Tree fall disturbance and *Quercus* population structure: A case study of two montane sites

Christopher M. Leander, Ryan M. Owens, and Rafael D. Rosengarten

Abstract: *Quercus* tree falls are important in maintaining forest structure and diversity at Cerro Cuericí. We hypothesized that wind is a more important factor than slope in causing tree falls, and that turnover would be higher in sites more heavily uprooted by high winds resulting in smaller trees on average. We measured the DBH (diameter at breast height) of *Quercus*, and counted tree falls in two sites: a flat, wind-exposed ridge, and a wind-sheltered slope. While tree falls did not differ between sites, DBH of sub-canopy *Quercus* was significantly smaller on the ridge than the slope. The DBH distributions of *Quercus* also differed significantly between sites. Disturbance frequency does not seem to be driving this pattern. These differences in forest structure may be related to variation in timing of recruitment or growth rate.

Key Words: forest dynamics, oak, recruitment, tropical montane forest

Introduction

Oak trees (*Quercus* spp.) dominate the forest canopy of the mountain ridges and slopes on the Cerro de la Muerte, Cartago Province (Janzen 1983). Frequency of *Quercus* tree falls (i.e., disturbance) is important in maintaining forest structure and diversity (Bellow 1998). Both slope and mechanical stress induced by wind cause tree falls (Dyhrman et al. 1993), and wind tends to be higher on mountain ridges than leeward slopes. We hypothesized that wind disturbance is a more important factor than slope in causing tree falls, and that oaks in a more highly disturbed area would be smaller due to higher rates of turnover. We therefore predicted that there would be a greater number of fallen trees on a mountain ridge than a leeward slope, and that the oak trees in the more disturbed area would have a smaller mean diameter at breast height (DBH) than those in the less disturbed area.

Methods

We sampled *Quercus* at two sites along the loop trail at the Cuericí Research Station, Costa Rica. One site was a flat ridge top exposed to the prevailing northeast wind (ridge site). The second site was on a south-facing slope protected from the wind (slope site). In each site we marked one 150 pace section of trail. We then stratified both sites into five subdivisions of 30 paces. We walked five 50 m belt transects, one per 30 pace subdivision, perpendicular to the trail. Transects intersected the trail at randomly chosen distances from the edge of each subdivision.

We measured the DBH of each sub-canopy *Quercus* encountered within 1.75 m of the center of each belt. We excluded any *Quercus* shorter than the height of the measurer (approximately 2 m). Assuming that canopy-height *Quercus* would be more widely spaced than sub-canopy trees, we measured the DBH of each canopy *Quercus* encountered within 3 m of the center of each belt. We also counted the number of fallen trees encountered in each belt.

T-tests were used for comparisons across sites and sub-canopy DBH was log-transformed for analysis. To meet the assumptions of a Chi-square analysis to test for differences between ridge and slope DBH distributions, data had to be combined into non-uniform size ranges (bins). Bin sizes were the same across sites in the analysis. For ease of interpretation, results are presented in histograms with uniform-sized bins.

Table 1. T-test results for five dependant variables of *Quercus* populations in the ridge and slope sites at Cuericí Biological Station, Costa Rica.

Variable	Ridge		Slope		t	df	P
	Mean	SE	Mean	SE			
Tree falls (#/transect)	5.6	1.29	5.25	0.85	0.21	7	0.84
Canopy DBH (cm)	77.1	6.37	84.4	7.86	-0.73	24	0.47
Density canopy (trees/m^2)	0.009	0.002	0.008	0.002	0.52	8	0.62
Density sub-canopy (trees/m^2)	0.052	0.007	0.034	0.009	1.69	8	0.13
Canopy: sub-canopy ratio	0.31	0.07	0.62	0.24	1.25	8	0.25

Results

We found no difference in the number of tree falls, the DBH of canopy *Quercus*, the density of canopy or sub-canopy *Quercus*, or the ratio of canopy to sub-canopy *Quercus* abundance between sites (Table 1).

Mean sub-canopy *Quercus* DBH was significantly smaller on the ridge than the slope (Welch's ANOVA, $F = 18.39$, $df = 1$, $P < 0.0001$; Fig. 1). The size distributions (as measured by DBH) of *Quercus* were significantly different between sites ($\chi^2 = 16.147$, $df = 158$, $P = 0.0028$; Figs. 2 and 3).

Discussion

We did not observe a significant difference in the number of tree falls (an index of

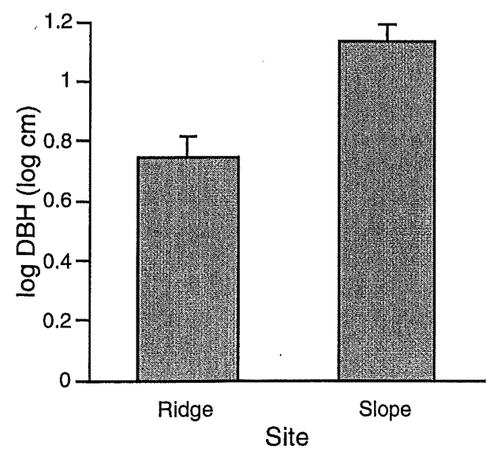

Fig. 1. Mean log DBH of sub-canopy *Quercus* (± 1 SE) in ridge (n = 47) and slope (n = 30) sites near Cuericí Biological Station, Costa Rica.

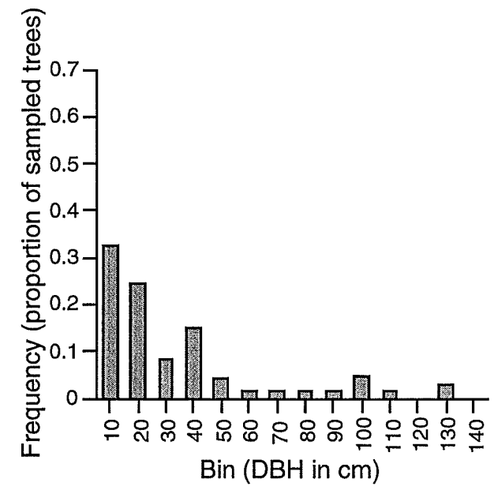

Fig. 2. Size classes (DBH) of *Quercus* on protected slope at Cuericí Biological Station, Costa Rica. Five belt transects used were each 50 m x 6 m (n = 42 trees).

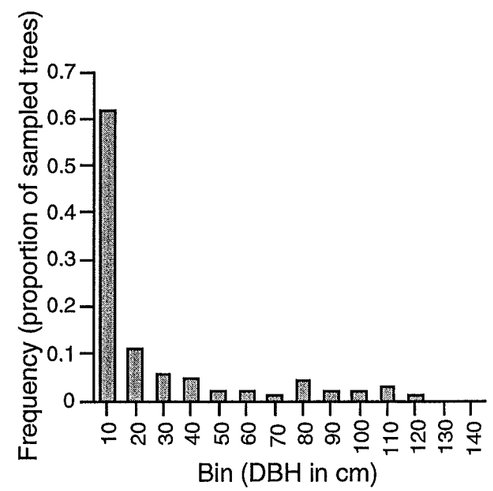

Fig. 3. Size classes (DBH) of *Quercus* on wind-exposed ridge at Cuericí Biological Station, Costa Rica. Five belt transects used were each 50 m x 6 m (n = 61 trees).

disturbance) between the ridge and slope sites. Under equal conditions, it could be expected that slope would be a major factor in causing tree falls, due to decreased soil stability and the asymmetry of tree support structures. However, our data seem to suggest that wind and slope contribute to disturbance equally in the two sites we examined. Similar rates of disturbance should produce similar forest structure at both sites. Indeed, the mean DBH of canopy trees, the density of canopy and sub-canopy trees, and the ratio of canopy to sub-canopy tree abundance did not differ between sites. These similarities suggest that the processes that determine *Quercus* forest structure, recruitment, growth rate, and/or mortality, may be similar at both sites.

Sub-canopy DBH and the overall DBH distribution, however, varied significantly between sites. The ridge population structure was strongly biased towards trees with a DBH between 1 and 10 cm. The distribution at the slope site was more even than that of the ridge. These differences could be attributed to variation in timing of recruitment or growth rate. The timing of acorn masts could differ between sites, affecting the average age of the understory, or the growth rate of slope trees is higher than the growth rate on the ridge. Further, recruitment and growth rate are likely affected by the under-story composition and density.

Bamboo was more dominant in the slope under-story than on the ridge. Carlos Solano, the proprietor of the study site land, has proposed that *Quercus* undergoes a rapid increase in recruitment following the senescence of bamboo stands at the end of a flowering cycle (pers. comm.). Future research should quantify oak response to the bamboo cycle. Understanding the relationship between tree fall disturbance and oak recruitment and growth patterns is central to interpreting the Cerro forest population structure.

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