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Advantageous Development of Buttresses displayed in Quercus spp.

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ABSTRACT

The many hypotheses aimed at describing the physiological, morphological, environmental forces contributing to buttress development have not clearly shown definitive evidence regarding what selective forces are responsible for buttress formation. One hypothesis that has little documented research available is that the presence of buttresses allows for an increased abundance of organic matter and inhibits nutrient leaching from the soil, thus providing the tree with a greater quality soil for localized growth. Twenty-five different soil samples were collected and analyzed for potassium, nitrogen, phosphorus, and pH from both the base of buttressed *Quercus spp.* and a control site in the cloud forest of Monteverde, Costa Rica. No significant difference was found in the relationship between the presence of buttresses and an increased amount of N, P, K, or a more suitable pH. Results found may be due to nutrient use by the roots of buttressed trees or a slower rate of decomposition due to decreased temperatures in lower montane wet forests verses lowland tropical forests.

RESUMEN

Hay muchas hipótesis que apuntan a describir las fuerzas fisiológicas, morfológicas y ambientales que contribuyen al desarrollo de gambas, pero no se ha mostrado evidencia definitiva con respecto a qué fuerza selectiva es responsable de su formación. Una hipótesis que ha sido poco investigada predice que con la presencia de gambas se aumenta la abundancia de la materia orgánica e inhibe la lixiviación de nutrientes de la tierra, así proporciona al árbol con un sustrato más nutritivo para el crecimiento. Veinticinco muestras diferentes de tierra fueron analizadas en el contenido de potasio, nitrógeno, fósforo, y de pH en la base de árboles de *Quercus y* un sitio control cerca, en el bosque nuboso de Monteverde, Costa Rica. Ninguna diferencia significativa se encontró en la relación entre la presencia de gambas y el aumento de N, P, K, o de un pH más adecuado. Los resultados encontrados puede estar relacionados al uso de nutrientes por las raíces de las gambas o a una tasa más lenta de descomposición debido a la baja humedad y temperaturas en el bosque montano bajo, comparado con los bosques de bajura tropicales.

INTRODUCTION

Buttresses are structures that develop at the base of tree trunks from strip-like regions of enhanced cambial activity that extends from the trunk to the upper side of certain roots (Fisher 1982). The degree of cambial activity determines the height and plank like form or relative thickness of the buttress (Fisher 1982). General characteristics of trees that display buttresses are: emergent trees of 30 m in height or more, trees on flood plain areas where drainage is poor, and trees growing where shallow soils primarily made up of clay occur (Smith 1979; Richards 1996). As altitude increases, the presence of buttresses usually decreases, however, buttresses can still be found at higher elevations, but are less abundant.

Many tree species in the tropics display buttressed roots. In Monteverde (1500 m elevation), Costa Rica, along the Tilarán Mountain Range in the province of Puntarenas the most abundant species exhibiting buttresses is *Quercus spp.* (Mauricio Garcia, pers. com,). *Quercus spp.* (Fagaceae) are large canopy trees (20-35 m), common on ridges and peaks in the cloud forest (Haber et al. 2000). Trunks of *Quercus spp.* are usually buttressed with twisted branches and are covered in epiphytes (Haber et al. 2000). The four species of *Quercus* found in the Monteverde are: *Q. brenesii, Q. insignis, Q. corrugata,* and *Q. seemannii* (Hartshorn 1983; Haber et al. 2000).

A theory widely excepted in the scientific community is that buttresses are an adaptation to wind or gravitational forces acting upon the tree (Smith 1979; Hartshorn 1983; Richards 1996). In this case the buttress would be offering the tree increased structural support especially where poor drainage and shallow soil were a factor. Buttress development may be selected for as a competitive mechanism, which inhibits other trees from establishing themselves nearby. Thus, using nutrients valuable to the buttressed species (Black and Harpe l979). A less researched idea is that buttresses provide the tree with more nutrients, which is a limited resource in tropical soils. By creating cavities for litter, water, and a hospitable habitat for soil organisms, buttresses presumably would supply the tree with more organic matter, thus creating the availability of a higher quality soil.

Phosphorus, nitrogen, and potassium are elements that most frequently limit plant production (Brady and Weil 1996). Soil pH affects the plants ability to use what elements are available in the soil; therefore it is an important factor to analyze when looking at P, N, and K (Killham 1994). A good supply of N stimulates root growth and development as well as tile uptake of other nutrients (Taize and Zeiger 1991). Nitrogen is available for plant uptake through two different ways: one being through the breakdown of atmospheric dinitrogen gas by microorganisms and the other being through the soil organic matter present on the forest floor. Potassium plays an important role in reducing the amount of water lost from leaf stomata and increasing the ability of root cells to take up water from the soil. Animal waste and plant residues are primarily responsible for potassium elements found in the soil (Brady and Weil 1996). Potassium is normally abundant in soils, but in highly acidic soils, K is especially prone to loss by leaching, erosion and runoff. Phosphorus aids in photosynthesis, N fixation, and root growth; particularly development of lateral roots and fibrous rootlets: Phosphorus compounds are released when organic residues and humus decompose. (Brady and Weil 1996).

Adaptations to nutrient poor environments occur in any region soils are infertile, but because poor soils are common in the tropics, nutrient conservation mechanisms are often associated with tropical species. A common plant adaptation to nutrient poor soils is the production of a large root biomass, often with the concentration of root biomass on or near the soil surface. However, buttress development might be an additional adaptation to nutrient poor soil. (Jordan 1985)

I hypothesize that tree buttress presence on *Quercus spp.* is an adaptation to poor tropical soils. Trees that display buttresses do so because they allow for more organic matter to accumulate in an area optimal for nutrient capture by the roots. Buttresses may also limit the amount of nutrients lost due to leaching, by funneling the nutrient rich water towards the tree for uptake. I hypothesize that an increase in area between the buttress planks may yield an increase in soil quality. Also, I am proposing that the greater the slope of the ground that a *Quercus spp.* reside on the lesser amount of N, P, and K will be found due to a higher rate of nutrient leaching.

MATERIALS AND METHODS

Twenty-five buttressed *Quercus spp.* were sampled from a plot of forest in the Estación Biológica Monteverde in Puntarenas, Costa Rica. For each tree the slope was measured using a clinometer. The area of ground, upslope from each *Quercus spp.*, between the buttress planks (collecting area) was measured. This was done by taking two measurements: first, the distance between the terminal ends of the two planks was measured, and second, the distance from the trunk to the center point between the terminal measurement (assuming a triangular form). Once organic matter was cleared from the collecting area a soil sample (150 ml) was taken from the top layer (0-5 cm deep) directly in the middle of the triangular formation of the collecting area. A control sample was then taken to the left of the tree sample directly parallel (on the same slope) to it, 1.5 m away from the site of the buttress sample (outside the buttress area). The availability of N, P, and K were then measured, in the control and the tree sample, using the LaMotte soil analysis kit. The pH was measured using an Okatun pH meter after mixing three parts distilled water and one part soil for each sample.

A paired t-test was conducted looking for differences between pH, P, K, and N in the buttress sample and the control sample. Regressions were done between area and the soil elements, slope and area, and slope and the soil elements. All statistical test ran were done with Stat view 5.0.

RESULTS

There was no significant difference found in the pH level between the buttress and the control (Paired t-test, $p = 0.7698$) (Fig. 1). The amount of N found in the buttress samples was not significantly different from the control (Paired t-test $p = 0.7955$) (fig. 2). There was no significant difference in P between the buttress samples and the control (Paired t-test, $p = 0.2543$) (Fig. 3). The amount of K found in the buttress samples was not significantly different from the control (Paired t-test, $p = 0.2413$) (Fig. 4).

Slope did not show a significant relationship to, area (Simple regression, $p = 0.2544$; $R^2 =0.056$) (Fig. 5), N (Simple regression, $p = 0.4188$; $R^2 = 0.029$)(Fig. 6), P (Simple regression, $p = 0.5283$; $R^2 = 0.018$) (Fig. 7), or K (Simple regression, $p = 0.1058$; $R^2 = 0.11$) (Fig. 8) in the buttress samples.

Slope did not show a significant relationship to the control samples (Simple regression, N, $p = 0.1969$; $R^2 = 0.071$; P, $p =0.8172$; $R^2 = 0.002$; K, $p = 0.0306$; $R^2 = 0.118$).

Slope did not have a significant effect on the pH level of buttress samples (Simple regression, $p = 0.2292$; $R^2 = 0.062$) or the control samples (Simple regression, $p = 0.8172$; $R^2 = 0.002$).

Area did not have a significant effect on N (Simple regression, $p = 0.1125$; $R^2= 0.071$), P (Simple regression, $p = 0.4980$; $R^2 = 0.02$), or K (Simple regression, $p = 0.0816$; $R^2= 0.126$). Area did not have a significant effect of pH (Simple regression, $p = 0.2700$; $R^2= 0.053$).

DISCUSSION

For nutrients to be available for uptake they must be in a soluble form and must be located at the root surface. The existing supply of nutrients in contact with the root eventually becomes depleted and more nutrients are needed to replenish the depleted portion. This is done in three ways: root interception (roots continually grow into new undepleted soils), mass flow (dissolved nutrients are carried along with the flow of soil water towards the root), and by diffusion (nutrient ions continually moving from areas of greater concentration towards the nutrient depleted areas of lower concentration) (Brady and Weil 1996). As a result the similar levels of N, P, and K (Fig. 2-4) measured from the collecting area of buttresses in comparison to the control might be due to a significant amount of nutrient uptake being done by the roots. The control samples were all taken from an area of ground where no apparent vegetation was growing, therefore, the amount of nutrients present wasn't being depleted by plant uptake whereas the buttress samples were all taken in close vicinity to the roots and amount derived could possibly be lower due to the active depletion and use of the nutrients. (Brady and Weil 1996).

Temperature in Monteverde is lower compared to lowland tropical areas. When temperature is present in greater amounts it acts as a catalyst for decomposition (Brady and Weil 1996). Plants rely on N, P, and K to release ions in a form that is available for uptake by the decomposing of organic matter. In tropical areas of higher temperatures and humidity you would expect to find a higher decomposition rate and thus a higher value of N, P, and K availability (Jordan 1985). While sampling it was noticed that much of the organic matter collected in the buttresses was not well decomposed. Sampling was done toward the end of the dry season, which, could contribute to the slow rate of decomposition. Sampling during the rainy season, when more moisture was available for decomposition, or sampling done from lowland tropical area might have resulted in different findings.

Nitrogen (Simple regression, $p = 0.4188$; $R^2 = 0.029$)(Fig. 6), P (Simple regression, $p = 0.5283$; $R^2 = 0.018$) (Fig. 7), and K (Simple regression, $p = 0.1058$; $R^2 = 0.11$) (Fig. 8) all showed no significant relationship relating an increased slope with a decreased amount of nutrient availability in the buttress samples. No significance was found in the control samples relating increased slope to decreased nutrient availability (Simple regression, N, $p = 0.1969$; $R^2 = 0.071$; P, $p =0.8172$; $R^2 = 0.002$; K, $p = 0.0306$; $R^2 = 0.118$). This result may also be due to sampling during the dry season. Leaching rates are highest when the soil is saturated with water and runoff is a occurring regularly (Jordan 1985).

The collecting area of the trees sampled did not show a relationship of increasing nutrients with increasing area, as originally hypothesized. This could be due to the lower temperatures in higher elevational tropical areas compared to lowland tropical areas, where decomposition allows for a greater nutrient availability (Brady and Weil 1996).

Other existing hypotheses propose that buttressing is strongly selected for as a means of achieving support. It has been noticed that trees growing on poor substrate often have buttresses, but in extra tropical areas buttress presence isn't as prevalent even in swampy areas where the substrate offers almost no support (Smith 1972). Mechanical stain and tension could also be stimuli for buttress production, producing asymmetrical growth and strengthening of the roots (Smith 1972; Richards l996). In a study done by Young and Perkocha (1994), buttresses formation was greatest on the side of the tree away from the direction of crown asymmetry; suggesting that buttresses formation is at least partly due to tensile pressure acting on the tree. Numerous studies have been done on the effects wind force has on buttress development. In some reports buttress formation has been noticed to be pronounced on the leeward side. This hypothesis is often disputed due to the contradicting elevational and latitudinal gradient where buttress presence decreases with increasing latitude and increasing elevation (temperate and high elevational areas have higher wind velocities) (Smith 1972). It is possible that buttress growth is a competitive mechanism; deterring other plants from establishment. An obvious increase in individual space occupied at ground level inhibits available space for rooting by other plants Black and Harpe 1979). Buttressed trees provide defense against soil rooted woody vines (more energy is expended to establish on a buttressed tree vs. an unbuttressed tree) which when established in large numbers can lead to tree damage and possible mortality (Black and Harpe 1979).

Numerous studies have been done trying to describe which factors cause buttress formation. Evidence, for, and against many of these factors exists in scientific literature; therefore, further studies need to be done before a consensus can be reached. It is most likely that a multitude of factors are responsible for buttress presences and it is doubtful that a definitive answer will ever be fully realized or accepted.

ACKNOWLEDGEMENTS

I would like to thank Mauricio Garcia for all his guidance and prudent knowledge. Andrew was a savor and helped me locate seven more buttressed *Quercus spp.* when I thought there were no more to be found. I would like to thank Rick Smith for allowing me the use of his Creedance Clearwater CD, which kept soil analysis bearable after the fourth hour. And last but not least, I would like to thank my nerdery companions.

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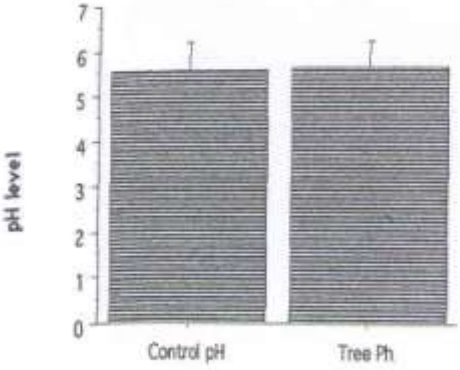

Figure 1. The mean pH level of the soil did not show a significant difference between buttressed trees and the control (Paired t-test, p = 0.7698; N = 25).

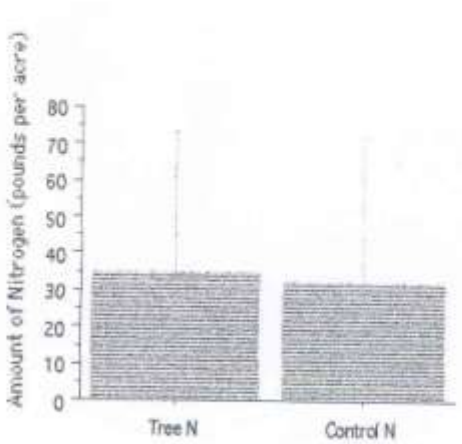

Figure 2. The mean nitrogen level did not show a significant difference between buttressed trees and the control (Paired t-test, p = 0.7955; N = 25).

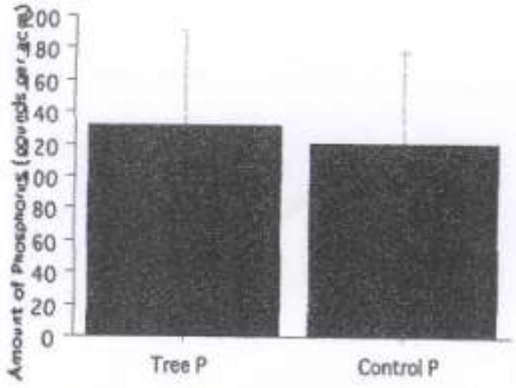

Figure 3. The mean phosphorus level did not show a significant difference between buttressed trees and the control (Paired t-test, p = 0.2543; N = 25).

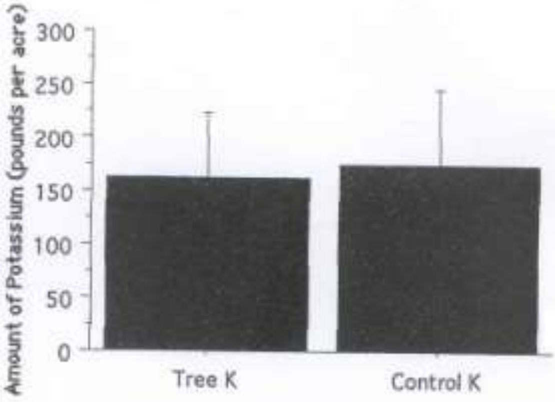

Figure 4. The mean potassium level did not show a significant difference between buttressed trees and he control (Paired t-test, p = 0.2413; N = 25).

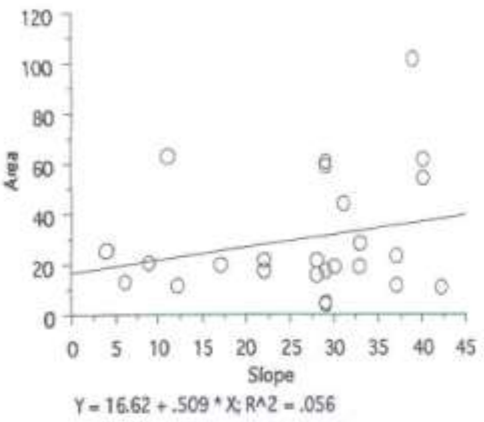

Figure 5. Slope does not show an effect in the amount of area (Simple regression, p = 0.2544; R2 = 0.056).

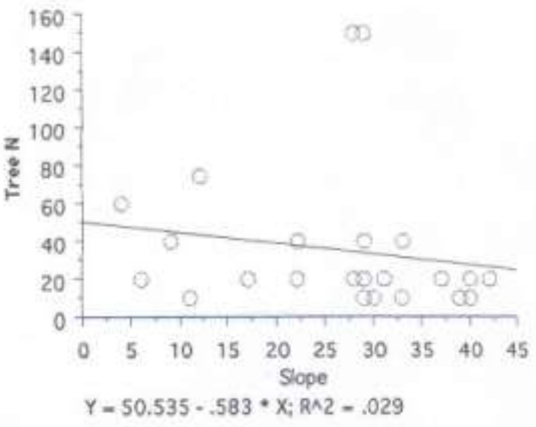

Figure 6. Slope does not show an effect in the amount of nitrogen (Simple regression, p = 0.4188; R2 = 0.029).

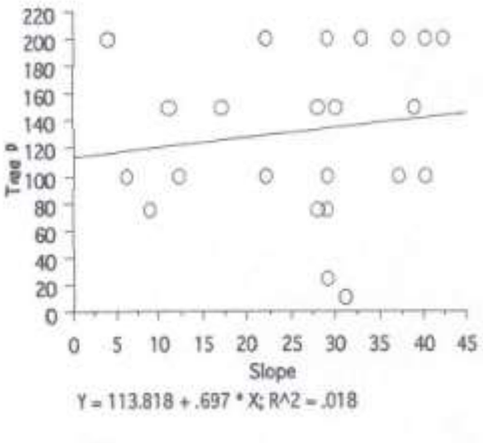

Figure 7. Slope does not show an effect in the amount of phosphorus (Simple regression, p = 0.5283; R2 = 0.018).

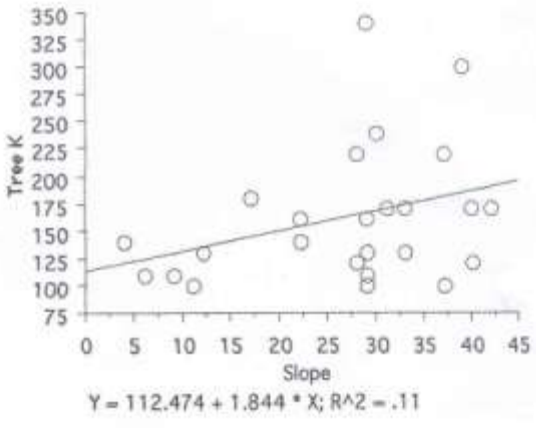

Figure 8. Slope does ont show an effect in the amount of potsassium (Simple regresssion, p = 0.1058; R2 = 0.11).