Theory vs. Practice: Optimal growth angles for oak trees growing on slopes

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Abstract: Understory trees growing on inclined surfaces face a tradeoff in growth angle between light optimization and minimization of mechanical stresses. We examined oak (*Quercus* spp.) trees on three hillsides of varying slope on a tropical mountain to determine the relationship between growth angle and hill slope. The angle of *Quercus* varied among hillsides, but hill slope and growth angle were only weakly related. We conclude that the prediction of an optimal angle for tree growth is an oversimplification, and that local environmental characteristics probably play a more important role in determining tree growth angle than hillside slope alone.

Key Words: growth optimization, oak, Quercus, *shade tolerant*

Introduction

Understory trees on inclined surfaces face a tradeoff between growing in a direction that favors optimal light exposure and growing in a direction that minimizes mechanical stresses. Valladares (1999) theorized that trees would achieve optimal exposure to light by growing perpendicular to the slope of the hill. He further theorized that mechanical stresses (e.g., torque) would be minimized through vertical growth (Valladares 1999). Thus, there may exist some optimal intermediate angle at which tree growth is maximized, but this theory has not been tested (D. R. Peart, pers. comm.). We surveyed oak trees (*Quercus* spp.) on mountain slopes at Cerro De La Muerte to examine the relationship between growth angle and hill slope. We predicted that the optimal angle for tree growth would be farther from the vertical with increasing hill slope.

Methods

Sampling sites were located on three hillsides of varying slope in the vicinity of "the bench" on the east end of the Loop Trail near Estación Cuericí on Cerro de la Muerte, Costa Rica: low incline (5-12°), moderate incline (18-25°), and steep incline (33-38°). Analysis showed that the sites differed significantly in slope, as intended (ANOVA, $F = 1133.94$, df = 2, 188, $P < 0.0001$). Criteria for site selection included a large area of approximately even slope and a closed canopy (ca. 75%). At each site, we haphazardly selected a canopy-level *Quercus* and ran a 30 m transect perpendicular to the incline of the hill. From every canopy-level *Quercus* within a 10 m belt of this initial transect, we ran another transect (20 m long and 6 m wide) directly down the slope of the hill. In each transect we measured the DBH (diameter at breast height) and tree angle of every *Quercus* over 4 cm in DBH, and the slope of the hill. Tree angles were defined as the effective angle from the base of the tree to the center of its canopy. Both hill slope and tree angles were measured using a clinometer. The effects of site and transect were assessed with a nested ANOVA (transect within site). We determined the relationship between hill slope and tree angle using linear regression.

Results

Most *Quercus* trees in the study area were not oriented at 90° to the horizontal, but at some angle less than 90°, leaning down the hill slope on which they grew (Fig. 1). There was a weak but highly significant relationship between tree angle and hill slope ($r^2 = 0.18$, df = 1, $P < 0.0001$; Fig. 1), with trees on steeper slopes growing farther from the vertical than trees on shallow slopes. Tree angle was significantly affected by the site (nested ANOVA, $F = 18.52$, df = 2, $P < 0.0001$) and by the transect in which the tree was located (nested ANOVA, $F = 2.13$, df = 9, $P = 0.03$; Fig. 2). DBH did not

explain differences in tree angle ($r^2 = 0.02$, df = 1, $P = 0.033$; Fig. 3).

Discussion

As predicted, tree angles differed significantly among the three sites of different slope. However, the fact that only 18% of the variance was explained by slope implies that slope was not a major factor in determining tree angle (Fig. 1). The significant effect of transect on angle (Fig. 2) suggests that local environmental conditions were more important than slope in determining *Quercus* growth angle. Although trees may grow farther from the vertical on steeper slopes to maximize light as Valladares (1999) hypothesized, the lack of a strong relationship between hill slope and tree angle in this study suggests that his theory is too limited. A tree's growth direction may be determined by the location of the nearest canopy gap rather than simply by the shortest distance from the base of the tree to the canopy.

Oak trees are shade-tolerant (D. R. Peart, pers. comm.) and may respond differently from shade-intolerant species, as predicted by Valdares (1999). Thus, further studies could examine the effects of hill slope on the angle of shade-intolerant species. More importantly, another study could examine local environmental conditions, such as proximity to canopy gaps, to determine whether gap location is indeed the main factor affecting tree growth angle.

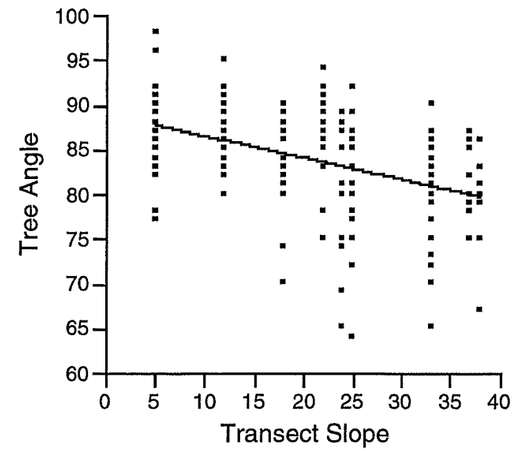

Fig. 1. Change in *Quercus* angle as a function of transect slope.

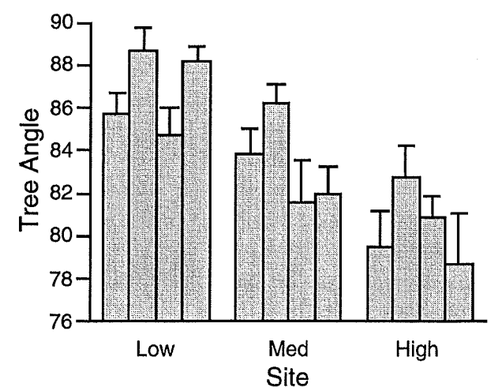

Fig. 2. Effect of transect and site on mean *Quercus* angle (mean ± 1 SE). Each bar represents a transect within a site, and the transects are arranged from lowest to highest slope within each site.

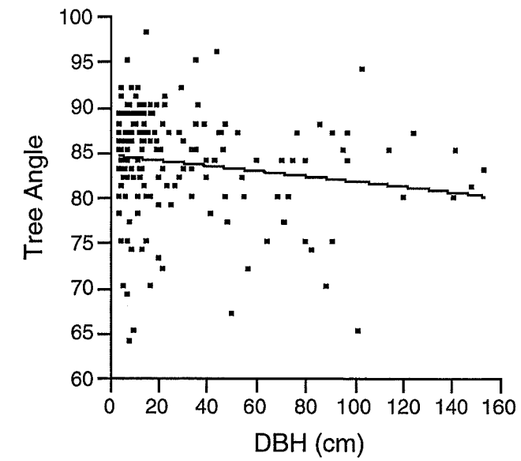

Fig. 3. Change in *Quercus* angle as a function oftree size (DBH - diameter at breast height). ($n = 191$, $r2 = 0.02$, df = 1, $P = 0.033$)

Literature Cited

Valladares, F. 1999. Architecture, ecology, and evolution of plant crowns. In F. I. Pugnaire, F. Valladares and M. Dekker, editors. Handbook of functional plant ecology. New York, NY, USA.