

Palatability of tree foliage to chewing insects: a comparison between a temperate and a tropical site

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Abstract

The leaf palatability of 10 temperate and 10 tropical tree-species was compared in two woodland sites, in Switzerland and Papua New Guinea. Relative palatability was estimated by scoring damage visually during feeding trials with numerous species of chewing insects, drawn from the local pool of species. The average palatability temperate foliage to its local community of chewing insects was significantly higher, by a factor of 2.3, than that of tropical foliage. In multiple regression analyses considering different plant-related variables, 71 % of the variance in leaf palatability could be accounted for by the number of young leaves or leaflets recorded during the field-study and by the average leaf area. Based upon food acceptance in laboratory conditions, the proportion of insect morphospecies which behaved as generalists was higher at the temperate site (44 %) than at the tropical site (18 %). These results reflect intrinsic differences between deciduous trees growing at the temperate site and evergreen trees growing at the tropical site.

Keywords: Host specificity, insect herbivores, leaf flush, leaf palatability, Papua New Guinea, Switzerland.

Résumé

Les "saveurs" relatives du feuillage de 10 espèces ligneuses tempérées et de 10 espèces ligneuses tropicales ont été comparées dans deux parcelles boisées situées en Suisse et en Papouasie Nouvelle-Guinée. La saveur relative de chaque espèce a été déterminée en comparant visuellement au laboratoire les dommages infligés au feuillage par de nombreuses espèces d'insectes défoliateurs, appartenant au pool d'espèces locales. La saveur moyenne du feuillage tempéré était significativement plus élevée, d'un facteur 2.3, que celle du feuillage tropical. Lors d'analyses de régression multiples considérant différentes variables inhérentes aux arbres étudiés, 71 % de la variation dans la saveur du feuillage des arbres étudiés était expliquée par le nombre de jeunes feuilles ou folioles dénombrées lors de l'étude et par la surface moyenne des feuilles. La proportion des morpho-espèces d'insectes qui se comportaient comme des généralistes en conditions de laboratoire était plus élevée au site tempéré (44 %) qu'au site tropical (18 %). Ces résultats reflètent des différences intrinsèques entre arbres caduques croissant au site tempéré et arbres sempervirents croissant au site tropical.

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INTRODUCTION

The leaf palatability of particular plant species is often estimated by measuring or scoring damage by a few generalist species, such as certain snails (GRIME *et al.*, 1968; WRATTEN *et al.*, 1981), slugs (CATES & ORIANS, 1975; RATHCKE, 1985), grasshoppers (OTTE, 1975), caterpillars (MACLEAN & JENSEN, 1985; EDWARDS *et al.*, 1986), leaf-cutting ants (ROCKWOOD, 1976) or a combination of a few different taxa (READER & SOUTHWOOD, 1981). As emphasized by CATES & ORIANS (1975), different herbivores have unique evolutionary histories and, most probably, different physiologies. Thus, herbivores may respond differently to morphological and chemical defenses of plants and it may be inappropriate to generalize too much from the results obtained with a particular species or group of species (CATES & ORIANS, 1975). For this purpose, a community-based, multispecies, approach may be of particular interest (*see* JONES & LAWTON, 1991).

It is generally assumed that tropical foliage is less palatable to insect herbivores than is temperate foliage (e.g. JANZEN, 1973, 1985). One of the reasons invoked regularly for this is the abundance and diversity of chemical defenses in tropical plants (e.g. LEVIN, 1976; KRISCHIK & DENNO, 1983; COLEY & AIDE, 1991). However, to date, there has been no critical study aimed at quantifying differences in leaf palatability between temperate and tropical foliage. Insect species encountering both temperate and tropical foliage in natural conditions, and, therefore, adequate for testing these differences, are extremely rare. This calls for independent tests to be performed with different insect species in temperate and tropical regions, using a common scale of measurement. Furthermore, the protocol should, as far as possible, minimize intra- and inter-specific variation in insect fitness, to ensure that measurements of palatability do not simply reflect the preferences of a few voracious species.

In two independent studies, performed in Switzerland and Papua New Guinea (BASSET & BURCKHARDT, 1992; this paper), the leaf palatability of particular tree-species was estimated with regard to the local community of chewing insects associated with these trees. Although the sampling methods used for collecting herbivores differed in the two studies, their scope and duration were similar, and, in particular, the protocol used to measure leaf palatability was identical. This paper investigates (a) whether the foliage at the temperate site is more palatable to its local community of chewing insects than the foliage at the tropical site; and (b) which plant-related attributes, easily measurable in the field, best explain the observed scores of palatability for all tree species.

MATERIAL AND METHODS

Study sites

The temperate site encompassed the lower slopes of the Swiss Jura situated in the Vendôme-Bonmont area: Grande Côte and Petite Côte de Bonmont, Combe de la Mey, Les Deplumeaux (Vaud, Switzerland, approximately 46° 25' N, 6° 09' E). Sampling was restricted to an altitude of 600-750 m. The woodlands in this area represent a mosaic of associations including principally *Lathyro-Quercetum*, *Coronillo-Quercetum*, *Cardamino-Fagetum* and *Luzulo-Fagetum* (*see* BASSET & BURCKHARDT, 1992). The

mean annual air temperature in the area is approximately 10 °C and mean annual rainfall is 1 300 mm (meteorological stations of Changins and Chésereux, respectively, 7 and 3 km from the study site).

Sampling at the tropical site was performed on the slopes of Mt Kaindi, near and within the grounds of the Wau Ecology Institute, Wau, Papua New Guinea (7° 24' S, 146° 44' E). Altitude of collecting ranged from 1 100-2 362 m (summit). Mt Kaindi has been cleared locally, leaving a mosaic of grasslands and forest patches. The main forest formations encountered on the slopes include lower and mid-montane rain forest (JOHNS, 1982). The former shows some variation with *Castanopsis acuminatissima* (oak forest), or *Araucaria cunninghamii* and *A. hunsteinii* (*Araucaria* forest) gaining dominance, or *Elmerrillia*, *Litsea* and *Cryptocarya* being among the common species (mixed lower montane forest). *Pandanus* spp. are frequent in wet areas. The mid-montane forest is characterized by *Nothofagus pullei* and *N. grandis* (*Nothofagus* forest) with epiphytic lichens, mosses, ferns and orchids being abundant (JOHNS, 1982). The climate may be classified as "humid to perhumid mesothermal with little or no water deficit" (MCALPINE *et al.*, 1983). Mean annual air temperature is 21.1 °C at 1 200 m and 14.7 °C on the summit, and the mean annual rainfall is 1 887 mm and 3 104 mm at these same altitudes (GRESSITT & NADKARNI, 1978).

Study plants

Ten woody and broad-leaved plant species (native forest trees and shrubs) were studied at each site (table I). Most species were common and widespread at the study sites. As far as possible, they were chosen as representatives of different plant families and included both pioneer and persistent species. At the temperate site, all trees were deciduous, whereas at the tropical site, all were evergreen with the exception of *Ficus nodosa* and *Cordia dichotoma*. These choices accounted for local differences between study sites: most broad-leaved tree species in Vendôme-Bonmont are deciduous, whereas in Wau, broad-leaved evergreen species dominate with a few deciduous species. Since it was not always possible to identify trees with certainty in the field, some were combined into "aggregates" (table I). Hereafter, the host plants and aggregates are designed by their generic names.

Insect sampling

At both sites, chewing insects were collected exclusively from the foliage of the study trees. Sampling at the temperate site was performed from April to October 1990. Accessible branches of trees (<2 m high), were visually searched at random during the day for insects. Sample time and number of sampling occasions were identical for each tree species (several tens of hours of observation; see further details in BASSET & BURCKHARDT, 1992).

Sampling at the tropical site was performed from February to July 1992, encompassing occasional wetter and drier periods. When the foliage of trees could not be sampled from the ground, the single rope technique provided access to the crowns (PERRY, 1978). Insects were collected alive during both day and night by hand-collecting, beating and branch-clipping. Sampling effort was identical for each tree species (180 beating samples, about 30 m² of foliage clipped and several tens of hours of observation).

Insect testing

The following protocol was used at each study site. Live insects were stored in plastic vials, at room temperature and in conditions of near-saturated relative humidity. They were provided with fresh foliage of the tree species from which they were collected, until they died or accepted food. In the latter case, identification numbers corresponding to Operational Taxonomic Units (OTUs, *i.e.* morphospecies) were assigned to the insects. This procedure (a) prevented inclusion of incidental species in the analyses (*i.e.* those resting on the foliage but not feeding); and (b) reduced the influence on the results of parasitised specimens, or other insects with abnormal behavior. As far as possible, each assigned individual was tested once on another plant species during 24 h and then moved randomly to another plant species for a similar test, until the 9 other study species had been provided. Each

TABLE I. - Study trees, their successional status (*Pi* = pioneer, *Pe* = persistent) and the number of OTUs of chewing insects collected from their foliage. For aggregates, the first-named species indicates the most common host in the study area.

Hosts	Plant family	Status	No. OTUs
a) Temperate trees			
<i>Salix caprea</i> L. and hybrids	Salicaceae	Pi	22
<i>Corylus avellana</i> L.	Betulaceae	Pi	15
<i>Fagus sylvatica</i> L.	Fagaceae	Pe	19
<i>Quercus petraea</i> Lieblein - <i>Q. robur</i> L. - <i>Q. pubescens</i> Willd. aggr.	Fagaceae	Pe	19
<i>Crataegus oxyacantha</i> L. - <i>C. monogyna</i> Jacq. aggr.	Rosaceae	Pi	17
<i>Sorbus aria</i> Crantz and hybrids	Rosaceae	Pi	19
<i>Acer opalus</i> Miller and hybrids	Aceraceae	Pe	14
<i>Fraxinus excelsior</i> L.	Oleaceae	Pe	11
<i>Lonicera xylosteum</i> L.	Caprifoliaceae	Pe	6
<i>Viburnum lantana</i> L.	Caprifoliaceae	Pi	3
b) Tropical trees			
<i>Elmerrillia tsiampacca</i> (L.) Dandy	Magnoliaceae	Pe	18
<i>Cinnamomum culilaban</i> (L.) Presl	Lauraceae	Pe	16
<i>Piper plagiophyllum</i> K. Sch. & Laut.	Piperaceae	Pi	18
<i>Ficus nodosa</i> Teys. & Binn.	Moraceae	Pi	43
<i>Pipturus argenteus</i> Wedd.	Urticaceae	Pi	37
<i>Castanopsis acuminatissima</i> A. DC.	Fagaceae	Pe	68
<i>Caldcluvia brassii</i> Hoogl.	Cunoniaceae	Pi	32
<i>Aleurites moluccana</i> Willd.	Euphorbiaceae	Pe	18
<i>Melicope denhamii</i> (Seem.) T. Hartley	Rutaceae	Pe	15
<i>Cordia dichotoma</i> Forst.	Boraginaceae	Pi	30

specimen collected was tested, unless many individuals of the same OTU were collected. Thus, the number of specimens tested per OTU varied greatly, from one to several tens. Insects molting during trials were provided the original foliage from which they were collected from: these individuals were further tested once they resumed feeding. Both young and mature leaves were used in the trials, as seasonal availability of leaf cohorts permitted.

Feeding damage was scored visually on a logarithmic scale, as follows: 0: no feeding; 1: attempting to feed; 10: moderate feeding; 100: extensive feeding. This procedure emphasized regular feeding as compared to food-probing. Further, this simple scale of scores ensured that there were no shifts in the scoring behaviour of the author between the temperate and tropical sites. To minimize possible differences among tested individuals of a particular OTU, and differences due to varying leaf age, the results of the feeding trials were judged conservatively: for a particular OTU, the highest score recorded for any individual of that OTU, regardless of leaf age, was the score assigned to that OTU.

An index of leaf palatability was calculated by summing scores of all OTUs tested on a particular tree species and dividing this value by the number of OTUs tested on this species. Values of this index range theoretically from 0 to 100 and allow comparison among plant species, as in READER & SOUTHWOOD (1981). When species were collected on several host-trees, the scores of these species were considered for each of the hosts. Since insects were tested but not scored on the hosts from which they were collected, palatability scores are independent of the number of insect species collected from the tree species considered.

Measurement of plant-related variables

Several plant-related attributes, which could potentially influence leaf palatability and which could be easily determined in the field from several tree individuals or from the literature, were considered

for each study tree. These were: mean water content and specific weight of mature leaves (leaves oven-dried for 24 h, number of samples >10); two measurements of taxonomic isolation: number of congeneric and confamilial plant-species, as reported in the Swiss flora of AESCHIMANN & BURDET (1989) and in the New Guinean checklist of HÖFT (1992); mean leaf/leaflet area ($n > 50$); mean ratio of largest width to length in mature leaves ($n = 40$); mean tree height ($n > 10$); leaf pubescence (relative classes of density of hair cover, from 1 to 8); number of newly emerged leaves/leaflets recorded; and total leaf area sampled during the course of the study. The last two variables were determined by hand-collecting and branch-clipping samples at the temperate and tropical sites, respectively. Plant-related variables are detailed for each study tree in appendix I.

Data analysis

Scores of relative palatability are likely to be inflated when two or more of the test plant species belong to the same family, particularly if these plant species share many oligophagous herbivores. Since it was not possible to choose temperate tree species in a way that they all belonged to different plant families, temperate data were corrected before they were compared with their tropical counterparts. This was achieved by ignoring results of feeding tests of a particular OTU if tested on the same plant family from which the OTU was collected. Results are detailed both prior to and after modification of temperate data. Since the data used in the analyses satisfied the assumption of normality (Kolmogorov-Smirnoff-Liliefors tests, $p > 0.05$), they were not transformed. The influence of plant-related variables on leaf palatability was tested using stepwise forward multiple regression analysis.

RESULTS

At the temperate site, most of the insects considered in the analyses belonged to the following families (in order of decreasing abundance): Geometridae, Curculionidae, Tenthredinidae, Chrysomelidae, Noctuidae, Oecophoridae and Tortricidae. At the tropical site, the following families were well represented: Geometridae, Chrysomelidae, Curculionidae, Lymantriidae, Noctuidae and Tortricidae. Overall, 145 and 295 OTUs were tested in feeding trials on temperate and tropical foliage, respectively. Although the number of OTUs tested on each tree species was roughly similar within each site, more OTUs were tested at the tropical site (average 161 OTUs tested per tree species, *see* table II) than at the temperate site (average 56 OTUs). This may reflect the high species richness of herbivores in Papua New Guinea, but as sampling methods differed between sites, species richness data are not directly comparable between sites.

The leaf palatability to local insect herbivores was significantly lower for tropical trees than for temperate trees (table II), both when scores for temperate foliage were considered prior to and after modification of temperate data (t -tests, $t = 5.13$, $p < 0.001$ and $t = 4.85$, $p < 0.001$, respectively). Average leaf palatability scores were about 2.3 times higher for temperate foliage (mean and s.e. 40.16 ± 3.31) than for tropical foliage (18.02 ± 3.15). When trees from both sites were pooled, deciduous trees were significantly more palatable than evergreens ($t = 5.47$, $p < 0.001$). In comparison with temperate trees, tropical trees had a significantly higher specific leaf weight (a measurement related to leaf toughness, $t = 3.61$, $p < 0.01$), higher leaf area ($t = 3.68$, $p < 0.01$) and exhibited significantly fewer young leaves during the course of the field study ($t = 6.51$, $p < 0.001$) (*see* appendix I).

The multiple regression analysis of leaf palatability and the available plant-related variables was highly significant, with the total number of young leaves or leaflets recorded during the sampling period entering first in the regression and the

TABLE II. - Palatability scores (prior to and after modification of temperate data, see text) and number of OTUs tested on study trees.

Tree	Palatability Scores		No. OTUs tested
	Prior	After	
a) Temperate trees			
<i>Salix</i>	52.06	52.06	51
<i>Corylus</i>	45.25	45.25	48
<i>Fagus</i>	57.69	55.10	67
<i>Quercus</i>	38.61	32.49	56
<i>Crataegus</i>	44.15	41.14	53
<i>Sorbus</i>	43.28	38.70	50
<i>Acer</i>	49.73	49.73	71
<i>Fraxinus</i>	34.79	34.79	63
<i>Lonicera</i>	23.70	23.12	53
<i>Viburnum</i>	27.54	29.22	52
b) Tropical trees			
<i>Elmerrillia</i>	-	15.49	160
<i>Cinnamomum</i>	-	10.72	156
<i>Piper</i>	-	5.52	161
<i>Ficus</i>	-	35.97	152
<i>Pipturus</i>	-	10.65	168
<i>Castanopsis</i>	-	16.24	163
<i>Caldcluvia</i>	-	17.41	161
<i>Aleurites</i>	-	33.30	164
<i>Melicope</i>	-	11.77	161
<i>Cordia</i>	-	23.12	160

mean area of leaves entering second. Together, these two variables explained 71 % of the variance in leaf palatability (table III). In contrast, the influence of other variables (leaf water content, specific leaf weight, taxonomic isolation of the host, ratio width/length of leaves, host height, leaf pubescence, total leaf area sampled and number of OTUs tested) was not obvious. In particular, dummy variables accounting for the successional status of the tree (pioneer or persistent) and its location (temperate or tropical) did not improve the regression.

TABLE III. - Summary of results of forward stepwise multiple regression analysis with leaf palatability as the dependent variable.

	R ²
Step 1: Enter Total No. young leaves/leaflets recorded	0.63
Step 2: Enter Leaf area	0.74
Final equation: Palatability = 0.884 + 0.018 *** Young leaves + 0.066 * Leaf area F = 24.50 ***, adjusted R ² = 0.71	

* P ≤ 0.05, *** P ≤ 0.001.

In order to appraise the feeding specificity of the OTUs tested, the following proportion was calculated for each study site: number of OTUs feeding on four or more tree species: number of OTUs tested four or more times. This simple comparison showed that, regarding food acceptance in laboratory conditions, the

proportion of OTUs which behaved as generalists was higher at the temperate site (32 "generalist" OTUs against 72 tested, 44 %, corrected data) than at the tropical site (41 OTUs against 226, 18 %).

For temperate data, since several OTUs could be identified and their host range checked in the relevant literature (see BASSET & BURCKHARDT, 1992), host specificity could in some cases be compared with the results of feeding trials. Agreement was generally good and confirmed for 31 of the 38 cases (82 %) which could be examined in this regard. In 6 out of the 7 discordant cases, the literature showed a generalist habit, with some reported host-plants not belonging to the test plants, whereas feeding trials indicated a specialist habit. From a community perspective, the discrepancy between the proportion of tree-feeding specialists as recorded from the literature and as estimated with feeding experiments was low (46 species out of 118, 39 % and 25 species out of 72, 35 %, respectively). This occurred because the emphasis of the experimental protocol was on recording possible feeding on hosts belonging to different plant families, rather than recording feeding on related hosts and the number of such hosts accepted.

DISCUSSION

The procedure used in the present study offers several advantages for measuring leaf palatability, one of the major ones being simplicity. Secondly, testing herbivores with plants belonging to different plant families provides a first estimate of food acceptance and herbivore host-specificity. This point is particularly interesting when faunas are known inadequately, such as those in many parts of the tropics. The temperate data suggested that the results of feeding trials were in reasonable agreement with host range as reported in the literature. Yet, it is well-recognised that insects tend to accept more plant species in laboratory conditions than in the wild, particularly when test-plants are closely related (e.g. ROWELL *et al.*, 1983). Although using the present data it may be unsafe to discuss the actual number of hosts accepted, field observations suggest that a simple specialist/generalist dichotomy may be applied safely when the insects have been tested on several hosts and when the results of the tests are without ambiguity (*i.e.* systemic rejection or acceptance of test-plants).

However, the shortcomings of these measurements are equally obvious. Firstly, they refer to short-term palatability of both young and mature foliage, measured at the end of 24 h-periods, not to long-term estimates of insect fitness and survivorship. Secondly, scores of damage were used instead of actual measurements of biomass or leaf area ingested. Thirdly, no plant material was used as controls, so that in certain cases, rejection may be due to satiation rather than to deterrence or avoidance, although it is probable that the high number of herbivores tested minimised this problem. In addition, the choice of a control plant is not straightforward (see RICHARDSON & WHITTAKER, 1982, for a critique of palatability measured with reference to control plants), particularly when comparing temperate and tropical foliage. Lastly, the procedure did not allow assessment of the influence of intraspecific variability in leaf palatability (see ROWELL *et al.*, 1983).

The results indicate that, for the tree species considered and for the duration of the field study, the foliage of trees at the temperate site was more readily

accepted and fed upon by its local community of chewing insects than was the foliage of trees at the tropical site. Although the number of tree species tested was low, the results are independent of phylogenetic relationships at family level and, therefore, the probability of this reflecting a real difference between the two study sites is high. This can be interpreted as (a) the leaf palatability of trees tested being higher at the temperate site than at the tropical site; and (b) chewing insects at the temperate site being more generalized feeders than at the tropical site. Both concepts depend on each other to some degree: plant biochemistry (and concomitant leaf palatability) could be either a cause or a consequence of insect host range. The former interpretation predominates in the ecological literature (e.g. EHRlich & RAVEN, 1964; FEENY, 1975; SCHULTZ, 1988). This reasoning is also followed in the present discussion. Two independent observations of the present study indicate the contrast between the palatability of deciduous and evergreen trees at the temperate and tropical sites. Firstly, deciduous trees as a group were significantly more palatable than evergreens (and note the high palatability scores of *Ficus* and, to a lesser extent, of *Cordia*, two tropical deciduous species). Secondly, in a multiple regression analysis considering trees from both sites, most of the variance in leaf palatability could be accounted for by the number of young leaves or leaflets recorded during the field-study. Usually, leaf turnover is much higher in deciduous trees than in evergreens (e.g. MOONEY & GULMON, 1982).

This interpretation stands in line with the conclusions of several other studies of leaf palatability, which has been shown to be influenced by the successional status of the plant (e.g. CATES & ORIAN, 1975; READER & SOUTHWOOD, 1981), and more particularly by the life-expectancy of leaves (RATHCKE, 1985; SOUTHWOOD *et al.*, 1986) and the deciduous habit of the plant (MACLEAN & JENSEN, 1985). Since usually leaf lifespan in deciduous trees is shorter and they grow faster than evergreens (e.g. MOONEY & GULMON, 1982), this appears to be consistent with the "growth-rate theory" of COLEY *et al.* (1985). This theory proposed that the intrinsic growth rate of plant-species determined the optimal amount and type of their chemical defenses: usually, slower growing species on nutrient-poor sites are better defended than faster growing species on nutrient-rich sites. In short, fast growing trees, such as deciduous temperate trees with a high leaf turnover, may be more palatable to insect herbivores due to a lower commitment to chemical defenses and, possibly, a high content of free nitrogen per leaf area (see MOONEY & GULMON, 1982; READER & SOUTHWOOD, 1981).

Leaf production as a variable may help to predict the leaf palatability of evergreen and deciduous trees, and, to a lesser extent, that of tropical and temperate trees. However, the causal factor promoting the high palatability of deciduous trees (and, therefore, of most broad-leaved temperate trees) was not identified in this study. Further investigation of the palatability of broad-leaved deciduous and evergreen trees to both chewing and sap-sucking insects in the tropics may shed light on this issue.

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APPENDIX I. - Plant-related variables determined for each tree species (see text for details).

Tree	Water (% DW)	Weight ($g^{-4} \times cm^{-2}$)	Congeneric (no. sp.)	Confamilial (no. sp.)	Area ¹ (cm^2)	Width (ratio)	Height (m)	Hairs ² (classes)	Young leaves (no.)	Total Area ³ (m^2)
<i>Salix</i>	59.4	51.2	28	32	27.0	0.50	6.5	8	2531	14.7
<i>Corylus</i>	61.5	27.2	1	10	42.4	0.76	3.5	4	1832	18.7
<i>Fagus</i>	54.5	32.0	1	6	35.0	0.69	35.0	1	3291	19.8
<i>Quercus</i>	51.5	68.7	4	6	42.4	0.60	35.0	4	1080	16.4
<i>Crataegus</i>	54.4	64.3	2	137	13.7	0.65	4.0	2	2118	4.6
<i>Sorbus</i>	54.6	40.6	6	137	61.7	0.67	15.0	7	1699	27.8
<i>Acer</i>	58.3	39.1	6	6	98.0	1.23	12.0	1	1704	40.0
<i>Fraxinus</i>	65.4	54.6	2	6	24.5	0.40	20.0	1	1730	17.0
<i>Lonicera</i>	65.1	27.6	8	15	12.8	0.61	2.0	6	1696	3.3
<i>Viburnum</i>	64.3	55.3	2	15	79.1	0.70	2.5	4	1176	25.7
<i>Elmerrillia</i>	60.6	99.6	2	4	251.8	0.43	19.4	5	66	28.0
<i>Cinnamomum</i>	49.7	108.2	21	278	92.0	0.43	7.0	1	345	20.8
<i>Piper</i>	74.4	41.7	100	126	192.3	0.94	4.5	2	108	28.9
<i>Ficus</i>	61.6	81.4	138	165	417.1	0.81	16.3	4	408	25.3
<i>Pipturus</i>	64.8	67.6	12	222	121.6	0.45	4.2	8	681	24.7
<i>Castanopsis</i>	48.8	91.8	1	24	45.0	0.32	17.2	2	1068	26.6
<i>Caldclavia</i>	53.9	131.5	5	48	173.3	0.54	4.4	6	623	26.7
<i>Aleurites</i>	64.5	76.0	1	426	237.5	0.81	16.3	3	87	26.9
<i>Melicope</i>	61.9	88.1	37	167	127.7	0.61	6.1	7	356	29.3
<i>Cordia</i>	72.5	40.1	5	46	82.6	0.68	12.7	2	394	28.0

¹ Mean leaf area, double sided. ² Higher classes denote increasing pubescence. ³ Total leaf area sampled.