number of leaves on the plant (Fig. 2). One possible explanation is that herbivore encounters with shrubs are independent of shrub size, in which case larger shrubs would sustain less damage per leaf than smaller shrubs. This could explain the pattern in Fig. 2 if herbivore search patterns differ between primary and secondary forests, perhaps because they are different species or because of the increased aggregation of shrubs in the secondary forest (Table 1). Additional studies should investigate the relationship between biodiversity and parasitism by pathogens and other classes of parasitism, especially as they affect species whose densities vary across diversity gradients of forest ecosystems.

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An evaluation of the structural function of buttresses in cloud forest trees

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Abstract: Although mechanical support is often proposed as a function of buttresses, evidence for support function is limited. If the main function of buttresses is support, then buttress volume should increase as the need for support grows, e.g., on steep slopes. Contrary to the support hypothesis there was no significant relationship between the total buttress volume and slope. Downhill buttress volume averaged more than twice the uphill volume, and the largest buttress was usually located on the downhill side. However, this pattern also seems counter to the support hypothesis, and might be best understood as a developmental artifact. Other explanations for buttresses deserve consideration, including the possibility that there is no adaptive function.

Key Words: mechanical support, tree height, tree morphology

Introduction

Tropical plants exhibit an assortment of unusual morphological features. The function of some such features, such as buttresses, are not well understood. Proposed explanations for buttresses include nutrient conduction (Janzen 1983), catchments for organic material and mechanical support (Henwood 1973). The hypothesis that buttresses function as mechanical support has been reviewed extensively, yet definitive conclusions have remained elusive.

Henwood (1973) proposed that buttresses help trees bear their gravitational load. To test this theory, we compared the total uphill and downhill buttress volume on trees subject to similar wind conditions on slopes of varying degrees. We hypothesized that a tree maximizes its fitness by building up large buttresses only when necessary, resulting in patterns of buttress volume and distribution around the bole that vary with slope. If buttresses have an important structural function, then trees on steeper slopes should have greater total buttress volume because of an increased need to counter gravitational force.

Methods

On 19 January 2002, we sampled 26 canopy trees with buttresses in Monteverde, Puntarenas Province, Costa Rica. Sampled trees were at least 10 m apart and within 25 m of the main trail near La Estación Biológica. We excluded trees with more than one bole, small trees with buttresses indistinguishable from the trunk and trees with buttresses extending higher than 2 m. All sample trees were on the Pacific (leeward) side of the mountain ridge in primary cloud forest and were apparently subjected to similar wind conditions. Twenty-five of the 26 trees were on east facing slopes. For each tree, we measured the length, width, and height of each buttress, tree diameter above the highest buttress (DAB) and tree height (with clinometer). We recorded the slope and aspect of the tree's location and scored the orientation of each buttress as uphill or downhill. Volume of each buttress was estimated as length•width•height/2.

We evaluated correlations across trees between diameter, slope, number of buttresses and total buttress volume (log transformed). We used a chi-square test to see if the location of the largest buttress on each tree was related to slope.

Results

Our sample included trees on slopes ranging from 9 – 52°. Diameters ranged from 0.28 – 0.81 m, and total buttress volume ranged

from 380 – 9.43•10^5 cm^3. Slope was not correlated with number of buttresses, total buttress volume or diameter (Table 1). However, tree diameter was positively correlated with number of buttresses and total buttress volume (Table 1). Multiple regression models that included diameter did not reveal any significant effects of slope or slope x diameter on number of buttresses/tree or total buttress volume.

The largest buttress on each tree was located on the downhill side on 23 of the 26 trees sampled ($\chi^2 = 15.38$, df = 1, $P < 0.001$). As uphill volume increased, downhill volume increased twice as much (y = 0.01 + 0.29 • downhill volume; $r^2 = 0.59$, df = 24, $P < 0.001$ for test that slope = 1; Fig. 1). We were unable to obtain reasonable estimates of tree height.

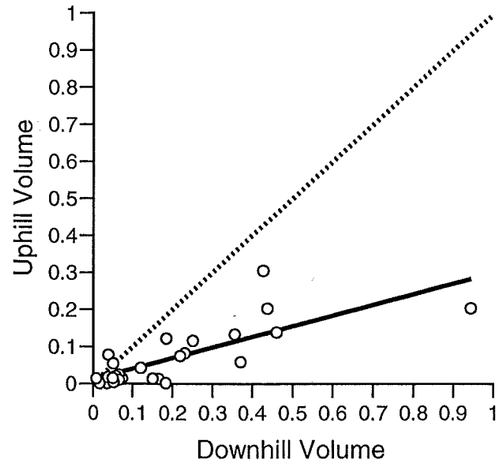

FIG. 1. Relationship between uphill buttress volume and downhill buttress volume in trees in the Monteverde cloud forest. Downhill volume was generally greater than uphill volume (most points lie below line of equality).

Discussion

Neither total buttress volume nor the proportion of buttress volume that was uphill vs. downhill was correlated with slope. This argues against the hypothesis that buttresses serve as structural support. Our prediction assumed that tress have developmental plasticity in buttress formation (and that structural support from buttresses would be more important on steeper slopes). It could still be that buttresses are an adaptation for structural support but trees lack the ability to facultatively increase buttresses on steep slopes. If so, buttressed trees should be underrepresented in treefalls relative to their size and frequency in the forest.

The only evidence for developmental plasticity in buttresses was that they were larger on the downhill side (Fig. 1). This seems counter to the optimal engineering solution for maximizing structural support (the same volume of buttress could brace the trunk from a higher fulcrum from the uphill side), further weakening the structural support hypothesis. Large downhill buttresses seem more likely to be a developmental artifact. The point at which buttresses become distinguishable from the trunk occurs at about the same level up the bole of a given tree, whether the buttress reaches the ground on the uphill or downhill side. So for uphill buttresses, the height of the buttress (or the distance from the buttress attachment on the trunk to the ground) is necessarily shorter than the height of downhill buttresses. Thus the buttress volume tends to be greater on the downhill side.

TABLE 1. Correlations across trees between slope, tree diameter, number of buttresses per tree and total buttress volume (log transformed) (N = 26 trees).

	Slope	Diameter	Buttresses/Tree
Diameter	0.22	--	--
Buttresses/Tree	-0.07	0.59**	--
Log (Total Buttress Volume)	0.25	0.79***	0.74***

** $P < 0.01$, *** $P < 0.001$

From these results we argue for more careful consideration of other hypotheses to explain buttress morphology in tropical forests. Neither the litter catchment hypothesis nor the nutrient conduction hypothesis easily explains the relatively high volume of downhill buttresses. One adaptive hypothesis that still seems plausible is that buttresses minimize soil erosion around the lower trunk by distributing stem-flow of water (which can be intense during heavy rains) over a larger area. If this were true, buttressed trees should have exposed roots less frequently than non-buttressed trees, and should appear in treefalls less often than expected based on their size and frequency in the forest. Finally, it could be that there is no adaptive explanation for buttresses. This would seem most plausible if phylogenic analyses indicate that buttresses have evolved within only a few taxa.

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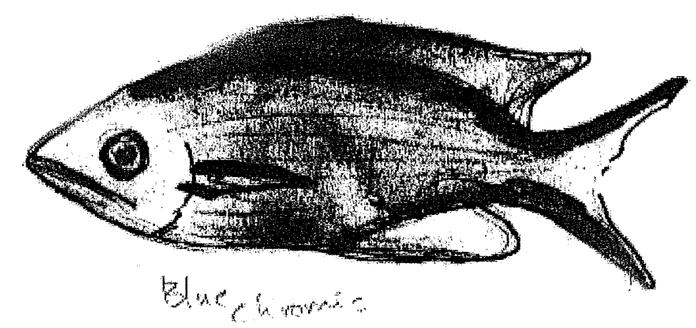

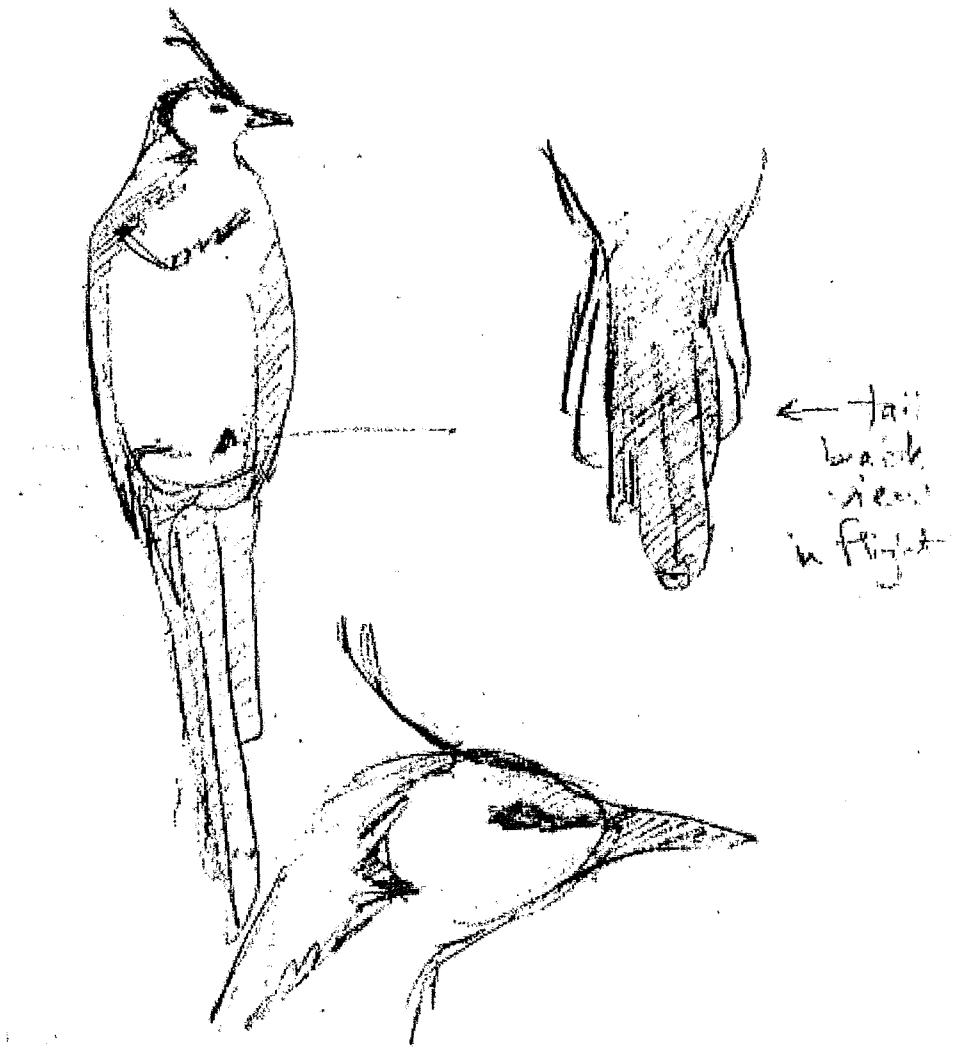

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