Variation in leaf trichomes and nutrients of *Wigandia urens* (Hydrophyllaceae) and its implications for herbivory

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Abstract. Leaf trichome variation was studied in a population of *Wigandia urens* (Hydrophyllaceae) in relation to water availability, diversity of herbivorous insects, and grazing rates. Plants of *W. urens* have glandular and urticant (stinging hairs) trichomes, and it is possible to distinguish two types of leaves: "smooth" leaves with only glandular trichomes and "bristly" leaves with both types of trichomes. Density of urticant trichomes was negatively correlated with weekly mean precipitation. Fourteen species of insects in five different orders feed on leaves of *W. urens* throughout the year. Grazing rates varied according to type and age of leaves. Grazing rates were lower in smooth than bristly young leaves but the rates were similar for mature leaves. Secondary metabolites, screened using qualitative methods, showed similar classes of compounds in both types of leaves. Bristly leaves had significantly higher concentrations of nitrogen, phosphorous and water and these nutritional differences were well correlated with the differences in grazing rates between bristly and smooth leaves.

Key words: *Wigandia urens* – Leaf trichomes – Herbivory – Intraspecific variation – Insects diversity

The role of pubescence as a physical barrier against herbivores has widely been reported in wild (Johnson 1953; Gilbert 1971; Levin 1973; Johnson 1975) and cultivated plant species (Stephens 1959; Broersma et al. 1972; Johnson 1975). Trichomes are distinctive biochemical compartments containing classes of compounds with different degrees of toxicity against herbivores or pathogens (Thurston and Lersten 1969; Thurston 1970; Levin 1973; Rodríguez 1983; Stipanovic 1983; Rodríguez et al. 1984; Kelsey et al. 1984). The most obvious examples are plants with stinging hairs found in the families Urticaceae, Euphorbiaceae, Loasaceae and Hydrophyllaceae (Thurston and Lersten 1969).

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Density of pubescence is correlated to basic physiological processes like water potential relations and photosynthesis (Ehleringer 1982, 1984; Ehleringer and Björkman 1978). Leaf pubescence is a very plastic trait that changes seasonally (Ehleringer and Björkman 1978), along aridity gradients (Johnson 1975; Ehleringer 1984) or within individual plants (Johnson 1975). Intraspecific variation in other chemical and physical traits has been widely reported in plants (Denno and McClure 1983) but the ecological and evolutionary consequences of this variation to plant-herbivore interactions are still in discussion.

Wigandia urens (Ruiz and Pavón) HBK (Hydrophyllaceae) is a very common shrub occupying different types of habitats. This species has glandular and urticant trichomes on leaves and stems. Presence and density of urticant trichomes are very variable and may be correlated with the heterogeneity of the environment. Deterring properties of leaf trichomes and toxic secondary compounds of leaves have been reported for plants of this species (Gómez et al. 1980). However, 17 species of herbivorous insects have been previously reported on this species in a seasonal xeric community in Mexico (Carbajal-Moreno 1975). Thus, *W. urens* constitutes a good system to analyze the interaction among environmental factors (humidity and disturbance), leaf pubescence variation (differences in trichomes) and herbivory. In this study, we compare grazing rates on bristly and smooth leaves of *W. urens* in relation to the following plant traits: a) type of trichomes, b) nitrogen, phosphorous and water content; and c) secondary compounds in both types of leaves. We also analyze relationships between environmental moisture and trichome density, and diversity of herbivores with disturbance.

Materials and methods

Species

Wigandia urens is a perennial shrub that usually colonizes open and disturbed sites. The classification of Mexican species of *Wigandia*

has been done using morphological characters including leaf trichomes as one of the main criteria. Nash (1979) reviewed the Hydrophyllaceae of Veracruz State, Mexico and described two varieties of *W. urens*, var. *urens* and var. *caracasana*, based on pubescence of leaves, petioles and stems. However, Ochoa (1976) found that leaf trichomes were a very variable character that cannot be used as a definitive criterion. We also observed a high degree of spatial and temporal variation in the density of trichomes even in a single population or on an individual plant. Thus, we studied *W. urens* as a single species.

Two types of trichomes are found on the leaves of *W. urens*: glandular and urticant stinging hairs. Glandular trichomes are smaller (0.7–1.0 mm) with a pedicel of four or five cells and multicellular head with a sticky secretion. Urticant stinging hairs are longer (3.0–6.0 mm), straight and sharp, and contain an irritant substance. Leaves without stinging hairs but with glandular ones we designated as smooth; leaves with both types of trichomes were called bristly. Because density of urticant trichomes varied between leaves we chose leaves with the highest density (>40 stinging hairs per cm^2) for all the observations. Smooth leaves were easily identified in the field. No leaves were found without any kind of trichomes. Plants of this species contain flavonoids (flavonoid 5, 4′-dihidroxi-7-metoxiflavona and 5, 4′-dihidroxi-6, 7-dimetoxiflavona) and terpenoids (farsenol-quinona and wigandol) (Gómez et al. 1980). However, these presumptive defensive characteristics of *W. urens* do not deter 17 phytophagous insect species that use different parts of this plant (Carbajal-Moreno 1975).

Study site

All the observations were done in the reserve "Pedregal de San Angel" (124.5 ha) in the campus of Universidad Nacional Autónoma de México (UNAM) in Mexico City. The vegetation is dominated by a herbaceous stratum with a few small shrubs and trees. This vegetation is classified as xerophytic scrub and it has more than 300 plant species (Rzedowski 1954). Elevation is 2225 m, mean annual temperature is 15.5° C, and the annual precipitation is 870 mm. This locality has a rainy season from June to October and a dry season from November to May.

Grazing rates

Three cohorts of young smooth and bristly leaves were tagged on July 24 (cohort A), October 3 (cohort B), and November 11 (cohort C). On November 12 an additional cohort (cohort D) of buds on both types of plants were tagged. We defined a cohort as a group of leaves of the same age independently of the size of the plant. Sample sizes of each cohort depended on the availability of both types of leaves in the field. The level of damage was measured periodically (every 8–15 days) with a transparent 0.5 mm grid. This grid was placed on the adaxial surface of the leaves covering all the leaf in a way that we could count the number of visible points coinciding with the holes of the lamina (as a product of herbivore damage), as well as the whole leaf. We calculated an index of leaf area removed (in percentage) as the quotient of the number of points registered (ruptured) to the total number of points of the grid covering the total leaf area. Grazing rates (%/day) were calculated by dividing the leaf area removed by the number of days between two consecutive measurements. Percentages of grazing rate values were arcsin transformed and compared between bristly and smooth leaves following the procedures of Zar (1974) and Snedecor and Cochran (1967) when the variances were not homogeneous. Actual data are reported in all cases.

Seasonality and diversity of insects

The diversity of insects, including both larvae and adults, was estimated from data from two censuses (October 1 and November 14) in six transects of 25 m, three in the interior and three at the edge of the reserve using the Shannon-Wiener index. The edge of the reserve was more disturbed (more light, near roads) than the interior. Ninety-six leaves per census were chosen with a plotless method (Poole 1974). We estimated the age of these leaves (according to their size, position on the branch, texture and color), type of trichomes and presence of phytophagous insects. Seasonality of phytophagous insects on *W. urens* was determined with regular observations through a year on plants in a permanent plot used for a long-term demographic study (Cano-Santana 1987). All specimens of insects are deposited in the collection of Instituto de Biología, UNAM. Comparison between diversity indexes were done following Zar (1974) procedures.

Density of trichomes and water availability

We counted the density of urticant trichomes on leaves of three ages in three months with different weekly mean precipitation to relate age of leaves, density of trichomes and availability of water in the environment. Data of daily precipitation were obtained from the meteorological station on the UNAM campus. Density of trichomes was counted directly with a stereomicroscope.

Chemical analyses

Leaves of intermediate age were collected from different plants of *W. urens* in the morning (9–10 a.m.) and used for chemical analyses. Nitrogen and phosphorous contents were analyzed on bristly and smooth leaves using an Autoanalyzer Technicon II (TIS 1977a, b) with a Kjeldahl method (McKenzie and Wallace 1954). The water content was estimated using the following method:

$$\text{Water content} = \frac{FW - DW}{FW}(100)$$

where $FW = $ fresh weight of a single leaf and $DW = $ its dry weight (dried in an oven at 60° C for 48 h).

Screening of secondary metabolites was done on hexanic and metanolic extracts; flavonoids with Shinoda-test, esteroids with Liebermann-Burchard-test, phenols with Ferric Chloride-test, and glucosides with Molisch-test (Domínguez 1973).

Results

The grazing rate was significantly higher in bristly young leaves (BY) than smooth ones (SY) in the cohort A ($t = 2.842$; $P < 0.01$) and cohort C ($t = 2.05$; $P < 0.05$). Differences were not significant for buds or for bristly or smooth leaves of intermediate and mature ages (Table 1). These values suggest that some herbivores eat bristly young leaves with more intensity than smooth ones, but by the time leaves are mature rates of grazing are the same.

In this study, we found only fourteen species of phytophagous insects on the leaves of *W. urens* contrasting with the 17 species found by Carbajal-Moreno (1975). These insects had different seasonalities (Table 2). At the beginning of the study (J–A) only three species were found on *W. urens*; but by mid-July, there were nine phytophagous species. Some are considered host-specific to *W. urens* (*Sphinx lugens* and *Aconophora pallescens*) based on experimental studies (Cano-Santana 1987). Others, like larvae of *Lophoceramica pyrrha*, usually eat leaves of *W. urens* and *Buddleia cordata* in natural con-

ditions but experimentally can eat more than 10 species of plants (Cano-Santana and Oyama unpublished). Shannon-Wiener diversity indexes estimated for the interior of the reserve were 0.303 in October and 0.166 in November, and for the edges were 0.408 and 0.405 respectively (Table 3). The diversity index was significantly higher in the edge of the reserve than in the interior in both October (t=15.189; $P<0.001$) and November

(t=50.501; $P<0.001$). Plants at the interior of the reserve showed a significantly higher diversity index in October than in November (t=20.365; $P<0.001$) but not at the edge of the reserve (t=0.563; $P>0.05$).

The ratio of bristly and smooth leaves (B:S) and the weekly mean precipitation were negatively correlated in the interior (r= −0.685; $P<0.001$) and edge (r= −0.838; $P<0.001$) of the reserve (Table 4). The

Table 1. Grazing rates (%/day) for four cohorts of bristly and smooth leaves of *Wigandia urens*. Means±1. SE are presented. Number of leaves measured in each cohort in parentheses. Age of leaves: B=buds, Y=young, I=intermediate, and M=mature

Cohort	Leaf age	Grazing rates		t*	P
		Bristly leaves	Smooth leaves		
A	Y	0.41±0.09 (36)	0.14±0.3 (48)	2.842	<0.01
B	Y	0.15±0.06 (50)	0.08±0.14 (53)	0.74	n.s.**
	I	0.10±0.06 (47)	0.12±0.04 (49)	1.63	n.s.
	M	0.18±0.06 (33)	0.20±0.07 (36)	0.12	n.s.
C	Y	0.14±0.05 (102)	0.04±0.01 (101)	2.050	<0.05
	I	0.09±0.03 (61)	0.09±0.04 (47)	0.03	n.s.
D	B	0.01±0.01 (52)	0.01±0.01 (50)	0.22	n.s.

* Data were arcsin transformed and t-test corrected when variances were not homogeneous (Snedecor and Cochran 1967). Percentage values presented without transformation.
** n.s. $P>0.05$

Table 3. Number of insects of each species and the Shannon-Wiener diversity indexes for the interior and edge sites at Pedregal de San Angel in two samplings. Sample size in all cases = 288 leaves

Species	October		November	
	Interior	Edge	Interior	Edge
Collaria sp.	83	127	142	90
Aconophora pallescens	0	1	0	1
Myzus persicae	4	1	7	19
Graphocephala sp.	1	3	0	0
Membracidae sp. 1	0	1	0	0
Sphinx lugens	0	1	0	0
Baratra configurata	1	0	0	0
Lophoceramica pyrrha	4	10	0	1
Sabulodes matrona	1	0	0	0
Sphenarium sp.	5	44	8	25
Total	99	188	157	136
Shannon-Wiener index	0.303	0.408	0.166	0.405

Table 2. Seasonality of insects associated with leaves of *Wigandia urens* in both the interior and edge sites at the Pedregal de San Angel. Rainy season months are underlined

Species	Seasonality (months)											
	J	F	M	A	M	J	J	A	S	O	N	D
Hemiptera												
Collaria sp.	*	*	*	*	*	*	*	*	*	*	*	*
Homoptera												
Aconophora pallescens Stal.						*	*	*		*	*	*
Myzus persicae (Sulzer)	*	*	*	*	*	*	*	*	*	*	*	*
Graphocephala sp.[a]												
Unidentified sp. 1[a]												
Lepidoptera												
Sphinx lugens Walk.							*	*	*	*	*	
Baratra configurata Walk.						*	*	*	*	*		
Autographa biloba (Steph)				*		*				*	*	
Lophoceramica pyrrha (Druce)							*	*	*	*	*	*
Sabulodes matrona Druce[a]												
Diptera												
Liriomyza sp.				*	*	*	*	*	*			
Orthoptera												
Sphenarium sp.							*	*	*	*	*	*
Ichthyotettix mexicanus Saussure					*		*	*	*	*	*	*
Oecanthus sp.[a]												

[a] Data not recorded

Table 4. Ratio of bristly (B) and smooth (S) leaves of *Wigandia urens* in relation to the daily mean precipitation (DMP) for different periods during a year in two zones within the Pedregal reserve. Number of leaves sampled is represented in parentheses. – data not recorded

Period	DMP (mm)	Ratio B:S	
		Interior	Edge
Feb28–Mar20	0.00	1.39 (374)	–
Mar21–Apr3	0.14	1.61 (305)	–
Apr4–18	3.08	0.19 (214)	–
Aug13–Aug26	5.12	0.03 (160)	0.25 (123)
Aug27–Sep9	2.50	0.10 (74)	0.11 (90)
Sep10–Sep24	3.35	0.17 (54)	0.09 (75)
Sep25–Oct10	3.03	0.11 (123)	0.72 (93)
Oct19–Oct24	0.17	0.29 (106)	1.75 (99)
Oct25–Nov7	0.00	0.92 (69)	3.00 (96)

Table 5. Concentration of water (% fresh weight), nitrogen, and phosphorous (% dry weight) in bristly and smooth leaves of *Wigandia urens*. Means ± 1SE are presented. n = sample sizes

	n	Bristly leaves	Smooth leaves	t	P
Water	16	72.2 ± 0.6	61.9 ± 0.9	9.95	< 0.0001
Nitrogen	10	3.25 ± 0.15	2.63 ± 0.09	5.34	< 0.001
Phosphorus	10	0.22 ± 0.01	0.15 ± 0.01	4.85	< 0.001

nitrogen, phosphorous and water contents were significantly higher in bristly leaves than smooth ones (Table 5). Tests for esteroids, flavonoids, phenols and glucosides were positive; alkaloids and saponins were negative. Because no differences in secondary compounds were found between bristly and smooth leaves, more detailed chemical analyses were not continued.

Discussion

Presence of pubescence is a very common feature in higher plants (Kelsey et al. 1984) and its adaptive value is generally thought to be related to the water economy of plants (Ehleringer 1982, 1984; Ehleringer and Björkman 1978; Rodríguez 1983) and to plant defenses against herbivores and diseases (Levin 1973; Rodríguez 1983; Kelsey et al. 1984). Plant water economy is related to trichomes either through an increased reflection of solar radiation which reduces leaf temperature, or by increasing the thickness of the boundary layer. In both cases, the transpirate rate is reduced and thus the content of water is potentially increased in the leaves if all other factors are equal (Ehleringer 1984). In *W. urens* the higher content of water in bristly than in smooth leaves is consistent with a role for trichomes of increased reflection of solar radiation. During the dry season, new buds have the highest density of trichomes, they are totally white (Z. Cano-Santana and K. Oyama pers. obs.). Increases in leaf pubescence density are common along aridity gradients (Johnson 1975; Ehleringer 1984) and may change seasonally (Ehleringer et al. 1976; Ehleringer and Björkman 1978) independent of plant species. Seasonal declines in the moisture content of plant leaves reduce the

suitability of leaves as food for leaf chewing insects (Feeny 1970; Mattson 1980; McClure 1980; Scriber and Slansky 1981; Kraft and Denno 1982). In *W. urens*, bristly leaves had higher contents of moisture and grazing rates were also higher on bristly leaves even with the presence of urticant trichomes.

In *W. urens* bristly leaves also had higher content of nitrogen and phosphorous. These nutritional properties were well correlated with the higher grazing rates suffered by bristly young leaves (e.g. herbivores preferred nutritionally rich foliage irrespective of trichome density) although this difference in grazing rate decreased with increasing leaf age. In any case, however, these results do not fit the suggestion that leaf pubescence may play a role in reducing herbivory by serving as a physical barrier to animal penetration or by emiting toxic or repellent compounds (Levin 1973; Johnson 1975). Experimental studies with *Lophoceramica pyrrha* and *Sphinx lugens* showed that larvae of these species grow better on a diet of bristly leaves than smooth leaves (Cano-Santana 1987; Cano-Santana and Oyama unpub.) suggesting that pubescence is not always an advantage to plants as a defensive mechanism against adapted insects (but see below). This is well illustrated in studies of plants with agronomical importance (Poos and Smith 1931; Wolfenburger and Sleesman 1963; Lukefahr et al. 1968; Starks and Merkle 1977; Benedict et al. 1983) but much less in wild plants. Plant hair-like trichomes act as a physical barrier keeping smaller insects away from the leaf surface (Stipanovic 1983). This is the case for *Collaria* sp., a very small and common insect on *W. urens*, which significantly preferred smooth young and intermediate leaves (Cano-Santana 1987).

At every site, there is a certain amount of temporal and spatial variation in vegetation structure, and the range of conditions may require different plant responses. The degree and frequency of disturbance may enhance or reduce perfomance of plants. Consequently, the patterns of spatial distribution of insects may be influenced not only by feeding preferences but by disturbance. At the Pedregal reserve, edge zones are more disturbed and insects may be attracted by artificial light resulting in higher insect diversity compared with interior zones.

Polymorphic and plasticity properties of plants of *W. urens* are related with herbivores with different levels of specialization (Cano-Santana 1987; Cano-Santana and Oyama unpub.). In the field, insect species were observed on different types of leaves or plants of *W. urens*. For example, *Autographa biloba* and *Baratra configurata* were usually found on bristly leaves of small plants and *S. lugens*, *L. pyrrha* and *Collaria* sp. were associated with large plants of *W. urens*. Experimentally, *Sphenarium* sp. and *S. lugens* prefer mature bristly leaves while males of *Ichthyotettix mexicanus* fed also bristly leaves but of different age (Cano-Santana and Oyama unpub.). Herbivores should respond in predictable ways to temporal and spatial changes in the quality of their host plants as food (Raupp and Denno 1983). Because of the changes in nutrients, moisture, structural defenses, and allelochemicals in leaves as they age and the impact of leaf age on herbivore fitness, we would expect some tissues to be preferred over others and the distribution of

herbivores in time and space to reflect this preference. *Wigandia urens*, as in other cases (Whitham 1981, 1983; Whitham and Slobodchikoff 1981), displays a mosaic of resources with different qualities in time and space that determine its present interaction with a set of diverse herbivores in the reserve of Pedregal de San Angel.

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