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UNDERSTANDING TROPICAL MONTANE REFORESTATION:

A COMPARISON OF SOIL AND THROUGHFALL NUTRIENTS IN PRIMARY AND
SECONDARY FORESTS OF MONTEVERDE, COSTA RICA

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Abstract

Attempts to accelerate reforestation in tropical montane forests have been ineffective. One of the greatest obstacles to reforestation is the restoration of depleted nutrient capital to facilitate forest growth. A natural source of allochthonous nutrients was sought to enhance the soil nutrient budget of the secondary forest and facilitate plant growth. Epiphytes catalyze the deposition of allochthonous nutrients in the primary forest where they are abundant. In secondary forests, epiphyte abundance is severely diminished due to inhospitable canopy structure. This study compared the plant-availability of nitrate, phosphate, and potassium in soil and precipitation under a primary forest, mid-succession secondary forest, and recently abandoned pasture near Monteverde, Costa Rica. It was expected that soil and throughfall nutrient concentration decreases from the primary forest, to the secondary forest, to the pasture. Soil nitrate and phosphate concentrations were greatest in the primary forest and lowest in the secondary forest. Soil potassium concentration was equivalent in primary and secondary forest soil but higher in the pasture due to previous inputs from cattle excreta. No statistically significant difference in throughfall concentration was observed for nitrate or phosphate between any sites. Potassium concentration in throughfall was significantly higher in forest sites than the pasture. Epiphytes perform substantial ecosystem functions and recruit allochthonous nutrients that increase the total nutrient pool but throughfall may not be a significant nutrient transport mechanism.

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Introduction

Ecological damage from tropical deforestation is difficult to repair. Deforestation alters habitat determining factors such as insolation, temperature, humidity, hydrology, soil fertility, and species composition. The extent that deforestation impairs an ecosystem corresponds to the method of destruction, duration of disturbance, and use of deforested land. Facilitating tropical reforestation requires overcoming obstacles that are costly, require intense manual labor, and are often ineffective. Successful restoration efforts involve characterizing impacts of deforestation and determining methods to resolve them.

In Costa Rica, one of the most destructive forms of deforestation is the development of pasture. Nutrient capital in pasture systems is an important determinant of sustainable use and restoration potential. The majority of nutrients in natural tropical forests are held in biomass and rapidly recycled. Pastures can account for 84% of anthropogenic erosion in Costa Rica (Hartshorn et al., 1982). The most common mechanism of deforestation to produce pasture is burning. Fire initially results in a beneficial increase in soil nutrient content due to the rapid release of stored nutrients from biomass. After about three years of cultivation as pasture, soil nutrients are depleted and limit pasture productivity (Uhl et al., 1988). Declining pasture productivity frequently results in pasture abandonment. Abandoned pastures offer an opportunity for reforestation but the loss of nutrient pools is a significant barrier to overcome.

Trees can become established in abandoned pastures and develop a community that undergoes secondary succession. Secondary succession following deforestation occurs over a long time scale and achieves an incomplete representation of the original community. In order to expedite reforestation through secondary succession it is necessary to increase the

chance that a secondary forest becomes established and matures. This requires ameliorating changes in microclimate and soil properties while facilitating the reestablishment of native communities (Holl et al., 1999). Secondary forests are unlike the primary forest in many physical, structural, and biological characteristics. Primary tropical forests are dominated by broad trees with a closed canopy and sparse under-story. Secondary forests are dominated by a community of pioneer plants which are herbaceous and grow rapidly without forming a broad canopy. When secondary succession proceeds under natural conditions, such as tree falls in gap succession, the pioneer community is replaced by a climax community. Given enough time, the secondary forest may begin to resemble the primary forest in physical, structural, and species characteristics in unaltered tropical forests. The enduring impact of deforestation, however, inhibits the pace and efficacy of secondary succession.

Successful experiments to improve reforestation have been conducted in the lowland dry forest of Guanacaste in northwest Costa Rica. In the Guanacaste Conservation Area, fire suppression and pest control has cost effectively enabled expansion and merging of forest fragments in abandoned pasture (Janzen, 1988). However, in montane regions of the Guanacaste Conservation Area this strategy has been ineffective and the development of reforestation plots is stunted (Carmona, pers. comm.). Montane reforestation is especially difficult because pastures incur more erosion and cooler temperatures than lowland areas, slowing forest growth. Montane reforestation can proceed with moderate success following land tilling, but this strategy is undesirable since it incurs additional loss of soil, is expensive, and is technically impossible on some montane slopes (Carmona, pers. comm.).

Organic farms can cost effectively improve soil by harnessing natural nutrient input with methods like intercropping with legumes (Jordan, 2004). Similar strategies that

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incorporate organisms to improve nutrient capital of ecosystems during restoration should be developed. Epiphytic plants potentially fulfill this role but they are disproportionately impacted by deforestation and unaided by current reforestation strategies. Epiphytes are a diverse plant community that lives on other plants without parasitizing the host. Orchids, bromeliads, bryophytes, ferns, and less represented groups share this lifestyle but are not related by taxonomic lineage. Convergent evolution of the epiphyte niche has been documented in at least 83 families of vascular plants and montane neotropical forests harbor the world's highest density and diversity (Gentry and Dodson, 1987). Orchids are the most diverse group of angiosperms and are especially abundant at low-mid montane elevations. Orchids are vulnerable to extinction and valuable for conservation biology because they exploit narrow niches and have highly specialized symbionts (Nadkarni et al., 2001). Bromeliads create especially important ecosystem structures because the phytoelmata creates a canopy water tank (Nadkarni et al., 2001). Bryophytes rapidly establish, grow, reproduce, and decay, fulfilling the crucial roles of moisture retention and forming detritus (Pocs, 1980).

Maintaining species diversity in tropical forests is an important component of all conservation and reforestation goals. Increasingly, understanding the ecosystem function of epiphyte diversity in the tropics is an important topic in conservation of biodiversity (Nadkarni et al., 2001). Epiphytes are important to ecosystem function because they are adapted to capture allochthonous nutrients and influence the nutrient concentration of rainwater. Precipitation and dry deposition are important nutrient inputs for forests that potentially refill nutrient pools depleted by erosion (Lovett, 1994). In montane tropical forests, precipitation and cloud water deposition have important roles in biogeochemical cycles because cloud mist that saturates the forest can contain 3-10 times more nutrients than

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bulk precipitation (Weathers et al., 1998). Epiphytes are productive in montane forests because they are frequently immersed in nutrient-rich cloud mist and are physiologically adapted to promote the deposition and retention of nutrients derived from cloud mist (Zotz and Hietz, 2001). Aerodynamic friction that epiphytes add to the canopy promotes condensation of cloud mist. At the community level, abundant epiphytes may enhance short term nutrient flux by capturing nutrients carried in cloud mist and wind.

The substantial nutrient pool sequestered in epiphytic biomass can exceed the biomass of terrestrial trees in some tropical forests (Nadkarni, 1984). Dead canopy organic matter composes 50-60% of epiphytic biomass (Ingram and Nadkarni, 1993). As epiphytic litter accumulates in branches and decomposes, allochthonous nutrients become available to the ecosystem. Decomposing canopy organic matter derived from epiphytes produces canopy soils that are more fertile than the humus layer of terrestrial soil because it harbors a richer microbial community (Vance and Nadkarni, 1990; Clark et al., 2005).

Nutrients contained in the canopy become available to terrestrially rooted trees via precipitation. Precipitation in forests is divided into three major classes including throughfall, stemflow, and canopy drip. Throughfall occurs when rainfall passes through the canopy to the forest floor. Stemflow is a similar process where precipitation runs down the trunks of trees. Canopy drip is a process unique to humid forests that occurs when air is saturated with mist that condenses on surfaces. Water passing through the canopy becomes enriched in some nutrients and depleted of others because the canopy community absorbs and excretes nutrients (Jordan, 1980). Rapid nutrient fluxes arise from fine litter dynamics and throughfall from which plants extract nutrients (Proctor, 1987). Nutrient rich precipitation facilitates forest growth by transporting dissolved nutrients that are immediately

available to terrestrial plants (Parker, 1983). Rapid nutrient fluxes are vital to plant growth in montane regions where decomposition and weathering of bedrock, sources of long term nutrient flux, occur very slowly. Epiphytes have a potentially crucial symbiotic relationship with terrestrial plants by capturing allochthonous nutrients and incorporating them in rapid nutrient cycles (Benzing, 1998). This is a reasonable expectation since host trees must support more than twice their own biomass to permit such abundant epiphyte growth.

Little effort has been made to characterize the different nutrient dynamics in primary and secondary forest canopies or to facilitate canopy restoration. The structures of primary and secondary forests are dramatically different because primary forests consist of a diverse community of large trees that produce broad horizontal branches that support an abundance of epiphytes (Nadkarni, 1984). Secondary forests consist of narrow trees that grow rapidly and produce vertical columns (Steininger, 2000). The poor substrate formed by the vertical structure of potential host trees, microclimate, and edge effects can alter epiphyte communities in secondary forests (Merwin et al., 2003). Lack of host tree availability corresponds to decreased abundance and altered composition of vascular epiphyte (Cascante-Marin et al., 2006) and bryophyte (Sillet et al., 1995) communities in secondary forests. The biomass of a secondary forest surveyed in Monteverde consisted of 95% dense wood that is excluded from rapid-nutrient cycles and it contained 0.5% of the epiphytic biomass found in an adjacent primary forest (Nadkarni et al., 2004). The impact of epiphyte scarcity in secondary forest communities in Monteverde is poorly understood but potentially substantial.

It is possible that secondary forests would benefit from allochthonous nutrients naturally acquired by epiphytes because residual soil nutrients may be depleted more rapidly than new nutrients become available. Soil nutrient limitations may forestall the development

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of mature forest structures that supports epiphyte communities. Since epiphytes are important to primary montane forest biodiversity, microclimate, and nutrient cycling, reforestation strategies should ameliorate differences between primary and secondary forest epiphyte communities. It is necessary to assess differences between nutrient input in primary and secondary forests to determine if a difference may influence reforestation success.

This research assesses the nutrient concentrations of soil and precipitation in deforested and undisturbed habitats in Monteverde, Costa Rica. The Monteverde region is a mosaic of primary forests, secondary forests, agriculture, and urban land. The climate of the pacific slope of Monteverde, where most deforestation occurs, strongly influences the resilience of the landscape to the physical changes associated with deforestation (Nadkarni and Wheelwright, 2000). A wet season with frequent heavy rain from May through November promotes erosion and leeching of nutrients while a short dry season from January through March brings strong trade winds that limit productivity.

Primary forests in Monteverde host unprecedented epiphyte diversity. More than 250 vascular epiphytes have been found in 4 ha (Ingram, 1996) and 206 species of epiphytic bryophytes have been found in 6 ha (Holz et al., 2002). Vascular epiphytes of Monteverde are primarily orchids, ferns, and bromeliads (Ingram et. al., 1996). Bryophytes are strongly dominated by hepatics and mosses in Monteverde (Gradstein et. al., 2001). A recent study of epiphyte dispersal in secondary forests characterized typical mid-succession secondary forest trees that host sparse epiphyte communities (Cascante-Maren et al., 2006).

Rain, throughfall, and soil samples were collected at a primary forest, secondary forest, and pasture study sites in Monteverde. Samples were analyzed for nitrate, phosphate, and potassium. It is expected that, on average, soil and throughfall nutrient concentration

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decreases from the primary forest, to the secondary forest, to the pasture. These hypotheses are based on the role of epiphytes in montane tropical forest nutrient cycling and the capacity of primary and secondary forests to support epiphyte communities.

Methods

Site Description

The Ecolodge San Luis Research Station is a 62 ha campus near Monteverde, Costa Rica that is owned and operated by The University of Georgia. The climate is classified as humid and pre-montane (Haber, 2000). Soil and rainwater samples were each collected from two sampling locations within primary forest, secondary forest, and pasture study sites (Figure 1). The distance between each study site was minimized as much as possible to obtain a representative study site in each forest type. Slight elevation differences existed because the pacific slope decreases in elevation from northeast to southwest. However, all sites were within the pre-montane elevation range.

The primary forest study site is a section of primary forest adjoining the Monteverde Cloud Forest Preserve. Epiphytes, especially bryophytes, are abundant on tree trunks, branches, and branch junctions. The secondary forest study site was on the Camino Real Trail where a cattle pasture has undergone secondary succession for 35 to 40 years. Secondary forest sampling locations were under closed canopies dominated by pioneer species, such as *Cecropia*, and characterized by an absence of epiphytes. A recently abandoned cattle pasture along the Camino Real Trail served as the control study site. The pasture was once contiguous with the Camino Real secondary forest study site but it has been used regularly as recently as 2005. The pasture study site is dominated by tall grasses and small interspersed seedlings that do not form a closed canopy.

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Soil Sampling

Soil samples were randomly collected six times in primary forest, secondary forest, and pasture study sites. Soil samples were taken with a plastic corer (~100 ml). Large detritus was removed and samples were dried for two days in a plastic weigh tray. Dry soil samples were sifted through a 2 mm plastic mesh to obtain 2.5 +/- 0.02 g. A sodium bicarbonate ($NaHCO_3$) digestion of soil samples simultaneously extracted plant-available nitrate, phosphate, and potassium (Schoenau and Karamanos, 1993). The digestion mixture was agitated with a magnetic stir bar at 120 rpm. The coarse extract mixture was filtered through filter paper (medium porosity and slow flow rate) followed by filtration through a 0.45 μm sterile filter into a 50 ml sterile plastic tube. Filtrate was stored at -20°C.

Rainwater Sampling

Rain collectors were constructed by affixing a plastic funnel to a 1 L plastic bottle. Collectors were deployed at each sampling location daily for 24+/-3 hours for 8 days in July 2006. Samples were syringe filtered through a 0.45 μm sterile filter into a 50 ml sterile plastic tube and stored at -20°C.

Nutrient Assessment

Nitrate and phosphate concentrations were determined using a Cary Bio100 UV/Visible Spectrophotometer, 10 mm quartz cuvette, and Cary WinUV Simple Reads (version 3.0). Potassium concentrations were determined using an Perkin Elmer AAnalyst 800 Atomic Absorption Spectrophotometer and WINLAB 32 AA (version 6.2). Serial dilutions of KNO_3, KH_2PO_4, and KCl dissolved in ddH_2O or $NaHCO_3$ extracting solution were used to produce linear regressions for nitrate, phosphate, and potassium determinations in precipitation and soil samples, respecitvely.

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TRI solution (1g sodium salicylate, 0.2g NaCl, 0.1g ammonium sulfamate per 100 ml

0.01M NaOH) was used to determine nitrate concentration in precipitation and soil extract

(Yang et al., 1998). Standards and samples (1 ml) were evaporated with TRI solution (0.5

ml) in a 60°C oven overnight. Cooled resins were wetted with 1 ml concentrated H_2SO_4,

swirled to mix, and cooled. Distilled H_2O (5 ml) was added, swirled to mix, and allowed to

cool. Finally, 40% NaOH (5 ml) was added, swirled to mix, and cooled. Absorbance of each

solution was measured at 410 nm using a UV/Vis Spectrophotometer.

Ammonium molybdate was used to colorimetrically determine the concentration of

phosphate in soil extract (Murphy and Riley, 1962). A mixed reagent (125 ml 5M H_2SO_4,

37.5 ml 0.23M ammonium molybdate, 75 ml 0.1M ascorbic acid, 12.5 ml 0.004M potassium

antimonyl tartrate) was prepared. The mixed reagent (4 ml) was added to soil extract (5 ml)

and diluted to 25 ml with ddH_2O. Absorbance was read after color development (15 min)

using a UV/Vis Spectrophotometer at 712 nm.

Phosphate in precipitation samples was determined using molybdate and malachite

green (Motomizu et. al, 1983). A reagent mixture [0.68M molybdate (300 ml), concentrated

H_2SO_4 (47 ml), and 2×10^{-3}M malachite green (250 ml)] was prepared. Each sample (5 ml)

was mixed with reagent mixture (0.75 ml), 7.5M H_2SO_4 (2.5 ml), and 1% poly(vinyl alcohol)

color stabilizing solution (0.25 ml). Absorbance was read using a UV/Vis spectrophotometer

at 650 nm.

Potassium concentration in soil and precipitation was determined by atomic

absorption spectroscopy at 766.5 nm in an oxidizing air-acetylene flame. Samples were

diluted 2x and 20x in 10 ml and 100 ml volumetric flasks for precipitation and soil extract,

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respectively. To suppress ionization interferences all standards and samples were made to 0.1% CsCl during dilution (PerkinElmer, 2000).

Data Analysis

A stratified randomization design was used for statistical blocking analysis of nutrient concentration in precipitation. Each study site was considered a stratum and the average concentration of two sampling locations per precipitation event were used to improve precision. ANOVA single factor ($\alpha=0.05$) was used to detect statistically significant differences between strata for all rainfall events in the study period.

Soil samples were collected at random in each strata and a statistically significant difference in soil nutrient content was tested for all samples within each stratum. ANOVA single factor ($\alpha=0.05$) was used to determined statistically significant differences between nutrient concentrations from different study sites.

Results

A statistically significant difference ($p<0.05$) was detected between the nutrient concentration of soil samples taken from different study sites for nitrate, phosphate, and potassium ($p=0.015, 0.008, 0.006$, respectively) (Figure 2). Primary forest soil contained the highest mean, median, maximum, and minimum concentration of nitrate and phosphate. The pasture study site had the second highest concentration of plant-available nitrate and phosphate, and the highest concentration of potassium. The secondary forest site had the most nitrate and phosphate deficient soil. Mean potassium was slightly higher in the secondary forest than in the primary forest, whereas median potassium was slightly lower. The maximum value in the secondary forest, but not the primary forest, was greater than the

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mean pasture concentration, although no statistically significant difference was observed between forest sites (Table 1).

Some precipitation samples were lost when plastic containers cracked in storage requiring different n values to be used in analysis (Table 2). No statistically significant difference in throughfall nutrient concentration was detected for nitrate or phosphate (p= 0.823, 0.162, respectively), but a statistically significant difference in potassium concentration (p= 0.005) was detected between the pasture and forest study sites (Figure 3). Although mean nitrate and phosphate concentrations were not significantly different between study sites the distribution of data differed. Nitrate and phosphate concentrations had a compact inter-quartile range at the primary forest sites. However, the secondary forest had a broader range of values and much broader inter-quartile range than the other study sites. Potassium concentration in precipitation was significantly higher in the primary forest than in the pasture. The primary forest range is greater and it has the broadest inter-quartile range (Figure 3).

A published hypothetical model of tropical soil nutrient concentration following disturbance was used create predictions and evaluate these data (Figure 4A). The primary literature revealed limitations to the scope of this model for describing soil nutrient patterns. An alternative model that describes 40 years of succession following disturbance and is consistent with the data reported in this study is presented (Figure 4B).

Discussion

Nitrate, phosphate, and potassium availability can limit plant growth. This study was conducted in late July which coincides with the wet season and peak plant productivity. The

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amount of plant-accessible nitrate, phosphate, and potassium extracted underestimates the total amount of nitrogen, phosphorous, and potassium present in soil, respectively. However, for a short-term soil study these nutrients are ideal because they can be simultaneously extracted from soil to indicate short term nutrient flux and availability (Schoenau and Karamanos, 1993). The expectation that a statistically significant difference of soil nutrient concentration could be detected between primary forest, mid-succession secondary forest, and an abandoned pasture was confirmed.

As expected, the primary forest had the most nitrate and phosphate per gram of soil. However, the prediction that the secondary forest would have an intermediate amount of plant-available nutrients in the soil was not supported. Instead, the pasture showed the second highest concentration of nitrate and phosphate. Pasture soil fertility was expected to decrease due to physical characteristics of pasture, including high wind exposure, erosion, and low decomposer populations. These factors have a greater effect on pasture than on mid-succession secondary forests.

Reading et al., (1995) integrated numerous soil studies to produce a simplified theoretical model of changes in nutrient concentration over time (Figure 4A). This model predicts an increase in soil nutrient concentration when a tropical forest is burned, followed by a decrease in nutrient concentration during cultivation, and a return to undisturbed nutrient concentrations after abandonment. When tropical forests are burned or cleared for pasture the initial increase in nutrient content is due to release of nutrients from debris. These nutrients persist for approximately two years before becoming exhausted by cultivation (Buschbacher et al., 1988). When a pasture is abandoned and allowed to revert to forest, the model suggests that soil nutrient availability will increase until it is as nutrient-rich as the

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undisturbed forest (Reading et al., 1995). Based on the model by Reading et al., (1995) an increase of soil nutrient availability during succession was expected to be observed in Monteverde. However, the findings of this study are not consistent with the theoretical predictions of pasture succession.

Several factors limit use of the theoretical model to describe secondary succession in pasture. First, the simplified model neglects the differences in nutrient dynamics under slight and intense pasture use. Second, the model ignores the influence of large herbivore waste. Third, pasture grasses form thick root mats that trap nutrients, slowing the rate of nutrient decline. Pasture grass root mats retain higher amounts of nutrients than forest humus but these nutrients are stored in soil instead of biomass (Feigl et al., 1995). Fourth, young forests efficiently withdraw available nutrients from soil and mobilize tightly bound minerals. The result is that nutrients become proportionally distributed between soil and biomass in a manner similar to primary forests (Uhl and Jordan, 1984). Similar proportional distribution of nutrient pools between primary and secondary forests may lead to an erroneous conclusion that secondary forests are not nutrient limited. However, the total nutrient pool was depleted at the time the original forest was cleared and fewer total nutrients are present in the secondary forest. Finally, secondary forests rapidly accumulate biomass but the majority of this biomass ultimately enters rapid nutrient flux cycles (Brown and Lugo, 1990). Therefore, measurements of plant-available nutrients in secondary forests may indicate relatively rich soil, consistent with the theoretical model, but the measurements overestimate the ecosystem value of these nutrients. When long lived trees replace herbaceous plants in mid- to late-secondary forests, a portion of the total nutrient pool is immobilized in biomass and no longer cycled through the soil.

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To my knowledge, no preexisting soil nutrient data for study sites used in this research exist. The data reported here demonstrate significantly less nitrate and phosphate are available in mid-succession secondary forest soils than in nearby pasture and primary forest soils. The decrease in secondary forest nutrient availability is likely due to the influence of the regenerating forest. The conclusion that residual total nutrient pools have been immobilized in secondary forest biomass and are no longer present in the soil is consistent with the data reported here.

To be useful for understanding soil nutrient dynamics on a scale suitable for reforestation, a more long-term model than that proposed by Reading et al. (1995) is needed. An alternative hypothetical model that distinguishes between total nutrient pools and plant-available nutrients found in the soil is proposed (Figure 4B). As a pasture progresses through secondary succession the total biological nutrient pool slowly increases because new nutrients are extracted from parent material and are absorbed from the atmosphere. Soil nutrient availability initially increases as rapid nutrient fluxes and fine litter dynamics enrich the humus layer. However, over time the forest transitions to more long-term nutrient fluxes and these nutrients are immobilized in tree structures. At this point, there is a net sequestration of nutrients. The forest soil may become nutrient depleted and limit forest growth. This model is most applicable for understanding growth limiting nutrients, such as nitrate and phosphate in this study, because nutrient conservation adaptations of plants target limiting nutrients.

Declining soil phosphate concentration may limit forest succession as it becomes incorporated into biomass. Nitrate is made available by bacteria that fix nitrogen from atmospheric sources but phosphate must weather from parent material (Bautista-Cruz and

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Castillo, 2005). The decline in available nitrate reported in this study must not have occurred through the same mechanism as phosphate because forest growth promotes bacterial productivity. The nitrogenase enzyme used by bacteria to fix nitrogen can be deactivated by oxygen so most nitrogen fixing bacteria symbiotically live in the anoxic root nodules of legumes (Raymond et al., 2004). Nitrogen fixation produces ammonia which is converted into nitrate and immediately absorbed by plants. Thus, nitrate produced by nitrogen fixing bacteria is rapidly incorporated in biomass and not observed in the soil unless produced in excess. Soil nitrate levels may not rise until nitrogen utilized by plants is mineralized through decay and the nitrogen demand of the forest is satisfied. Although allochthonous nitrate is created by nitrogen fixing bacteria, the nitrogen fixation process may not keep pace with forest demand. Low soil nitrate concentration can be expected in mid-succession secondary forests.

Potassium concentrations in the soil varied differently than nitrate and phosphate. Potassium concentrations in primary and secondary forest soils were similar. The pasture site had significantly more potassium than either forest study sites. Pasture grazed by large herbivores contains significantly more soil potassium due to excreta than adjacent herbivore-excluded areas (Carran and Theobald, 2000). Potassium increases nitrogen uptake by plants and leaching of other cations, especially Mg and Ca (Kayser and Isselstein, 2005). High potassium and low nitrate concentrations in pasture sites is supported by this study.

The spatial distribution of cattle excreta in pasture follows no significant pattern over time, producing concentrated patches of nutrients randomly distributed in the pasture (Kohler et al., 2006). Dissimilarly, stemflow/root induced double-funneling of precipitation redirects water and nutrients to soil located at the base of canopy trees, localizing a high concentration

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of potassium that lasts for decades (Johnson and Lehmann, 2006). Secondary forest trees effectively withdraw potassium from soil and concentrate it around their roots, reducing the ambient concentration in upper soil horizons. Thus, secondary forest trees that may be established randomly will reduce the random distribution of high potassium concentration throughout the soil. Although the total potassium pool in secondary forests is likely more than or equal to the potassium pool in pasture, concentrated potassium is not observed in secondary forest soil.

Soil nitrate concentration also increases due to the influence of large herbivore excreta but does not saturate deep soil layers like potassium (Carran and Theobald, 2000). Nitrate is rapidly cycled into organic forms such as ammonia but potassium does not have an organic form. Soil colloids are small insoluble minerals in soil with a large surface area and negative charge that bind soils cations such as Ca, Mg, and K. Potassium ions contained in herbivore excreta associate with soil colloids and are not readily leached on slopes. In contrast, excreted nitrate is an anion with organic forms that do not persist in the soil (Sakadevan et al., 1993). In Monteverde, excreta from grazing herbivores increases soil nitrate and potassium concentrations in pasture soil. Two years or more post-abandonment, potassium concentrations remain higher in pasture than in the primary forest and nitrate concentration is lower than in the primary forest. 35-40 years since cattle excreta was excluded from the secondary forest the maximum and mean potassium concentrations are slightly higher, though not significantly, than in the primary forest. The persistent increase in potassium concentration suggests that mid-succession secondary forests are not nutritionally limited by potassium.

Based on this study, it is possible that nutrient limits to reforestation in Monteverde are most detrimental when the forest transitions from the herbaceous, early-succession, plant communities to long-lived mature forest trees. Low levels of plant available nitrate and phosphate in the soil of mid-succession secondary forests may act to stall or severely delay forest succession to a mature state. In tropical montane forests, this can occur before horizontal structures necessary for the native abundance of mature epiphyte communities develop. Epiphytes catalyze nutrient deposition which may counteract nutrient losses, especially phosphate, in mature forests (Bautista-Cruz and Castillo, 2005). Restoration of this allochthonous nutrient input mechanism in secondary forests may be critical to improving reforestation.

If epiphytes significantly increase nutrient input, then this effect may be observed in high throughfall nutrient concentrations. This study tested the prediction that the high abundance of epiphytes in the primary forest significantly enriches nutrient concentration of throughfall. Secondary forest canopies, with low epiphyte abundance, were not expected to significantly enrich throughfall. No statistically significant difference was found between study sites for nitrate and phosphate because variation between rainfall events was large within each stratum. A statistically significant difference in potassium concentration was found between forest and control sites, but not between primary and secondary forests. Sampling with roving collectors can reduce variability in nutrient determinations between rainfall events to less than half of the variability of experiments using fixed collectors (Holwerda et al., 2005). Fixed collectors were used in this experiment but improving collection procedures to reduce variability may enable finer resolution potential differences between strata.

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The high variation in nitrate and phosphate concentration reported in secondary forest throughfall is due to one of the two sampling locations consistently having higher concentrations of nitrate and phosphate than the other. Consistent with gap succession models, pioneer and climax tree species in mid-succession secondary forests intermingle such that some trees have high leeching rates while other species have high nutrient conservation characteristics (Lawton and Putz, 1988). The influence of terrestrial tree leaching may explain the broader inter-quartile range of secondary forest nitrate and phosphate throughfall concentrations. Forest vegetation around the sampling sites was not identified to species in this experiment because the overall structure of the canopy, mid-succession forest lacking epiphytes, was the independent variable. However, at this stage of succession the relative age and species composition of canopy trees can influence throughfall nutrient content. To minimize this possible source of variation more samples per strata are needed.

This study was unable to account for terrestrial plant leachate mixing with epiphytic leachate in throughfall. Plants in secondary forests do not immobilize nutrients in long term flux cycles like mature forest trees. Therefore, canopy leaching from terrestrial vegetation may occur in greater quantity in secondary forests than primary forests. Conversely, epiphytes exploit a nutrient limited niche and conserve nutrients extremely efficiently. Since it is not possible to distinguish between sources of nutrients observed in throughfall samples, the ability to quantify epiphytic addition of allochthonous nutrients is limited. More epiphyte derived nutrients may be present in primary forest throughfall, whereas more terrestrial derived nutrients may be present in secondary forest throughfall. This may explain the failure to detect significantly different distributions between study sites. An experiment that

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isolates epiphyte community nutrient cycles from terrestrial community nutrient cycles may resolve the total exchange of nutrients between canopy and terrestrial pools.

Concentration of potassium in precipitation was significantly different between pasture and forest study sites. As expected, forest canopy communities enrich throughfall with potassium. Potassium becomes enriched in tropical forests throughfall throughout the tropics but nitrate or phosphate enrichment is inconsistent (Parker, 1983). The substantial percent increase of potassium in throughfall could be the reason that a statistically significant difference between pasture and forest was detected for potassium but not for nitrate or phosphate. The unexpectedly similar distribution of potassium concentration in primary and secondary forest throughfall may suggest that the low epiphyte abundance in secondary forests has minimal impact on the allochthonous input. This is consistent with the similar soil potassium concentration in primary and secondary forests in Monteverde.

Throughfall can be a poor indicator of the total epiphyte contribution to tropical forest nutrient pools because epiphytes can absorb nutrients from rainfall (Jordan, 1980). Throughfall may not be an important route of epiphyte derived nutrient transport as compared to litterfall (Hietz et al., 2002). Since most allochthonous nutrients are first incorporated into epiphyte communities, most of these nutrients are probably made available to terrestrial plants through fine litter dynamics rather than throughfall nutrient enrichment. The ability of epiphytes to trap and absorb nutrients has been reported to vary depending on forest location (Nadkarni and Matelson, 1991) and likely varies annually within forests due to seasonal metabolic demands of epiphyte communities. At certain times of the year epiphyte communities may be less beneficial to forest growth than others but the cumulative long-term benefit should be assessed.

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Potential differences between total and average throughfall nutrient loading and depletion due to leaching and absorption by terrestrial trees or epiphytes must be qualified by an observation of ecosystem structure. Since epiphytes absorb nutrients from throughfall in mature forests, decreased throughfall nutrient concentration should not be reported as an ecosystem loss. Although throughfall nutrient concentration in primary and secondary forests may be similar, the location of nutrient pools is important. Similar throughfall concentrations in primary and secondary forests do not rule out the important role of epiphytes in nutrient cycling.

Many studies of epiphyte nutrient pools are limited to old growth trees with horizontal branches that permit climbing, admitting a bias to the results (Barker and Pinard, 2001). Even where secondary forest trees do form horizontal branches to support epiphytes, the bulk contribution of epiphyte communities to the secondary forest nutrient pools is low (Nadkarni et al., 2004). Since much of the epiphyte-derived nutrient pool in the canopy is held in dead organic matter, the age of the forest community may be more important than its abundance. Dead canopy organic matter forms crown histosols as it decomposes. These soils are formed from decaying organic matter and are stabilized in the canopy by epiphytic structures.

The plant-available nutrients conserved by crown histosols make them proportionally more important to the Monteverde ecosystem than implied by their mass (Nadkarni et al., 2002). While the nutrients contained in crown histosols are a small portion of the total nutrient pool, they are exploited by plants. Terrestrial trees of mature forests in Monteverde have evolved canopy roots to exploit the valuable nutrient reserve contained in crown histosols (Nadkarni, 1981). Like terrestrial soils, crown histosols develop over time.

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Nutrients can be leached from these arboreal soils to be absorbed by terrestrial trees from the forest floor or they can be tapped by arboreal roots that mature forest tree species have developed during coevolution. Due to delays between the abandonment of pasture and when forest trees become established, mature, develop horizontal structure, and recruit epiphytes, it might take centuries for crown histosols to develop. Contributing to crown histosols might be the most important role of epiphyte communities in the development of mature forest nutrient pools. To reach an ecologically important threshold, this nutrient pool may require the most long-term restoration of all nutrient pools in the secondary forest.

In order to develop a comprehensive strategy for the restoration of nutrient pools in secondary tropical montane forests it is necessary to evaluate potential natural sources of allochthonous nutrients. This study requires a distinction between statistically significant differences and ecologically important differences in throughfall nutrient concentration between study sites. Even though a statistically significant difference in throughfall nutrient concentration was not detected in this study, the throughfall nutrient concentration is so dilute that it is not likely to accelerate reforestation. However, allochthonous nutrient input catalyzed by epiphytes is probably important to long term maintenance of soil fertility in mature forests. The extended time of low epiphyte abundance during secondary succession insufficiently counterbalances diminished nutrient pools resulting from deforestation. Epiphyte communities increase plant biodiversity, provide resources to animal communities, moderate daily microclimate variation, and harbor nutrients involved in both long and short term nutrient flux. Therefore, the presence or absence of epiphytic communities in the canopy is important to consider for reforestation goals.

Literature Cited

Barker, M.G., Pinard, M.A. 2001. Forest canopy research: sampling problems, and some solutions. Plant Ecology. 153: 23-38.

Bautista-Cruz, A., Castillo, R.F. 2005. Soil Changes During Secondary Succession in a Tropical Montane Cloud Forest Area. Soil Science Society of America Journal. 69: 906-914.

Benzing D.H. 1998. Vulnerabilities of Tropical Forests to Climate Change: The Significance of Resident Epiphytes. Climatic Change. 39: 519-540.

Brown, S., Lugo, A.E. 1990. Tropical Secondary Forests. Journal of Tropical Ecology. 6: 1-32.

Buschbacher, R., Uhl, C., Serrao, A. S. 1988. Abandoned pastures in eastern Amazonia. II. Nutrient stocks in the soil and vegetation. Journal of Ecology. 76: 682-699.

Carmona, F. 2004. Guanacaste Conservation Area Restoration Manager. Associated Colleges of the South: Costa Rica Field Study. Personal Communication.

Carran, R.A., Theobald, P.W. 2000. Effects of excreta return on properties of grazed pasture soil. Nutrient Cycling in Agroecosystems. 56: 79-85.

Cascante-Marin, A., Wolf, J.H.D., Oostermeijer, J.G.B., den Nijs, J.C.M., Sanahuja, O., Duran-Apuy, A. 2006. Epiphytic bromeliad communities in secondary and mature forest in a tropical premontane area. Basic and Applied Ecology, 7: 520-532.

Clark, K.L., Nadkarni, N.M., Gholz, H.L. 2005. Retention of Inorganic Nitrogen by Epiphytic Bryophytes in a Tropical Montane Forest. Biotropica. 37: 328-336.

Feigl, B.J., Melillo, J., Cerri, C.C. 1995. Changes in the origin and quality of soil organic matter after pasture introduction in Rondonia. Plant and Soil. 175: 21-29.

Gentry, A.H., Dodson, C.H. 1987. Diversity and Biogeography of Neotropical Vascular Epiphytes. Annals of the Missouri Botanical Garden. 74: 205-233.

Gradstein, S.R., Griffin, D., Morales, M.I., Nadkarni, N.M. 2001. Diversity and habitat differentiation of mosses and liverworts in the cloud forest of Monteverde, Costa Rica. Caldasia. 23: 203-212.

Haber W.A. 2000. Plants and Vegetation. Nadkarni NM, Wheelwright NT (eds), Monteverde ecology and conservation of a tropical cloud forest. Oxford Press: New York

- 23 -

Hartshorn, G, Hartshorn, L., Atmetlla, A., Gomez, L.D., Mata, A., Mata, L., Morales, R. Ocampo, R., Pool, D., Quesada, C., Solera, C., Solorzano, R., Stiles, G., Tosi J., Umana, A., Villalobos, C., Wells, R. 1982. Costa Rica Country Environmental Profile: A Field Study. Agency for International Development contract No. 000-C-00-1004-00. Centro Cientifico Tropical, San Jose, Costa Rica.

Hietz, P., Wanek, W., Wania, R., Nadkarni, N.M. 2002. Nitrogen-15 natural abundance in montane cloud forest canopy as an indicator of nitrogen cycling and epiphyte nutrition. Oecologia. 131: 350-355

Holl, K.D. 1999. Factors limiting tropical rain forest regeneration in abandoned pasture: Seed rain, seed germination, microclimate, and soil. Biotropica. 31: 229-242.

Holwerda, F., Scatena, F.N., Bruijnzeel, L.A. 2006. Throughfall in a Puerto Rican lower montane rain forest: A comparison of sampling strategies. Journal of Hydrology. 327: 592-602.

Holz, I., Gradstein, S.R., Heinrichs, J., Kappelle, M. 2002. Bryophyte Diversity, Microhabitat Differentiation, and Distribution of Life Forms in Costa Rican Upper Montane *Quercus* Forest. The Bryologist. 105: 334-348.

Ingram, S.W., Ferrell-Ingram, K., Nadkarni, N.M. 1996. Floristic Composition of Vascular Epiphytes in a Neotropical Cloud Forest, Monteverde, Costa Rica. Selbyana. 17: 88-103.

Ingram, S.W., Nadkarni, N.M. 1993. Composition and distribution of epiphytic organic matter in a neotropical cloud forest, Costa Rica. Biotropica. 25: 370-383.

Janzen, D.H. 1988. Management of Habitat Fragments in a Tropical Dry Forest: Growth. Annals of the Missouri Botanical Garden. 75: 105-116.

Johnson, M.S., Lehmann, J. 2006. Double-funneling of trees: Stemflow and root-induced preferential flow. Ecoscience. 13: 324-333.

Jordan, C.F. 2004. Organic farming and agroforestry: Alleycropping for mulch production for organic farms of southeastern United States. Agroforestry Systems. 61: 79-90.

Jordan, C.F., Golley, F., Hall, J., Hall, J. 1980. Nutrient Scavenging of Rainfall by the Canopy of an Amazonian Rain Forest. Biotropica. 12: 61-66.

Kayser, M., Isselstein, J. 2005. Potassium cycling and losses in grassland systems: a review. Grass and Forage Science. 60: 213-223.

- 24 -

Kohler, F., Gillet, F., Reust, S., Wagner, H.H., Gadallah, F., Gobat, J.M., Buttler, A. 2006. Spatial and seasonal patterns of cattle habitat use in a mountain wooded pasture. Earth and Environmental Science. 21: 281-295.

Lawton, R.O., Putz, F.E. 1988. Natural Disturbance and Gap-Phase Regeneration in a Wind Exposed Tropical Cloud Forest. Ecological Society of America. 9: 764-777.

Lovett, G.M. 1994. Atmospheric Deposition of Nutrients and Pollutants in North America: An Ecological Perspective. Ecological Applications. 4: 629-650.

Merwin, M.C., Rentmeester, S.A., Nadkarni, N.M. The influence of host tree species on the distribution of epiphytic bromeliads in experimental monospecific plantations, La Selva, Costa Rica. Biotropica. 2003, 35(1), 37-47.

Motomizu, S., Wakimoto, T., Toei, K. 1983. Spectrophotometric Determination of Phosphate in River Waters with Molybdate and Malachite Green. Analyst. 108: 361-367.

Murphy, J., Riley, J.P. 1962. A Modified Single Solution Method for the Determination of Phosphate in Natural Waters. Analytica Chimica Acta. 27: 31-36.

Nadkarni, N. M. 1981. Canopy roots: convergent evolution in rainforest nutrient cycles. Science, 214: 1023-1024.

Nadkarni, N.M. 1984. Epiphyte biomass and nutrient capital of a neotropical elfin forest. Biotropica. 16: 249-256.

Nadkarni, N.M., Matelson, T.J. 1991. Fine litter dynamics within the tree canopy of a tropical cloud forest. Ecology. 72: 2071-2082.

Nadkarni, N.M., Merwin, M.C., Nieder, J. 2001. Forest Canopies, Plant Diversity. Encyclopedia of Biodiversity. 5: 27-40.

Nadkarni, N.M., Schaefer, D., Matelson, T.J., Solano, R. 2002. Comparison of arboreal and terrestrial soil characteristics in a lower montane forest, Monteverde, Costa Rica. Pedobiologia. 46: 24-33.

Nadkarni, N.M., Schaefer, D., Matelson, T.J., Solano, R. 2004. Biomass and nutrient pools of canopy and terrestrial components in a primary and a secondary montane cloud forest, Costa Rica. Forest Ecology and Management. 198: 223-236.

Nadkarni and Wheelwright. 2000. Monteverde. New York: Oxford University Press. .

Parker, G.G. 1983. Throughfall and Stemflow in the Forest Nutrient Cycle. Advances in Ecological Research. 13: 58-133.

PerkinElmer. 2000. Analytical Methods for Atomic Absorption Spectrometry. Perkin Elmer, Inc: 83.

Pocs, T. 1980. The epiphytic biomass and its effect on the water balance of two rainforest types in the Ulugur Mountains (Tanzania, East Africa). *Acta Botanica Hungarica Plantarum*. 26: 143-167.

Proctor, J. 1987. Nutrient Cycling in primary and old secondary rainforests. Applied Geography. 7: 135-152.

Raymond, J., Siefert, J.L., Staples, C.R., Blankenship, R.E. 2004. The natural history of nitrogen fixation. Molecular Biology and Evolution. 21: 541-554.

Reading, A.J., Thompson, R.D., Millington, A.C. 1995. Humid Tropical Environments. Blackwell Publishers Ltd. Cambridge, Ma: 305-307.

Sakadevan, K., Mackay, A.D., Hedley, M.J. 1993. Influence of sheep excreta on pasture uptake and leaching losses of sulfur, nitrogen and potassium from grazed pastures. Australian Journal of Soil Research. 31: 151-162.

Schoenau, J.J., Karamanos, R.E. 1993. Sodium Bicarbonate-Extractable P, K, and N. Soil Sampling and Methods of Analysis, M.R. Carter, Ed., Chapter 7. Canadian Society of Soil Science. Lewis Publishers.

Sillett, S.C., Gradstein, S.R., Griffin, D. 1995. Bryophyte diversity of Ficus tree crowns from intact cloud forest and pasture in Costa Rica. The Bryologist. 98: 251-260.

Steininger, M.K. 2000. Secondary forest structure and biomass following short and extended land-use in central and southern Amazonia. Journal of Tropical Ecology. 16: 689-708.

Uhl, C., Bushbacher, R., Serrao, E.A. 1988. Abandoned pastures in eastern Amazonia. Journal of Ecology. 76: 663-681.

Uhl, C., Jordan, C.F. 1984. Succession and nutrient dynamics following forest cutting and burning in Amazonia. Ecology. 65: 1476-1490.

Vance, E., Nadkarni, N.M. 1990. Microbial biomass and activity in canopy organic matter and the forest floor of a tropical cloud forest. Soil Biology and Biochemistry. 22: 677-684.

Weathers, K., Likens, G., Borman, F., Bicknell, S., Borman, H., McDowell, W., Siccama, T., Smiley, D., Tarrant, R. 1988. Cloud water chemistry from ten sites in North America. Environmental Science and Technology. 22: 1018-1026.

- 26 -

- 27 -

Yang, J.E., Skogley, E.O., Schaff, B.E., Kim, J.J. 1998. A Simple Spectrophotometric Determination of Nitrate in Water, Resin, and Soil Extracts. Soil Science Society of America Journal. 62: 1108-1115.

Zotz, G., Hietz, P. 2001. The physiological ecology of vascular epiphytes: current knowledge, open questions. Journal of Experimental Botany. 52: 2067-2078.

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Table Legends

Table 1. Soil nutrient concentration (and standard error), median, maximum and minimum values for nitrate, phosphate, and potassium in pasture, secondary forest, and primary forest study sites in mg/g soil. For all study sites, *n=6*.

Table 2. Precipitation events (*n*), nutrient concentration (and standard error), median, maximum and minimum values for nitrate, phosphate, and potassium in pasture, secondary forest, and primary forest study sites in mg/L.

Table 3. R^2 values of standard linear regressions used to determine nitrate, phosphate, and potassium concentration in soil and precipitation analysis.

Table 1

Soil		Pasture	Secondary Forest	Primary Forest
Nitrate	Mean (Standard Error)	0.035 (0.002)	0.026 (0.002)	0.039 (0.004)
	Median	0.036	0.025	0.038
	Maximum	0.040	0.031	0.055
	Minimum	0.026	0.020	0.028
Phosphate	Mean (Standard Error)	0.015 (<0.001)	0.014 (<0.001)	0.018 (0.001)
	Median	0.015	0.014	0.017
	Maximum	0.016	0.016	0.022
	Minimum	0.014	0.013	0.015
Potassium	Mean (Standard Error)	0.562 (0.065)	0.384 (0.061)	0.363 (0.041)
	Median	0.617	0.348	0.358
	Maximum	0.716	0.628	0.500
	Minimum	0.309	0.248	0.258

Table 2

Precipitation		Pasture	Secondary Forest	Primary Forest
Nitrate	*n*	6	5	5
	Mean (Standard Error)	0.285 (0.043)	0.289 (0.060)	0.322 (0.026)
	Median	0.304	0.299	0.319
	Maximum	0.426	0.435	0.402
	Minimum	0.151	0.150	0.256
Phosphate	*n*	7	6	6
	Mean (Standard Error)	0.030 (0.006)	0.056 (0.014)	0.038 (0.007)
	Median	0.026	0.049	0.042
	Maximum	0.054	0.110	0.056
	Minimum	0.012	0.015	0.018
Potassium	*n*	6	5	5
	Mean (Standard Error)	1.318 (0.176)	3.171 (0.336)	2.594 (0.482)
	Median	1.477	2.865	2.378
	Maximum	1.700	4.409	4.164
	Minimum	0.583	2.457	1.448

Table 3

Nutrient	Soil	Precipitation
Nitrate	0.960	0.998
Phosphate	0.991	0.989
Potassium	0.999	0.997

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Figure Legends

Figure 1. A 1997 aerial photograph of study site locations in the Monteverde-San Luis region. Photo Source: Cascante-Marin et al., 2006.

Figure 2. Modified box plots comparing concentration of soil nutrients (mg/g soil) for A) nitrate (p= 0.015), B) phosphate (p= 0.008), and C) potassium (p= 0.006) between study sites.

Figure 3. Modified box plots comparing concentration of precipitation nutrients (mg/L) for A) nitrate (p=0.823), B) phosphate (p=0.162), and C) potassium (p=0.005) between study sites.

Figure 4. Hypothetical models that represent tropical soil nutrient flux following deforestation compared to stable nutrient levels in undisturbed forest soil. A) Published model of soil nutrient flux (Reading et al., 1995). B) An alternative hypothetical model that represents potentially limiting soil nutrients is depicted. The first 10 years of the alternative model match that proposed by Reading et al., 1995. This alternative model spans 40 years and reflects a decrease in limiting soil nutrients as the forest transitions from a early- to mid-succession and immobilizes nutrients in biomass.
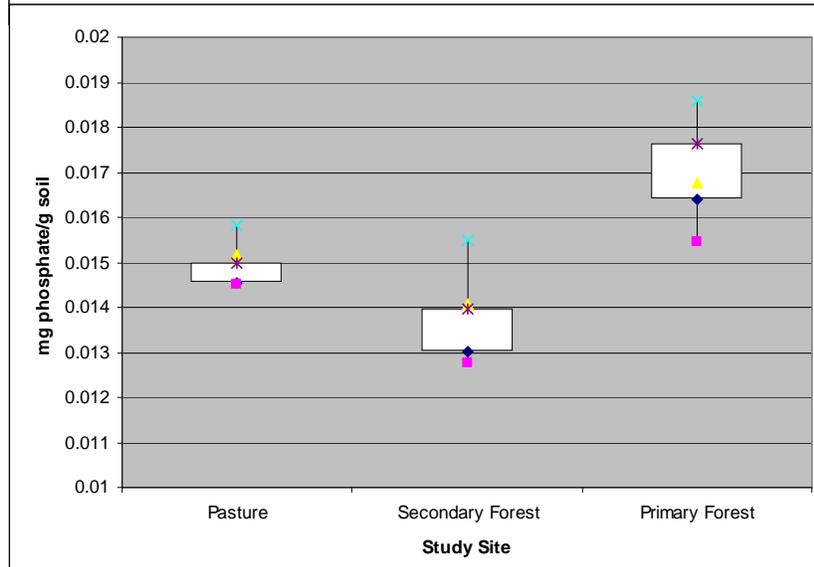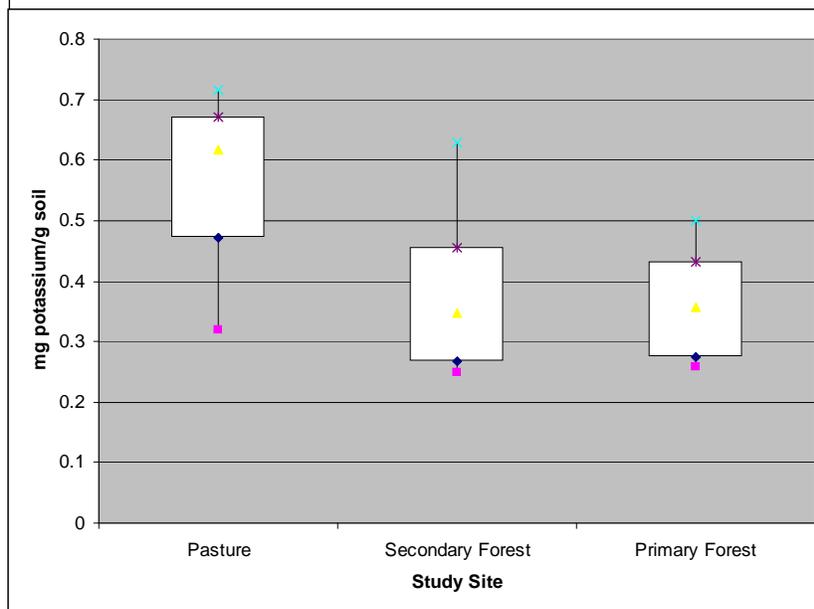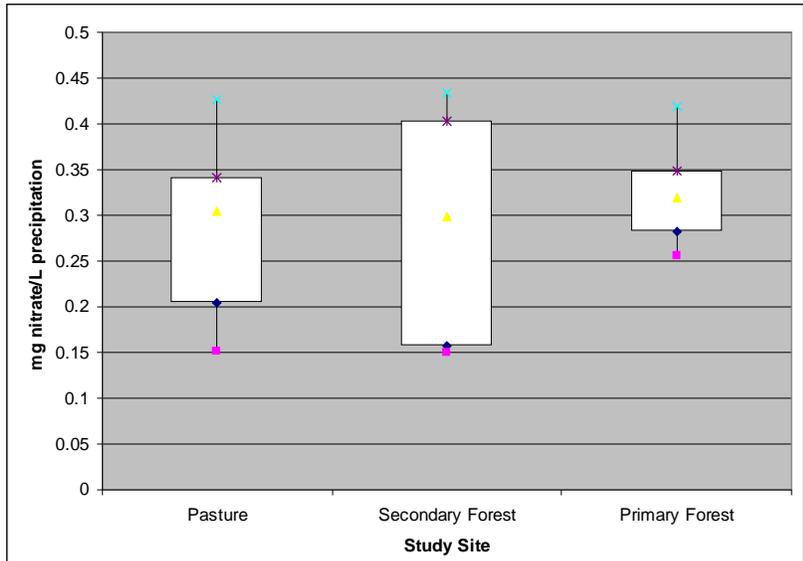
- 30 -

Figure 1
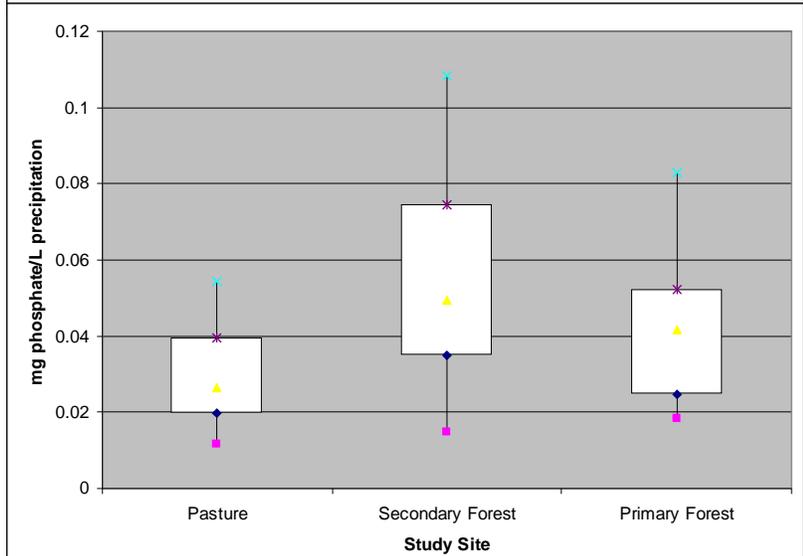
Figure 2

A

B

C

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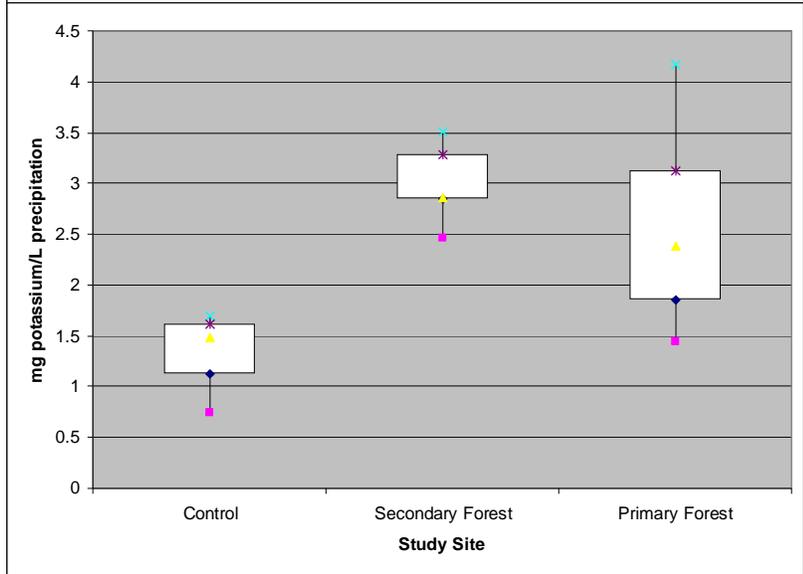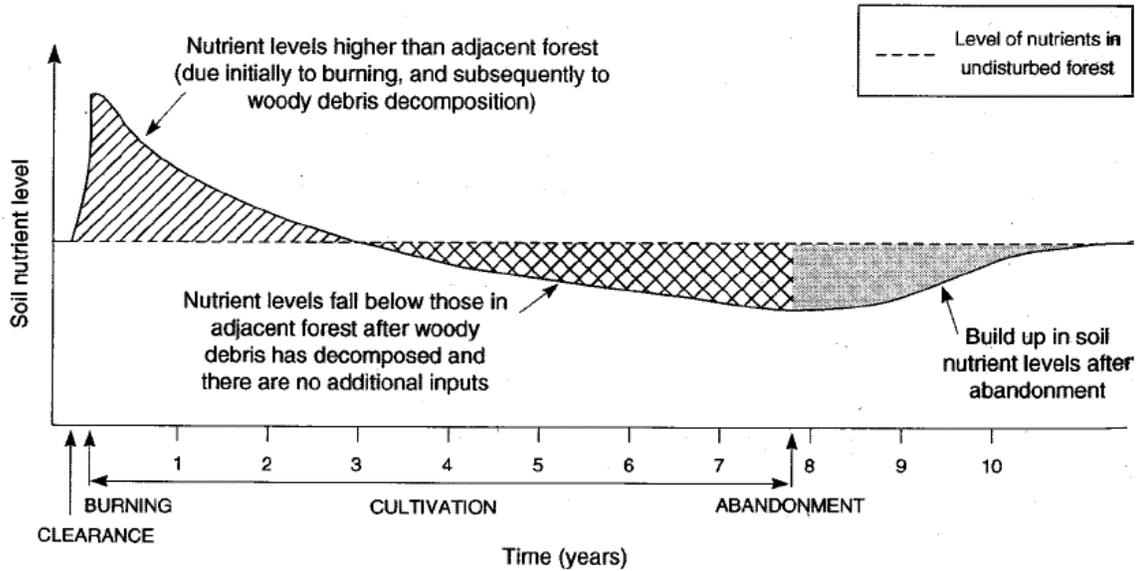Figure 3
A

B

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- 33 -
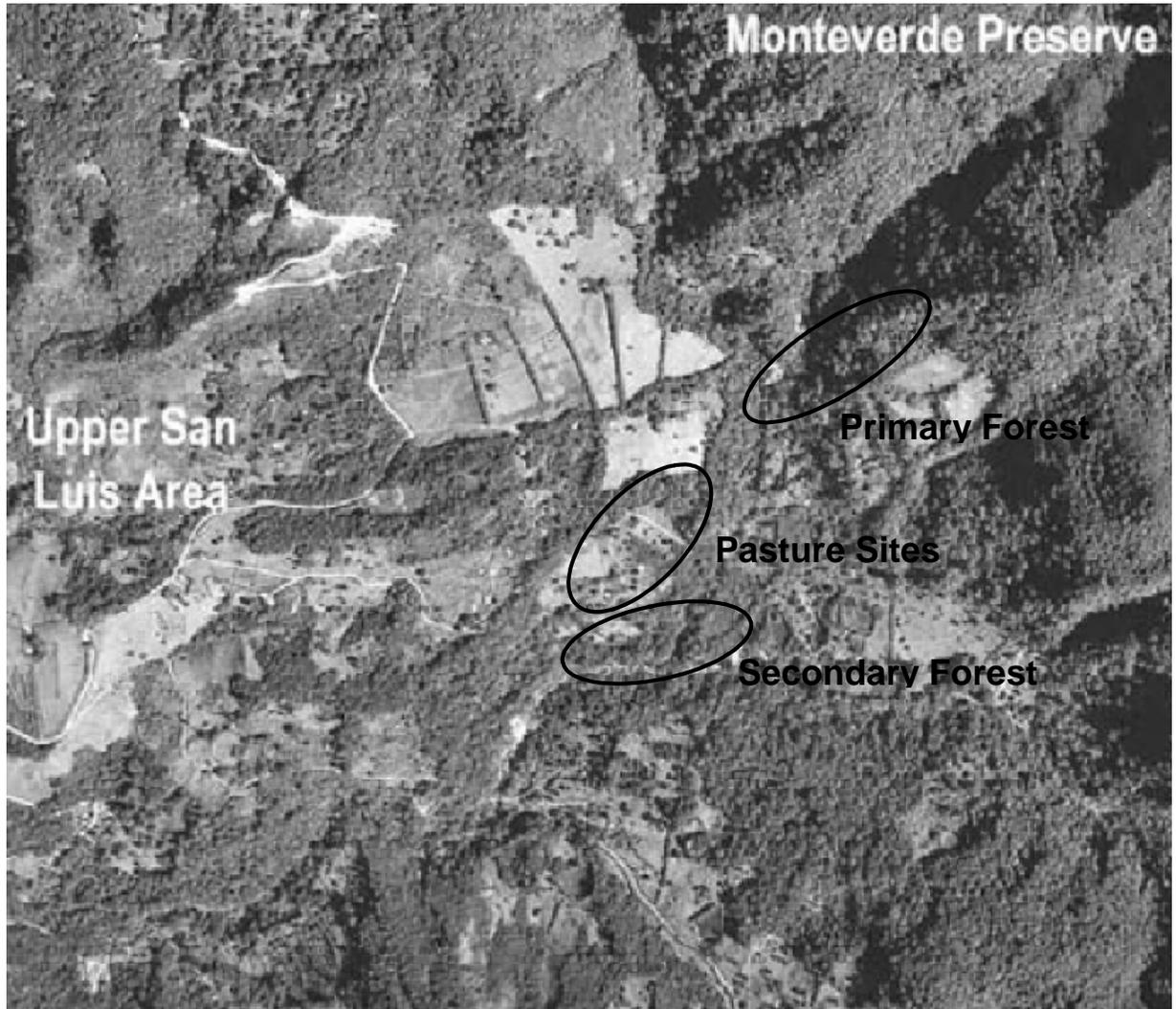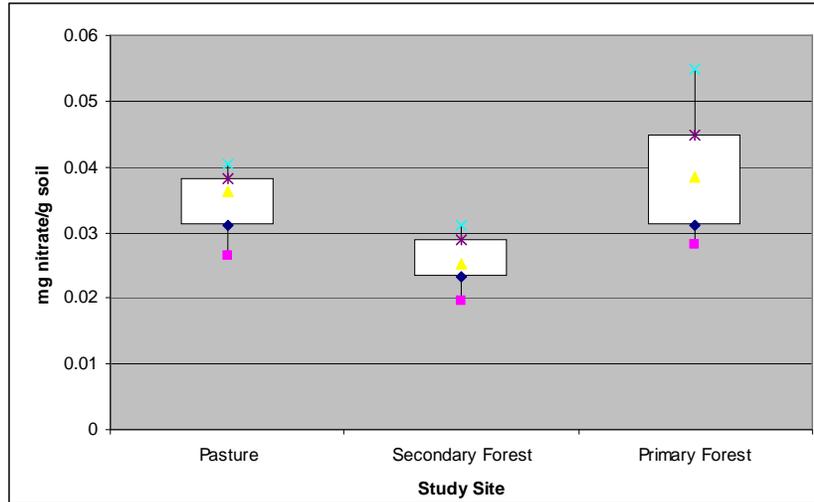
Figure 4
A

Reading, A.J., Thompson, R.D., Millington, A.C. 1995. Humid Tropical Environments. Blackwell Publishers Ltd.

B

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