The three-minute trial period shows only the ant's initial reaction to the vine segment (which may be a general response to disturbance) rather than the specific behaviors used to remove an intruding vine. The effect of an intruding vine on the condition of the *A. collinsii* host would not be immediate. A longer trial period may be necessary to document the full range of behaviors used for vegetation removal.

Literature Cited

Janzen, D. H. 1983. *Pseudomyrmex ferruginea* (Hormigea del Cornizuela, Acacia-Ant). Pp. 762-764 *in* D. H. Janzen, editor. Costa Rican Natural History. University of Chicago Press, Chicago, Illinois,USA

Harsh above the marsh?
Changes in leaf morphology with decreasing height above the water table

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Abstract. We tested for changes in leaf morphology, leaf area, pubescence, and waxiness along a transect spanning a 0-7 m elevational range above the marsh, at Palo Verde National Park. We assumed that the water table deepened with increasing elevation, reducing water availability. There was no trend in leaf area with elevation. Pubescence increased, and waxiness declined with elevation. The presumed water gradient may not exist, or other factors may be more important in determining leaf morphology.

Key Words: dry deciduous forest, moisture stress, pubescence, leaf area

Introduction

In dry habitats water stress is an important factor shaping leaf morphology. High leaf temperatures inhibit physiological processes. Plants use water to carry out the light reaction in photosynthesis. The uptake of carbon dioxide via the opening of stomata is a source of leaf water loss, especially in C_3 plants. Evaporation of water by leaves facilitates the uptake of water and nutrients, and reduces high leaf temperature.

Leaves exhibit several adaptations to dry environments. In small leaves, heat loss due to convection is greater, so less evaporative cooling is required. Pubescence on the top of the leaf can reduce water loss if reflectivity is increased, reducing heat absorption. Hair on lower leaf surfaces may reduce transpiration by extending the leaf's boundary layer.

Consequently, we predicted that leaf pubescence and cuticular waxiness would increase along a presumed gradient in water availability above the marsh, and that leaf area would decrease over the same gradient.

Methods

We sampled leaves from woody plants along an elevational transect 1 km northwest of the OTS field station in Palo Verde National Park, Guanacaste, Costa Rica. The transect began at marsh level and continued up slope to an elevation 7 m above the marsh. The total length was ca. 150 m. The starting position was randomized along the marsh edge within a 20-pace range. Elevation was measured using marsh level as a benchmark, and sighting successive 1 m intervals of elevation with a clinometer.

Plants with a dbh > 10 cm were sampled in a 5 m-wide swath along the transect, those with a dbh 5-10 cm within a 3 m-wide swath, and those with dbh <5 cm and at least 1 m high, within a 1m swath. A basal area index (Σdbh^2) was calculated for both single and multiple stemmed plants. Leaf type, compound or simple, was recorded. Each plant canopy was examined carefully by two people, to select a single leaf that "best represented the average sized leaf on the tree." Leaf area was estimated as the blade length times maximum width. For compound leaves, areas were measured both for the entire leaf and for a typical leaflet. Leaf samples were then ranked separately in each of the following categories: pubescence on top (none, low, medium, and high), pubescence on bottom (none, low, and high), and waxiness (none, low, medium, or high).

Fallen leaves were also measured along the transect in 16.3 cm x 16.3 cm quadrats at 0, 1, 2, 3, and 4 m elevations above the marsh. Leaves with >50% of their area within the quadrat were collected, and an area index calculated, as above, as maximum length x maximum width.

Results

Pubescence increased for the upper leaf surface with increasing elevation (G-test, G=13.6, P=0.035; Fig.1) and also, but not significantly, for the lower surface (G-test, G=6.3, P=0.18). Upper pubescence also decreased significantly with increasing leaf area (G-test, G=11.6, P=0.07), and upper and lower pubescence were positively associated (G-test, G=41.3, P<0.0001).

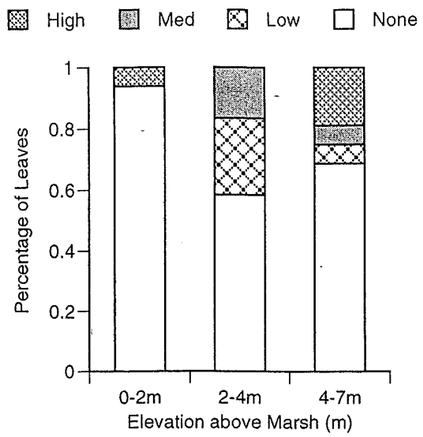

Fig. 1. Degree of pubescence on the top of leaves of woody plants at various elevations above marsh level at Palo Verde, CR. (G=13.6, p=0.035, n=44).

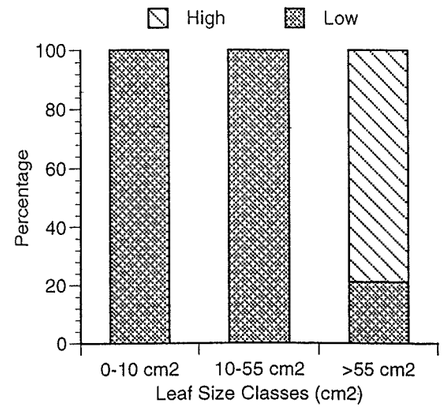

Fig. 3. Relation between degree of waxiness of leaves and leaf size classes in woody plants at Palo Verde, CR (G=36.9, p=0.0001, n=44).

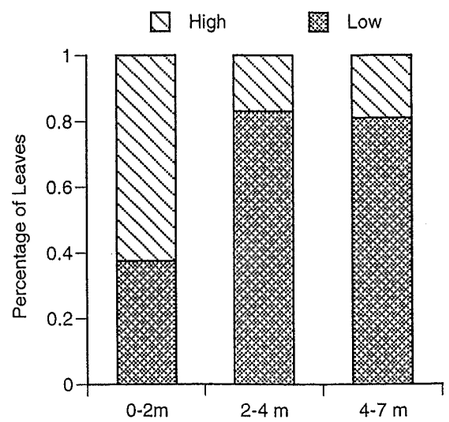

Fig. 2. Incidence of high and low waxiness in woody plants at various elevations above marsh at Palo Verde, CR. (G=9.04, p=0.01, n=44).

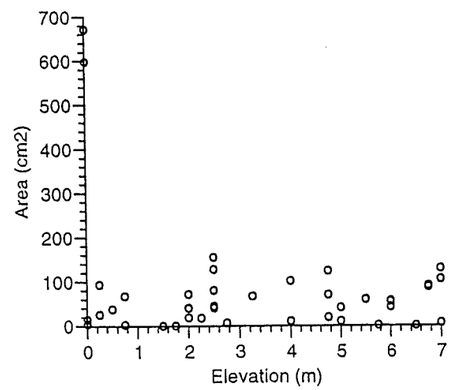

Fig. 4. Relation between leaf area and height above marsh in woody plants at Palo Verde, CR.

Contrary to our prediction, waxiness decreased with elevation (G-test, G=9.0, P=0.01; Fig. 2). There was no correlation between leaf area and elevation in either the fresh (Fig. 4.) or dry leaf samples (not shown). Waxiness also increased dramatically with leaf areas >50cm2 (G-test, G=36.9, P<0.0001; Fig. 3).

Discussion

In accordance with our predictions, pubescence on the top of the leaves increased in frequency with increasing elevation, as did bottom pubescence (the latter not significantly). The greater waxiness in the large leaves may compensate for moisture loss resulting from the greater heat load of large leaves.

The lack of the predicted trend in leaf area, and the contrary trend in waxiness, cast our assumptions about the water stress gradient into

doubt. First, deep tap roots may reach into the water table. Second, moisture stress may not be as important a factor in determining leaf morphology as other influences, such as herbivory. Finally, most species collected were deciduous; therefore, their leaves are dropped during the dry season, in which moisture stress is greatest. During the growing season, moisture stress may not be the dominant factor selecting for leaf morphology.