RETENTION AND MORPHOLOGY OF LEAVES OVER AN ENVIRONMENTAL GRADIENT AT PALO VERDE, COSTA RICA

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Abstract: Moisture and nutrient levels decrease with elevation on limestone ridges in tropical dry forests in Guanacaste, Costa Rica. We hypothesized that leaf area and retention would decrease, while leaf toughness would increase with elevation, in response to presumed physiological stresses over the elevational gradient. Evergreens were heavily concentrated at lower elevations, as predicted. Among deciduous woody plants, leaf traits did not change with elevation, probably because these plants escape water stress by early leaf loss in the dry season.

Keywords: Leaf morphology, elevation gradient, tropical dry forest, Palo Verde, land adaptation

INTRODUCTION

In tropical dry forests, the ridges and upper slopes generally lack soil; therefore, moisture and nutrients decrease with elevation as soil depth decreases (Janzen 1983).

We examined leaf morphology of woody species along a 100 m elevation transect running up to a limestone ridge, in a tropical dry forest in Palo Verde National Park. We predicted three trends: first, we expected leaf area to decrease with elevation due to increased mechanical and desiccation stress from wind and solar insolation; second, we predicted that leaf toughness would increase with elevation, conserving nutrients and acting as cost-effective means to deter herbivory; finally, we expected that leaf retention would decrease with elevation, because water stress may become critical at high elevations during the dry season.

METHODS

We sampled understory and canopy woody species over a 100m elevational change from near a marsh to near the Sendero Guyacan, behind the Palo Verde Biological Station, Palo Verde National Park, Costa Rica, on January 13 and 14, 2008.

Starting near the junction of Cerros Calizos and Mirador Guayacan trails (138 m asl), we sampled at each 10 m interval (measured with GPS), down the Cerros Calizos trail, At each interval, we established a sample point 5 m off the trail, choosing the left or right side randomly, and maintaining elevation constant.

At one site (38 m) by the junction of Sendero Pizote, we encountered trailside construction that precluded sampling on one side. On the other side, we proceeded 10 m beyond the disturbance along Sendero Pizote, and a further 5 m at right angles to that trail on a randomly chosen side.

Around each sample point, we sampled the nearest three trees with diameter at breast height (DBH) > 5 cm, and the nearest three woody understory plants 1-3 m tall.

From each individual sampled, we collected a leaf that represented the mean leaf morphology of that tree, if leaves were present and within reach, and recorded genus and family where possible. We sampled 23 canopy and 29 understory plants. We defined a leaf retention index as 1 = 0% leaf cover, 2 = < 50%, 3 = > 50% leaf cover, 4 = 100% leaf cover (yellowing leaves), 5 = 100% leaf cover (green leaves), and 6 = 100% leaf cover on an evergreen species. We multiplied leaf length and maximum width to calculate a leaf area index, and computed the mean leaf area index for each elevation. We used a toughness index, giving each leaf a score of 1 (least tough), 2 (medium toughness), or 3 (most tough). We noted pubescence on the bottom of each leaf as follows: 1 (none), 2 (small) or 3 (large).

We $\log_{10}$-transformed mean leaf area to equalize variances and correct non-normality.

RESULTS

We observed a total of 12 families, with 20 samples from unknown genera (unknown canopy = 7, unknown understory = 13). *Erythroylon* was the most abundant family or genus sampled followed by Fabaceae and Guazuma (Table1). Leaf retention increased significantly with elevation (r^2 = 0.83, df = 9, P = 0.0001). This was due entirely to the presence of evergreen trees at lower elevations: when we excluded evergreens , there was no significant trend in the timing of leaf loss with elevation (r^2 = 0.08, df = 9, P = 0.37).

There was no trend in leaf area with elevation, for either canopy (r^2 = 0.001, df = 7, P = 0.93) or understory species (r^2 = 0.23, df = 9, P = 0.13). Mean toughness was not significantly related to elevation for canopy trees (r^2 = 0.05, df = 7, P = 0.55), and was marginally significant for understory plants (r^2 = 0.32, df = 9, P = 0.07), with a trend toward greater toughness at low elevations.

All of the evergreen leaves sampled occurred at lower elevations, starting at 38 m and ending at 88 m (Fig 2). Only deciduousness had a significant effect on toughness (r^2 = 0.34, df = 53, P = 0.0063), with evergreen leaves much tougher than deciduous ones. There was no significant relationship between leaf pubescence and elevation for evergreen (r^2 = 0.00, df = 10, P = 94) or deciduous plants (r^2 = 0.05, df = 44, P = 0.11). Evergreens dominated woody plants at lower elevations (n = 12, Fig. 2), while they were conspicuously absent from higher elevations.

Table 1. Numbers of individuals sampled from each family/genus by understory/canopy

Family/Genus	Total Understory	Total Canopy
Apocynaceae	1	0
Burseraceae	0	1
Erythroxylon	12	1
Euphorbia	1	2
Fabaceae	2	6
Guiacum	1	0
Guazuma	2	1
Jaquinia	0	1
Luehea	0	4
Sapotaceae	0	5
Tabebuia	1	4
Tiliceae	0	1
Unknown	13	7

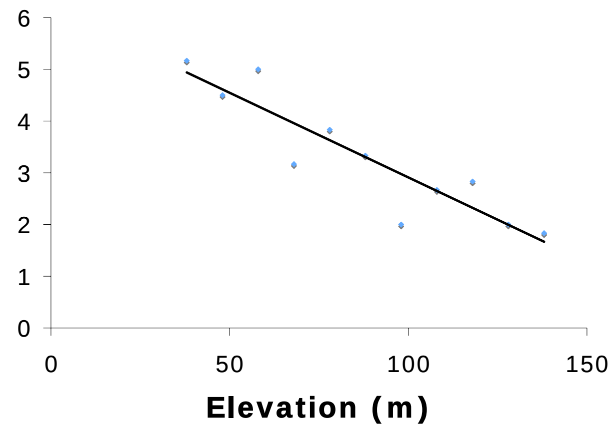

Figure 1. Trend in mean leaf retention by woody plants along an elevation gradient up a limestone ridge at Palo Verde, Costa Rica.

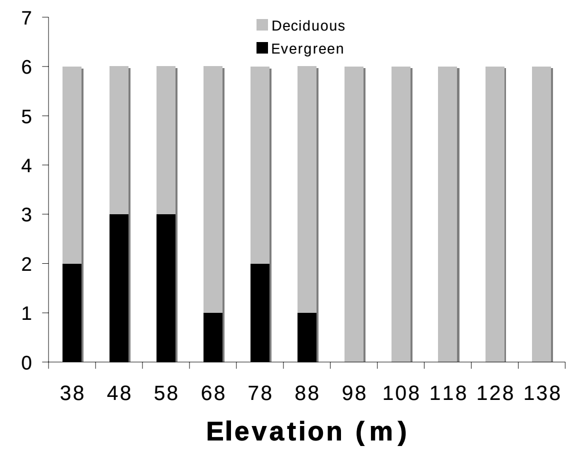

Figure 2. Proportions of evergreens sampled in woody plants along an elevation gradient up a limestone ridge, at Palo Verde, Costa Rica.

DISCUSSION

Vegetation retained fewer leaves with increasing elevation (Fig. 1), supporting our hypothesis that high elevation plants are early deciduous. Surprisingly, the trends we observed were dictated almost entirely by the concentration of evergreens at lower elevations.

Our results are consistent with the severe environmental gradients corresponding to elevation along our transect up to the limestone ridge. This was apparent in the complete absence of evergreens between 98 and 138 m, i.e. on the higher (and steeper) slopes.

Evergreens typically have tougher leaves than deciduous species, because leaf longevity makes investment in herbivore defense cost effective (Givnish 2002). Thus explains the marginally significant trend in understory plants for greater toughness at lower elevations.

Among deciduous trees, leaf area did not change with elevation. Deciduous plants escape the water stress that would occur if they maintained leaves in the dry season, by abscising leaves at the end of the wet season. Thus, it is not surprising that early deciduous plants did not follow the predicted trend in leaf area.

Evergreens can survive the dry season lower on the elevational gradient, where the soil probably retains more moisture during the dry season. Our results suggest that the elevational trends we observed were dominated by the extreme costs of maintaining leaves in a seasonally xeric environment.

LITERATURE CITED

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