

**SIZE OF AND DAMAGE ON SHOOTS OF *PASSIFLORA*
SUBEROSA (PASSIFLORACEAE) INFLUENCE OVIPOSITION SITE
SELECTION OF *HELICONIUS ERATO PHYLLIS* (FABRICIUS)
(LEPIDOPTERA, NYMPHALIDAE)**

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ABSTRACT. Oviposition site selection of *Heliconius erato phyllis* (Fabricius, 1775) (Lepidoptera, Nymphalidae) was studied when size of and damage on shoots were variable in a natural population of *Passiflora suberosa* Linnaeus (Passifloraceae), and through sequential and simultaneous choice experiments performed under insectary conditions. Females showed marked oviposition preference for undamaged and largest shoots of *P. suberosa*. Eggs were mostly laid on the terminal buds of intact shoots under natural conditions. In simultaneous choice trials, females preferred to oviposit on shoots from which leaves (ten) were removed but the terminal bud maintained to those where leaves were kept but the terminal bud was cut out. In sequential choice trials, they did not lay eggs on shoots from which the terminal bud was removed. Females preferred to oviposit on large to short intact shoots in both sequential and simultaneous choice trials. Females laid eggs preferentially on shoots with the greatest leaf area when most plants were intact in the field during early spring. Later in fall, when mostly large, old shoots were damaged or in a reproductive stage (less desirable for oviposition), oviposition intensity was highest on the shortest, youngest shoots of *P. suberosa*. Thus, females might rank these quality attributes higher than size while selecting shoots for oviposition. The consequences of ovipositing selectively on intact, large shoots of *P. suberosa* are discussed from the view point of *H. erato phyllis* larval performance.

KEY WORDS. Lepidoptera, *Heliconius*, *Passiflora*, oviposition behavior, host plant selection

Plant characteristics have been shown to influence many herbivorous insect, in terms of host preference for oviposition. While selecting hosts for oviposition, oligophagous insects usually discriminate between different host plant species (WIKLUND 1975, 1981; SINGER 1986; BERNAYS & CHAPMAN 1994). Their discrimination may be also strongly affected by variation within individual plants (JONES 1991; BERNAYS & CHAPMAN 1994), which may not necessarily be overridden by host plant species effects. On the contrary, host-choice based on host species may

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be less important than on host choice based on intraspecific plant attributes, in those insects that specialize on plant individuals or tissues in a particular phenological category (e.g. CATES 1980; LEWIS 1982; THOMAS 1987). Such insects might not show preference for a particular host species, and as suggested by THOMAS (1987), may still have as narrow a diet as a monophagous species that feeds on many plant tissues.

Passion vine butterflies (Nymphalidae: Heliconiinae) are associated with a narrow range of host plants in a given location as has been observed throughout the neotropics (see BENSON *et al.* 1976; BROWN 1981; GILBERT 1991). Oviposition preference within the range of host plants of some oligophagous heliconiine has also been experimentally demonstrated (COPP & DAVENPORT 1978; SMILEY 1978; MENNA-BARRETO & ARAÚJO 1985; PERICO & ARAÚJO 1991). In addition, field observations have strongly suggested that larvae of most passion vine butterflies feed preferentially on particular parts of their host plants, and that these are chosen for oviposition (see ALEXANDER 1961; BENSON *et al.* 1976; BENSON 1978). That heliconian butterflies select hosts for oviposition based upon qualitative attributes of these preferred plant parts has been also suggested (BENSON *et al.* 1976; BENSON 1978). However, little experimental work has been reported on the influence of intraspecific variation of passion vine attributes on oviposition behavior of these butterflies. Field observations carried out by LOPES (1991) suggest *Heliconius erato* (Linnaeus, 1758) females choose for oviposition shoots with "fast" over "slow" growth meristem in passion vine populations of Serra do Japi, São Paulo.

The work reported here is part of a more general study concerning the influence of host plant characteristics on oviposition site selection behavior of *Heliconius erato phyllis* (Fabricius, 1775), a common butterfly in southern Brazil (BROWN & MIELKE 1972). *H. erato phyllis* is oligophagic in Rio Grande do Sul State (RS), eggs and larvae being found primarily on *Passiflora suberosa* Linnaeus, in areas where this passion vine predominates (PERICO & ARAÚJO 1991). *Passiflora suberosa* is in fact one of the most abundant passion vines occurring in RS, but it is not the most preferred for oviposition or most suitable as food for *H. erato phyllis* larvae, as judged by laboratory studies (MENNA-BARRETO & ARAÚJO 1985; PÉRICO & ARAÚJO 1991). Thus, it is suspected that use of *P. suberosa* over other more preferred or more suitable host plants for larvae (e.g. *P. misera* Humboldt, Bonpland & Kunth and *P. elegans* Masters) may be mediated at local basis by variation intrinsic to these host plant populations, such as their relative availability and phenology (see CATES 1980; SOLOMON 1981; COURTNEY & FORSBERG 1988), or due to variation in preference of females within populations (see WIKLUND 1981; PAPAJ & RAUSHER 1983; ARAÚJO 1987; JONES 1991). In the present study, it is addressed this question by determining *H. erato phyllis* ovipositional response to variation in size of and damage to host plants, based upon samples taken in a natural population of *P. suberosa* and on ovipositional choice experiments carried out under insectary conditions.

MATERIALS AND METHODS

Study Site and Sample Procedure

Field studies were conducted on a *Passiflora suberosa* population in the Águas Belas Experimental Station (FEPAGRO), Viamão County, RS, from November 1, 1994 to May 1, 1995. Shoot samples were taken along an approximately 2m wide and 200m long trail, located in an *Eucalyptus*-plantation. The vegetation was characterized by a patchy native flora mixed with *Eucalyptus*-trees. *P. suberosa* predominates in the herbaceous stratum, at some places covering totally the trail ground. Other *Passiflora* vines were sparsely found in the area, including *P. misera*, *P. elegans*, *P. caerulea* Linnaeus, *P. alata* Dryander and *P. edulis* Sims.

Samples were taken at 45-day intervals, fifty on each date. Sampling points were randomly selected and identified by stretching a tape measure on the trail. Then, *P. suberosa* shoots located nearest to sorted positions were cut out and individually placed in plastic bags. A pilot study showed that *H. erato phyllis* eggs occur at very low densities in the area, which would make comparison difficult between plants with and without eggs within samples. To make such comparison possible, all *P. suberosa* plants located along the trail were concurrently inspected, and those shoots bearing *H. erato phyllis* eggs were also collected, until a number of ten to be reached on each date. In the laboratory, all shoots were carefully examined for the presence of other insect eggs and larvae, and classified according to their phenology and presence of intact terminal bud (made up of apical meristem, leaf primordia and overlapping leaves) (Fig. 1A). Those shoots where the terminal bud was absent, wilted or dried up, were considered as "damaged" (Fig. 1B,C). Then, shoots were pressed, air dried and their leaf area determined with a Li-Cor[®] portable leaf area meter.

Plants and insects

Passiflora suberosa plants (n = 70) used in the oviposition choice tests were transplanted at a very early developmental stage from the field study area into 3.8-liter pots, and grown in a large outdoor screened cage. Pots were provided with 50cm high wooden frame supports for shoot growth.

Heliconius erato phyllis females used in the ovipositional choice trials were collected in Porto Alegre County, RS. They were wing marked with an felt-tip pen (Pilot[®]), and maintained in a 2.6 x 4.5 x 5.6m outdoor screened insectary, located at the Zoology Department of Federal University of Rio Grande do Sul State, Porto Alegre. Females were fed twice a day (early morning and afternoon) with a mixture of 7.5g sucrose, 1.5g commercially available honey bee-pollen (AGA[®]) and distilled water (50ml). The solution was placed in yellow sponges set on small, red color, plastic vials. To resemble natural conditions, the insectary was provided with non host-plants (mostly *Impatiens balsamina* Linnaeus, *Lantana camara* Linnaeus, *Euphorbia pulcherrima* Willdenow ex Klotzsch, *Monstera deliciosa* Liebm. and an unidentified *Pilea* Lindley species). A few potted *P. suberosa* plants were offered for oviposition. Eggs were removed from plants during daily inspections. As already noted for other *Heliconius* populations that were maintained under similar insectary

conditions (e.g. GILBERT 1972), behavior and oviposition rates (averaged over 3 eggs/individual/day) among kept females were apparently identical to that of wild individuals. To control for variation among individuals, females were randomly selected, and never used in consecutive days or more than two times in a given test. Dead or senescent females (indicated by wing-scale loss, or low oviposition rate during the tests) were replaced accordingly throughout the experimental period.

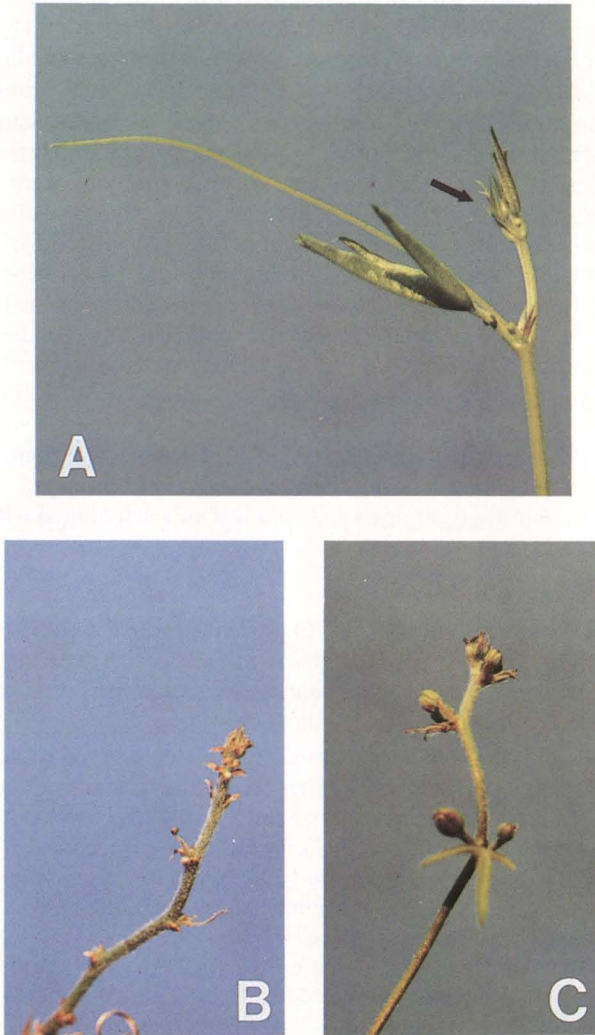


Fig. 1. Terminal portion of *P. suberosa* shoots. (A) With intact terminal bud (arrow), (B-C) with damaged terminal bud.

Ovipositional choice experiments

Trials were conducted from December 1994 to March 1995, in an adjacent outdoor insectary (2.0x6.0x1.8m) equivalent to that described previously (including non-host plants).

Sequential and simultaneous choice trials (*sensus* SINGER 1986) were performed to determine the relative importance of presence of terminal buds and size of *P. suberosa* shoots in relation to oviposition site selection of *H. erato phyllis*. Three shoot types (= treatments) were used for evaluating effects related to the presence of terminal buds: 1) with ten leaves and terminal bud; 2) with leaves removed and terminal bud kept; 3) with ten leaves and terminal bud cut out (Fig. 2). Three treatments were also used for testing shoot size effects: 1) large shoots - 40cm long, with ten leaves (**B + L**, Fig. 2); 2) medium - 30cm long, with seven leaves; 3) small - 15cm long, with three leaves. Plants were standardized for size by removing extra tissue, the main shoot being the only one left in each pot prior to using plants in the tests. *H. erato phyllis* eggs were laid individually on *P. suberosa* plants under field conditions, in an expected daily oviposition rate varying from 3 to 5 eggs per female (DUNLAP-PIANKA *et al.* 1977). Due to these aspects, a ratio of five plants per female was used for all treatments in the experiments.

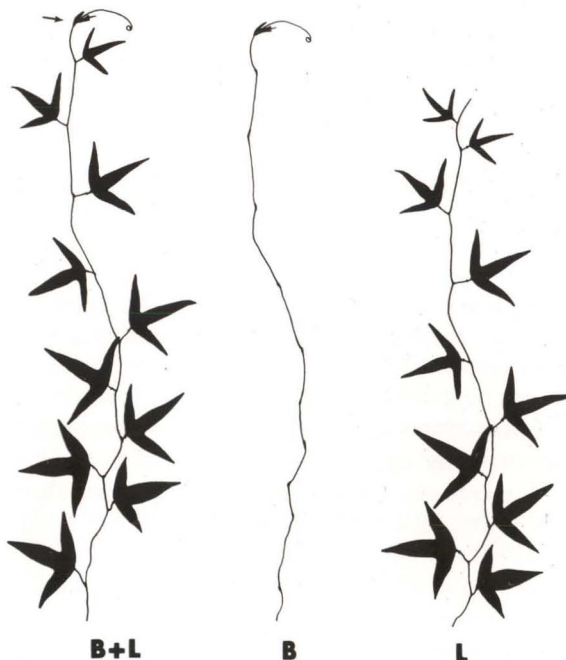


Fig. 2. Schematic representation of *P. suberosa* shoots used in the ovipositional choice experiments. (**B + L**) With ten leaves and terminal bud (arrow); (**B**) with leaves removed and terminal bud kept; (**L**) with ten leaves and terminal bud cut out. To facilitate visualization, tendrils and stipules associated with open leaves were not included.

A diel oviposition profile determined for *H. erato phyllis* prior to this study showed that most oviposition activity occurs from 8 a.m. to 5 p.m., thus tests were conducted during this time interval. In the simultaneous choice trials, all shoot types were introduced simultaneously in the insectary, and the oviposition response was quantified through the entire experimental period (9 hours each day). For the sequential choice trials, the experimental period was divided into three 3h-intervals; the insectary was divided by nylon screens into three 3-m sections, where shoots were distributed according to type. Females were moved among sections at the end of these pre-determined intervals during the tests.

Only one female was tested each day, and each experiment lasted for 20 days (= number of replicates). Plants were carefully inspected for egg deposition at the end of each period, when eggs were counted and removed. Females, plants, pot position in the insectary and order of treatment to be tested in a given day in the sequential choice trials were all randomized.

Results from ovipositional choice experiments were expressed as average daily oviposition rates per female (\pm standard errors), unless noted. Data were log transformed for the analysis of variance, following criteria described in SOKAL & ROLHF (1981). Where analyses of variance were significant, differences among treatments were tested using Tukey multiple comparison tests, $\alpha = 0.05$. Non-parametric statistical tests followed procedures described in SIEGEL (1956).

RESULTS

Field studies

There was considerable variation in number of shoots with intact terminal buds and plant phenology in the *P. suberosa* population among samples. From a total of 246 collected shoots, 174 (70.75%) had undamaged terminal buds. Proportion of shoots with intact terminal buds decreased from 87.23% at the first sample (spring) to 36.0% on the last sample date (fall) (Fig. 3A). Reproductive structures (flowers or fruits) were present in 63 (25.61%) of the total collected shoots. Contrary to trend noted for terminal bud damage, proportion of shoots with reproductive structures increased progressively from 14.9% at the first sample (November) to 44.0% in April, and decreased again in the last sample taken in early May (Fig. 3B).

The inspections for egg deposition performed in the *P. suberosa* plants located along the trail showed that females oviposited exclusively on intact terminal portion of shoots. From a total of 43 shoots that were collected with eggs, 25 (60%) had them located on the terminal buds. In the remaining egg-bearing shoots, they were found on open leaves and tendrils located near the terminal bud (Fig. 4).

There was great variation in leaf area among shoots in the *P. suberosa* population. It ranged from 2.84 to 463.5cm² among collected shoots (average of 83.71 \pm 74.51cm² per shoot). There was no indication that average leaf area of shoots varied among sample dates in the population (Fig. 5). There was also pronounced variation in leaf area among egg-bearing shoots. Eggs were laid on shoots with leaf area varying from 5.58 to 463.5cm² (average of 120.36 \pm 82.72cm²). The average

size of egg-bearing shoots decreased progressively throughout field evaluations. As indicated by the first two samples, females selected shoots for oviposition that had greater leaf area than the average in the population during later spring. However, in the last sample, during early fall, they chose shoots with lower leaf area than the population in average (Fig. 5). Although data were not included here, total length and number of leaves per shoot decreased in a similar way to leaf area through the experimental period (E. Mugarbi-Oliveira unpublished data).

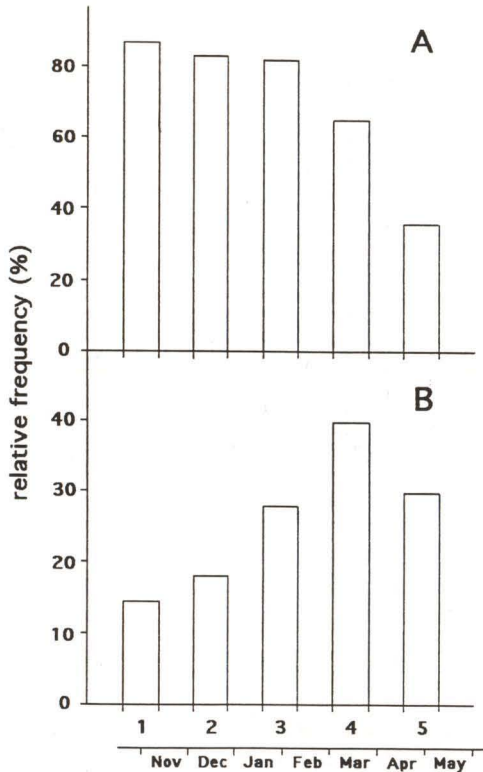


Fig. 3. Seasonal variation in number of *P. suberosa* shoots with undamaged terminal buds (A) and under reproductive stage (B) at Águas Belas Experimental Station, Viamão County, Rio Grande do Sul, 1994/95. Numbers from 1 to 5 represent 45-day sample intervals.

Ovipositional choice tests

Presence of terminal buds on *P. suberosa* shoots significantly affected *H. erato phyllis* oviposition site selection in the insectary experiments. In the simultaneous choice trials, there was no oviposition on shoots from which terminal buds were cut out. Also, oviposition intensity was significantly greater on shoots bearing ten leaves and terminal bud than those where only the terminal buds were kept (Fig. 6A). In the sequential choice trials, oviposition on shoots without terminal buds was

lower than those with ten leaves and terminal buds or terminal buds only (Fig. 6B). There was also a significant shoot size effect on oviposition site selection. Oviposition intensity significantly decreased with a decrease in shoot size in the simultaneous choice trials (Fig. 7A). Females laid eggs on small plants at significantly lower intensity than in medium or large size plants in the sequential choice trials (Fig. 7B).

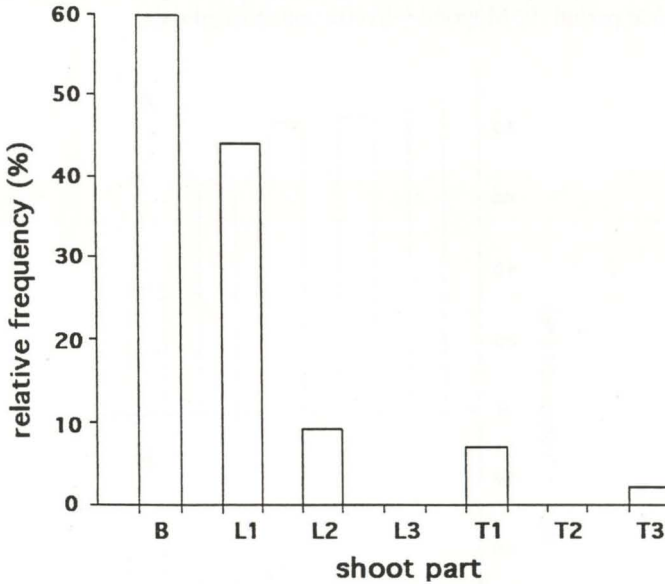


Fig. 4. Parts of *P. suberosa* shoots used for oviposition by *H. erato phyllis* at Águas Belas Experimental Station, Viamão County, RS, 11/1/94–5/1/95. (B) Terminal bud; (L) open leaf, (T) tendril; (1-3) position in relation to shoot apex.

DISCUSSION

Both field and insectary results from this study showed that presence of intact terminal bud is an important factor in determining selection of a given *P. suberosa* shoot for oviposition by *H. erato phyllis*. In accordance with LOPES (1991) observations for a *H. erato phyllis* population of Serra do Japi, São Paulo State, eggs are only found on the subterminal portion of *P. suberosa* shoots at Águas Belas Experimental Station. Young leaves have been recognized as the preferable oviposition site of *H. erato phyllis* for a number of *Passiflora* vines (CRANE 1955; ALEXANDER 1961; BENSON 1978; LOPES 1991). Our field results further demonstrated that intact *P. suberosa* shoots are preferred to those with damaged terminal buds, thus adding evidence to the suggestion made by BENSON (1978) in that *H. erato phyllis* females evaluate host plant quality before oviposition. The simultaneous and sequential choice trials performed in this study showed that females reject to oviposit on shoots from which terminal buds were cut out. They also indicated that females recognize shoot size, preferring the largest shoots for oviposition.

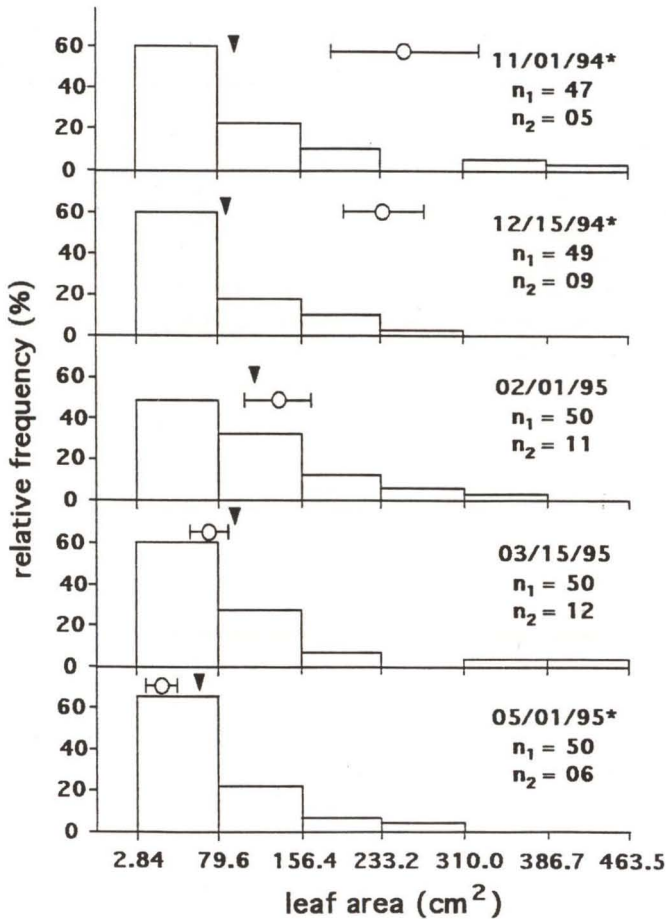


Fig. 5. Seasonal variation in leaf area on shoots of *P. suberosa* at Águas Belas Experimental Station, Viamão County, RS, 1994/95. The average leaf area of the total collected shoots (n_1) is indicated by closed triangles. Open circles and associated bars indicate the average leaf area (\pm standard error) of shoots bearing eggs (n_2) of *H. erato phyllis*. Asterisks indicate significant statistical difference in leaf area between shoots with and without eggs (Mann-Whitney U, one-tailed test, $\alpha = 0.05$).

It has been inferred from other studies that evolution of plant species preference among oligophagous insects is shaped at least in part by plant suitability as larval food (e.g. WIKLUND 1975; SINGER 1983; LEATHER 1985; HAMILTON & ZALUCKI 1993a,b). Similarly, it is expected that preference for oviposition on a given plant part to be also related to suitability of the corresponding tissue as larval food. Results from preliminary studies carried out in our laboratory (D. Rodrigues and G.R.P. Moreira unpublished data) strongly suggest that choice of *H. erato phyllis* females for oviposition on intact, new growing shoots of *P. suberosa* has important consequences on larval survival and growth rates. First and second instar

larvae when transferred to *P. suberosa* shoots having only old leaves have reduced survivorship probability (30 and 60%, respectively), when compared to those reared since the beginning on intact shoots with terminal bud (100% of survivorship). Transference of the first two larval instars to old leaves also leads to a significant delay in larval development. On the other hand, there is no effect on survivorship and growth rates of larvae when they are initially reared on intact leaves and then transferred at third, fourth, or fifth instars to old leaves. Thus, the presence of young leaves is crucial for success of early larval instars of *H. erato phyllis*, and may constitute the natural selection mechanism by which the behavior of laying eggs on intact, subterminal portion of *P. suberosa* shoots is maintained in the population (D. Rodrigues and G.R.P. Moreira unpublished data).

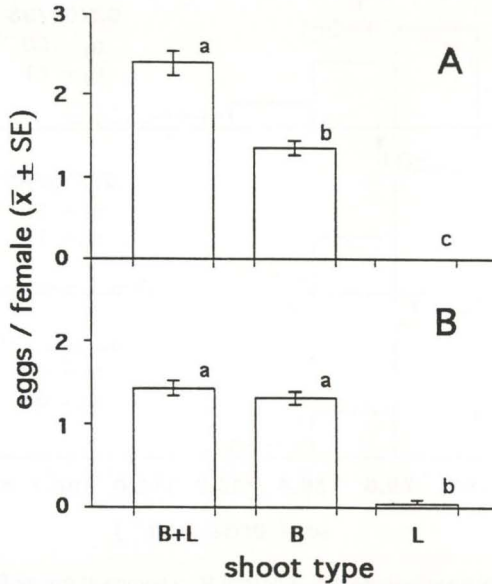


Fig. 6. Egg-laying response of *H. erato phyllis* to variation in *P. suberosa* shoot structure in simultaneous (A) and sequential (B) choice trials. (B + L) With ten leaves and terminal bud; (B) with leaves removed and terminal bud kept; (L) with ten leaves and terminal bud cut out. Values followed by the same letter are not significantly different (Anova, alpha = 0.05; Tukey multiple comparison tests, alpha = 0.05).

The first results obtained from another study in progress at our laboratory indicate that size of shoots chosen for oviposition might also influence *H. erato phyllis* larval development. When fed with *P. suberosa* leaves, this species needs to consume from 105.5 to 205.92cm² (average of 148.58cm²) of leaf area for completion of the larval stage (C.A. Barcellos and G.R.P. Moreira unpublished data). At any given time for the *P. suberosa* population sampled in the present study, total leaf area of more than half of shoots was lower than that required for larval development of *H. erato phyllis*. From a natural selection perspective, it would be expected that given a choice, females should lay eggs on those shoots with the

greatest leaf area, to ensure a satisfactory development for offspring. In the present study, such a response was observed in the first two field samples and on both simultaneous and sequential choice trials. Nevertheless, females laid eggs on shoots with leaf area lower than the average in the *P. suberosa* population in the last two samples. It is supposed that in such cases larvae starve before pupation, or find another suitable shoot for feeding. However, such nutritional and behavioral consequences of laying eggs on shoots with lower leaf area than that required for larval development remains to be tested for *H. erato phyllis*. BENSON *et al.* (1976) inferred eventual starvation for some individuals of *H. erato*, as judged by the presence of adults with reduced size found in insect collections. Larvae of another specialized young leaf feeder, *Heliconius hewitsoni* Staudinger starve before pupation when eggs are laid on short shoots of *Passiflora pittieri* Masters in Costa Rica (DUCKETT 1989).

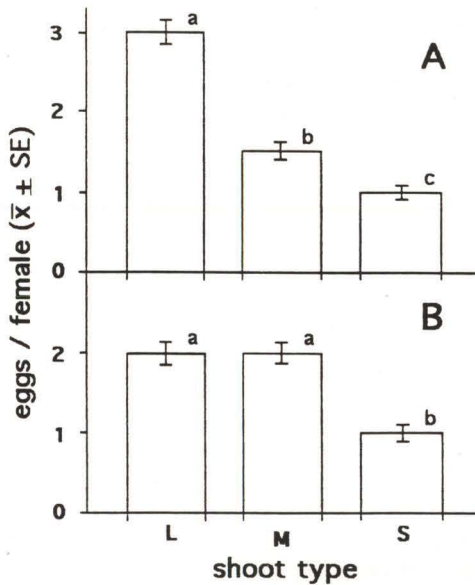


Fig. 7. Egg-laying response of *H. erato phyllis* to variation in *P. suberosa* shoot size in simultaneous (A) and sequential (B) choice trails. (L) Large, with ten leaves and 40cm long; (M) medium, with seven leaves and 30cm long; (S) small, with three leaves and 15cm long. Values followed by the same letter are not significantly different (Anova, $\alpha = 0.05$; Tukey multiple comparison tests, $\alpha = 0.05$).

Since there was not oviposition on damaged shoots, it is supposed that qualitative attributes might be more important than size as criteria to choose shoots for oviposition by *H. erato phyllis*. Thus, the progressive decrease in size of those shoots that were selected for oviposition could have resulted first from the concurrent decrease in number of intact shoots available in the *P. suberosa* population throughout the experimental period. Damage on shoots were mainly due to insect feeding, including unidentified flea beetles (Coleoptera, Chrysomelidae), larvae

from notodontid moths and other passion vine butterflies besides *H. erato phyllis*. Second, the size decrease of shoots chosen for oviposition could also be related to changes in phenology of *P. suberosa* plants. That is, females probably prefer to lay eggs on vegetative rather than reproductive stage plants. From the 43 shoots collected with eggs, only four (6.98%) were in reproductive stage (flowers present); the number of these shoots increased progressively in the population up to the end of summer. Thus, the shortage of plants in appropriate phenological category could also be important in forcing females to choose for oviposition the smallest, new growing shoots during early fall. It is suspected that *H. erato phyllis* oviposition on shoots with "fast" growth meristem in preference to "slow", reported by LOPES (1991), may result from these phenology changes on *P. suberosa* plants. Preliminary observations made (G.R.P. Moreira unpublished data) suggest shoots of *P. suberosa* grow in a similar way to that described by LONGINO (1984) for *P. pittieri* in Costa Rica. At the beginning, shoot elongation rate is high, it levels off as shoots leaf out, and apparently growth is reduced with the start of reproduction. Choice tests using shoots under vegetative and reproductive stages should be conducted in the future to better evaluate the influence of plant phenology on *H. erato phyllis* oviposition site selection.

It has been demonstrated that insect host plant use is influenced by at least three other major component, besides host suitability: insect host finding behavior and preference, and density of potential hosts (JAENIKE 1978, 1990; SOLOMON 1981; WIKLUND 1981; SINGER 1983, 1986; COURTNEY & FORSBERG 1988; JONES 1991). It is showed experimentally in this study that *H. erato phyllis* lays eggs only on the terminal portion of *P. suberosa* shoots, and that intraspecific variation in host plant attributes, such as damage and size of shoots, influences host selection for oviposition. Thus, a two component form of discrimination based on both within- and between-plant species attributes may hold for *H. erato phyllis*, as has been suggested for other oligophagous insects (e.g. THOMAS 1987). In other words, if within the host plant species range, *H. erato phyllis* chooses suitable shoots for oviposition irrespective of which species those shoots come from, it is expected that field distribution of eggs and larvae will be influenced by the relative abundance of these host plant species. *H. erato phyllis* uses a relative wide number of *Passiflora*-species as hosts, and although it was not yet experimentally tested, differences on host plant species use have been recognized for a number of southeastern Brazilian populations of this passion vine butterfly (BENSON *et al.* 1976). In Rio Grande do Sul State, local variation in distribution of *H. erato phyllis* eggs and larvae among *Passiflora* species seems to reflect the relative abundance of the most preferred and suitable host plants (*P. misera*, *P. capsularis* Linnaeus, *P. suberosa*, *P. elegans*), judging by field data provided by MENNA-BARRETO & ARAÚJO (1985), PÉRICO & ARAÚJO (1991) and LUTZ (1995), and observations made in the present study. We are now carrying out a more detailed investigation concerning the underlying mechanisms of oviposition host selection in *H. erato phyllis*, using different densities of *P. misera* and *P. suberosa* as hosts, to examine in particular choice based on plant variation compared to that on host species.

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