# Effects of tree buttresses on nutrient availability and macroinvertebrate species richness

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## ABSTRACT

This study tested the hypothesis that buttress microhabitats collect more leaf litter and have greater macroinvertebrate species richness, thereby increasing the leaf decomposition rate and providing more nutrient-rich soil for the tree. Leaf litter deposition and decomposition rates, soil fertility (pH, [N], [P], |K]), and macroinvertebrate species richness (S, Smarg) were compared between microhabitats in buttressed and non-buttressed trees and open areas in the lower montane cloud forest of Monteverde, Costa Rica. Results showed no significant difference between microhabitat types for soil pH levels (Kruskall-Wallis test, H= 3.188), soil [N] (Kruskall-Wallis test, H= 3.388), soil [P] (Kruskall-Wallis test, H= 6.215), soil [K] (Kruskall-Wallis test, H= 4.304), deposition rates (Kruskall-Wallis test, H= 3.599), or decomposition rates (Kruskall-Wallis test, H= 1.746). There was no significant difference in species richness (S) between buttressed trees and non-buttressed trees (Kruskall-Wallis post hoc, q = 1.72) or between non-buttressed trees and open areas (Kruskall-Wallis post hoc, q = 2.64). However, the difference in S between buttressed trees and open areas was significant (Kruskall-Wallis post hoc, q = 4.36). Results suggest that increased leaf litter biomass in buttresses is due to their functioning as collection cavities. Similarities in soil fertility and decomposition rates may be attributed to edaphic and leaf litter heterogeneity within microhabitats. It is apparent that buttress microhabitats are unique in structure, microclimate, and macroinvertebrate community complexity; however results of this study are inconclusive as to whether buttresses actually provide the tree with more nutrients. The role of buttresses in improving local soil quality needs to be further examined, with more consideration given to spatial heterogeneity within microhabitats.

## RESUMEN

Este estudio probó la hipótesis que sostiene reunir de microhábitats más basura de hoja y tiene riqueza más grande de especie de macroinvertebrate, con lo cual aumentando la tasa de la descomposición de hoja y proporcionando más tierra rica de alimento nutritivo para el árbol. Deposición de basura de hoja y tasas de descomposición, la fecundidad de tierra (pH, [N], *[P]*, [K]), y riqueza de especie de macroinvertebrate (S, $S_{marg}$) fueron comparados entre micro hábitats en sostuvo y no sostuvo árboles y abre áreas en el bosque más bajo de nube de montane de Monteverde, Costa Rica. Los resultados mostraron no diferencia significativa entre de tipo micro hábitats para niveles de pH de tierra (la prueba de Kruskall Wallis, H = 3.188), la tierra [N] (la prueba de Kruskall Wallis, H = 3.388), la tierra [P] (la prueba de Kruskall Wallis, H = 6.215), la tierra [K] (la prueba de Kruskall Wallis, H = 4.304), las tasas de deposición (la prueba de Kruskall Wallis, H = 3.599), ni las tasas de la descomposición (la prueba de Kruskall Wallis, H = 1.746). No había la diferencia significativa en la riqueza (S) de la especie entre sostuvo árboles y no sostuvo árboles (Kruskall Wallis anuncia este, q=1.72) o entre no sostuvo árboles y abre áreas (Kruskall Wallis anuncia este, q = 2.64). Sin embargo, la diferencia en el S entre sostuvo árboles y abre áreas eran significativo (Kruskall Wallis anuncia este, q = 4.36). Los resultados sugieren que la biomasa aumentada de basura de hoja en contrafuertes está debido a su funcionar como cavidades de colección. Las similitudes en la fecundidad de tierra y tasas de descomposición pueden ser atribuidas al edaphic y la heterogeneidad de la basura de la hoja dentro de micro hábitats. Es aparente que ese micro hábitats de contrafuerte es extraordinario en la estructura, en el microclima, y en la complejidad de la comunidad de macroinvertebrate, sin embargo los resultados de este estudio son no decisivos en cuanto a si contrafuertes proporcionan verdaderamente el árbol con más alimentos nutritivos. El papel de contrafuertes a mejorar la calidad local de tierra necesita ser aún más examinado, con *más* consideración dada a la heterogeneidad espacial dentro de micro hábitats.

# INTRODUCTION

The adaptive role of buttressing in tropical canopy trees is an issue of longstanding debate among scientists that has prompted the formulation of several hypotheses. Buttresses may be a response to mechanical strain and tension (Richards 1996; Smith 1972), a defense against nearby plant competitors or woody vines (Black 1979), a physical support (Richards 1996; Hartshorn 1983; Smith 1972), or a means to improve local soil quality. The latter "nutrient hypothesis", which is the focus of this study, proposes that buttress cavities improve the collection of organic debris and moisture. Buttress microhabitats would support a richer detritivore macroinvertebrate community, increasing decomposition rates and thus increasing the amount of nutrients available to the tree.

Nitrogen, Phosphorous, and Potassium are elements that most frequently limit plant production (Brady and Weil 1996), while soil pH affects the plants' ability to absorb these nutrients from the soil (Killham 1994). Nitrogen is important for the growth and development of roots as well as the uptake of other nutrients (Taize and Zeiger 1991). Phosphorous reduces the amount of water loss from stomata and increases the roots' ability to absorb water. Potassium aids in photosynthesis, N-fixation, and root growth. Buttressing, which may enhance the availability of these nutrients through increased decomposition rates, would therefore be advantageous in nutrient-poor tropical soils (Jordan 1985).

Soil fertility is improved by increased rates of leaf litter deposition and decomposition. Buttresses may aid in the accumulation of excess leaf litter. Nguyen (1996) showed that the bowl-shaped microhabitats formed between tension buttresses and the trunk base contained greater leaf litter abundance in comparison to down-slope buttress microhabitats. Decomposition rates increase with increased moisture, temperature (Jordan 1985), and detritivore community diversity, as leaf litter macroinvertebrates, along with bacteria and fungi, are vital for the transformation of dead organic matter to essential soil nutrients. Nguyen (1996) showed that buttresses are significantly higher in moisture content. A diverse macroinvertebrate community may be more attracted to buttresses as they decrease exposure to sunlight and wind (Marks 1995). In previous studies, positive correlations have been found between arthropod invertebrate abundance, richness, and diversity and environmental factors such as higher moisture levels (LeDoux 1988; Frith and Frith 1990), greater depth of leaf litter (Seidler 1992; Lee 1993; Marks 1995), and leaf litter heterogeneity (Lee 1993). These are all conditions that are likely to appear in buttresses, therefore creating a suitable microhabitat for a more diverse macroinvertebrate community and increasing rates of decomposition.

The purpose of this study is to determine whether buttresses increase the nutrients available to the tree. This will be determined by examining differences in soil fertility (pH, [N], [P], [K]), deposition and decomposition rate, and invertebrate species richness between buttressed and non-buttressed trees. I propose that buttressed trees will have increased soil fertility, greater deposition and decomposition rate, and greater macroinvertebrate species richness than non-buttressed trees.

# METHODS

## Study Site

This study was conducted at 1550-1650m secondary forest of the Pacific slope near the Estación de Biológica de Monteverde, Costa Rica (10° 18' N, 84° 48' W), from October 18, 2003 to November 18, 2003 (the end of the rainy season). It typically rained in the afternoon and often throughout the night for the duration of this study.

## Sampling Procedure and Analysis

Ten buttressed trees and ten non-buttressed trees were chosen without regard to species. Ten open areas served as control sites to compare the effects of being near a buttressed or non-buttressed tree.

*Soil fertility.* Soil samples were collected from 18 sites (six samples per microhabitat type) by first clearing away organic matter and then removing the top layer of soil (0-5 cm deep). Soil pH, [N], [P], and [K] were measured using a LaMotte soil analysis kit. A Kruskal-Wallis test was run to determine whether there was a difference in soil fertility between microhabitat types.

*Decomposition rate.* A mesh bag containing 100 g of dry, heterogeneous leaf-litter was secured at each of the 30 study sites on 10/23/03. After 23 days, the bags were collected and the mass of the leaf litter was measured again, yielding decomposition rates. A Kruskal-Wallis test was run to determine whether there was a difference in decomposition rate between microhabitat types.

*Deposition rate.* An open-topped, wire-mesh box was secured in each of the 30 study sites on 10/29/03. The mass of fallen leaf-litter was measured in the field on 11/3/03, 11/8/03, and 11/14/03. Boxes were emptied each time to prevent overflow. The total mass of litter deposited per study site during the 17-day period was used to calculate deposition rates. A Kruskal-Wallis test was run to determine whether there was a difference in deposition rate between microhabitat types.

*Macroinvertebrate species richness.* A leaf litter sample was collected from each of 18 study sites (six samples per microhabitat type). Macroinvertebrates were separated from leaf litter samples using Berlese funnels for 24 hours. The species richness (S) was counted for each sample, and the number of individuals (N) was counted for three samples of each microhabitat type. The Margalef index of species richness ($S_{marg}$) was calculated for those nine samples. A Kruskal-Wallis test was used to determine whether there was a difference in S between microhabitat types. Kruskal-Wallis post hoc tests were then run to determine whether there were differences in S between individual pairs of microhabitats.

# RESULTS

## Soil Fertility

There was no significant difference between microhabitat types for pH levels (Kruskal-Wallis test, H= 3.188), [N] (Kruskal-Wallis test, H= 3.388), [P] (Kruskal-Wallis test, H= 6.215), or [K] (Kruskal-Wallis test, H= 4.304). [P] was nearing significance, with mean values (in lbs/acre) of 58.3, 35.0, and 108.3 for buttressed trees, non-buttressed trees, and open areas, respectively (Table 1).

## Deposition Rate

There was no significant difference between microhabitat types for deposition rates (Kruskal-Wallis test, H= 3.599). Mean values between microhabitat types are reported in Table 1.

## Decomposition Rate

There was no significant difference between microhabitat types for decomposition rates (Kruskal-Wallis test, H= 1.746). Mean values between microhabitat types are reported in Table 1.

## Macroinvertebrate Species Richness (S)

There was a significant difference between microhabitat types for S (Kruskal-Wallis test, H= 9.680). Further analysis showed a significant difference in S between buttressed trees and open areas (Kruskal-Wallis post hoc, q= 4.36, Fig. 1). There was no significant difference in S between buttressed trees and non-buttressed trees (Kruskal-Wallis post hoc, q=1.72), but while there was also no significant difference in S between non-buttressed trees and open areas (Kruskal-Wallis post hoc, q= 2.64), the difference was approaching significance. The $S_{marg}$ values for buttressed trees appear to be higher than non-buttressed trees, and significantly higher than open areas, which would correspond with the results for S, however, no statistical analyses could be performed due to small sample size (Fig. 2).

## DISCUSSION

It was thought that buttressed trees would have increased soil fertility, a greater deposition and decomposition rate, and greater macroinvertebrate species richness than non-buttressed trees. However, the results of this study showed no significant difference between microhabitat types for any of the parameters studied. A significant difference in macroinvertebrate species richness was found between buttressed trees and open areas, with a difference nearing significance between non-buttressed trees and open areas.

### Soil Fertility

In a previous study, no correlation was found between buttressed *Quercus spp.* and increased [N], [P], and [K] or more beneficial pH levels (Platt 2003). It was suggested that the similar nutrient levels between buttressed trees, non-buttressed trees, and the control are due to a significant amount of root nutrient absorption. Similarly, in this study, as no trees were present near the control, nutrient depletion was probably not due to tree root absorption. Therefore, it is possible that excess nutrients available to the buttressed and non-buttressed trees were more rapidly absorbed, accounting for the similarities in soil fertility among microhabitats (Denslow 1987). This may explain why [P] was nearing significance ($p= 0.0580$), with buttressed and non-buttressed trees having much lower average P levels than open areas (Table 1). As P is often a limiting factor in plant growth, it is likely that the trees were absorbing the available P, accounting for higher levels in the open areas. The extreme heterogeneity of leaf litter in tropical forests may also cause edaphic heterogeneity within microhabitats (Marks 1995; Maheswaran and Gunatilleke 1988), attributing the similarities in soil fertility to spatial scale and sample size.

### Deposition Rate

Similarities in leaf deposition rate between microhabitats show that the cavities of buttresses do not have higher rates of leaf fall than the bases of non-buttressed trees or open areas. However, Nguyen (1996) showed that buttresses are significantly higher in leaf litter depths, indicating that buttresses actually do function as collection cavities. Marks (1995) showed that increased leaf litter biomass was found below trees with epiphytes, which may have been influential in changing deposition rates between microhabitats. Also, the control open areas were in more disturbed secondary forest patches that contained more understory growth, more pioneer species, and smaller trees, a characteristic of treefall gaps. These areas typically have more wind and larger, faster growing leaves (Denslow 1987), which may have caused more leaf litter of larger size to be blown into the collection boxes, rather than falling in directly. Due to the steep slopes of the study sites, the bases of non-buttressed trees on the upslope side may have accumulated leaf litter in the same way that buttressed trees do. However, it seems more likely that there is more movement of leaf litter near non-buttressed trees and open areas, so further studies should consider deposition rates at different spatial and temporal scales.

**Macroinvertebrate Species Richness** (S)

The results of this study showed a significant difference in macroinvertebrate species richness between buttressed trees and open areas. The difference in macroinvertebrate species richness between non-buttressed trees and open areas was approaching significance, while the difference between buttressed and non-buttressed trees was not. Spatial heterogeneity within microhabitats may account for these differences. Microhabitats are extremely complex, heterogeneous, and dynamic. Small-scale differences in structure, moisture level and orientation of habitats has major effects on invertebrate diversity, with communities being influenced by factors such as epiphytes, depth of leaf litter, nutrient availability, and species immigration (Marks 1995). Increased leaf litter biomass increases litter heterogeneity and creates unique niches for organisms to inhabit. Also, as different types of leaves have different decomposition patterns (Maheswaran and Gunatilleke 1988) greater accumulations of leaf litter of different leaf types would cause nutrients to be released at different times in different forms, thereby supporting a more diverse invertebrate community (Ezcurra and Becerra 1987). Further studies should examine macroinvertebrate species richness and the effects of heterogeneity within microhabitats to determine the benefits of buttressing in trees.

## Leaf Decomposition

There was no significant difference between microhabitats for leaf decomposition, which may be a reflection of climatic conditions or macroinvertebrate communities. Climatic conditions within microhabitat types probably vary greatly, although they were not directly tested in this study. Previous studies, however, have shown that buttresses contain greater moisture levels than other microhabitats (Nguyen 1996). This study did show a significant increase in macroinvertebrate species richness for buttressed trees, but it did not appear to affect the decomposition rate. Decomposition rates vary for different leaf types (Maheswaran and Gunatilleke 1988) which may account for similarities in leaf decomposition rates. Differences in leaf litter heterogeneity may have a large impact on the patterns and time-scale of decomposition within microhabitats. Future studies may control for species in leaf litter to determine differences in decomposition rates based on buttress microhabitat conditions and macroinvertebrate communities alone.

## Concluding Remarks

The "nutrient hypothesis" for buttressing explored in this study has not been rejected, nor has it been fully supported. Buttress microhabitats are damper, appear to function as collecting cavities for leaf litter, and harbor more species-rich macroinvertebrate communities. However, whether these microhabitat conditions increase decomposition rate and improve local soil fertility remains to be determined. Future studies should focus on differences in edaphic and leaf litter heterogeneity within buttress microhabitats. It seems likely that the complexity of buttress formation in tropical trees is due to a combination of factors and will not be fully explained by any single hypothesis.


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**Table 1.** The mean (standard deviation) values for [N], [K], [P], pH, deposition rate and decomposition rate between microhabitat types. Concentrations are measured in lbs/acre, and rates are in g/day. [P] levels are nearing significance (Kruskal-Wallis test, p = 0.0580) with open areas containing much higher concentrations.

| | **Buttress** | **Non-buttress** | **Open area** | **n** |
|---|---|---|---|---|
| **Parameter** | **Ave. x (s.d.)** | **Ave. x (s.d.)** | **Ave. x (s.d.)** | |
| **[N]** | 76.667 (64.70) | 40 (17.89) | 25 (17.61) | 6 |
| **[K]** | 173.333 (76.60) | 216.667 (48.03) | 161.667 (22.29) | 6 |
| **[P]** | 58.3 (20.41) | 35 (23.45) | 108.3 (73.60) | 6 |
| **pH** | 6.3 (0.17) | 6.13 (0.16) | 6.3 (0.21) | 6 |
| **Dep. Rate** | 0.599 (.294) | 0.605 (.284) | 0.415 (.314) | 10 |
| **Decomp. Rate** | 0.946 (.556) | 0.705 (.310) | 0.698 (.355) | 10 |

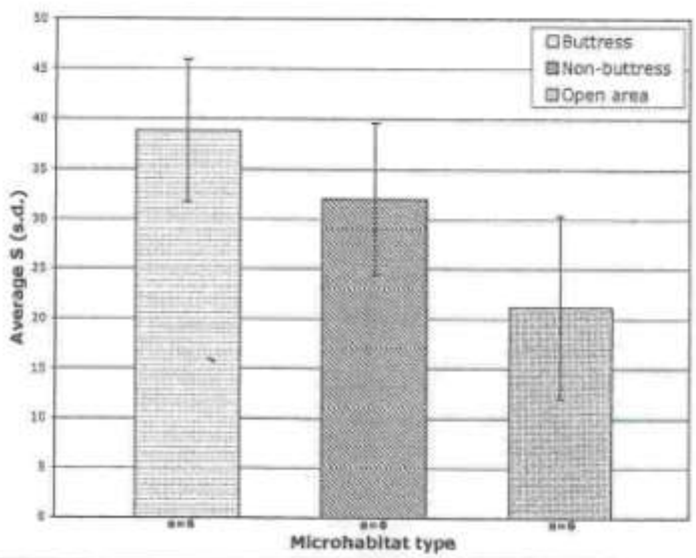


Figure 1. Comparison of species richness (S) between microhabitat types. Buttressed trees have a significantly higher macroinvertebrate species richness than open areas (Kruskal-Wallis post hoc test, q= 4.36).

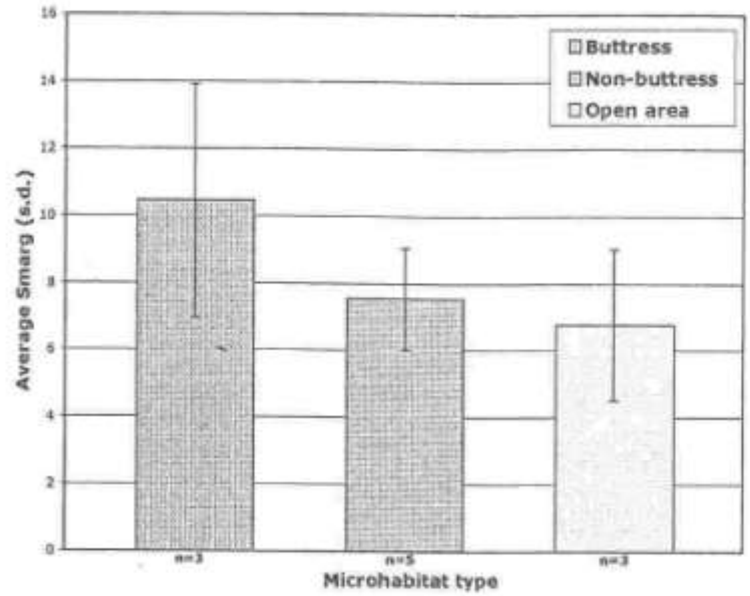


Figure 2. Comparison of Margalef index for species richness ($S_{marg}$) between microhabitat types. Buttressed trees appear have greater species richness than open areas, although no statistical tests were run due to small sample size.