THE TRADEOFFS OF TILTING: AN ANALYSIS OF NON-VERTICAL GROWTH IN A MONTANE TROPICAL FOREST

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Abstract: On steep forested slopes, trees could gather more light and reach the canopy faster if they grow non-vertically, so the benefits of tilt might outweigh its costs (such as increased risk of getting uprooted). Before the effects on tree tilt of environmental factors such as light availability can be meaningfully considered, it is necessary to know that tree tilt is an adaptive trait of the trees to their surroundings, and not a mere response to ground slope and gravity. To distinguish between these possibilities, I built a mathematical model of tilt, and tested it against real data from Cuerici. The cost-benefit model of tilt found that tilting should be more beneficial on steeper ground, and predicted that if tilting is adaptive, then shade intolerant species should show more tilt than shade tolerant species because they cannot survive in low light. I sampled twenty trees in the steep forest of Cuerici, and found no significant relationship between either ground slope or compensation point and tree tilt, but I did detect evidence that trees grow towards increasing light. These mixed results show that tree tilt is likely to be the result of both the physical constraints of growing on a slope and the remarkable plasticity of trees to adapt their shape to their environment.

Key Words: torque, compensation point, tapering, game theory, parameter space

INTRODUCTION

Reaching the canopy is critical to the survival and reproductive success of all canopy trees (Clark and Clark, 2001). On a steep slope, trees with unconstrained phototropic growth would be tilted so as to gather more light, and reach the canopy at a lesser height (Figure 1). However, tilted trees are subject to torque from gravity, which increases the risk that they will snap or get uprooted. As a result, tilting might come at the cost of additional wood for supportive structures (Leohle, 1986). Trees on slopes cannot simultaneously grow in such a way as to maximize light and to minimize physical stress.

If the light gradient is non-vertical, then trees might benefit from growing such that they tilt their trunks in the direction of increasing light availability. Of course there is an alternative non-adaptive explanation that could explain tilted tree trunks. For trees growing on slopes, there is less downhill ground for supporting roots, and gravity acting on this asymmetry could force trees to be tilted. Understanding the causes and consequences of tilting tree trunks could help elucidate the effect of landscape topography on forest architecture.

I created a model to theoretically consider the cost and benefit of tilted growth. I explored the net effect (defined as benefit - cost) of tilt and calculated the optimal amount of it for any given ground slope. I compared net effect of tilt of shade tolerant and shade intolerant trees, and compared the model's predictions with real data from the hilly forest of Cuerici, Costa Rica.

If tilting is an adaptive trait (i.e., which produces a net benefit), then it should be optimized with respect to the life history of the tree. Shade tolerance is a variable trait that seems like it would matter to the optimization of trunk tilting; shade intolerant trees (high light compensation points) should tilt more than shade tolerant trees (low light compensation points) because the benefits of reaching the canopy are greatest for trees that are relatively shade-intolerant. Under the alternate hypothesis that tilting is a nonadaptive response to gravity, there should no relationship between light compensation point and tilt.

METHODS

Model formulation

To model the benefit and cost of tilt, I assumed that the benefit was proportional to the difference between the vertical and tilted lengths (noted 'C' and 'H') that the tree would have to grow to reach the canopy, and that the cost was proportional to the torque incurred due to gravity. From these assumptions, I derived the following equations (see Appendix):

(1) $B(\alpha,\beta) = \lambda.C.(1-\cos(\alpha)/\cos(\alpha-\beta))$
(2) $C(\alpha,\beta) = k.C.(\cos(\alpha)*\sin(\beta)/\cos(\beta-\alpha))$

where α is the angle of the ground (relative to horizontal, Figure 1), β is the angle of the tree (relative to vertical), $B(\alpha,\beta)$ is the benefit function, $C(\alpha,\beta)$ is the cost function, k is the proportionally constant for cost (which itself is proportional to the mass of the canopy times the force of gravity), λ is the proportionality constant for benefit, and C is the height of the canopy (see Appendix).

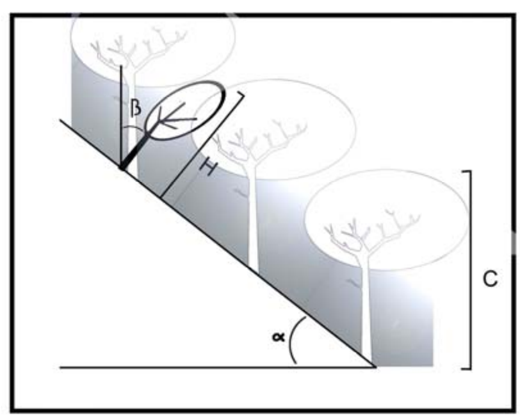

FIGURE 1. Graphic representation of the model parameters C, H, α, and β to investigate the effect of ground slope (α) on tree tilt (β).

I examined the shape of the benefit and cost functions, and explored parameter space in terms of α, β, and the λ/k ratio. Because trees with higher compensation points need to reach the canopy faster, the benefits to tilt would be greater than those of trees with lower compensation points, while the costs would be roughly similar. Therefore, I compared the higher and lower compensation point groups by evaluating model behavior for each group with parameters set at (λ, k) = (10,1) and (λ, k) = (2,1), respectively.

Data collection

I sampled twenty large trees under the canopy on the hills of the primary forest of Cuerici, Costa Rica. I walked in a random compass direction for a random number of steps (< 100 steps), and then sampled the nearest tree of height greater than 7 m. For each tree, I estimated α by putting a piece of tape on the tree at eye-level, walking 3 meters downhill along the hill's gradient (i.e. the direction of steepest descent), and sighting the tape with a clinometer. I estimated the angle of the tree's tilt by resting the clinometer on its trunk at breast height ($\beta 1$) and measuring trunk tilt, and then standing next to the trunk and sighting the center of mass of the canopy ($\beta 2$). For every tree the estimated position of the center of gravity fell along the axis of the tree tilt, so $\beta 1$ and $\beta 2$ can be compared. Both $\beta 1$ and $\beta 2$ were square-root transformed to improve normality. I aligned myself with the hill gradient (i.e. the axis along which it rises most steeply) and recorded the hill aspect (degrees relative to north), then aligned myself with the axis of the tree's tilt, and recorded the tree aspect. I estimated the alignment of the hill gradient and the tilt axis by taking the difference of these two aspects. I recorded the circumference of each tree at breast height and ground level, and estimated tree height, position in the canopy (dominant, co-dominant, intermediate, overtopped) and percent live crown by the ratio of height of first leafy branch to tree height.

The trees above the median percent live crown were assigned to the high light compensation point (shade intolerant) group and the rest were assigned to the low light compensation point (shade tolerant) group. To estimate tapering, I calculated the ratio of trunk cross sectional area at breast height relative to that at ground level. Finally, to estimate the relative strength of the tree's base, I calculated the ratio of trunk radius at ground level relative to tree height.

RESULTS

The model predicted that the benefit of tilt is maximized when $\beta = \alpha$ (i.e., when the tree is perpendicular to the ground), and increases with increasing α (Figure 2, top panel). The cost of tilt increased non-linearly with increasing β, and decreased with increasing α (Figure 2, bottom panel).

Combining these two functions, and weighting the benefit and cost functions in two different ways showed increasing net benefit of tilt with increasing ground slope, and increasing optimal β with increasing α (Figure 3). Thus the model predicts little or no benefit from tilting at low ground slopes (small α values), but as α increases, tilting is predicted to become increasingly favored and optimal tilt is predicted to become more extreme relative to vertical as the ground slope increases. Finally, the model justified that higher compensation point trees should be more tilted, since they benefit more from tilt, and have higher optimal β values for a given ground slope (Figure 3, top panel).

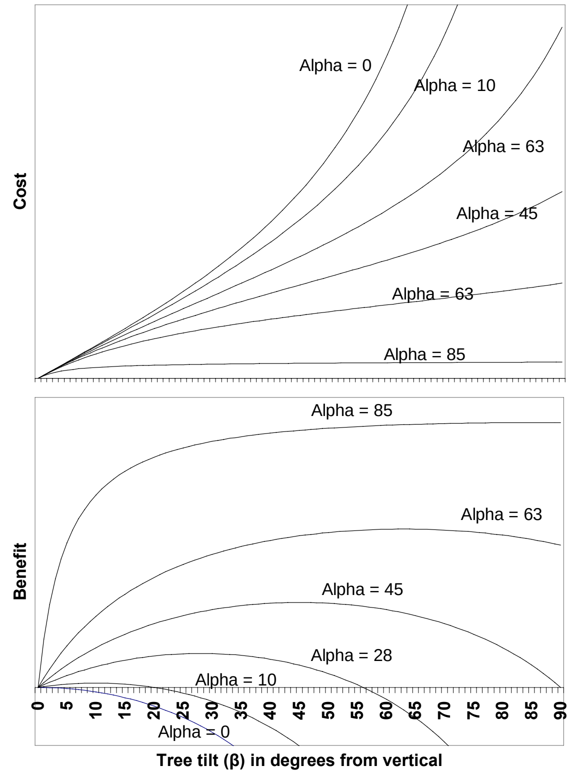

FIGURE 2. Estimated cost (top panel) and benefit (bottom panel) of tilted growth given by equations (1) and (2) for six fixed α values, where α is the angle of the ground relative to horizontal, and β is the angle of the tree relative to vertical.

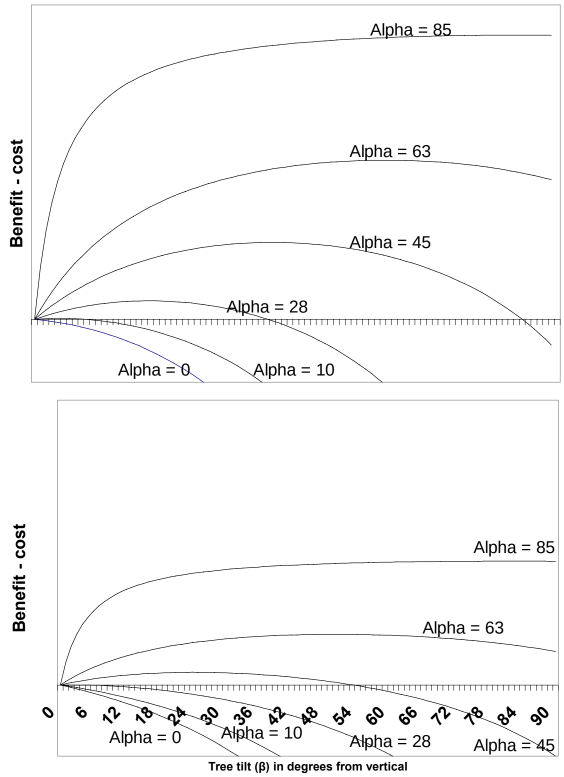

FIGURE 3. Cost-benefit analysis of tilted growth as given by $B(\alpha,\beta) - C(\alpha,\beta)$ from equations (1) and (2) for six fixed α values, where α is the angle of the ground relative to horizontal, and β is the angle of the tree relative to vertical. The top panel represents $(\lambda,k) = (10,1)$ to simulate high compensation point trees, while the bottom panel represents $(\lambda,k) = (2,1)$ to simulate low compensation point trees. Positive values indicate that the model predicts a net gain given these parameters.

In the primary forest of Cuerici, ground slope was clearly related to tree growth form: e.g., large trees (>7m in height) were off vertical by mean ± SE = 10.9 ± 10.5°, and all the trees tilted downhill: mean aspect difference ± SE = 12.2º ± 30.0º; t = -23.8, df = 17, $p < .0001$; t-test based on the expected mean (by the law of large numbers) of 180 º if the two aspects were independent of one another).

However, several other results were contrary to that predicted by the model. There was not a strong relationship between ground slope and tree tilt (F = 1.07, df = 1, 18, p = 0.31, Figure 4). There was no significant difference in tilt between trees classified as having the low and high compensation points (t = 1.24, df = 18, p = 0.23).

There was no relationship between tilting and tapering (F = 0.81, df = 1,18, p = 0.38) or tilting and base strength (F = 1.18, df = 1, 18, p = 0.29). Canopies were asymmetrical, and were larger downhill: comparing $\beta 1$ and $\beta 2$ showed that the center of gravity of the canopy was significantly further downhill than would be expected given the tilt at the base of the tree (paired-t = 1.86, df = 18, p = 0.04).

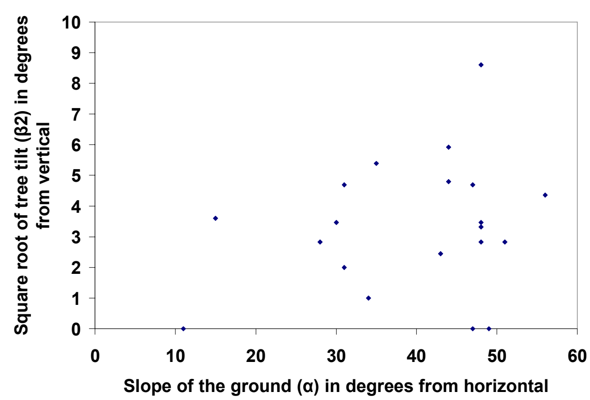

FIGURE 4. Scatterplot of tree tilt ($\beta 2$) by ground slope (α) of twenty trees in the forest of Cuerici, Costa Rica.

DISCUSSION

In general, model predictions regarding the effect of ground slope and light compensation point on tree tilt were not supported by the data. This could be due to some of the model's assumptions (e.g., for large β values the cost remains proportional to torque) or simplifications (e.g., it does not account for tree age, which should correlate which canopy mass and affect k). Despite these limitations, the model provided a structured theoretical investigation into the effects of ground slope and tree tilt on optimal growth, and it would become more valuable if future studies could estimate the parameters λ and k.

The data did not support the hypothesis that the cost of tilt would be visible in the tapering and larger basal area of the trunk. Root density and risk of getting uprooted are probably more correlated with tilt, and would reflect its true cost. The result that compensation point did not affect tilt is inconsistent with it being an adaptive, optimized trait. However, this was not a robust result because the compensation point data were based on rough estimates within a small range of low compensation points (all the study trees were quite shade tolerant). Furthermore, it might be impossible to sample trees with a high compensation point growing under the canopy (which would be necessary to avoid introducing confounding variables) since such shade intolerant trees are unlikely to survive there. Yet, it has been shown that canopies become more developed in regions of greater light (Leohle, 1986), and I found that tree canopies extended farther downhill. This is consistent with the highest light availability being in the direction in which a tree tilts, as would be expected if tilting were adaptive.

If tilting is indeed adaptive, then its long term dynamics could be analyzed with game theory. The optimal amount of tilt in this study was calculated based on the assumption that most canopy trees are vertical. But as more trees become tilted to optimize light, the benefit function would slowly change shape, and it would become more advantageous to grow vertically again. The rate at which this shift happens would determine the stability of the state of dynamic equilibrium between tilted and vertical tree populations.

LITERATURE CITED

Clark, D.A., and D.B. Clark. 2001. Getting to the Canopy: Tree Height Growth in a Neotropical Rain Forest. Ecology 82: 1460-1472.

Loehle, C. 1986. Phototropism of Whole Trees: Effects of Habitat and Growth Form. American Midland Naturalist 116: 190-196.

APPENDIX: MODEL DERIVATION

$H = C \cos(\alpha)/\cos(\beta-\alpha)$

$\text{Benefit} = \lambda\ (C - H)$

$\text{Cost} = F \times d\ .\ k$

$\quad = k\ .\ H\ .\ \sin(\beta)$

$\quad = k\ .\ C \cos(\alpha)/\cos(\beta-\alpha)\ .\ \sin(\beta)$