

Variation in herbivory within and among plants of *Daphne laureola* (Thymelaeaceae): correlation with plant size and architecture

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Summary

1 Herbivory by noctuid moth larvae (Lepidoptera, Noctuidae) on plants of *Daphne laureola* L. (Thymelaeaceae) was studied under natural conditions in a south-eastern Spanish montane habitat. The main objective of the study was to determine how size and architectural features correlated with herbivory level (mean percentage leaf area removed by the end of the larval growth season) and herbivore load (mean number of caterpillars recorded per day) both among and within plants.

2 A significant correlation was found between herbivore load and herbivory level of individual plants. Herbivory levels differed widely (range = 0.1–12.8% leaf area) and were considerably smaller than those often used in artificial defoliation experiments.

3 Variation among plants in the incidence of noctuid larvae was directly related to the number of leaf whorls, and inversely to the mean basal diameter of stems. These responses to size and architectural traits may be explained by discrimination by ovipositing females.

4 Within plants, larvae preferentially selected leaf whorls having shorter supporting stems and lower branching orders. Movement costs may be reduced by larvae using plant architectural traits as cues for within-plant food selection.

5 The reasons for and potential implications of the different features used by adult noctuids discriminating between plants and by their larvae selecting leaf whorls are discussed.

Keywords: food selection, foraging behaviour, insect herbivory, Noctuidae, plant architecture

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Introduction

The evolutionary implications of plant–herbivore relationships cannot be understood without elucidating (1) why all individuals in a plant population are not equally damaged, and whether differences in herbivory levels are random, relate to environmental conditions or depend on intrinsic (i.e. potentially heritable) plant features and (2) whether differential herbivory has fitness-related consequences for either the plant, the herbivores, or both (reviewed in Karban 1992; and Marquis 1992). Some recent studies have focused on characteristics extrinsic to individual plants, such as microhabitat conditions (Lincoln & Mooney 1984; Bowers *et al.* 1992; Dudt & Shure 1994), recent herbivory history (McCrea & Abrahamson 1987) and interaction with natural enemies (Moran 1984; Hare 1992; Ohsaki & Sato 1994). Other analyses have considered relationships between her-

bivory levels and plant genotypes (Marquis 1990; Fritz 1990; Bowers *et al.* 1992) and, more rarely, associated phenotypes (Dirzo & Harper 1982; Nuñez-Farfán & Dirzo 1994). A third line of investigation concentrates on individual variation in phenotypic traits, such as secondary chemistry (Dirzo & Harper 1982; Zangerl & Berenbaum 1993), phenology (Moran & Whitham 1990), physical characteristics of foliage (Howard 1988) or plant gender (Elmqvist & Gardfjell 1988; Boecklen *et al.* 1990).

Most investigations on correlates and consequences of variation in herbivory have adopted an experimental approach whereby herbivory levels are simulated artificially and/or plants are cultivated under controlled conditions. Comparatively few studies have examined the phenotypic correlates of individual plant variation in herbivore load and foliage loss under natural field conditions. We focused on the basis for the interaction between *Daphne laureola* and

Table 1 Effects of size and architectural plant traits on individual variation in herbivore load (caterpillars per day) and herbivory level (% leaf area removed), as assessed by multiple regression analyses. Only variables contributing significantly (or marginally so) are shown. Significance levels tested using randomization methods. *b* = standardized regression coefficient

Variable	Caterpillars/day $R^2 = 0.613, P = 0.02$		Leaf area removed $R^2 = 0.214, P = 0.05$	
	<i>b</i>	<i>P</i>	<i>b</i>	<i>P</i>
Number of leaf whorls	0.8285	0.0002		
Mean stem diameter	-0.3749	0.0684	-0.4788	0.0174

its major herbivores (lepidopteran larvae) by investigating how variation in size and architecture among shrubs relates to differences in herbivory in the field.

Variation in plant architecture could influence herbivory rates via its effects on the foraging costs and behaviour of caterpillars. Plant size and architecture have been considered to explain differences in herbivory between species (Lawton 1983), but more rarely among conspecifics. Out of a total of 43 studies reviewed by Marquis (1992: Table 13.3) that examined the effect of plant characters on intraspecific variation in herbivore damage, only four considered architectural traits.

A realistic assessment of herbivory levels experienced by individuals of *D. laureola* was obtained by evaluating the overall damage caused by invertebrate herbivores (Maddox & Root 1987; Marquis 1990). In some trees the consequences of herbivory depend on location effects (Heichel & Turner 1984; Marquis 1988), but intracrown variation in herbivory has not been documented previously for shrubs. Within-plant variation in herbivory was therefore studied in addition to among-plant differences. A comparison of within- and among-plant analyses may illustrate possible conflicts between preferences of lepidopteran larvae and host selection by ovipositing females (Thompson 1988).

The specific questions addressed in this study are thus: (1) Do *D. laureola* plants differ significantly in size and architectural traits, and in herbivory levels? (2) are individual differences in herbivory among *D. laureola* plants related to variation in size and architectural traits, (3) do herbivores exhibit within-plant selection and (4) are within- and among-plant choices consistent?

STUDY SPECIES

Daphne laureola L. (Thymelaeaceae) is a long-lived evergreen shrub that, in the Mediterranean region, occupies preferentially the undergrowth of shady mountain forests. In the study area flowering occurs in February–March, shortly before new leaves are produced. Fruits (single-seeded drupes) ripen in early June, earlier than most fleshy-fruited plants in the area, and are heavily consumed by mice and birds

(Obeso 1985; Hulme 1992). Plants shed their oldest leaves in early summer.

D. laureola plants consist of a variable number of erect stems that rise at ground level from a common trunk (Fig. 1). Leaves are found only at the distal end of each branch, forming a single, well-defined leaf whorl. Individual stems may remain undivided or may ramify into two, three or four branches, which also may branch again or remain undivided. Variation among plants in the number, length and degree of branching of stems generates a broad spectrum of architectural types in this species. From the viewpoint of slow-moving, flightless invertebrate herbivores that have to crawl along bare stems to reach leaf whorls (e.g. lepidopteran larvae), food resources within *D. laureola* plants occur as widely spaced packages. Each of these provides food in excess of individual requirements during a single foraging bout, but the need for regular search presumably implies certain costs in terms of time and energy.

Foliage-feeding lepidopteran larvae were the most frequent herbivores on *D. laureola*. Mammalian herbivores do not browse on *D. laureola* plants, probably because of the presence of a variety of toxic and repel-

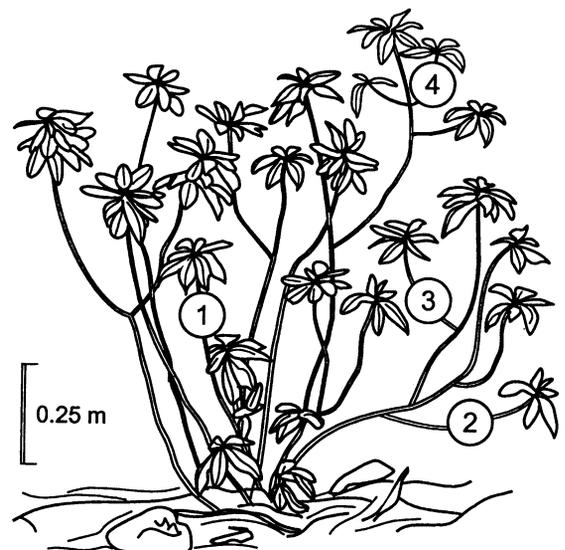


Fig. 1 Characteristic architecture of a *Daphne laureola* plant. Numerals denote the different branching orders associated with individual leaf whorls.

lent substances in the foliage (Hegnauer 1973). Grasshoppers were occasionally observed on study plants but their damage (which could be easily distinguished from that caused by caterpillars) was not recorded. Some geometrid larvae were also observed sporadically on *D. laureola* plants but, as they were never seen feeding on the foliage, were not considered further. All larvae recorded feeding were from noctuid moths (Noctuidae). The most abundant species were *Trigonophora flammea* Esper. (44.1% of total records) and *Noctua janthe* Bkh. (38.4%). Other species observed were *Pseudenargia ulicis* Staud. (10.2%) and *Noctua 'fimbriata'* (= *N. fimbriata* Schreb. + *N. tirrenica* Bieb., Spdl. & Hngk.) (7.3%) (for taxonomic identity see Yela 1992). In the study region these noctuid species are all polyphagous on a variety of herbaceous and woody plants (J. L. Yela, personal communication; *T. flammea*, for instance, is known to feed on such disparate plants as *Crataegus*, *Quercus*, *Arbutus*, *Phillyrea*, *Narcissus* and *Paeonia*, in addition to *Daphne*). We only evaluated the importance of caterpillars as consumers of foliage (largely young leaves), although they also consume flowers and unripe fruits.

Noctua janthe larvae were most frequent on *D. laureola* early in the season (April to mid-May). Larvae remained inactive during daytime, hidden in the litter beneath the plants, and climbed at night to the leaf whorls to feed. They did not usually feed on the same leaf whorl during consecutive nights. This species belongs to the 'short pupal duration' group of Mediterranean Noctuidae (Yela & Herrera 1993) and adults emerge early in the summer, shortly after pupation. Larvae of *Trigonophora flammea* were most frequent on *D. laureola* from early May to mid-June, when pupation occurred. Their foraging behaviour was found to vary with age. From the first to fourth instars, larvae are green-coloured, remain hidden during daytime among the leaves of *D. laureola* plants, and feed on the same leaf whorl for several nights. After entering the fifth instar, they become brown-coloured and hide in the litter beneath the plants during the daytime, climbing to the leaf whorls every night to feed. At this stage, they did not feed on the same leaf whorl during consecutive nights. *Trigonophora flammea* passes the summer as pupa ('long pupal duration' group of Yela & Herrera 1993), and adults emerge by early October.

Methods

The study was carried out during April–June 1994 on a population of marked *Daphne laureola* individuals ($N = 28$ plants) located in the Sierra de Cazorla (Jaén province, south-eastern Spain), on a north-facing slope at 1235 m a.s.l. (CA site in Yela & Herrera 1993). The marked shrubs were part of other investigations (Yela & Herrera 1993; and J. L. Yela, unpublished), and represented a random subsample of the local *D.*

laureola population. Nearest neighbour distances between marked plants ranged between 0.2–30 m, and the total study area was about 1500 m². At the study site, *D. laureola* grows as an understorey shrub in a dense mixed forest, with *Quercus rotundifolia*, *Q. faginea*, *Pinus nigra*, *Phillyrea latifolia* and *Juniperus oxycedrus* as dominant tree species, and *Rubus ulmi-folius*, *Crataegus monogyna* and *Rosa canina* as dominant shrubs.

PLANT CHARACTERISTICS

Plant structure was characterized according to separate size and architectural measures, although relationships may exist between the two types of features.

Size traits are single measurements that provide an overall characterization for an individual plant. For each marked plant we used the number of leaf whorls, the height of the tallest stem ('plant height' hereafter) and the geometric mean of the major diameters of the plant's vertical projection (assimilating it to an ellipse) as estimates of plant size.

Measurements used to characterize the architecture of marked plants were made on individual leaf whorls, and thus provided a series of replicates per plant that reflected intraplant variation in structure and characteristics of stems and leaf whorls. Measurements were made in late June, when all caterpillars had either been collected for other studies or had already left the plants to pupate. We characterized all the leaf whorls where caterpillars had been previously recorded, which had been marked during observation sessions ('marked whorls' hereafter) and up to a maximum of 10 leaf whorls (depending on plant size) chosen haphazardly among unmarked ones ('control whorls' hereafter). Since herbivores had not been chemically or physically excluded from plants, the limitations of enclosure-based approaches (Strauss 1988) did not apply, but the control whorls could have been fed upon by caterpillars on dates when no observations were made. However, only 40% of control whorls had at least one leaf with $\geq 26\%$ area removed, in comparison with 82% of marked whorls ($\chi^2_1 = 74.6$, $P < 0.0001$). This indicates that control whorls actually represent a reliable sample of leaf whorls that were less often selected by caterpillars.

For both marked and control whorls, we measured the length (from ground level to the insertion of the first leaf) and basal diameter (at ground level) of the supporting stem, counted the number of leaves and determined the branching order. Branching order was taken as the number of forks occurring from the base of the stem (which was considered as the first fork) up to the leaf whorl under consideration, i.e. the number of forks a climbing larva had to pass over to reach the leaf whorl (Fig. 1). Average branching order thus reflects the internal complexity of the plant from the viewpoint of foraging larvae. By computing weighted

plant means, architectural data can be used to make among plants as well as within plant comparisons.

INCIDENCE OF HERBIVORES

The incidence of herbivores on marked *D. laureola* plants was assessed both as the frequency of occurrence of caterpillars during nocturnal censuses ('herbivore load') and as the proportion of leaf tissue removed ('herbivory level').

Herbivore load

In order to determine the natural herbivore load on marked plants we made efforts to disturb caterpillars as little as possible. Observations of larvae were conducted at night (from 21.00 hours to 24.00 hours GMT), when they were active and most conspicuous. Observations were conducted on two consecutive nights each week over the whole study period, to enable short-term variation in the distribution of caterpillars to be assessed. Plants were checked in a different order on each night to avoid possible artefacts due to larval activity rhythms. On each occasion, the foliage of all marked plants was carefully examined at close range using a headlamp to detect active caterpillars. We recorded the taxonomic identity of every caterpillar observed and marked one leaf of the whorl on which it was feeding. Different colours of plastic tape were used for marking on different dates.

Herbivory level

For every current year leaf in all marked and control whorls the proportion of leaf area removed by the end of the larval growth season was estimated. Individual leaves were classified into one of 6 herbivory classes according to the percentage leaf area removed: 0, no signs of herbivory; 1, 1–5% area removed; 2, 6–25%; 3, 26–50%; 4, 51–75%; and 5, > 75%. An overall estimate of herbivory level for each leaf whorl was obtained as:

$$\bar{H} = \frac{\sum_{i=1}^{i=5} n_i H_i}{\sum_{i=0}^{i=5} n_i}$$

where n_i = number of leaves in herbivory class i , and H_i = midpoint of herbivory class i , as defined above. \bar{H} represents a weighted average of the proportion of area removed per leaf in each whorl. Reduction of a continuous measurement scale (percentage leaf area removed) to an ordinal one (the class score used here) may lead to biased estimates of mean herbivory (Williams & Abbott 1991), but this analytical simplification allows for more extensive sampling and thus larger sample sizes. Furthermore, in our study system there are no reasons to expect that potential biases would have a differential effect on the estimates

obtained for different plants or plant parts, hence estimates may be properly used for comparative purposes (see, e.g. Dirzo & Harper 1982; Fox & Morrow 1983; Núñez-Farfán & Dirzo 1988; Alliende 1989; for applications of similar herbivory indices).

Mean values of herbivory level were computed for control and marked whorls of all marked plants (except for a plant without caterpillar records and thus lacking marked whorls), and compared using paired t-tests. As expected, average herbivory levels were significantly greater in marked whorls than in control ones ($t = 5.48$, $N = 27$, $P < 0.0001$). This indicates that, although our sampling scheme was incomplete (only two observation nights a week), the observations provided a reliable assessment of the distribution of caterpillars within plants.

DATA ANALYSIS

For among-plant comparisons, plant means were computed for variables measured repeatedly within plants (architectural traits and herbivory level). However, measurements from control and marked whorls should not have the same influence on plant means. Control whorls are a random subset of all those remaining unmarked on a plant, while marked ones represent a complete enumeration of a subset that is determined by the presence of caterpillars on particular dates, and it is potentially nonrandom if caterpillars select the leaf whorls on which they feed. We therefore calculated weighting factors for control and marked whorls in each plant (F_C and F_M , respectively), and used them to compute weighted plant means. Weighting factors were calculated for each plant as

$$F_C = [(W_T - W_M) / W_T] / W_C, \text{ and}$$

$$F_M = (W_M / W_T) / W_M,$$

where W_M = number of marked whorls, W_C = number of control whorls and W_T = total number of leaf whorls on the plant.

Nonparametric statistical methods were used whenever data departed from normality or normality tests could not be performed reliably due to small sample sizes. Statistical analyses, unless otherwise stated, were conducted using procedures in the SAS package (SAS Institute 1989). The significance of differences among plant means was tested with Kruskal–Wallis analysis of variance (NPAR1WAY procedure). Relationships between variables were assessed using regression methods (REG procedure), and the significance of regression coefficients was tested using randomization methods (Noreen 1989; Manly 1991) when variables did not fulfil normality requirements. Within-plant differences between marked and control whorls were analysed using paired t-tests.

Results

AMONG-PLANT VARIATION

Plants differed both in size and architectural traits. There was broad variation in height (range 45–140 cm), number of leaf whorls (3–275), and both major (30–380 cm) and minor (10–170 cm) plant diameters. Plants also differed significantly in mean length ($H_{27} = 180.0$, $P < < 0.0001$) and mean basal diameter ($H_{27} = 222.7$, $P < < 0.0001$) of stems, mean number of leaves per whorl ($H_{27} = 150.7$, $P < < 0.0001$), and mean branching order of leaf whorls ($H_{27} = 120.9$, $P < < 0.0001$) (data for control and marked whorls combined for each plant).

We recorded 337 noctuid larvae over 22 observation nights. Both mean herbivory levels and herbivore loads differed widely between plants (Fig. 2). There was statistically significant individual variation in both the number of caterpillars recorded per observation session ($H_{27} = 133.4$, $P < < 0.0001$) and in the proportion of leaf area removed by the end of the study ($H_{27} = 118.4$, $P < < 0.0001$). These two variables were positively correlated across plants ($r_s = 0.508$, $P = 0.007$). A few plants had both high herbivory levels and comparatively few larval records (Fig. 2), and the significance of the relationship increases dramatically after removing these outliers from the analysis ($r_s = 0.764$, $P = 0.00003$). No information is available to explain the occurrence of these outliers, but the overall significant association across plants between herbivore load and herbivory level indicates, at least, that (1) our nocturnal observation scheme was sufficient to detect individual variation in caterpillar abundance; (2) observed differences among plants in leaf damage were consistent with differences in the abundance of herbivores; and (3) either can be used to describe individual variation in the incidence of herbivores.

To evaluate the influence of plant features on herbivore load and herbivory level, we conducted separate multiple linear regressions for each dependent variable (herbivore load and herbivory level) using a stepwise method. The independent variables con-

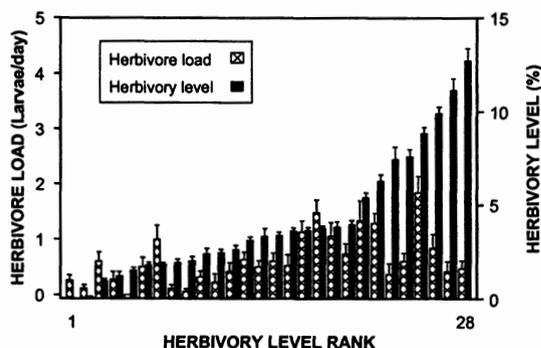


Fig. 2 Individual variation in mean (+ SD) herbivore load (caterpillars recorded/observation day) and herbivory level (% leaf area removed) in *Daphne laureola* plants.

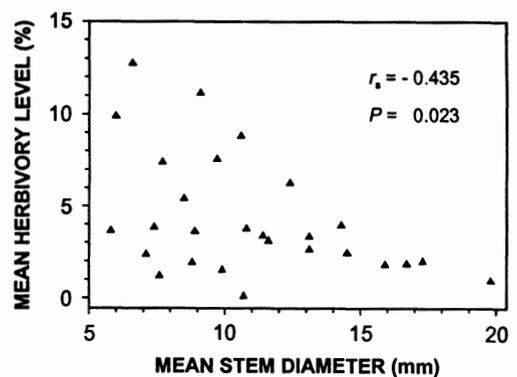


Fig. 3 Relationship between mean herbivory level (% leaf area removed) and mean basal stem diameter of individual *Daphne laureola* plants.

sidered were total number of leaf whorls, the square root of the product of major and minor diameters, plant height, and the weighted plant means for stem basal diameter, stem length, and number of leaves and branching order of leaf whorls. The significance level of those variables showing the largest effects were computed using randomization methods. Only total number of leaf whorls and the mean basal diameter of stems had significant effects on herbivory level and herbivore load (Table 1). Across plants, herbivore load was directly related to number of leaf whorls and inversely (although only marginally significant) to mean basal stem diameter. Herbivory level was inversely related to mean basal stem diameter (Fig. 3), with damage being predictably smallest among plants with the thickest stems. None of the other plant traits considered exhibited significant relationships with either herbivory level or herbivore load.

WITHIN-PLANT VARIATION

The difference between marked and control whorls in average stem basal diameter, stem length, branching order, and number of leaves was tested using paired t-tests. For each characteristic tested, data pairs were the respective within-plant averages for marked and control whorls. On average, leaf whorls where caterpillars had been recorded had significantly more leaves, lower branching order, and shorter stems than control ones (Table 2). Mean basal diameter was not different in control and marked whorls. These results suggest that caterpillars show some within-plant selection of feeding sites based on structural characteristics of leaf whorls and their supporting stems.

Discussion

AMONG-PLANT VARIATION

The proportion of leaf area removed by invertebrate herbivores has often been used to infer variation in the incidence of herbivores but simultaneous direct counts of the herbivores themselves are rare (e.g. Fritz 1990; Moran & Whitham 1990; Dudd & Shure 1994;

Table 2 Differences in architectural traits between control (no Noctuid larvae recorded) and marked (larvae recorded) leaf whorls. Significance was tested by comparison of control and marked mean values per plant using paired *t*-tests ($N = 27$ plants)

Variable	Population average		<i>t</i>	<i>P</i>
	Control	Marked		
Stem basal diameter (mm)	11.2 ± 3.9	10.4 ± 2.9	1.27	0.1122
Stem length (cm)	78.1 ± 20.4	63.5 ± 18.3	4.60	0.0001
Branching order	2.3 ± 0.5	2.0 ± 0.3	4.01	0.0005
Number of leaves	16.2 ± 3.2	17.9 ± 3.4	3.52	0.0016

Núñez-Farfán & Dirzo 1994). Conversely, studies analysing herbivore loads have not often related them to proportional losses in plant foliage (Cottan *et al.* 1986; Karban & Courtney 1987; Boecklen *et al.* 1990). The significant relationship found across individual plants between herbivore load (number of larvae recorded) and herbivory level (percentage leaf area eaten) indicates that estimates of foliar losses at the end of the season adequately reflected the defoliation intensity experienced by individual plants of *D. laureola*. Thus, at least in this species, measurements of leaf area removed may be reliably used to assess the distribution of invertebrate herbivores both among and within plants.

Significant differences were found among plants in levels of natural herbivory. Nevertheless, the observed range of plant means (0.1–12.8%) is considerably narrower than extremes of defoliation levels used in most experimental studies (20–100%; Heichel & Turner 1984; Elmqvist & Gardfjell 1988; Marquis 1988). Mean percentage (\pm SD) of leaf area removed in our study from *D. laureola* plants (4.3 ± 3.3) was similar to those reported in other studies examining herbivory levels under field conditions, which found herbivory means ($3.2 \pm 1.5\%$; Marquis 1988) and ranges of variation (1–9%, Dudd & Shure 1994; 5–9% and 0.9–7%, Cottan *et al.* 1986) much smaller than those used in experimental studies. These findings highlight the need for conducting pilot studies under natural conditions prior to undertaking artificial defoliation experiments. Defoliation treatments should then be chosen to be comparable to herbivory levels commonly faced by plants in the field, rather than only to the extreme figures experienced during herbivore outbreaks.

Individual variations in herbivory levels caused by insect larvae are usually linked to oviposition choice by the parent insects (Rausher 1983). In this study, differences among *D. laureola* plants were significantly related to plant size and structural features. Intensity of herbivory increased with number of leaf whorls, and declined with average basal diameter of stems. The larvae of the noctuid species involved are not specialist on *D. laureola*. Oviposition is therefore not likely to be highly specific, with females laying eggs at ground level in herbaceous plants close to one

of the host species. Female moths ovipositing near *D. laureola* plants might easily discriminate among these plants on the basis of their overall size, as reported for other lepidopteran species (Forsberg 1987; Karban & Courtney 1987); it seems less likely that they could use the basal diameter of stems as a cue in host selection. Larvae of *T. flammea* and *N. janthe* rarely appear to move between *D. laureola* plants (C. Alonso, personal observation), so larval selection between plants cannot explain observed patterns. Differential survivorship of caterpillars (Zangerl & Berenbaum 1993) on plants with stems of different thicknesses, perhaps related to structure-dependent difficulties faced by young larvae in reaching leaf whorls, could partly explain subsequent differences in both frequency of caterpillars and damage experienced by the plants.

The modest defoliation levels experienced by *D. laureola* during this study are representative for the species in the study region (C. M. Herrera, J. L. Yela, unpublished data). Such levels may or may not decrease plant reproduction or survival, but evolutionary responses to the correlation between plant traits and damage would require that the traits involved were heritable. Number and diameter of stems, the traits correlated with herbivory, presumably depend more on plant age, development and location in the habitat than on intrinsic plant features. Noctuid moth larvae therefore seem unlikely to act as selective agents on *D. laureola*, at least for the traits considered here.

WITHIN-PLANT VARIATION

Within plants, larvae occurred most frequently in leaf whorls characterized by lower branching order, shorter stems, and greater number of leaves. Since caterpillars are presumably unable to detect differences among leaf whorls in chemical or physical properties of foliage, if any, until they have reached the leaves (Schultz 1983), these results indicate that structural traits of stems are used as cues while accessing feeding sites. Larvae did not appear to discriminate among stems at ground level, as there were no significant differences between the basal diameters of control and marked whorls of the same plant, instead selection occurred at stem forks, favouring the shortest possible route to a leaf whorl (lower branching order).

Foliage is patchily distributed within *D. laureola* plants, occurring in the form of dense clusters of leaves separated by a network of rewardless stems. The nonrandom, architecture-related distribution of larvae among leaf whorls may thus reflect (1) a selective response to differences in the amount of foliage, aimed at increasing the food value of the patch chosen; (2) a behavioural response to the contrasting costs associated with foraging along stems of different length, directed at decreasing the movement costs required to reach the food patch; or (3) a combination of these two effects. The first explanation seems unlikely, since all leaf whorls provide a virtually unlimited food supply to larvae (the maximum amount of foliage that an individual larva can ingest during a feeding bout is some orders of magnitude smaller than the amount of foliage available). This is supported by the observation that 96.2% of marked whorls had mean herbivory levels < 30%, and no whorl was ever found with an herbivory level > 70% (despite potential re-visitation of the same leaf whorl on different dates). In contrast, larvae tended to occur most frequently in whorls with shorter stems, suggesting a role for movement costs in explaining their distribution within plants.

Schultz (1983) proposed that caterpillar face trade-offs among feeding costs, predation risks, and movement costs, and suggested that the last factor is the most important in nocturnal caterpillars. This suggestion is consistent with our interpretation of within-plant larval distribution, and also with the foraging behaviour exhibited by *T. flammaea*. Green-coloured larvae of this species, cryptic to visually orientated enemies, remained feeding on the same leaf whorl for several consecutive nights, thus reducing movement costs to a minimum. When risks increased as a consequence of colour change, the foraging pattern was altered to a daily movement between feeding sites in leaf whorls and hiding places beneath the plants. If reducing the movement actually diminishes foraging costs and, subsidiarily, reduces the duration of the larval period and also decreases predation risk, there could be selection for the use of architectural traits as cues for accessing foraging sites. Given the polyphagous behaviour of *T. flammaea* in this region, it is surprising that the species displays finely tuned behaviour when feeding on both *D. laureola* and other plant species (when feeding on *Narcissus longispathus*, *T. flammaea* also shows a colour-dependent activity pattern; C. M. Herrera, unpublished data). Thus the polyphagous condition does not necessarily mean reduced capabilities to adjust individual foraging behaviour to the characteristics of different host plants.

CONTRASTS BETWEEN AMONG- AND WITHIN-PLANT VARIATION

Correlates of herbivory load have been found to differ at the among- and within-plant levels. Among plants,

Table 3 Percentage of total population variance in architectural traits of leaf whorls that was accounted for by variation among and within plants

Variable	Among plants	Within plants
Stem basal diameter	36.0	64.0
Stem length	21.9	78.1
Branching order	22.0	78.0
Number of leaves	25.6	74.4
Average	26.4	73.6

differences in herbivore load are related to variation in number of whorls and (marginally) to mean stem diameter, while within plants they are related to variation in stem length, branching order, and number of leaves per whorl. This discrepancy may be attributed to differences between the choices exerted by ovipositing moths (among plants) and by the larvae (within plants), and probably depend on the relative amounts of variability exhibited by the studied traits at the two scales. For the architectural traits examined, the within-plant component accounted for roughly three times as much variance as the among-plant component (Table 3), thus providing considerable opportunities for larvae to take advantage of structural cues. Ovipositing females, on the other hand, were most likely constrained to use other cues in their selection, such as the number of leaf whorls. Insects may not use the same plant features when decisions are taken at different life history stages, or may be unable to do so. Ultimately, the implications of this phenomenon will depend on whether or not discrimination among conspecific plants (Rausher & Papaj 1983; Forsberg 1987; Karban 1992) or within plants (Whitham 1983) has demographical consequences for the insect species involved. In the case of *D. laureola*, further studies are needed to assess these demographical consequences.

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