A COMPARISON OF UNDERSTORY PLANT MORPHOLOGY ACROSS FOUR CLIMATIC REGIMES IN COSTA RICA

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Abstract. Plant morphology often varies as a function of abiotic factors. In spite of its small land area, Costa Rica has a wide range of climate types. We compared various aspects of sapling morphology in the understory and in treefall gaps in primary forests of four sites in Costa Rica. The four sites examined were: (1) Palo Verde - a tropical dry forest, (2) Monteverde - a mid-elevation cloud forest, (3) Corcovado - a Pacific lowland rainforest, and (4) La Selva - a Caribbean lowland rainforest. We also measured canopy density and light intensity at these sites. Stem diameter in relation to tree height was greatest in Palo Verde where light intensity was high. More leaves were tougher and had pubescence in the drier sites. There were more leaves with drip tips in the wetter sites. A greater proportion of trees at Palo Verde and in gaps had compound leaves. At all sites, leaves in gaps were larger and less tough. We discuss the possible physiological explanations for these patterns.

Key Words: climate, leaf morphology, primary forest, understory, treefall gaps

INTRODUCTION

Plant morphology is generally thought to vary with differences in climate (Brosh and Peet, 1997). One would expect to see different leaf types across the wide range of habitat types and climatic conditions in Costa Rica. This study examined several aspects of morphology of primary forest understory saplings across four sites in Costa Rica: Palo Verde, Monteverde, Corcovado, and La Selva. We asked the following questions: how does leaf morphology of forest shrubs and saplings vary across regions; are there differences among regions and between gap and understory species; and how does light availability in a forest vary among regions? We hypothesized that plant morphology would differ across sites of varying abiotic conditions and between gaps and understory habitats.

METHODS

We surveyed understory saplings along transects within gaps in four Costa Rican primary forests that varied in annual rainfall and elevation (Table 1). In each forest, we sampled eight understory sites located every 15 m along a transect and in 2 - 3 gaps chosen haphazardly within primary forest. At each site, within each forest, we measured the five dicot saplings (1 - 5 m tall) that were closest to the transect point. For each sapling, we measured height and diameter and recorded leaf dimensions, toughness, pubescence and morphotype. Leaf dimensions included blade length and maximum width. Toughness was measured as the average force required to pierce five different leaves with a leaf penetrometer. Morphotype characteristics included the presence of serration, drip tips, compound leaves, and pubescence. At each sampling site, we measured canopy density with a spherical densiometer and light intensity with a light meter. We calculated leaf area with width and blade length using the equation for an ellipse (π / 4 * L * W).

We performed regressions to compare the relationship between tree diameter and tree height across forests. We used two-way ANOVAs to test the effect of forest site and habitat (understory or gap) and their interactions on leaf toughness, area, canopy cover, and light intensity. We used a nominal logistic model to test the effects of forest site and habitat and their interactions on presence of serration, compound leaves, drip tips, and pubescence.

TABLE 1. Summary of mean annual rainfall and elevation for the four study sites.

Site	Mean Annual Rainfall (mm)	Elevation (m)
Palo Verde	1,000 - 1,500	3 - 183
Monteverde	1,500 - 2,000	1,200 - 1,800
Corcovado	plains: 3,000 - 3,800 uplands: 4000+ interior: 5,000 - 6,000	0 - 400
La Selva	3,991 ± 748	29 - 100

RESULTS

Stem diameter was significantly greater at Palo Verde. Regression analyses of tree height on stem diameter indicated that trees in Palo Verde tended to increase less in height per unit increase in diameter than trees at the three wetter sites (Fig. 1). Leaf toughness was significantly greater in Palo Verde and in understory habitats (Fig. 2). Trees in gaps had greater leaf area than trees in the understory. ANOVA results are summarized in Table 2.

There was a significantly higher proportion of compound leaves in Palo Verde than at the other three sites. In Corcovado and La Selva there tended to be more compound leaves in light gaps than in the understory. Serration did not differ across sites or habitat types. There tended to be more leaves with drip tips at La Selva and Corcovado than at Palo Verde. There were more pubescent leaves at Palo Verde and Monteverde than at the other two study sites. We used the nominal logistic model to test for effects of site and habitat on leaf type (simple vs. compound), presence or absence of serration, drip tips, and pubescence are presented in Table 3.

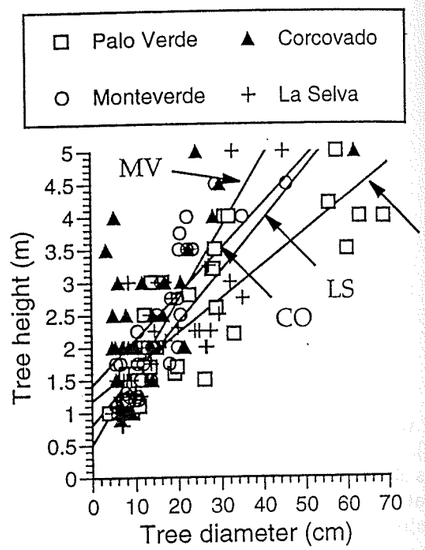

FIG. 1. Relationship between tree height and tree diameter across four study sites.

TABLE 2. Summary of ANOVA results.

Source	df	F-statistics			
		Leaf Toughness	Leaf Area	Canopy Cover	Light Intensity
Site	3	10.65***	1.63	4.91**	66.04***
Habitat	1	4.04*	12.66***	14.62***	365.58***
Site x Habitat	3	0.93	1.10	0.51	57.08***
Error	202	202	202	34	34

* P < 0.05; ** P < 0.01; *** P < 0.001

TABLE 3. Results of nominal logistic analyses.

Source	df	X^2 Values			
		Compound	Serration	Drip Tips	Pubescence
Site	3	12.80**	4.42	7.31+	10.52*
Habitat	1	0.00	2.46	0.01	0.91
Site x Habitat	3	1.76	2.91	3.06	1.86

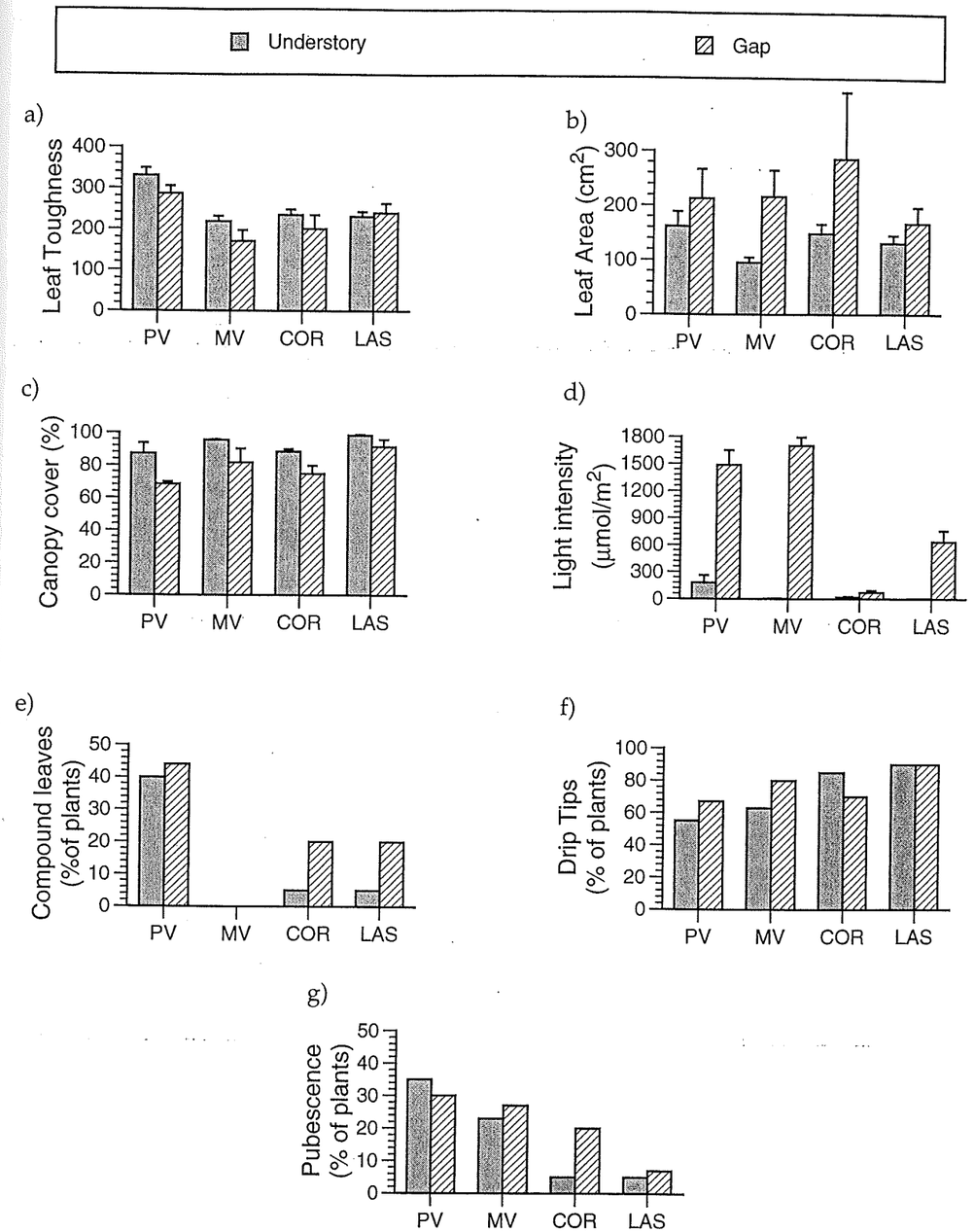

FIG. 2. Measures of leaf morphology and abiotic factors in the understory and tree gaps in four sites in Costa Rica.. (PV = Palo Verde; MV = Monteverde; COR = Corcovado; LAS = La Selva.)

DISCUSSION

Trees in the four sites sampled showed different growth strategies. In Palo Verde, where canopy cover was lowest, trees allocated relatively more resources toward enlarging trunk diameter than toward increasing in height. At Monteverde, Corcovado, and La Selva, where sunlight is a limiting factor, there is presumably vary strong selection to attain canopy-height as quickly as possible. Alternatively, the change in the ratio of trunk diameter to tree height between Palo Verde and the other sites could be explained by damage to saplings (broken stems) due to falling debris such as tree limbs and palm fronds, but if this were true we would have expected less height per diameter at Corcovado and La Selva where the canopy is taller and falling debris is known to result in frequent stem damage (D. B. Clark, pers. comm.).

As expected, we found significant variation in leaf morphology characteristics across the four sites. The need to keep water loss to a minimum in arid environments explains the higher leaf toughness and pubescence at Palo Verde than in the other sites. Gap-colonizers had larger, but less tough leaves than understory species. This is consistent with a strategy of photosynthetic surface area at the expense of the phenolics and fibers that influences leaf toughness (Coley, 1983). The greater presence of compound leaves in Palo Verde and in gaps at Corcovado and La Selva is most likely the result of a greater proportion of legumes in this area. The success of legumes in this kind of environment could be because nitrogen fixation (typical of legumes) is energetically costly and is most likely to be cost effective in areas of high light intensity and high photosynthetic potential. Serrated leaf edges are thought to increase early season photosynthesis by the expanding leaves of deciduous trees in areas with a seasonal dry season (Baker-Brosh and Peet 1996). However, we did not find more leaves with toothed margins in Palo Verde . Drip tips are thought to remove water from the leaf surface quickly and serve to reduce nutrient leaching as well as colonization by epiphylls. Consistent with this, we found more leaves with drip tips at sites with high annual rainfall than at sites with low annual rainfall.

LITERATURE CITED

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