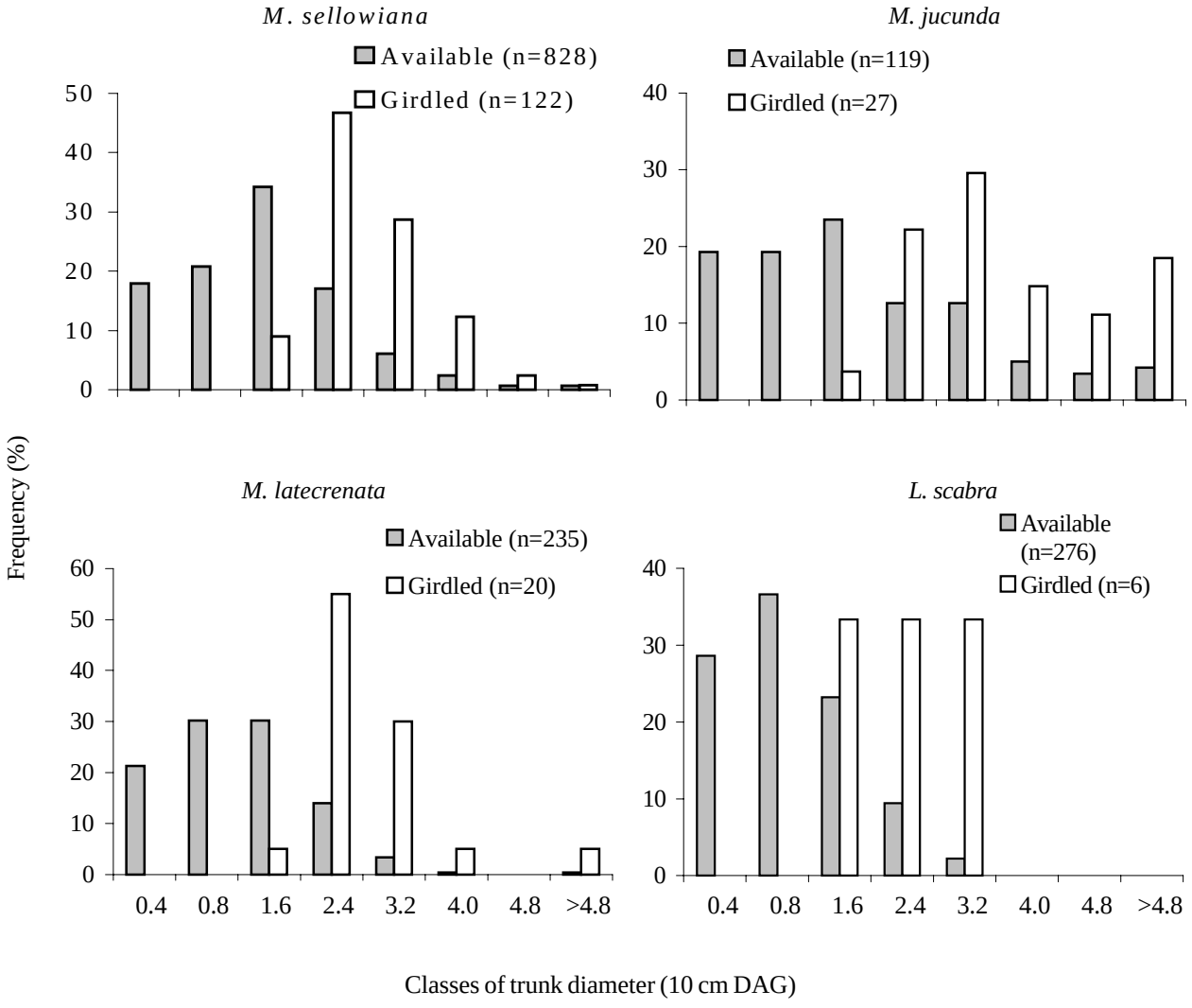

Figure 2. Frequency distribution for trunk diameter of trees of four Melastomataceae species that were girdled by *O. humeralis* and those that were not "available".

Discussion

Our results indicate that *O. humeralis* is a specialist associated with Melastomataceae. The other two *Oncideres* species in this study (*O. cervina* and *O. dejeani*) also used only one plant family as host. Beetles of this genus are generally specialists within plant families (Buck 1957, Hovore & Penrose 1982, Rice 1989, 1995, Di Iorio 1996, Berkov *et al.* 2000). In the present study, *O. impluviata* and *O. saga* used two plant families, and shared one Fabaceae species (*Inga* sp). Buck (1957) also reported in other region these two beetle species sharing one Fabaceae species (*Acacia decurrens* Willd.). The most common hosts were in the Melastomataceae and Myrtaceae of the order Myrtales, and are characterized by intra-xylematic phloem (Metcalfe & Chalk 1950). Plants with this anatomy present, apart from the external phloem, an additional layer of phloem (and parenchymatic cells) in the centre of the trunk, separated by rigid (lignified) xylem. In these hosts larvae can feed deep in the trunk, where the tissue is more nutritious and soft, and they are protected against parasitoids (Austin *et al*. 1994). *O. humeralis* larvae reach the central region of the Melastomataceae trunk through the bifurcations of the secondary branches (Paulino Neto 2003), which are rich in soft parenchymatic cells. Adaptation to intra-xylematic phloem may explain oligophagy in other cerambycid species (Papp & Samuelson 1981, Hanks *et al.* 1993a, Berkov *et al*. 2000).

The preference of *O. humeralis* for *M. sellowiana* support the general hypothesis that herbivores could prefer the most abundant host (e.g. Connell *et al*. 1984, Bernays & Chapman 1994), but the beetle also preferred the tree species of largest size, *M. jucunda*. In contrast, *L. scabra* individuals were least preferred and of smaller size. The other *Leandra* species (*Leandra* sp.1-4) may not have been attacked because trunk diameter was also too small,

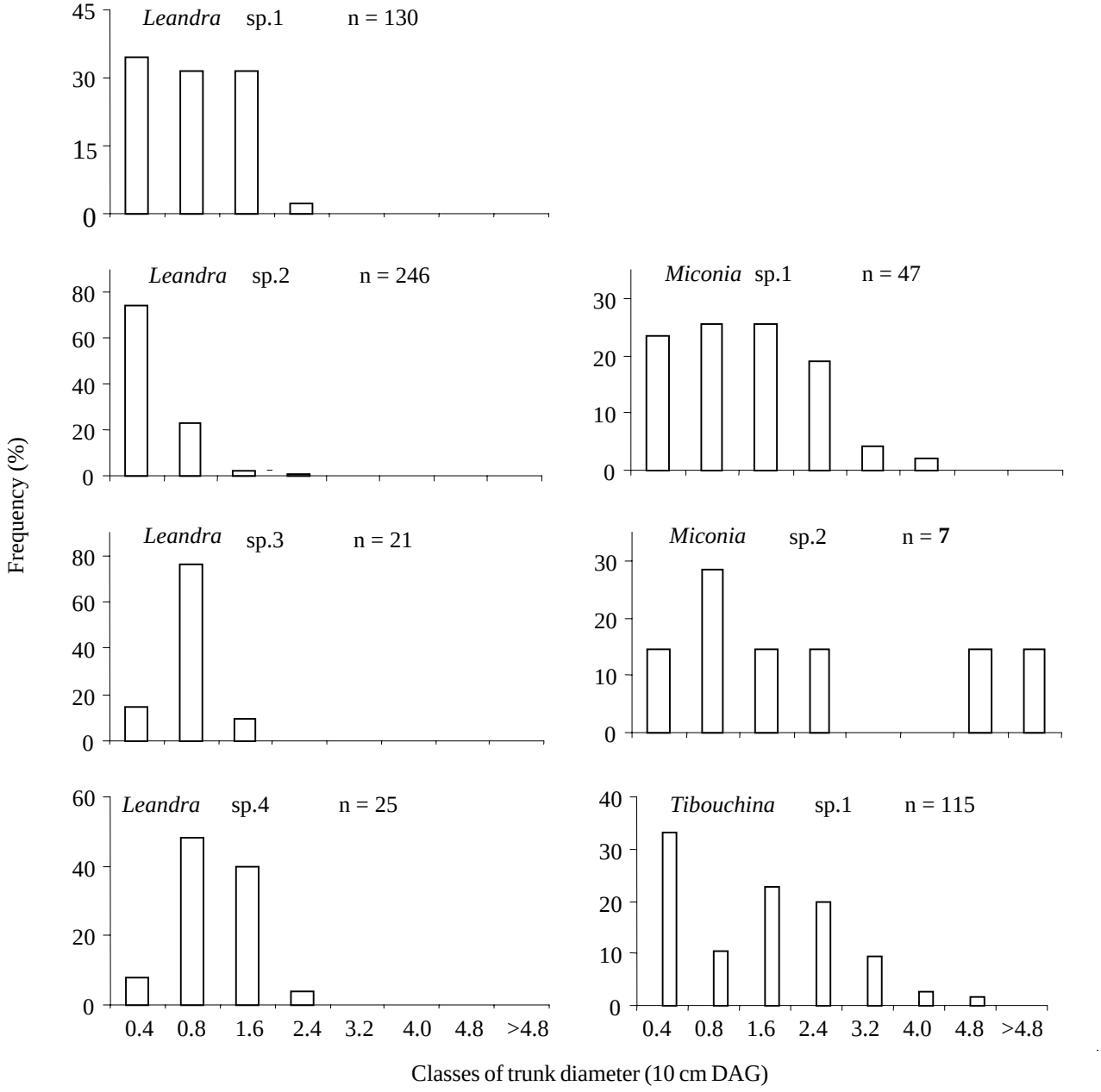

Figure 3. Frequency distribution for trunk diameters of Melastomataceae species not attacked by *O. humeralis*.

insufficient for colonization. However, there were individuals of *Miconia* sp. 1 and *Miconia* sp. 2 with similar diameters to those of the plants used by the beetles. They possibly were not attacked for not offering enough quality and quantity of nutrients for optimal larval development, or for having chemical defences or wood with inadequate physical characteristics. Moreover, *Miconia* sp. 2 was rare during this work (n = 7), making its encounter difficult for *O. humeralis*. *Tibouchina* sp.1 was not attacked by *O. humeralis*, even presenting many individuals with diameters similar to the plants used by the beetle. This is the only melastome species that occurs in a swampy environment (swamp) and is completely exposed to light. For this reason, eggs or larvae may be vulnerable to desiccation in this host. On the other hand, if the trunk falls on the ground, it may become saturated with water which will kill larvae. Hanks *et al.* (1999) showed that excess of moisture causes mortality in larvae of the cerambycid *Phoracantha semipunctata* F.

In general, *O. humeralis* selected trees of greater size, independent of host-plant species. Other studies showed that species of *Oncideres* also select trunks with specific diameters (Coulson 1979, Rice 1995, Caraglio *et al.* 2001). Coulson (1979) suggested that survival of wood boring insects is related to trunk diameter, since larger plants offer greater quantity of food and are capable of accommodating

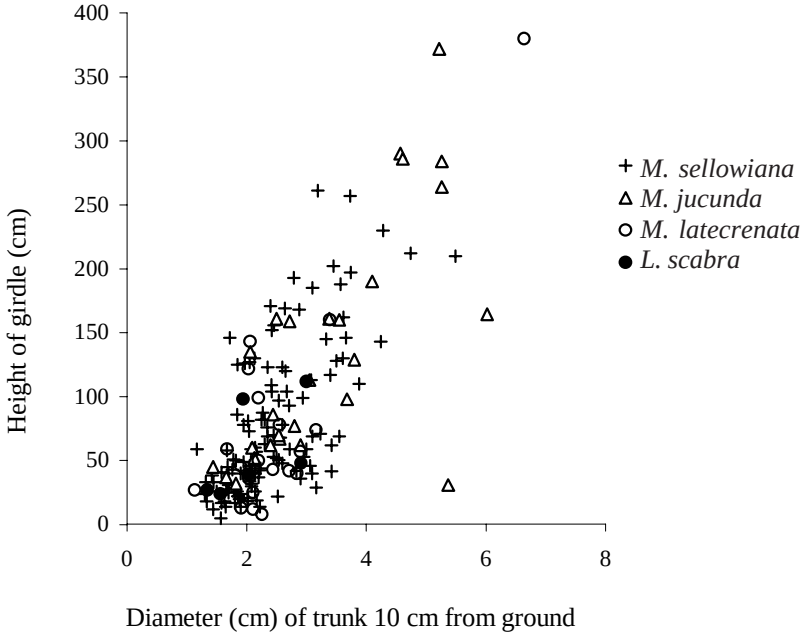

Figure 4. Relationship between trunk diameter at 10 cm above ground for four melastome species and girdle height by *O. humeralis*.

greater number of beetles, as well as protection against desiccation, bad weather, and natural enemies such as parasitoids. Our results showed that these beetles adjust the girdle height in function of the size of their host-plant, girdling trunks at lower points if plants are small and higher points if plants are larger, indicating that they are selecting particular diameters. These results suggest that there may be a trade-off between minimum diameter for larval performance and female effort during the plant girdle. If females chose branches that were too thick, they could take too much time to girdle them and would be exposed to predators for long time. Females of this beetle can stay for more than 7h laying eggs and girdling Melastomataceae trunks (Paulino Neto 2003).

Individuals of *M. sellowiana* with more secondary branches were preferred by *O. humeralis* females, indicating that, apart from the trunk diameter, the number of secondary branches can also influence the plant choice. The secondary branches are the females' oviposition sites and are the entrance door of the larvae in the first instars to reach the intra-xylematic phloem, located in the centre of the trunk (Paulino Neto 2003).

Table 2. Randomized-block ANCOVA examining the number of secondary branches between non-girdled and girdled plants by *O. humeralis*. The diameter at 10 cm above ground was the covariate.

Source of variation	df	*MS*	*F*	P
Block	30	7.366	1.31	0.237
Number of branches	1	65.581	11.62	0.002
Covariate	1	71.164	12.61	0.001
Error	29	5.642		

In conclusion, *O. humeralis* is specialist in Melastomataceae and uses four of the 11 available plant species, preferring *M. sellowiana* and *M. jucunda*, which are the most abundant and the one with greatest size, respectively. Females select larger plants, but adjusting the trunk girdle height as a function of the plant size. Apart from the size, the number of secondary branches also appears to be important in the host-plant choice.

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