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The community-wide and guild-specific effects of pubescence on the folivorous insects of manzanitas *Arctostaphylos* spp.

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Abstract. 1. Insect communities on 26 species of manzanita *Arctostaphylos* spp. (Ericaceae) were sampled in order to examine the effects of variation in foliar pubescence traits on a community of folivorous insects. Manzanitas vary widely in pubescence density, length, and glandularity both within and between species.

2. Linear models were fitted and evaluated to determine whether pubescence traits are associated with the species richness and abundance of folivorous insects after accounting for the effects of other relevant habitat and host-plant related characteristics.

3. Pubescence traits were clearly associated with both community-wide and guild-specific variation in the structure of the folivorous insect community of manzanitas, however the effects of pubescence were manifested primarily as effects on the abundance of folivores not on species richness. The species richness of folivorous insects on manzanitas was not associated with pubescence density or length but was associated positively with glandularity.

4. The abundance of all guilds except leaf-mining insects was lower on manzanitas having longer pubescence. In contrast, the abundance of external-chewing insects was higher on plants having denser pubescence and on plants having glandular pubescence.

5. Overall, the results suggest that both longer pubescence and the amount of contact between an insect and pubescence act quantitatively to decrease the abundance of external-feeding guilds of folivorous insects. The abundance of species in internal-feeding guilds that oviposit directly on leaves is unrelated to foliar pubescence traits in the host plant.

Key words. Abundance, *Arctostaphylos*, feeding guild, foliage, insects, manzanitas, pubescence, species richness.

Introduction

Numerous studies have shown that variation in glandularity or in trichome shape, length, and density can affect individual species of insects in at least four ways (Levin, 1973; Johnson, 1975; Turnipseed, 1977; Ribeiro *et al.*, 1994; Webster *et al.*, 1994). (1) Trichomes may prevent or enhance oviposition by affecting the security with which eggs are attached to leaves (Turnipseed, 1977; Khan & Agarwal, 1984; Ramalho *et al.*, 1984; Baur *et al.*, 1991; Lambert *et al.*, 1992; Webster *et al.*, 1994; Oghiakhe, 1995; Haddad & Hicks, 2000). Several studies have shown that glandular pubescence or dense pubescence are correlated with higher rates of oviposition, but at least one study found the opposite effect (higher: Lukefahr *et al.*, 1971; Benedict *et al.*, 1983; Navasero & Ramaswamy, 1991; Navon *et al.*, 1991; McAuslane, 1996; lower: Webster *et al.*, 1975). (2) Trichomes may interfere with the rate of movement of an insect over the leaf surface (Ramalho *et al.*, 1984; Gannon *et al.*, 1994; Webster *et al.*, 1994; Oghiakhe, 1995; Eisner *et al.*, 1998; Zvereva *et al.*, 1998; Malakar & Tingey, 2000). Hooked trichomes may even puncture or entrap insects trying

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to move over the leaf surface (Gilbert, 1971; Quiring *et al.*, 1992; Eisner *et al.*, 1998). Glandular exudates from trichomes may repel, attract, adhere to, or be toxic to insects that encounter them (Tingey & Gibson, 1978; Duffey, 1986; Lapointe & Tingey, 1986). (3) Insects that encounter trichomes while feeding may be inhibited from feeding or may suffer reduced growth, fecundity, and survival because trichomes are lower in nutritional quality than other leaf tissues (Benedict *et al.*, 1983; Lapointe & Tingey, 1986; Navon *et al.*, 1991; Lambert *et al.*, 1992; Papp *et al.*, 1992; Haddad & Hicks, 2000). (4) External-feeding insects that are small enough to live sheltered within the layer of foliar pubescence may be protected from natural enemies and/or moisture loss (Elsey, 1974; Treacy *et al.*, 1986; Ezcurra *et al.*, 1987; Woodman & Fernandes, 1991; Eisner *et al.*, 1998), however hooked and glandular trichomes can also cause direct mortality (Gilbert, 1971; Tingey & Gibson, 1978; Quiring *et al.*, 1992; Eisner *et al.*, 1998).

While studies on the effects of pubescence on individual species of insect are common, little empirical information is available, and no general theories have been proposed regarding the community-wide or guild-specific effects of pubescence on folivorous insects. Two studies that have made predictions about the effects of host-plant defences on the community of folivorous insects may provide some guidance in developing such general theories.

Mattson *et al.* (1988) examined all feeding guilds of folivorous insects and concluded that as the relationship between an insect and the tissues of the host plant becomes more intimate, the insect will be more susceptible to host-plant defences. They quantified the *intimacy of association* of each insect species with the host plant by a host intimacy rank, and calculated ranks as the 'proportion of the life cycle spent in intimate contact with living tissue × the proportion of body surface area exposed directly to host tissue.' Under their hypothesis, insects could escape the effects of pubescence either by spending little time in contact with tissue or by having a large body size. Using these rankings, Mattson *et al.* (1988) predicted that among the leaf-eating guilds, gall-forming insects would be the most susceptible to host-plant defences, such as tough tissues or toxic chemicals. Leaf-mining insects would be almost as susceptible as gall-formers, and sap-sucking insects would rank third in degree of susceptibility to host-plant defences. Finally, chewing insects that feed externally would have the lowest intimacy rank both because they are not embedded in host plant tissues like leaf-miners and gall-formers, and because a smaller proportion of their larger-sized bodies contacts the host plant.

In contrast, Cornell (1989) pointed out that leaf-mining and leaf-galling insects tend to be very small bodied and often feed selectively on specialised leaf tissues (DeClerck & Shorthouse, 1985; Kimmerer & Potter, 1987; Scheirs *et al.*, 1997, 2000, 2001), and suggested that the capacity for specialised feeding would allow leaf-mining and leaf-galling insects to be more successful than external-feeding insects in avoiding contact with structural and chemical defences within the host leaf.

Despite their differing predictions about guild-specific effects, Mattson *et al.* (1988) and Cornell (1989) agreed that the success of an insect will be inversely proportional to the amount of contact with host-plant defences. The amount of contact with host defences will be a function of the duration of contact and the body size of the insect. Extending Mattson *et al.*'s (1988) and Cornell's (1989) reasoning, the hypothesis proposed here was that the abundance and species richness of folivorous insects will be associated negatively with the level of pubescence of the host plant (density or length). Furthermore, it was hypothesised that the abundance and species richness of feeding guilds that avoid or have little contact with pubescence will be largely unaffected by foliar pubescence. Generally, sap-sucking insects will have the highest duration of contact with pubescence because they feed externally on foliage during both the juvenile and adult stages. Chewing insects contact leaf surfaces either mainly as juveniles (Lepidoptera) or as adults (Coleoptera). Although the orthopteroid orders contact leaf surfaces as juveniles and adults, it is conjectured that they escape the effects of pubescence due to their larger body size. It is expected that leaf-mining and leaf-galling insects will contact the leaf surface only at oviposition and emergence, however exceptions occur among some species of leaf-mining and gall-forming insect that can contact leaf surfaces transiently as they search for locations to initiate new mines or galls. Given their duration of contact with foliar pubescence, the abundance and species richness of sap-sucking insects should suffer the greatest negative effect, while leaf-mining and leaf-galling insects should experience the smallest negative effect. The effect of pubescence on chewing insects should fall between those of sap-sucking and mining and galling insects.

Pubescence may also have effects that are not proportional to the amount of contact, but rather depend on the mechanism by which pubescence affects folivorous insects (i.e. ovipositional interference, locomotory interference, feeding interference, and protection from natural enemies and moisture loss). For example, many species of sap-sucking insect are largely sedentary, so they may contact pubescence less than do more mobile insects. The ideas that the effects of pubescence on folivorous insects may be functions of the mechanism of effect, duration of contact, and an insect's body size are combined into a set of guild-specific predictions about the likely effects of variation in pubescence characteristics (Fig. 1). For example, if ovipositional interference is the primary mechanism by which pubescence affects folivorous insects, it is predicted that the abundance and species richness of guilds whose members oviposit directly on or into leaves will be affected adversely in proportion to the amount of pubescence (density or length). These predictions about the effects of pubescence on each guild, each mechanism of effect, and as a function of an insect's body size, are presented in Fig. 1.

To test these predictions, the relationship between foliar pubescence traits and community-wide and guild-specific species richness and abundance for the folivorous insects of manzanitas *Arctostaphylos* spp. were examined. Because

		Potential mechanistic effects of pubescence							
		Ovipositional		Locomotory		Feeding		Protection	
	Body size	Small	Large	Small	Large	Small	Large	Small	Large
Feeding guild	Chewing insects	–	–	–	None	–† None‡	–	+	None
	Sap-sucking insects	–	–	–	None	None	None	+	None
	Leaf-miners	–	NA	None	NA	None	NA	None	NA
	Leaf-gallers	–	NA	None	NA	None	NA	None	NA

†Prediction if small-bodied chewers ingest trichomes.
‡Prediction if small-bodied chewers avoid ingesting trichomes.

Fig. 1. The predicted effects of foliar pubescence traits on the guild-specific species richness and abundance of folivorous insects. – indicates that pubescence is predicted to be associated with lower species richness and abundance. + indicates that pubescence is predicted to be associated with higher species richness and abundance. 'None' indicates that pubescence is predicted to have no effect. 'NA' indicates that no prediction is applicable because these guilds comprise entirely small-bodied insects (Cornell, 1989; Connor & Taverner, 1997). Note that protective effects could only be positive or none, feeding and locomotory effects could only be negative or none, and ovipositional effects could be negative, positive, or none.

manzanitas vary in their pubescence traits from simple (hair-like) to glandular, from glabrous to dense, and from short to long, they are a convenient system with which to test the effects of pubescence on a community of folivorous insects. By examining the effects of pubescence within a single plant genus, variation in host-plant chemical defences and structural traits that may confound comparisons made between species in different genera or families should be minimised. Do pubescence traits affect the abundance or species richness of feeding guilds within the community of folivorous insects on manzanitas after accounting for habitat and host-plant related characteristics (e.g. geographic range, growth form, leaf size, habitat type)? To answer this question, a sampling regime was implemented to estimate species richness, abundance, and herbivory of the community of folivorous insect species on manzanitas varying in pubescence characteristics. Linear models relating the effects of pubescence traits on the species richness, abundance, and herbivory of the community of folivorous insects associated with manzanitas were built and evaluated.

Methods

Study area and species

In order to examine the effect of variation in the pubescence traits of manzanitas on the community of associated folivorous insects, 26 species of manzanita that varied widely in pubescence density, length, and glandularity were sampled (Table 1). *Arctostaphylos* is divided into two major lineages and species from both lineages were included in the study (Denford, 1981; Hileman *et al.*, 2001). Samples of manzanitas were collected at 27 sites within California's Coast Range between Sonoma and Santa Barbara Counties (39°N, 122°W and 34°N, 120°W) from June to August 1999 (Table 1). Sampling was restricted to sites within the Coast Range in an attempt to reduce environmental differences between study sites but obtain a range of pubescence levels.

Estimating insect abundance, species richness, and chewing damage

To estimate the abundance and species richness of folivorous insects from each species of manzanita at each site, an average of seven shrubs per species per site was sampled independently and randomly. Three twigs from each shrub were randomly selected, bagged, and removed from each shrub, each twig having 50–100 leaves. Among the 26 species of manzanita and 27 sites, a total of 42 manzanita species–site combinations was sampled. Because manzanitas display substantial within-species variation in pubescence traits at different sites, each species–site combination was treated as an independent observation (Table 1).

Most manzanita species at each site were sampled both early and late in the growing season, and early and late season samples for each manzanita species–site combination were combined to obtain estimates of species richness and abundance, however it was not possible to collect at a few sites on both occasions. Some of the estimates of species richness and abundance therefore consisted of the early and late season collections combined, while other samples included data from only one sampling date. Estimates of the total abundance of folivores or the total leaf area sampled were used to account for the effects of variation in sampling effort between species–site combinations on species richness or abundance respectively. Variation in leaf size, the number of shrubs sampled, the size of twigs removed, and the number of times that a species–site combination was sampled all contributed to variation in

Table 1. Sampling sites, manzanita species, and average pubescence traits.

					Pubescence	
Site	Habitat	Growth form	Species	Glandular	Density (number/mm^2)	Length (mm)
R. L. Stevenson State Park	Mixed	Shrub	*A. canescens*	Absent	210.6	0.27
R. L. Stevenson State Park	Mixed	Tree-like	*A. manzanita*	Absent	9.6	0.20
Sugarloaf Ridge State Park	Oak Wood	Tree-like	*A. viscida*	Absent	23.4	0.25
Harrison Grade Road	Chaparral	Shrub	*A. bakeri*	Absent	47.5	0.29
Austin Creek Recreation Area	Oak Wood	Tree-like	*A. viscida*	Absent	59.2	0.28
Mt George	Chaparral	Shrub	*A. stanfordiana*	Absent	0.8	0.11
Mt George	Chaparral	Shrub	*A. canescens*	Absent	154.2	0.32
Bothe-Napa State Park	Oak Wood	Tree-like	*A. manzanita*	Absent	42.2	0.27
Mt Tamalpais State Park	Chaparral	Shrub	*A. glandulosa*	Present	57.6	0.34
Mt Tamalpais State Park	Chaparral	Shrub	*A. canescens*	Absent	144.2	0.48
Mt Tamalpais State Park	Chaparral	Prostrate	*A. hookeri*	Absent	50.5	0.20
Bolinas Ridge	Chaparral	Shrub	*A. glandulosa*	Present	49.9	0.34
Bolinas Ridge	Chaparral	Shrub	*A. nummularia*	Absent	30.1	0.42
Bolinas Ridge	Chaparral	Tree-like	*A. virgata*	Present	1.8	0.16
El Corte de Madera Preserve	Mixed	Tree-like	*A. regismontana*	Present	69.6	0.43
Anderson County Reservoir	Chaparral	Tree-like	*A. glauca*	Absent	0.1	0.11
China Grade	Mixed	Shrub	*A. nummularia*	Absent	16.2	0.15
China Grade	Mixed	Tree-like	*A. andersonii*	Present	43.6	0.36
China Grade	Mixed	Shrub	*A. tomentosa*	Absent	128.3	0.38
Bonny Doon	Mixed	Tree-like	*A. silvicola*	Absent	189.4	0.48
Bonny Doon	Mixed	Shrub	*A. tomentosa*	Absent	148.4	0.56
Bonny Doon	Mixed	Shrub	*A. nummularia*	Absent	2.8	0.19
Manzanita Park	Dune	Shrub	*A. pajaroensis*	Absent	4.4	0.17
Manzanita Park	Dune	Prostrate	*A. hookeri*	Absent	0.7	0.08
West Fort Ord	Dune	Shrub	*A. tomentosa*	Absent	191.6	0.49
West Fort Ord	Dune	Prostrate	*A. pumila*	Absent	89.5	0.29
Jack's Peak County Park	Chaparral	Shrub	*A. tomentosa*	Present	8.5	0.28
Jack's Peak County Park	Chaparral	Shrub	*A. hookeri*	Absent	0.8	0.08
Toro County Park	Chaparral	Shrub	*A. montereyensis*	Present	7.2	0.23
Toro County Park	Chaparral	Shrub	*A. tomentosa*	Absent	86.4	0.46
Morro Bay State Park	Chaparral	Shrub	*A. pechoensis*	Absent	0.9	0.16
Montana de Oro State Park	Dune	Shrub	*A. morroensis*	Absent	238.1	0.34
Near Morro Bay State Park	Dune	Shrub	*A. sp.*	Absent	248.9	0.33
See Canyon Road	Chaparral	Shrub	*A. pechoensis*	Absent	2.0	0.14
Mt Lowe	Chaparral	Shrub	*A. luciana*	Absent	142.6	0.25
Cuesta Ridge Botanical Area	Mixed	Tree-like	*A. obispoensis*	Absent	73.8	0.34
South Atascadero	Chaparral	Shrub	*A. pilosula*	Absent	108.0	0.23
La Panza Range	Chaparral	Tree-like	*A. glauca*	Absent	0.1	0.00
La Panza Range	Chaparral	Shrub	*A. pilosula*	Absent	51.8	0.34
Burton Mesa	Dune	Shrub	*A. rudis*	Absent	6.3	0.26
Burton Mesa	Dune	Shrub	*A. purissima*	Absent	1.1	0.11
Purissima Hills	Mixed	Shrub	*A. tomentosa*	Absent	2.7	0.19

sampling effort. The total leaf area collected in each sample was estimated using digital photography and image analysis software.

Data on insect abundance, species richness, guild membership, and body size were collected. The abundance and species richness of each feeding guild were estimated by counting and identifying each insect species collected. All insects were identified to family level and each distinct form was assigned to morphospecies. Morphospecies was treated as provisional species for the analyses. Specimens of all intact insect morphospecies were sent to the U.S.D.A. Systematic Entomology Laboratory at the United States National Museum of Natural History for further identification. Each morphospecies was assigned to feeding guilds using the field observations, information in the literature (Stehr, 1987, 1991; Borror *et al.*, 1989), or, in a few instances, information provided by taxonomists associated with the Systematic Entomology Laboratory. The body length of subsamples of specimens of each morphospecies was measured to estimate body size. The community of folivorous insects on manzanitas was divided into four guilds: leaf-mining, leaf-galling, sap-sucking, and chewing insects. Skeletonising and leaf-tying insects were included in the guild of chewing insects.

To estimate the amount of foliar damage caused by skeletonising and chewing insects, the percentage of leaf area either removed or skeletonised for each leaf that had suffered damage from chewing insects was estimated, and the length of the leaf was measured. Digital photography and image analysis software were used to gather length and area data for each leaf in a random sample of 50–100 leaves from each manzanita species at each site. Regression analysis of leaf area on leaf length was performed for each manzanita species at each site. Using measurements for the proportion of leaf area damaged and the length-area regression for each species at each site, the actual leaf area removed or skeletonised by chewing insects in each sample was estimated.

Estimating habitat and host-plant attributes

To account for host-plant related factors other than leaf pubescence that have been suggested to affect insect species richness and abundance, various host-plant attributes were estimated using field and laboratory samples. While visiting each site, each manzanita species was classified into three growth forms (low prostrate shrub <0.5 m, typical shrub 0.5–2 m, and tree-like shrub >2 m); the habitat type (chaparral, oak woodland, mixed evergreen forest, coastal dune) was recorded; and the number of congeneric species of manzanita present was determined. Geographic range was estimated as the number of counties in California in which each species of manzanita is found because only two of the 26 species have distributions that extend beyond California (V. T. Parker and M. Vasey, pers. comm.). Fifty to 100 leaves were sampled randomly from each species at each site, and digital photography and image analysis software were used to estimate average leaf size for each species.

Most studies on the effects of pubescence on insects have examined the effect of variation in pubescence density while only a few studies have examined the effects of pubescence length (Papp *et al.*, 1992; Oghiakhe, 1995). To estimate average pubescence density and length, five to nine plants (median = 6) were selected randomly from each manzanita species at each site, and two or three leaves (median = 2) were selected from each plant. Pubescence density was estimated by counting the number of hairs within one randomly selected square millimetre on the lower surface of each leaf (avoiding major veins) using a dissecting microscope and an ocular micrometer (0.05 mm accuracy) at $\approx 580\times$ magnification. The length of three randomly selected hairs on the lower surface of each leaf was measured at $\approx 600\times$ magnification. In a preliminary analysis, no significant differences in pubescence density or length were found among different leaf age-classes, so leaf ages were not distinguished (Raupp & Denno, 1983).

Statistical analysis

Linear models were fitted and evaluated to determine whether the species richness and abundance of the community of folivorous insects on manzanitas are associated with pubescence traits, after accounting for the effects of other habitat and host-plant related characteristics. The procedure for building and evaluating models consisted of four parts.

Histograms of both untransformed and log-transformed data for species richness and abundance [$\log_{10}(\text{variable} + 1)$] were examined. Histograms of both untransformed and angularly transformed data for the proportion of leaf area damaged were also examined. In general, species richness was approximately Poisson distributed when not transformed. The abundance variables lacked a consistent response, but in most cases were distributed approximately normally when transformed logarithmically. The proportion of leaf area damaged was approximately normally distributed when transformed.

Models appropriate for the underlying distribution of the response variable were fitted. When transformations normalised the distributions of the response variable, ordinary least squares regression was used. When response variables were approximately Poisson distributed, generalised linear models were fitted using a log-link function and accounting for over-dispersion (McCullagh & Nelder, 1989; Agresti, 1996; Connor *et al.*, 1997). Models that included all of the relevant predictor variables were built hierarchically (Table 2). Because none of the predictor variables was highly inter-correlated, multi-colinearity was not a problem.

To account for variation in sampling effort, the total abundance of folivores was forced into each model of species richness, and the total leaf area sampled was forced into each model for the abundance of folivores. Analyses were carried out on the subset of the species–site combinations that were visited twice, and on all species–site combinations for the second sampling period. Because these analyses yielded results that were identical in pattern to those obtained from the full set of data, only the results for the complete set of data are reported here.

The effects of all five of the habitat and host-plant related variables after accounting for sampling effort were examined. Habitat and host-plant related variables that had significant partial t-values were retained. Finally, the effects of pubescence traits after accounting for the effects of sampling effort and relevant habitat and host-plant related variables were tested. Pubescence variables that had significant partial t-values after accounting for the effects of sampling effort and habitat and host-plant related variables were retained. If pubescence traits were included in the final model, variation in species richness or abundance was concluded to be associated with pubescence traits. The final model for each response variable was of the general form:

$$\begin{aligned}\textit{Response variable} &= \textit{sampling effort} + \textit{significant habitat}\\ &\quad \textit{or host-plant related variables}\\ &\quad + \textit{significant pubescence variables}\end{aligned}$$

To determine the adequacy of each model, the residuals from each model were examined to check for outliers and patterns in the data. Finally, to determine whether each

Table 2. Descriptions of the response and predictor variables.

Category	Variable (number of groups or categories)	Abbreviations	Units
Response variables	Species richness (four feeding guilds)		Number of species
	Abundance (four feeding guilds)		Number of individuals
	Proportion of leaf area damaged by external-chewing insects (leaf area removed, skeletonised, and combined)		Proportions
Predictor variables			
Sampling effort	Total leaf area sampled		cm^2
Habitat and host plant related	Average leaf size	leaf size	cm^2
	Habitat type [chaparral (hab1), oak woodland (hab2), mixed forest (hab3), or coastal dunes (hab4)]	hab	Categorical
	Plant growth form [prostrate shrub (1), shrub (2), or tree-like shrub (3)]		Categorical
	Number of local species of *Arctostaphylos* spp.	congen	Number of species
	Geographic range of each host plant species	range	Number of counties in California
Pubescence traits	Glandularity (glandular or non-glandular)	gland	Categorical
	Average pubescence density	den	Number of hairs per mm^2
	Average pubescence length	len	mm^2

model accounted for a significant amount of variation in the response variable, or a significant reduction in residual deviance respectively, the *F*-test and R^2-values for each ordinary least squares model and the deviance-difference χ^2-values for each generalised linear model were examined.

Linear models were also fitted using similar procedures to examine the relationships between average body size and pubescence traits for each feeding guild; no adjustment was made for sampling effort.

Results

A total of 7317 arthropod specimens was collected, of which 6265 were folivorous insects. Altogether, 209 distinct insect morphospecies were collected from manzanita foliage. On average, leaf-galling insects occurred in the highest densities, followed by leaf-mining and sap-sucking insects (Fig. 2). Chewing insects occurred at much lower densities. On average, leaf-mining and sap-sucking insects each comprised $>40\%$ of the species of folivorous insect on each host (Fig. 3). Leaf-chewing and leaf-galling insects together accounted for the remaining 17% of species. Although the total number of species of chewing insect was relatively high (54 species; Table 3), the average abundance of chewing insects was low (Fig. 2). Foliar damage by chewing insects accounted for an average of only 2.5% of the total leaf area sampled (Fig. 4). All feeding guilds had body sizes averaging <10 mm in length (Table 3).

Pubescence traits were highly variable both among species and among sites within a single manzanita species. Within species, pubescence density ranged from 2.7 to 191.6 trichomes per mm^2 and length ranged from 0.19 to 0.49 mm (*A. tomentosa*; Table 1). Among all species of manzanita, pubescence density ranged from 0.1 to 248.9 trichomes per mm^2, and length ranged from <0.01 mm to 0.56 mm (Table 1). Because there was no strong correlation between pubescence density and length ($r = 0.643$), these traits were treated as independent response variables. Six species of manzanita and seven of the 42 species–site combinations had glandular trichomes.

Effects of pubescence on community structure

The community-wide and guild-specific species richness of folivorous insects on manzanitas was not associated with pubescence density or length (Table 4), however the total

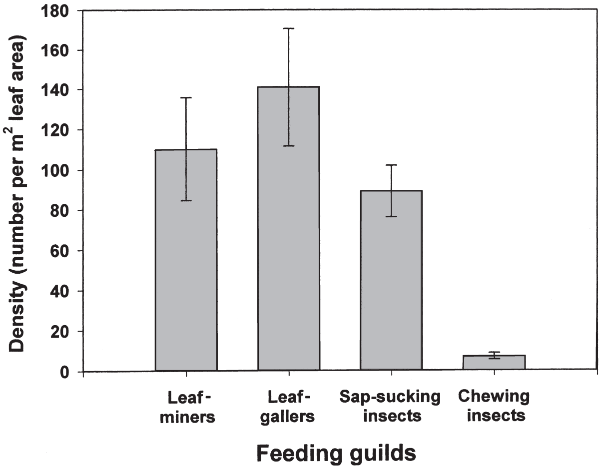


Fig. 2. Abundances of each feeding guild on species of manzanita at sample sites in California (mean ± SE).

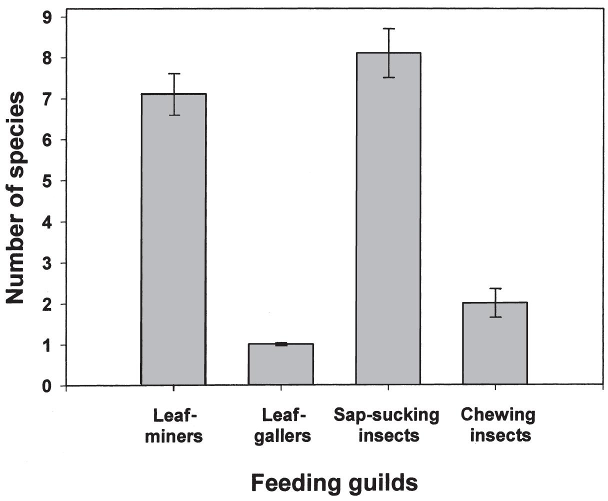


Fig. 3. Species richness of each feeding guild on species of manzanita at sample sites in California (mean ± SE).

abundance of folivores was associated positively with the presence of glandular trichomes (Table 4). Although the presence of glandular trichomes factored into the final models for the species richness of sucking and chewing insects with significant partial *t*-values, the deviance-difference χ^2 revealed that the overall model did not result in a significant reduction in residual deviance. Models were not built for the species richness of galling insects because this guild was represented by a single species.

On the other hand, pubescence traits had strong community-wide and guild-specific effects on the abundance of folivorous insects on manzanitas. The abundance of all folivorous guilds except leaf-mining insects was associated negatively with pubescence length (Table 5). The negative association between folivore abundance and pubescence length occurred both within and among manzanita species (Fig. 5). In contrast, chewing insects were higher in abundance on plants with denser pubescence and on plants bearing glandular trichomes (Table 5). None of the pubescence variables influenced the amount of damage caused by chewing insects on manzanitas (Table 6).

No community-wide associations were detected between the body sizes of folivores and pubescence traits, and only one association for guilds. The average body size of chewing insects was higher on plants with glandular trichomes ($F_{4,37} = 4.838$, $P < 0.01$) than on plants lacking glandular trichomes.

Table 3. Total species richness and average body size of each folivore guild.

Guild	Total species richness	Average body size (mm) (±SE)
Leaf-miners	42	6.13 (1.24)
Leaf-gallers	1	1.40 (0.00)†
Sap-sucking insects	58	3.63 (0.24)
Chewing insects	54	9.03 (0.79)

†Standard error is zero because the calculation for average body size is based on a single species.

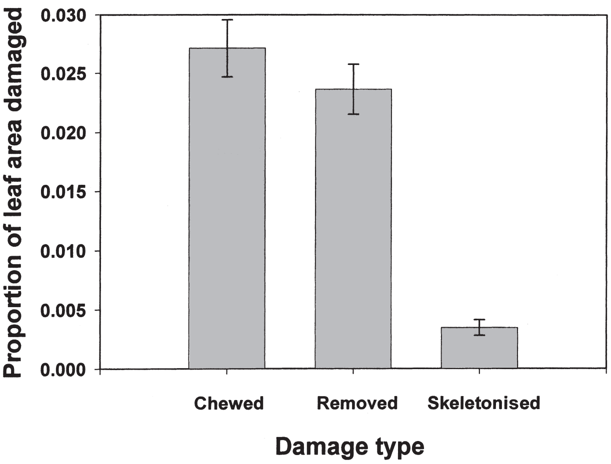


Fig. 4. Average proportion of leaf area damaged by external-chewing insects on species of manzanita at sample sites in California (mean ± SE). The values for chewed equal the sum of the leaf area skeletonised and the leaf area removed completely.

Effects of habitat and host-plant related variables

Some of the habitat and host-plant variables were associated with community-wide or guild-specific variation in folivore abundance and species richness (Tables 3, 4, and 5). The species richness of leaf-mining insects differed among habitat types, and sucking insects were more abundant on shrubs with larger leaves. Folivore abundance was greatest on manzanitas in coastal dune and oak woodland habitat and lowest in chaparral and mixed forests. Manzanitas occurring sympatrically with more congeneric species had lower abundances of leaf-galling and chewing insects. Species of manzanita with wide geographic ranges suffered greater damage from chewing insects.

Discussion

Pubescence traits are clearly associated with both community-wide and guild-specific variation in the structure of the community of folivorous insects on manzanitas, however the effects of pubescence are manifested primarily as effects on folivore abundance not on species richness (Tables 4 and 5). The total abundance of folivores and the abundance of most feeding guilds were associated negatively with pubescence length (Table 5, Fig. 5). Leaf-mining insects were the only guild whose abundance was not associated with pubescence length or any other pubescence trait. In addition, the abundance of chewing insects, while associated negatively with pubescence length was associated positively with pubescence density and the presence of glandular trichomes

Table 4. Linear models for the species richness of folivorous insects on manzanitas. The sign of the coefficients for all habitat, host plant, and pubescence variables indicates the nature of the association with the response variable. Blank entries in the table indicate that either no habitat and host-plant variables or no pubescence traits were retained in the model. See Table 2 for definitions of abbreviations.

Response variables†	Constant	Herbivore abundance	Habitat and host-plant variables‡	Pubescence traits	Model§	χ^2	d.f.	*P*
All folivores	2.635	0.0015		0.228(gland)¶	GLM	58.90	39	0.021
Leaf-miners	1.335	0.0021	0.046(hab 1) + 0.138(hab 2) + 0.245(hab 3) − 0.429(hab4)		GLM	25.52	37	0.923
Sucking insects	1.877	0.0012	0.0326(leaf size)	0.323(gland)¶	GLM	32.80	38	0.708
Chewing insects	0.236	0.0029		0.400(gland)¶	GLM	28.17	39	0.900

†Species richness of leaf-galling insects is not relevant because there is only one species in this guild.

‡Habitat type and plant growth form are categorical variables. The regression coefficients shown for categorical variables are the effects for each of the k treatment levels rather than the $k-1$ model coefficients.

§Regression methods: GLM = generalised linear model.

¶Values for glandularity represent *presence* of glandular trichomes.

(Table 4). There was no evidence that pubescence levels affected large- or small-bodied folivores differentially on manzanitas.

Species richness of folivorous insects on manzanitas

The lack of an association between pubescence length or density and the community-wide or guild-specific species richness of folivorous insects on manzanitas could arise for a variety of reasons. The sampling techniques may have underestimated the species richness of chewing insects that may shelter during the day on plant parts that were not sampled. Furthermore, the estimates of species richness are based on morphospecies so such estimates are only preliminary. It seems unlikely, however, that either the underestimation of the richness of chewing insects or the pattern of over splitting or lumping of animals into morphospecies would mask strong associations between species richness and pubescence traits. Rather, the lack of an effect of pubescence on species richness, coupled with the observed reduction in abundance, indicates that pubescence traits seldom result in complete exclusion of a folivore, and thus no concomitant reduction in species richness.

Most of the habitat and host-plant traits were not associated with the species richness of folivorous insects on manzanitas (Table 4), however habitat type was associated with the species richness of leaf-mining insects. More species of leaf-mining insect were observed in oak woodland and mixed-forest habitats than in chaparral or coastal dune habitats. Two species of leaf-miner, *Marmara arbutiella* and *Coptodisca arbutiella* (Lepidoptera: Gracillariidae and Heliozelidae respectively), are known to use both *Arbutus* and *Arctostaphylos* as host plants (J. Powell, pers. comm.). *Arbutus menziesii* occurs in mixed forest habitats with *Arctostaphylos*. No leaf-mining insects are reported to use both *Quercus* and *Arctostaphylos* (Opler, 1974). Perhaps the observed habitat difference in species richness is related to microclimate differences and the availability of alternative hosts.

Abundance of folivorous insects on manzanitas

The strong negative association between both community-wide and guild-specific abundance for chewing, sap-sucking, and leaf-galling insects and pubescence length was unexpected. Many studies have documented an effect of pubescence density and glandularity on the abundance, herbivory, larval activity, and oviposition for species of chewing and sap-sucking insects (Smith & Poos, 1931; Becerra & Ezcurra, 1986; Khan *et al.*, 1986; Danielson *et al.*, 1987; Dimock & Tingey, 1988; Doss & Shanks, 1988; Soetens *et al.*, 1991; Goertzen & Small, 1993; Palaniswamy & Bodnaryk, 1994; Kanno, 1996; Malakar & Tingey, 1999; Chu *et al.*, 2000; among others). Yet, few studies have examined the effects of pubescence length on folivores (Turnipseed, 1977; Papp *et al.*, 1992; Webster *et al.*, 1994; Oghiakhe, 1995). The lack of an effect of pubescence density on the abundance of most guilds, however, and an effect opposite in sign to that of pubescence length for chewing insects, suggests that these traits may pose different obstacles to most folivore guilds.

The negative association between pubescence length and abundance for external-feeding guilds may be caused by locomotory or feeding interference. The fact that the abundance of leaf-mining insects on manzanitas is not associated with any pubescence trait suggests that interference with oviposition is unlikely to account for the lower abundance of external feeding guilds on plants with longer pubescence. Most leaf-mining insects contact the leaf surface only transiently, and oviposit by either cementing their eggs to the leaf surface or by inserting their eggs into the leaf (Connor & Taverner, 1997). Therefore, if longer pubescence is primarily an impediment to oviposition, it should also have resulted in lower abundance for leaf-mining insects.

The sole leaf-galling insect observed to attack manzanitas, *Tamalia coweni* (Homoptera: Aphidae), may also be affected by locomotory or feeding interference. Unlike many other leaf-galling insects that oviposit directly into the host leaf, *Tamalia coweni* lays its overwintering eggs at the base of the plant and must walk up to the leaves of the

Table 5. Linear models for the abundance of folivorous insects on manzanitas. The sign of the coefficients for all habitat, host-plant, and pubescence variables indicates the nature of the association with the response variable. Blank entries in the table indicate that either no habitat and host-plant variables or no pubescence traits were retained in the model. See Table 2 for definitions of abbreviations.

Response variables	Constant	Leaf area	Habitat and host-plant variables†	Pubescence variables	Model‡	F or χ^2	d.f.	P	R^2
All folivores	1.736	0.0001	-0.090(hab 1) + 0.074(hab 2) − 0.285(hab 3) + 0.301(hab 4)	-1.032(len)	OLS	16.38	5,36	2.03×10^{-8}	0.695
Leaf-miners	0.911	0.0001			OLS	10.35	1,40	0.00256	0.206
Leaf-gallers	1.867	0.0001	0.020(hab 1) − 0.084(hab 2) − 0.462(hab 3) + 0.526(hab 4) − 0.231(congen)	-1.411(len)	OLS	11.23	6,35	5.73×10^{-7}	0.658
Sucking insects	1.016	0.0002		-1.109(len)	OLS	27.51	2,39	3.53×10^{-8}	0.585
Chewing insects	1.762	0.0003	-0.457(hab 1) + 0.717(hab 2) − 0.977(hab 3) + 0.717(hab 4) − 0.251(congen)	0.917(gland)§ + 0.010(den) − 5.892(len)	GLM	161.14	33	<0.001	

†Habitat type and plant growth form are categorical variables. The regression coefficients shown for categorical variables are those associated with each category rather than the coefficients used in making the calculations.

‡Model: OLS = ordinary least squares, GLM = generalised linear model.

§Values for *glandularity* represent *presence* of glandular trichomes.

plant in order to initiate galls (Valenti & Gaimari, 1992; Miller, 1998). If pubescence prevents the wingless, parthenogenetic stem mother from moving over or probing into plant tissues, it could account for the reduced abundance found on plants with longer pubescence.

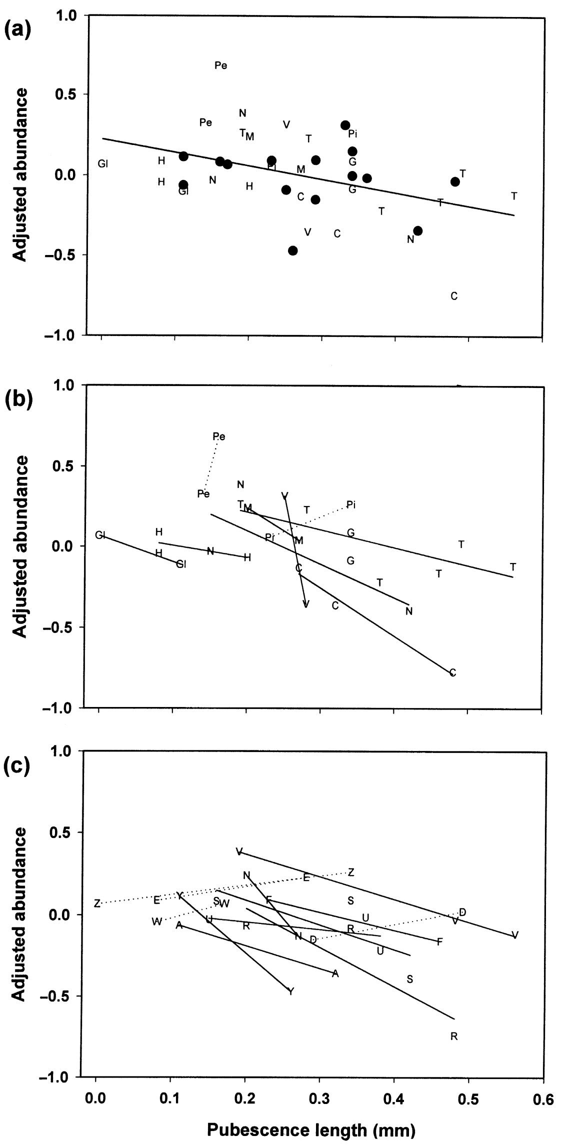


Fig. 5. The relationship between the abundance of all folivores and pubescence length after adjusting for sampling effort and other relevant habitat and host-plant related variables. The residual from the model folivore abundance = 1.736 + 0.001(leaf area) − 0.090 (habitat1) + 0.074(habitat2) − 0.285(habitat3) + 0.301(habitat4) is plotted on the *y* axis. (a) All combinations of species and sites. Solid circles represent manzanita species that were sampled at only one site. Species of manzanita sampled at two or more sites are represented by letters (C – *A. canescens*, G – *A. glandulosa*, GL – *A. glauca*, H – *A. hookeri*, M – *A. manzanita*, N – *A. nummularia*, Pe – *A. pechoensis*, Pi – *A. pilosula*, T – *A. tomentosa*, V – *A. viscida*). (b) Only species of manzanita sampled at more than one site. Lines represent the best-fit linear trend within species among sites (solid = positive, dotted = negative). (c) Sites where multiple species of manzanita were sampled (A – Mt George, D – West Fort Ord, E – Jack's Peak County Park, F – Toro County Park, N – R. L. Stevenson State Park, R – Mt Tamalpais State Park, S – Bolinas Ridge, U – China Grade, V – Bonny Doon, W – Manzanita Park, Y – Burton Mesa, Z – La Panza Range). Lines represent the best-fit linear trend among species within each site.

The abundance of chewing insects was also associated positively with pubescence density and glandularity, contrary to expectation (Table 5). A few studies have reported positive effects of pubescence density on oviposition and on the abundance of individual species of chewing insect (Robinson *et al.*, 1980; Lambert & Kilen, 1989; Navon *et al.*, 1991). Such positive associations could arise because of protection from desiccation or natural enemies, or if chewing insects prefer or can oviposit more effectively on leaves with dense pubescence (Treacy *et al.*, 1986; Eisner *et al.*, 1998). Glandular pubescence has been found to provide protection for sucking insects against their natural enemies (Belcher & Thurston, 1982; Obrycki & Tauber, 1984; Lovinger *et al.*, 2000). Alternatively, the higher abundance of chewing insects, and the higher species richness of folivores, in general, on glandular manzanitas may simply be a by-product of the fact that these folivores are more likely to be stuck on glandular leaf surfaces at the time of sampling, rather than being evidence that greater numbers of individuals or species of folivore are associated with plants having glandular pubescence.

The results contrast with the only other community-level study of the effects of pubescence on folivorous insects. Ezcurra *et al.* (1987) found that the abundance of sucking insects was higher on pubescent than on glabrous madrones (Ericaceae, *Arbutus xalapensis*), which are related closely to manzanitas (Hileman *et al.*, 2001), however just the opposite effect was found among sap-sucking insects on manzanitas. Ezcurra *et al.* (1987) suggested that pubescence might have protected the sucking insects of madrones from parasitoids. They also found that leaf-mining insects were less abundant on pubescent madrones, which they interpreted to indicate that leaf-mining insects on madrones are deterred at oviposition. On manzanitas, the abundance of leaf-mining insects was not associated with any pubescence trait.

Although several species of manzanita were sampled at more than a single site, each manzanita species–site combination was treated as an independent observation. If the estimates of abundance or species richness for manzanita species sampled multiple times do not act independently, they could distort the analysis, however examination of Fig. 5 suggests that the trends observed within species duplicate those observed between species, trends observed within site duplicate those observed between sites, and that variation in pubescence length within species is as great as variation among species. The most frequently sampled species of manzanita, *A. tomentosa*, displays considerable variation in pubescence length among sites, with lower folivore abundance at sites with longer pubescence (Fig. 5a,b). The strong negative association between folivore abundance and pubescence length observed *within* many manzanita species across multiple sites that can vary in their environmental

Table 6. Linear models for chewing damage caused by folivorous insects on manzanitas. The sign of the regression coefficients for all habitat, host-plant, and pubescence variables indicates the nature of the association with the response variable. Blank entries in the table indicate that no pubescence traits were retained in the model. See Table 2 for definitions of abbreviations.

Response variables	Constant	Leaf area	Habitat and host-plant variables	Pubescence variables	Model†	F	d.f.	P	R^2
Proportion of leaf area removed	0.1269	4.12×10^{-7}	0.0028(range)		OLS	5.33	2,39	0.009	0.2146
Proportion of leaf area skeletonised	0.0602	5.25×10^{-6}	0.0013(range)		OLS	5.29	2,39	0.009	0.2133
Proportion of leaf area chewed (removed + skeletonised)	0.1429	-2.42×10^{-6}	0.0031(range)		OLS	5.88	2,39	0.0059	0.2315

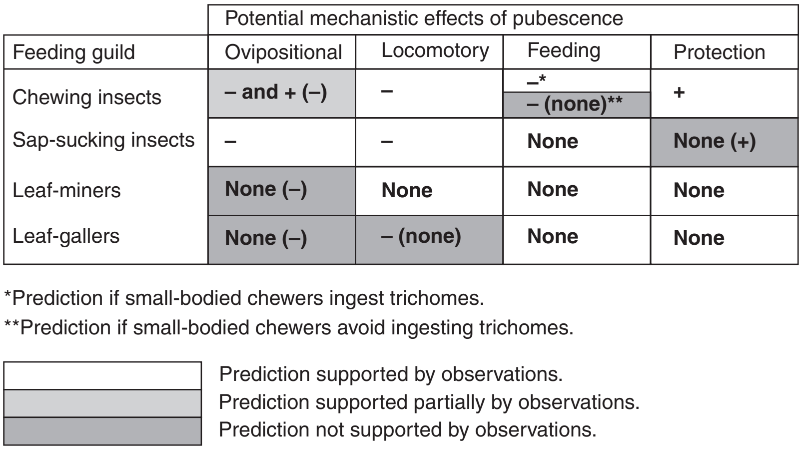
†Model: OLS = ordinary least squares.

characteristics adds further support to the argument that pubescence length is associated negatively with folivore abundance.

Synthesis

The overall pattern of results obtained supports the hypothesis that as both the level of pubescence and the amount that an insect contacts pubescence increase, the abundance of external-feeding guilds of folivorous insects will decrease (Fig. 6). Internal-feeding guilds that can avoid the leaf surface, such as leaf-mining insects, appear to be largely unaffected by pubescence traits. It is expected that for leaf-galling insects that oviposit directly onto leaves, pubescence would also have little effect on their host-plant use, however on *Arctostaphylos* spp., where the leaf-galling aphid *Tamalia cowenii* encounters pubescent stems and leaves while moving, ovipositing, feeding, and initiating galls, pubescence length is an obstacle to host-plant use. There was no evidence that the effects of pubescence traits on folivorous insects depend on body size (Fig. 6), however the sample sizes for body-size analyses were small, and body-size effects may be difficult to detect given the wide ontogenetic variation in body size. The overall pattern of effects suggests that foliar pubescence on *Arctostaphylos* spp. acts by interfering with the locomotion and/or feeding of insects that contact the leaf surface.

The associations between folivore abundance and pubescence length cannot be interpreted to indicate a causal relationship. Other foliar traits that are correlated with pubescence length may ultimately be responsible for the association between the abundance of folivores and pubescence length observed, however numerous experimental studies have demonstrated that pubescence traits have



	Potential mechanistic effects of pubescence			
Feeding guild	Ovipositional	Locomotory	Feeding	Protection
Chewing insects	– and + (–)	–	–* – (none)**	+
Sap-sucking insects	–	–	None	None (+)
Leaf-miners	None (–)	None	None	None
Leaf-gallers	None (–)	– (none)	None	None

*Prediction if small-bodied chewers ingest trichomes.

**Prediction if small-bodied chewers avoid ingesting trichomes.

□ Prediction supported by observations.

▨ Prediction supported partially by observations.

■ Prediction not supported by observations.

Fig. 6. Predicted and observed effects of foliar pubescence on the abundance of folivorous insects associated with manzanitas. Cell entries are observed effects followed by predicted effects in parentheses. In cells with only one effect reported, observation and prediction are in agreement. – indicates a negative effect, + indicates a positive effect. 'None' indicates that pubescence was predicted or observed to have no effect. Shading highlights the pattern of correspondence between observed effects and predicted effects, with darker shading indicating instances in which observations did not correspond with predictions. No body-size dependent effects were detected, so predictions based on body size were eliminated from the table. All negative effects appear to be due to pubescence length and all positive effects are due to pubescence density and glandularity.

mechanistic effects on folivorous insects. An examination of potential correlations between pubescence traits and other structural and chemical traits of foliage might permit elimination of such traits as causes of the effects observed (Soetens *et al.*, 1991; Matsuki & MacLean, 1994). Experimental manipulation of pubescence traits may also help to link pubescence length causally to community-wide and guild-specific effects on the abundance of folivorous insects (Khan *et al.*, 1986; Baur *et al.*, 1991; Zvereva *et al.*, 1998).

While strong associations were found between pubescence length and the abundance of guilds of folivorous insects, not all species within a guild may respond to pubescence in the same way. In their review of 14 species of folivorous arthropod that feed on cotton, Norris and Kogan (1980) illustrated that there is wide variation in the response of folivores within the same feeding guild to pubescence. Pubescent cotton plants showed some resistance to species of leaf-chewing and sap-sucking insects, but were also susceptible to other species in the same feeding guilds. Therefore, the results may characterise the average response of a guild or the response of the most abundant species within a guild to pubescence, not the response of all members of a guild.

This study focused on the effects of foliar pubescence on manzanitas, however pubescence on other plant parts, such as petioles and stems, may also affect folivorous insects. On manzanitas, pubescence occurs on the petioles and stems of some species. Pubescence should be expected to affect the successful movement of folivorous insects over any part of the plant. Future studies should examine the role of pubescence on different plant parts in deterring the activity of folivorous insects.

This study suggests strongly that a plant trait, pubescence, may have both community-wide and guild-specific effects on folivorous insects. To the extent that other plant traits have been shown to have strong and largely consistent effects on a variety of individual species of folivore, those traits may also be candidates to show community-wide and guild-specific effects on folivorous insects.

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References

Agresti, A. (1996) *An Introduction to Categorical Data Analysis*. Wiley, New York.

Baur, R., Binder, S. & Benz, G. (1991) Nonglandular leaf trichomes as short-term inducible defense of the grey alder, *Alnus incana* (L.), against the chrysomelid beetle, *Agelastica alni* L. *Oecologia*, **87**, 219–226.

Becerra, J. & Ezcurra, E. (1986) Glandular hairs in the *Arbutus xalapensis* complex in relation to herbivory. *American Journal of Botany*, **73**, 1427–1430.

Belcher, D.W. & Thurston, R. (1982) Inhibition of movement of larvae of the convergent lady beetle by the leaf trichomes of tobacco. *Environmental Entomology*, **11**, 91–94.

Benedict, J.H., Leigh, T.F. & Hyer, A.H. (1983) *Lygus hesperus* (Heteroptera: Miridae) oviposition and behavior, growth, and survival in relation to cotton trichome density. *Environmental Entomology*, **12**, 331–335.

Borror, D.J., Triplehorn, C.A. & Johnson, N.F. (1989) *An Introduction to the Study of Insects*, 6th edn. Harcourt Brace College Publishers, Fort Worth, Texas.

Chu, C., Freeman, T.P., Buckner, J.S., Henneberry, T.J., Nelson, D.R., Walker, G.P. *et al.* (2000) *Bemisia argentifolii* (Homoptera: Aleyrodidae) colonization on upland cottons and relationships to leaf morphology and leaf age. *Annals of the Entomological Society of America*, **93**, 912–919.

Connor, E.F., Hosfield, E., Meeter, D.A. & Niu, X. (1997) Tests for aggregation and size-based sample-unit selection when sample units vary in size. *Ecology*, **78**, 1238–1249.

Connor, E.F. & Taverner, M.P. (1997) The evolution and adaptive significance of the leaf-mining habitat. *Oikos*, **79**, 6–25.

Cornell, H.V. (1989) Endophage–ectophage ratios and plant defense. *Evolutionary Ecology*, **3**, 64–76.

Danielson, S.D., Manglitz, G.R. & Sorensen, E.L. (1987) Resistance in perennial glandular-haired *Medicago* species to feeding by adult alfalfa weevils (Coleoptera: Curculionidae). *Environmental Entomology*, **16**, 708–711.

DeClerck, R.A. & Shorthouse, J.D. (1985) Tissue preference and damage by *Fenusa pusilla* and *Messa nana* (Hymenoptera: Tenthredinidae), leaf-mining sawflies on white birch (*Betula papyrifera*). *Canadian Entomologist*, **117**, 351–362.

Denford, K.E. (1981) Chemical subdivisions within the genus *Arctostaphylos* based on flavonoid profiles. *Experientia*, **37**, 1287–1288.

Dimock, M.B. & Tingey, W.M. (1988) Host acceptance behaviour of Colorado potato beetle larvae influenced by potato glandular trichomes. *Physiological Entomology*, **13**, 399–406.

Doss, R.P. & Shanks, C.H. (1988) The influence of leaf pubescence on the resistance of selected clones of beach strawberry (*Fragaria chiloensis* (L.) Duchesne) to adult black vine weevils (*Otiorhynchus sulcatus* F.). *Scientia Horticulturae*, **34**, 47–54.

Duffey, S.S. (1986) Plant glandular trichomes: their partial role in defense against insects. *Insects and the Plant Surface* (ed. by B. Juniper and T. R. E. Southwood), pp. 151–172. Edward Arnold, London.

Eisner, T., Eisner, M. & Hoebeke, E.R. (1998) When defense backfires: detrimental effect of a plant's protective trichomes on an insect beneficial to the plant. *Proceedings of the National Academy of Sciences*, **95**, 4410–4414.

Elsey, K.D. (1974) Influence of plant host on searching speed of two predators. *Entomophaga*, **19**, 3–6.

Ezcurra, E., Gomez, J.C. & Becerra, J. (1987) Diverging patterns of host use by phytophagous insects in relation to leaf pubescence in *Arbutus xalapensis* (Ericaceae). *Oecologia*, **72**, 479–480.

Gannon, A.J., Back, C.E. & Walker, G.K. (1994) Feeding patterns and attachment ability of *Altica subplicata* (Coleoptera: Chrysomelidae) on sand-dune willow. *Great Lakes Entomologist*, **27**, 89–101.

Gilbert, L.E. (1971) Butterfly-plant coevolution: has *Passiflora adenopoda* won the selectional race with Heliconiine butterflies? *Science*, **172**, 585–586.

Goertzen, L.R. & Small, E. (1993) The defensive role of trichomes in black medick (*Medicago lupulina*, Fabaceae). *Plant Systematics and Evolution*, **184**, 101–111.

Haddad, N.M. & Hicks, W.M. (2000) Pubescence and behavior and performance of the butterfly *Papilio troilus* (Lepidoptera: Papilionidae). *Environmental Entomology*, **29**, 299–303.

Hileman, L., Parker, V.T. & Vasey, M.C. (2001) Phylogeny of Arbutoideae: implications for the Madro-Tethyan hypothesis. *Systematic Botany*, **26**, 131–143.

Johnson, H.B. (1975) Plant pubescence: an ecological perspective. *Botanical Review*, **41**, 233–258.

Kanno, H. (1996) Role of leaf pubescence in soybean resistance to the false melon beetle, *Atrachya menetriesi* Faldermann (Coleoptera: Chrysomelidae). *Applied Entomology and Zoology*, **31**, 597–603.

Khan, Z.R. & Agarwal, R.A. (1984) Ovipositional preference of jassid, *Amrasca biguttula biguttula* Ishida on cotton. *Journal of Entomological Research*, **8**, 78–80.

Khan, Z.R., Ward, J.T. & Norris, D.M. (1986) Role of trichomes in soybean resistance to cabbage looper, *Trichoplusia ni*. *Entomologia experimentalis et applicata*, **42**, 109–117.

Kimmerer, T.W. & Potter, D.A. (1987) Nutritional quality of specific leaf tissues and selective feeding by a specialist leafminer. *Oecologia*, **71**, 548–551.

Lambert, L., Beach, R.M., Kilen, T.C. & Todd, J.W. (1992) Soybean pubescence and its influence on larval development and oviposition preference of lepidopterous insects. *Crop Science*, **32**, 463–466.

Lambert, L. & Kilen, T.C. (1989) Influence and performance of soybean lines isogenic for pubescence type on oviposition preference and egg distribution by corn earworm (Lepidoptera: Noctuidae). *Journal of Entomological Science*, **24**, 309–316.

Lapointe, S.L. & Tingey, W.M. (1986) Glandular trichomes of *Solanum neocardenasii* confer resistance to green peach aphid (Homoptera: Aphididae). *Journal of Economic Entomology*, **79**, 1264–1268.

Levin, D.A. (1973) The role of trichomes in plant defense. *Quarterly Review of Biology*, **48**, 3–15.

Lovinger, A., Liewehr, D. & Lamp, W.O. (2000) Glandular trichomes on alfalfa impede searching behavior of the potato leafhopper parasitoid. *Biological Control*, **18**, 187–192.

Lukefahr, M.J., Houghtaling, J.E. & Graham, H.M. (1971) Suppression of *Heliothis* populations with glabrous cotton strains. *Journal of Economic Entomology*, **64**, 486–488.

Malakar, R. & Tingey, W.M. (1999) Resistance of *Solanum berthaultii* foliage to potato tuberworm (Lepidoptera: Gelechiidae). *Journal of Economic Entomology*, **92**, 497–502.

Malakar, R. & Tingey, W.M. (2000) Glandular trichomes of *Solanum berthaultii* and its hybrids with potato deter oviposition and impair growth of potato tuber moth. *Entomologia experimentalis et applicata*, **94**, 249–257.

Matsuki, M. & MacLean, S.F. (1994) Effects of different leaf traits on growth rates of insect herbivores on willows. *Oecologia*, **100**, 141–152.

Mattson, W.J., Lawrence, R.K., Haack, R.A., Herms, D.A. & Charles, P. (1988) Defensive strategies of woody plants against different insect-feeding guilds in relation to plant ecological strategies and intimacy of association with insects. *Mechanisms of Woody Plant Defenses against Insects* (ed. by W. J. Mattson, J. Levieux and C. Bernard-Dagan), pp. 3–38. Springer-Verlag, New York.

McAuslane, H. (1996) Influence of leaf pubescence on ovipositional preference of *Bemisia argentifolii* (Homoptera: Aleyrodidae) on soybean. *Environmental Entomology*, **25**, 834–841.

McCullagh, P. & Nelder, J.A. (1989) *Generalized Linear Models*. Chapman & Hall, London.

Miller, D.G. (1998) Life history, ecology and communal gall occupation in the manzanita leaf-gall aphid, *Tamalia coweni* (Cockerell) (Homoptera: Aphididae). *Journal of Natural History*, **32**, 351–366.

Navasero, R.C. & Ramaswamy, S.B. (1991) Morphology of leaf surface trichomes and its influence on egglaying by *Heliothis virescens*. *Crop Science*, **31**, 342–353.

Navon, A., Melamed-Madjar, V., Zur, M. & Ben-Moshe, E. (1991) Effects of cotton cultivars on feeding of *Heliothis armigera and Spodoptera littorialis* larvae and on oviposition of *Bemisia tabaci*. *Agriculture, Ecosystems and Environment*, **35**, 73–80.

Norris, D.M. & Kogan, M. (1980) Biochemical and morphological bases of resistance. *Breeding Plants Resistant to Insects* (ed. by F. G. Maxwell and P. R. Jennings), pp. 23–61. John Wiley and Sons, Inc., New York.

Obrycki, J.J. & Tauber, M.J. (1984) Natural enemy activity on glandular pubescent potato plants in the greenhouse: an unreliable predictor of effects in the field. *Environmental Entomology*, **13**, 679–683.

Oghiakhe, S. (1995) Effect of pubescence in cowpea resistance to the legume pod borer *Maruca testulalis* (Lepidoptera: Pyralidae). *Crop Protection*, **14**, 379–387.

Opler, P.A. (1974) Biology, ecology, and host specificity of microlepidoptera associated with *Quercus agrifolia* (Fagaceae). *University of California Publications in Entomology*, **75**, 1–83.

Palaniswamy, P. & Bodnaryk, R.P. (1994) A wild *Brassica* from Sicily provides trichome-based resistance against flea beetles, *Phyllotreta cruciferae* (Goeze) (Coleoptera: Chrysomelidae). *Canadian Entomologist*, **126**, 1119–1130.

Papp, M., Kolarov, J. & Mesterhazy, A. (1992) Relation between pubescence of seedling and flag leaves of winter wheat and its significance in breeding resistance to cereal leaf beetle (Coleoptera: Chrysomelidae). *Environmental Entomology*, **21**, 700–705.

Quiring, D.T., Timmins, P.R. & Park, S.J. (1992) Effect of variations in hooked trichome densities of *Phaseolus vulgaris* on longevity of *Liriomyza trifolii* (Diptera: Agromyzidae) adults. *Environmental Entomology*, **2**, 1357–1361.

Ramalho, F.S., Parrott, W.L., Jenkins, J.N. & McCarty, J.C. (1984) Effects of cotton leaf trichomes on the mobility of newly hatched tobacco budworms (Lepidoptera: Noctuidae). *Journal of Economic Entomology*, **77**, 619–621.

Raupp, M.J. & Denno, R.F. (1983) Leaf age as a predictor of herbivore distribution and abundance. *Variable Plants and Herbivores in Natural and Managed Systems* (ed. by R. F. Denno and M. S. McClure), pp. 91–124. Academic Press, Inc., New York.

Ribeiro, S.P., Pimenta, H.R. & Fernandes, G.W. (1994) Herbivory by chewing and sucking insects on *Tabebuia ochracea*. *Biotropica*, **26**, 302–307.

Robinson, S.H., Wolfenbarger, D.A. & Dilday, R.H. (1980) Antixenosis of smooth leaf cotton to the ovipositional response of tobacco budworm. *Crop Science*, **20**, 646–649.

Scheirs, J., De Bruyn, L. & Verhagen, R. (2000) A test of the C3–C4 hypothesis with two grass miners. *Ecology*, **82**, 410–421.

Scheirs, J., De Bruyn, L. & Verhagen, R. (2001) Nutritional benefits of the leaf-mining behaviour of two grass miners: a test of the selective feeding hypothesis. *Ecological Entomology*, **26**, 509–516.

Scheirs, J., Vandevyvere, I. & De Bruyn, L. (1997) Influence of monocotyl leaf anatomy on the feeding pattern of a grass-mining agromyzid (Diptera). *Annals of the Entomological Society of America*, **90**, 646–654.

Smith, F.F. & Poos, F.W. (1931) A comparison of the feeding habits of some species of *Empoasca*. *Journal of Economic Entomology*, **24**, 361–371.

Soetens, P., Rowell-Rahier, M. & Pasteels, J.M. (1991) Influence of phenolglucosides and trichome density on the distribution of insect herbivores on willows. *Entomologia experimentalis et applicata*, **59**, 175–187.

Stehr, F.W. (ed.) (1987) *Immature Insects*, Vol. 1. Kendall/Hunt Publishing Co., Dubuque, Iowa.

Stehr, F.W. (ed.) (1991) *Immature Insects*, Vol. 2. Kendall/Hunt Publishing Co., Dubuque, Iowa.

Tingey, W.M. & Gibson, R.W. (1978) Feeding and mobility of the potato leafhopper impaired by glandular trichomes of *Solanum berthaultii* and *S. polyadenium*. *Journal of Economic Entomology*, **71**, 856–858.

Treacy, M.F., Benedict, J.H., Segers, J.C., Morrison, R.K. & Lopez, J.D. (1986) Role of cotton trichome density in bollworm (Lepidoptera: Noctuidae) egg parasitism. *Environmental Entomology*, **15**, 365–368.

Turnipseed, S.G. (1977) Influence of trichome variations on populations of small phytophagous insects in soybean. *Environmental Entomology*, **6**, 815–817.

Valenti, M.A. & Gaimari, S.D. (1992) The manzanita leafgall aphid, *Tamalia coweni* (Cockerell) (Homoptera: Aphididae), and its association with the predator *Leucopis* sp. (Diptera: Chamaemyiidae). *Proceedings of the Washington State Entomological Society*, **54**, 972–977.

Webster, J.A., Inayatullah, C., Hamissou, M. & Mirkes, K.A. (1994) Leaf pubescence effects in wheat on yellow sugarcane aphids and greenbugs (Homoptera: Aphididae). *Journal of Economic Entomology*, **87**, 231–240.

Webster, J.A., Smith, D.H., Rathke, E. & Cress, C.E. (1975) Resistance to cereal leaf beetle in wheat: density and length of leaf-surface pubescence in four wheat lines. *Crop Science*, **15**, 199–202.

Woodman, R.L. & Fernandes, G.W. (1991) Differential mechanical defense: herbivory, evapotranspiration, and leaf-hairs. *Oikos*, **60**, 11–19.

Zvereva, E.L., Kozlov, M.V. & Niemelä, P. (1998) Effects of leaf pubescence in *Salix borealis* on host-plant choice and feeding behaviour of the leaf beetle, *Melasoma japonica*. *Entomologia experimentalis et applicata*, **89**, 297–303.

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