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Variation in leaf trichomes of *Wigandia urens*: environmental factors and physiological consequences

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Summary Seasonal and environmentally induced variation in the type and frequency of leaf trichomes of *Wigandia urens* (Ruiz & Pavón) Kunth (*Hydrophyllaceae*) was studied. Depending on the microsite, *W. urens* plants had smooth leaves with glandular trichomes or bristly leaves with both glandular trichomes and urticant trichomes (stinging hairs). Trichome density (number of urticant trichomes per unit leaf area) was higher in the dry season than in the wet season, and was significantly correlated with both temperature ($r = 0.353$, $P < 0.05$) and photosynthetic active radiation ($r = 0.313$, $P < 0.05$). Plants established in sun-exposed areas had trichome densities three times higher than those of plants established in shaded areas during the dry season, and 28 times higher during the wet season. At both exposed and shaded sites, trichome densities of the youngest leaves of young plants were higher than those of the youngest leaves of mature plants. In smooth and bristly leaves, transpiration rates decreased with increasing temperature during the day. However, smooth leaves had higher transpiration rates than bristly leaves at both exposed and shaded sites. In laboratory studies, trichome density was significantly ($P < 0.01$) reduced when small sun-grown plants (0.20–0.30 m tall) were either shaded or irrigated. In larger plants, also, irrigation significantly ($P < 0.01$) reduced trichome density relative to that of unirrigated controls.

Keywords: transpiration rates, water stress.

Introduction

Leaf hairs perform two distinct functions in plants: they provide a structural defense against herbivores (Levin 1973), and insulation against the environment (Esau 1965, Ehleringer et al. 1976, Rodríguez et al. 1984, Southwood 1986). The dual role of trichomes has been observed at the leaf level (Woodman and Fernandes 1991). However, few studies have assessed this dual role at the intra-population level (Cano-Santana and Oyama 1992*a*, 1992*b*, 1993).

Wigandia urens (Ruiz & Pavón) Kunth (*Hydrophyllaceae*) commonly occurs as a shrub or small tree in disturbed places in temperate and subtropical forests, along roadways and in abandoned fields in urban and suburban areas. Leaves of this species bear both glandular trichomes and urticant trichomes (stinging hairs). The presence and density of trichomes are correlated with aridity and herbivore pressure. Seventeen species of herbivores have been found on different parts of *W. urens* (Cano-Santana 1987). Some chewing herbivores like the grasshopper, *Sphenarium purpurascens* Charpentier, and larvae of the noctuid moth, *Lophoceramica pyrrha* Druce, cause severe defoliation of *W. urens* plants in some localities, indicating that the urticant trichomes do not deter the activity of these herbivores. Previously, we found that the presence and abundance of urticant trichomes on bristly leaves were correlated with tissue contents of water, N and P, which are higher in bristly leaves than in smooth leaves (Cano-Santana and Oyama 1992*a*). Furthermore, leaf nutrient status influenced the growth rate of *L. pyrrha* larvae (Cano-Santana and Oyama 1992*b*).

These findings raise the possibility that leaf trichomes of *W. urens* do not have a defensive role but serve primarily to reflect solar radiation and thereby restrict water loss, as has been reported for other plant species with leaf trichomes or spines (Ehleringer and Cook 1990, Woodman and Fernandes 1991). The two functions, defense against herbivores and the dissipation of radiant energy, are difficult to distinguish in *W. urens*, because of variation in both the type and density of trichomes and in the presence and abundance of herbivores.

In this study, we analyzed effects of light and water availability on the type and frequency of leaf trichomes of *W. urens*. We tested the hypothesis that variations in leaf trichomes influence physiological processes that indirectly affect plant–herbivore interactions.

Materials and methods

Site description

This study was done at the 146-ha Pedregal de San Angel reserve located on the campus of the National University of Mexico (UNAM) in Mexico City, Mexico (19º17′ N, 99°11′ W). Climate at the site is characterized by a dry season (from October to May) and a wet season (from June to September) (Rzedowski 1954) (Figure 1). The topography of the reserve reflects the activity of the Xitle Volcano located 21.5 km south. The vegetation, which resembles a mosaic as a result of heterogeneous soil conditions, comprises large tree species (*Buddleia cordata* Kunth and several introduced *Eucalyptus* spp.), small tree species (*W. urens*), shrubs (*Verbesina virgata* Cav. and *Senecio praecox* (Cav.) DC.) and herbs (*Muhlenbergia robusta* (E. Fourn.) Hitchc. and *Dahlia coccinea* Cav.) (Cano-Santana 1994).

Within the study area, *W. urens* exhibits variation in leaf trichomes dependent on soil depth (Cano-Santana and Oyama 1992*a*). Plants with smooth leaves bearing glandular trichomes are common along the edges of the reserve where the substrates are covered by a layer of soil. In contrast, in the inner part of the reserve, where rocky areas with almost no soil occur, plants growing in the crevices between rocks have bristly leaves bearing both glandular and urticant trichomes.

Field studies

Seasonal variation in leaf trichomes To investigate seasonal variation in leaf trichomes, we chose 30 *W. urens* plants, 0.3–1.0 m tall, growing at high density in a homogeneous area of the reserve. The number of urticant trichomes on the youngest leaf of each plant was recorded every month during the course of a year. This number was determined by counting the trichomes covered by a 1.41-cm^2 transparent plastic plate, placed in the center of the leaf blade.

The mean number of urticant trichomes per unit leaf area was studied in relation to monthly means of temperature and precipitation. Climatic data were obtained from a meteorological station located on the campus of the University.

Variation in leaf trichomes with environment and plant size We determined the effects of seasonal and environmental conditions on variation in leaf trichomes of *W. urens* plants growing in 20 × 30 m plots. One plot was unshaded with midday photosynthetic active radiation (PAR) of 1950–2440 μmol m^{-2} s^{-1}. The second plot was shaded by *Eucalyptus* trees and had a midday PAR of 130–1090 μmol m^{-2} s^{-1}. Plant height, height of the selected leaf, number of new leaves, number of trichomes per leaf, and leaf area were recorded for each plant.

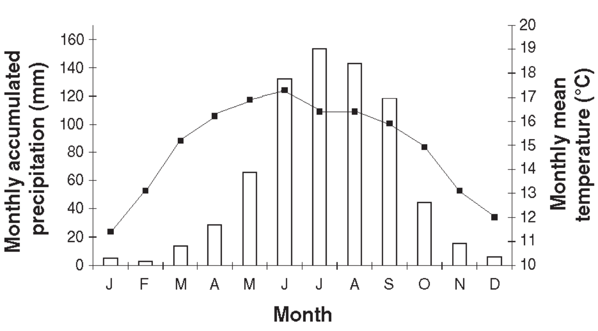

Figure 1. Monthly accumulated precipitation (bars) and mean temperature (■) at Pedregal de San Angel Reserve in Mexico City.

Data were evaluated by ANOVA (GLIM 3.77 statistical package), assuming a function of identity linkage and normal error (Zar 1974, Healey 1988).

Daily variation in transpiration with environment To compare leaf transpiration rates of smooth and bristly leaves in different environments, we selected four smooth and four bristly leaves. For each leaf type, two leaves were in a sun-exposed location and two in a shaded location. Leaf transpiration rates were measured with a porometer (LI-1600, Li-Cor, Inc., Lincoln, NE), and environmental temperatures were recorded, every hour from 0745 to 1445 h (solar time) (March 15, 1992).

Transpiration rate and trichome density The relationship between trichome density and leaf transpiration rate was investigated on March 17, 1992 (at 1300 h local time) in 50 randomly selected *W. urens* leaves from plants growing in a shaded area. Leaf transpiration rate, leaf temperature and photosynthetic active radiation were recorded for each leaf. Trichome density of each leaf was determined in the laboratory.

Experimental studies

To test effects of shade and irrigation on the presence and abundance of leaf trichomes of young *W. urens*, we chose 20 small plants of similar size (0.2–0.3 m stem height) growing in exposed conditions. The experimental design consisted in a 2 × 2 factorial with shading and irrigation as treatments. Shading was produced with wire mesh and dried leaves to simulate the shade produced by *Eucalyptus* trees. The maximum PAR received by the shaded plants at midday was 38% (about 386 μmol m^{-1} s^{-1}) of that received by the sun-exposed plants. Half the plants in each PAR treatment were irrigated daily with 5 l of water applied to a 50-cm^2-diameter area around each plant during the dry season (February 13 to May 11, 1992). Trichome density was recorded every 7 days on the youngest leaf of each plant.

To assess the effect of irrigation on leaf trichome variation, 10 mature plants between 1.0 and 1.5 m tall growing in an exposed area were supplied with 5 l of water on 87 days during the dry season (February 13 to May 11, 1992). Trichome density was recorded every 7 days on the youngest leaf of each of five randomly selected branches per plant. Treatment effects were evaluated by ANOVA (GLIM 3.77 statistical package), assuming a function of identity linkage and normal error (Zar 1974, Healey 1988).

Results

Field studies

Seasonal variation in leaf trichomes Mean monthly precipitation was negatively correlated with leaf trichome density of *W. urens* ($r = -0.295$, $P < 0.01$) (Figure 2). Trichome density increased during the dry season and decreased during the wet season. A negative correlation was also found between trichome density and mean monthly temperature ($r = -0.109$, $P < 0.01$).

Variation in leaf trichomes with environment and plant size Trichome density of *W. urens* leaves was three times higher in sun-exposed plants than in shaded plants during the dry season, and 28 times higher during the wet season (Table 1). As indicated in Figure 2, trichome density was higher during the dry season than during the wet season (Table 1).

Trichome density was also dependent on plant age (size). Young plants (0.20–0.3 m tall) had a higher trichome density than mature plants (1.0–1.5 m tall) in both exposed and shaded sites, although no significant correlation was detected during the wet season at exposed sites (Table 2).

Daily variation in leaf transpiration Transpiration rates decreased as temperature increased throughout the day in both smooth and bristly leaves, and in both exposed and shaded areas (Figure 3). At exposed sites, smooth leaves had higher transpiration rates than bristly leaves between 0745 and 1145 h (Figure 3a). Similar differences between smooth and bristly leaves were observed at shaded sites between 1045 and 1145 h (Figure 3b).

Transpiration and trichome density Trichome density was negatively correlated with leaf transpiration rate ($r = -0.281$, $P < 0.05$) (Figure 4). Smooth leaves had higher transpiration rates than bristly leaves; the highest values for smooth and bristly leaves were 62.0 and 34.8 µg H_2O cm^{-2} s^{-1}, respectively.

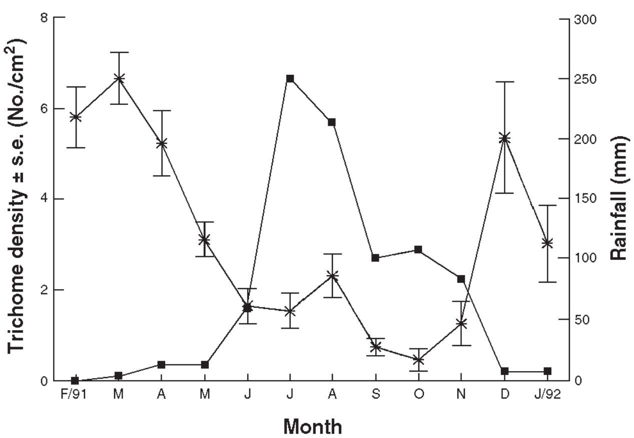

Figure 2. Trichome density (■) of leaves of *W. urens* and monthly accumulated precipitation (∗) during the study period ($r = -0.295$, $P < 0.01$).

Table 1. Mean density of trichomes (± 1 SE) on leaves of *W. urens* in two contrasting light environments and two seasons in the Pedregal de San Angel Reserve, Mexico City. Number of leaves are indicated in parenthesis.

	Density of trichomes (number cm^{-2})	
Season	Exposed site	Shaded site
Dry	8.7 ± 0.7 (150)	2.8 ± 0.4 (186)
Wet	5.6 ± 0.6 (196)	0.2 ± 0.1 (204)

Leaf trichome density was significantly correlated with temperature ($r = 0.353$, $P < 0.05$) and with photosynthetically active radiation (PAR) ($r = 0.313$, $P < 0.05$).

Experimental studies

Trichome density was significantly reduced in small sun-exposed plants (0.20–0.30 m stem height) in response to shading (ANOVA $F = 13.04$, $P < 0.01$) and irrigation (ANOVA $F = 25.63$, $P < 0.01$) treatments. The interaction between shading and irrigation was also significant (ANOVA $F = 9.91$, $P < 0.01$). In all treatments, initial trichome density was 5.9 cm^{-2}. After seven weeks, mean trichome densities of the youngest leaves of control plants increased to 11.4 cm^{-2}, whereas those in the shading and the irrigation treatments increased to 6.9 and 6.1 cm^{-2}, respectively. Mean trichome densities of the youngest leaves of plants in the shading + irrigation treatment decreased to 4.3 cm^{-2}. Irrigation of mature plants (> 1.0 m

Table 2. Correlation indices between density of trichomes of *W. urens* and plant height and leaf height. Sample size as indicated in Table 1. Significance: * = $P < 0.05$, ** = $P < 0.01$, and ns = $P > 0.05$.

	Exposed site		Shaded site	
Variable	Dry season	Wet season	Dry season	Wet season
Plant height	–0.428 **	–0.008 ns	–0.244 **	–0.164 *
Leaf height	–0.383 **	–0.002 ns	–0.293 **	–0.134 *

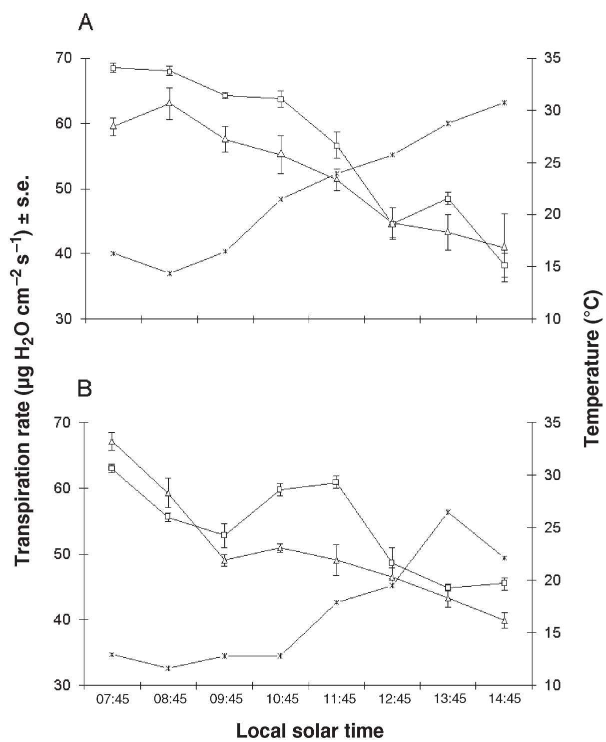

Figure 3. Transpiration rates of smooth (□) and bristly (△) leaves of *W. urens* in relation to environment temperature (∗) in open (exposed) (A) and shaded (B) sites.

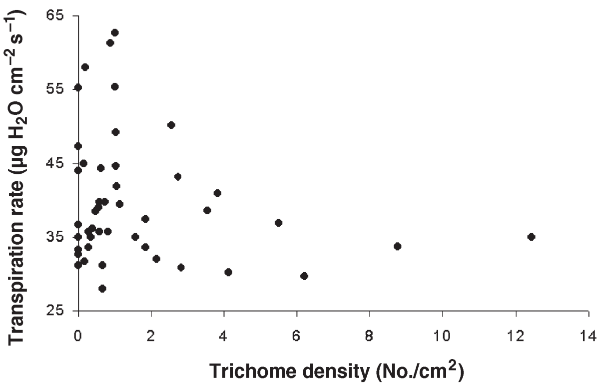

Figure 4. Correlation between leaf transpiration rate and trichome density in leaves of *W. urens* ($r = -0.281$, $P < 0.05$).

stem height) significantly reduced trichome density from 7.0 to 3.7 cm^{-2}, whereas in the control plants that were not watered, trichome density decreased by only 17% from 4.2 to 3.6 cm^{-2}.

Discussion

Leaf trichome density in *W. urens* was highly variable and depended on seasonal changes in light availability and soil water content. Trichome density decreased during the rainy season and increased during the dry season. Plants growing in sun-exposed areas (high PAR) had higher trichome densities than plants growing in shaded areas. Bristly leaves had lower transpiration rates than smooth leaves. Furthermore, trichome density decreased in response to irrigation and shade treatments.

Our observations indicate that leaf trichomes may help both to reflect incident solar radiation and dissipate absorbed heat, thereby reducing leaf temperatures and transpiration rates, as has been demonstrated for other plant species (Johnson 1975, Ehleringer and Mooney 1978, Ehleringer 1982, Ehleringer and Cook 1990, Woodman and Fernandes 1991). Pérez-Estrada (1993) reported that leaf temperatures of *W. urens* plants exposed to full sun do not exceed 26 °C. We conclude that, under non-drought conditions, *W. urens* plants control leaf temperature by leaf transpiration; however, under drought conditions, control of leaf temperature may depend on an increase in leaf pubescence (cf. Ehleringer 1982).

The variability of leaf trichomes on *W. urens* has several ecological consequences, particularly for plant–herbivore interactions. At the plant level, trichomes appear to provide both mechanical (presence and density of urticant and glandular trichomes) and chemical (urticant trichomes produce unknown irritant compounds) defenses, which are correlated with leaf and plant age. At the population level, these traits vary according to the microenvironment of the plant.

Although *W. urens* leaf trichomes appear to serve as a deterrent against some insect herbivores, there is also a positive relationship between the presence of urticant trichomes and damage by some herbivores including *Sphinx lugens* Walk. (*Sphingidae*) (Cano-Santana and Oyama 1993), *Lophoceramica pyrrha* (*Noctuidae*) and *Sphenarium purpurascens* (*Acrididae*). Thus, although hairy leaves deter some insect herbivores, the leaf physiological and metabolic processes associated with urticant trichome development appear to facilitate predation by other insect herbivores.

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