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Interciencia, vol. 25, núm. 5, agosto, 2000, pp. 254-259

Asociación Interciencia
Caracas, Venezuela

Available in: http://www.redalyc.org/articulo.oa?id=33904706
ENVIRONMENTAL GRADIENTS AFFECT FOREST STRUCTURE
IN PUERTO RICO’S LUQUILLO MOUNTAINS

Peter L. Weaver

SUMMARY

Forest structure and species richness vary along environmental gradients in the colorado forest of Puerto Rico’s Luquillo Mountains. Rainfall and temperature vary with aspect and elevation resulting in wetter conditions to the windward than to the leeward. A covariance model showed that: stem density increases significantly with elevation to the windward but not to the leeward; tree height decreases significantly with elevation on both windward and leeward exposures; total aboveground woody biomass decreases significantly with elevation on ridges to the windward; and organic matter increases significantly with elevation to the leeward. ANOVAs disclosed interactions between aspect and topography for species diversity and biomass. Species-area curves show the greatest number of species on ridges and the fewest in ravines.

RESUMEN

La estructura forestal y la riqueza de especies varían según gradientes ambientales en el bosque de colorado en las montañas de Luquillo en Puerto Rico. La precipitación y la temperatura varían con aspecto y elevación, resultando en condiciones más húmedas al barlovento que al sotovento. Un modelo de covarianza demostró que: la densidad de tallos aumenta significativamente con elevación en barlovento pero no en sotovento; la altura de árboles disminuye significativamente con elevación tanto en barlovento como en sotovento; la biomasa leñosa total sobre el terreno disminuye significativamente con elevación en crestas de barlovento; y la materia orgánica aumenta significativamente con elevación en sotovento. Curvas de especies-área muestran el mayor número de especies en crestas y el menor número en hondonadas.

Introduction

Changes in forest types (i.e., their species composition and structure) along elevational gradients were described in the Luquillo Experimental Forest (LEF) of northeastern Puerto Rico (Wadsworth, 1951; White, 1963), the Lesser Antilles (Beard, 1944, 1949), and Jamaica (Asprey and Robbins, 1953), about 50 years ago. Subsequent studies of gradients in the LEF showed changes in species composition associated with aspect, elevation, and topography within a single forest type (Weaver, 1991, 1994). Analyses of structural variation along gradients within particular forest types, however, have not been reported. The purpose of this research is to characterize topographic differences in species diversity, and to show changes in forest structure and soil organic matter content according to aspect, topography, and elevation within the colorado forest of the Luquillo Mountains.

The Study Site

Four forest types occupy the LEF (Wadsworth, 1951; Weaver, 1983, 1989a; Weaver and Murphy, 1990). The tabonuco forest, situated between 150 and 600 m in elevation, is named for Dacryodes excelsa Vahl, the tabonuco tree. Other major species reaching the 30-m canopy include Manilkara bidentata (A. DC.) Chev., Sloanea berteroana Choisy, and Buchenavia tetraphylla (Aublet) R. Howard. The forest contains >50 tree species per hectare.

The colorado forest, between 600 and 950 m, is characterized by Cyrilla racemiflora L., the colorado tree (Weaver, 1986). Other tree species commonly found in the canopy are Micropholis chrysophylloides Pierre, M. garcinifolia Pierre, and Henrietta squamulosa (Cogn.) Judd. Reaching 15 to 20 m in...
height, the colorado forest has >40 tree species per hectare.

The dwarf forest, growing between 950 m to the LEF’s 1,075 m summits, has about 15 tree species per hectare. Dwarf forest, high in stem density and rarely >5 m in height, is gnarled and epiphyte-laden. Common tree species that reach the canopy include Tabebuia rigida Urban, Ocotea spathulata Mez, M. garciniifolia, and Clusia clusoides (Griseb.) D’Arcy.

Palm brake, occurring above 500 m, is scattered along streams and on steep windward slopes. Palm brake, reaching 15 to 20 m in height, contains >30 tree species per hectare, but is dominated by Prestoëa montana (R. Grah.) Nichols, the sierra palm (Weaver, 1983). These same forest types in the Lesser Antilles are designated as lower montane rain forest, montane rain forest, dwarf forest, and palm brake, respectively (Beard, 1944; 1949).

According to the life zone system (Holdridge, 1967; Ewel and Whitmore, 1973), subtropical wet forest, sub-tropical rain forest, and sub-tropical lower montane forest are encountered while ascending the windward gradient. The descent along the leeward gradient passes through subtropical lower montane wet forest and sub-tropical wet forest. The forest designated as colorado (sensu Wadsworth), or montane rain forest (sensu Beard), is recognized as two life zones—subtropical lower montane rain forest and subtropical lower montane wet forest (sensu Holdridge). Hereafter, the term colorado forest will be used.

Methods

During 1981 and 1982, 25 groups of three plots (one each on ridge, slope and ravine topography) were selected between 620 and about 950 m elevation within the colorado forest (10 groups to the windward and 15 groups to the leeward). The groups were spaced at about 50 m intervals. The plots contained closed canopy forest and had varying aspects, slopes, and exposures. Ridge plots were entirely on convex topography, ravine plots were entirely on concave topography, and slope plots were on nearly uniform slopes without pronounced concave or convex features.

After preliminary observations, a 50 x 10 m plot size and a minimum stem diameter of 4 cm at breast height (dbh, or 1.4 m above the ground) were selected for sampling. Tree height for all stems was estimated to the nearest 0.1 m with an optical rangefinder. All species were identified using local taxonomic references (Little and Wadsworth, 1964; Little et al., 1974; Liogier, 1985-97).

The null hypothesis of the complete covariance model was that the effects of inter-

\[
Y = T + A + (T \times A) + E \]

where Y = the number of species per 500 m² plot, T = topography, A = aspect, and E = elevation. None of the component terms of the model was significantly correlated with elevation.

Aboveground woody biomass for all species was estimated by multiplying tree volumes by their respective oven-dry specific gravities. The latter were derived from local texts (Little and Wadsworth, 1964; Little et al., 1974) or directly from the U.S. Forest Service’s Wood Products Laboratory in Madison, Wisconsin.

Canopy closure on each plot was estimated from four densiometer readings taken at two points spaced about 20 m apart. The densiometer’s surface, a grid superimposed on a mirror, allows a direct estimate of canopy closure in percent by counting completely or partially shaded squares. At each densiometer point, two soil samples were collected to 50 cm depth with a soil probe. Soil contents were composited by plot and placed in collecting bags. Aboveground woody biomass (t/ha) and soil organic matter (kg/m²).

In the data analysis, the main effects of aspect, topography and elevation were considered along with interaction. Initially, for each parameter (Y), the complete model was:

\[
Y = \text{aspect} \times \text{topography} + \text{elevation} + (\text{aspect} \times \text{topography}) + (\text{aspect} \times \text{elevation})
\]
Figure 2. Tree species-area relationships for 25 ridge, slope, and ravine plots, each 500 m² in size, in the Colorado forest. In each instance, the vertical set of plots (ridge, slope and ravine) are from the same area within the forest.

Results and Discussion

The mean canopy closure for all plots was 91 percent. This indicates that the selected plots had closed canopies with occasional small openings among branches or between trees.

Species diversity gradients. The number of tree species averaged 15 per plot (Table I) and ranged from 5 to 28 (Figure 1). No significant relationships were demonstrated with elevation in the complete covariance model, probably because the high variability in species numbers per plot and the relatively small 0.05 ha sample plot size. Other trends were apparent, however. Leeward plots had a greater average number of species by topographic position than windward plots, and there is a decline in average numbers of species from ridge to slope to valley, regardless of aspect (Table I).

Moreover, the number of species on the most diverse plots tended to be concentrated at lower to intermediate elevations (Figure 1). The general decline in species numbers with elevation is a common phenomenon in both temperate and tropical forests (Beard, 1949; Wadsworth, 1951; Whittaker, 1956). With ascent from the tabonuco through the Colorado to the dwarf forest in the LEF, permanent plots average 45 to 55, 35 to 40, and 15 to 20 tree species, respectively (Weaver, 1987).

The lower mean number of tree species to the windward as compared to the leeward may be due to environmental factors. On the windward plots, the effects of greater rainfall and cloud cover are similar to those of higher elevation where solar insolation is reduced, soil water is increased, and the existence of permanent plots average 45 to 55, 35 to 40, and 15 to 20 tree species, respectively (Weaver, 1987).

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creased, and organic matter mineralization is slowed. Palms, well-adapted to wet conditions, are abundant (Ewel and Whitmore, 1973). Moreover, some dicotyledonous tree species common at lower elevations are probably less competitive under these saturated conditions; consequently, species richness is lower.

Species-area curves by topography for all plots show that ridges had the greatest cumulative number of species and ravines the least (Figure 2). These differences may be related to local gradients in forest height and drainage. Several of the LEF's rare tree species are relatively small in stature and survive in the shorter vegetation characteristic of better drained ridges and upper slopes (Weaver, 1989b). Also, tree density is greater on ridges than other topographies (Table I) assuring that the number of trees sampled is greater and more likely to include uncommon species.

**Tree density gradients.** The mean stem density for all 75 plots was 2174/ha and was significantly correlated with elevation to the windward but not to the leeward (Table I). Ultimately, the covariance model was reduced to two linear regressions of tree densities vs. elevation to the windward — one for ridge and slope plots combined, and the other for valley plots (Figure 3). An ANOVA of leeward densities showed that ravines had significantly fewer trees than ridges or slopes (Table I). The mean tree density for all temporary sample plots combined averaged about 15 percent higher than on the permanent colorado plots, which ranged from 1635 to 2190 trees/ha and had an average of 1860 trees/ha (Weaver, 1983). The differences between permanent and temporary plots reflect in part the small plot size used in this study and the selection of closed canopy stands for sampling.

**Tree height gradients.** The mean height for all dominant and codominant stems on the 75 plots was 12.7 m, and tree height was significantly related to elevation on both windward and leeward exposures (Table I). Individual plot mean heights ranged from 8.1 to 17.2 m. Differences among topographic positions by aspect were not significant to the windward, and ultimately the covariance model was reduced to a linear regression of tree height vs. elevation. To the leeward, two separate linear regressions were significant, one for ridge and slopes combined, and one for the valleys (Figure 4). Tree density and tree height are related to tree size. The colorado forest gradient in tree size is more pronounced to the windward than to the leeward. At low elevations, some plots had tree species characteristic of the tabonuco forest such as Dacryodes excelsa, Manilkara bidentata, and Ormosia krugii Urban (Weaver, 1991). These species tend to be larger than most of those in the colorado forest. In contrast, some plots at higher elevations, in particular to the windward, are exposed, and contain a dense, stunted vegetation (Beard 1944, 1949; Wadsworth, 1951). Numerous dwarf forest species, generally small in size, grow on these exposed sites.

**Biomass gradients.** The mean aboveground woody biomass for all 75 plots was 148.2 t/ha (Table I). Elevation did not explain a significant portion of the variance to the leeward; in contrast, topography, elevation, and their interaction were significant to the windward where biomass was correlated with elevation on ridge topography (Figure 5). The comparatively low aboveground woody biomass in ravines (Table I) was partially

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*Figure 3. Distribution of data points in the covariance model Y = E, where Y = the number of stems/ha and E = elevation, according to aspect. The elevational component of the model is significant at the 95 percent level to the windward but not to the leeward. Topography of sample plots is indicated.*

*Figure 4. Distribution of data points in the covariance model Y = E, where Y = the mean height of dominant and codominant trees on the 500-m² plots and E = elevation, according to aspect. The elevational component of the model is significant at the 95 percent level in both windward and leeward forests. Topography of sample plots is indicated.*
caused by differences in species compositions, stem densities, and tree sizes. Ravine plots contain numerous palms which average about 15 to 20 cm in dbh, whereas slopes and ridges contain proportionately more dicotyledonous species that occasionally attain much larger diameters. In a forest comprised of many small stems, a few large trees influence individual plot biomass values considerably, notably at low elevations on ridge plots to the windward.

Trends in plot basal areas and volumes parallel those of aboveground woody biomass (Weaver, 1987). Differences among topographic positions, however, are more pronounced for biomass than for those of basal area or volume. This is due to the lower specific gravities of species that characterize ravines. The palm, *Prestoea montana*, with a specific gravity of 0.26 g/cm$^3$, and the dicotyledonous species *Cecropia schreberiana* Miq. and *Sapium laurocerasus* Desf. with specific gravities of 0.29 and 0.38 g/cm$^3$, respectively, are common ravine species (Weaver, 1991). Their specific gravities are lower than those of canopy slope and ridge species which range from 0.50 to 0.70 g/cm$^3$. Similar topographic differences in specific gravity between tree species in ravines and those on slopes and ridges were observed in the montane forests of Costa Rica (Lawton, 1984).

**Organic matter gradients.**

The soil organic matter content in the top 50 cm of soil for all 75 plots combined was 33.8 kg/m$^2$ (Table I). Two separate analyses of organic matter content vs. elevation, each by aspect, showed a significant increase in organic matter to the leeward but not to the windward (Figure 6). Mean organic matter content, however, averaged slightly greater to the windward than to the leeward (Table I). Other factors being equal, organic matter of soils in humid forests should increase with a decrease in temperature, an increase in rainfall, or a decrease in the temperature/rainfall ratio (Brown and Lugo, 1982). With an increase in elevation, temperature decreases and both rainfall and cloud cover increase, raising soil water content and retarding the decomposition of organic matter (Grubb, 1971). The rain shadow phenomenon is characteristic of areas to the leeward of mountains lying in the path of moisture-laden winds from the ocean (Runcie, 1968). This effect accounts for the vertical displacement of lower montane forest to higher elevations on leeward slopes, a phenomenon observed
The organic matter content of soils on slopes tended to be greater than those of ridge or ravine soils to both the windward and leeward (Table 1). Wind and heavy rainfall in the Luquillo Mountains probably contribute to this phenomenon. Wind on exposed ridges could distribute leaves to the leeward of crests as was observed on steep topography in central New York State (Welbourn et al., 1981). Moreover, runoff from the ridges during heavy rains is rapid and should move organic matter down slope where it may be trapped locally in route or deposited in ravines. Earlier work adjacent to one of the plots in this study showed that the down slope export of organic matter ranged from 1 to 4 g/m²/day (Frangi and Lugo, 1985). Once in ravines, it is undoubtedly washed down stream during riparian zone flooding and peak streamflows that occur during heavy rains. A similar phenomenon of greater soil organic matter on slopes as opposed to ridges or concave topography was noted in Puerto Rico’s active coffee shade forests located on deep volcanic soils in the subtropical wet forest life zone (Weaver et al., 1987).

The organic matter content of soils in undisturbed forest at high elevations in the Luquillo Mountains is considerably greater than in the island’s secondary forests (Weaver et al., 1987). Soil samples taken to a depth of 23 cm during Puerto Rico’s 1980 secondary forest inventory averaged only 9.0 and 7.3 kg/m², respectively, for the subtropical moist and subtropical wet forest life zones. Greater organic matter concentrations in these forests were associated with more mature forest cover and greater standing volumes of timber (Weaver et al., 1987).

ACKNOWLEDGMENTS

Carlos Rivera assisted with field data collection. Dr. Peter G. Murphy, Michigan State University, reviewed an earlier version of the manuscript. Dr. Bernie Parresol, U.S. Forest Service in Asheville, made helpful comments on data analysis. Organic matter samples were processed in the International Institute of Tropical Forestry laboratory. Several of the specific gravities were determined at the Forest Products Laboratory, Madison, Wisconsin. This work was done in cooperation with the University of Puerto Rico, Rio Piedras.

REFERENCES