

PATTERNS OF MINERAL ELEMENT RETRANSLOCATION IN FOUR
SPECIES OF TROPICAL MONTANE FOREST TREES IN MONTEVERDE,
COSTA RICA

by
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ABSTRACT

PATTERNS OF MINERAL ELEMENT RETRANSLLOCATION IN FOUR SPECIES OF TROPICAL MONTANE FOREST TREES IN MONTEVERDE, COSTA RICA

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Retranslocated nutrients (i.e. those moved out of plants prior to loss through litterfall) comprise a significant fraction of available nutrients in trees but this availability can differ by up to 50% or more among species. This high interspecific variation in nutrient return indicates that tree species differentially affect stand-level soil quality, as well as overall tree fitness. In this study, I investigated the amounts and dynamics of nutrient cycling of six elements in the foliage of four species of trees in the upper montane forest of Monteverde, Costa Rica, and how much of that nutrient capital was transferred to the soil via litterfall. For all species combined, as hypothesized, elements useful for tree growth were retranslocated—with relatively high retranslocation rates of P and K—while all other elements were transferred to the soil in the litterfall. At the species level, retranslocation efficiency was highly variable over time. Significant interspecific differences existed in N ($p=0.001$), P ($p<0.001$), K ($p<0.001$), Na ($p=0.002$), but no significant differences existed for Ca and Al. The retranslocation efficiencies of both N and P were in the lower range when compared to other cloud forests. Relative to other cloud forests, the high nutrient contents found in tree foliage in this study suggest nutrients at Monteverde may not be as limiting as those in other cloud forests. The low rate of retranslocation suggests these nutrients are being recycled into the soil freely. In the future, the need for a more complete understanding of cloud forest nutrient cycling and ecology across multiple scales, one in which broad generalizations can be rooted in sufficient data, present great challenges for ecologists.

TABLE OF CONTENTS

1. Introduction.....	1
2. Objectives and Hypotheses.....	6
3. Materials and Methods.....	7
4. Results.....	12
5. Discussion.....	14
6. Conclusions.....	19
7. Bibliography.....	21
8. Tables and Figures.....	24

LIST OF TABLES

Table 1: Leaf and litterfall content.....	24
Table 2: Cross-study comparison.....	25
Table 3: Mean retranslocation proficiency	26
Table 4: Mean retranslocation efficiency	27
Table 5: Mean seasonal retranslocation efficiency	28

LIST OF FIGURES

Figure 1: Mean annual rainfall.....	29
Figure 2: Map of Costa Rica and Monteverde.....	30
Figure 3: Picture of primary forest plot	31
Figure 4: Picture of secondary research plot.....	32
Figure 5: Mean mineral percent retranslocation efficiency	33
Figure 6: Temporal changes in retranslocation efficiency.....	34
Figure 7: Seasonal retranslocation differences	35

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1. INTRODUCTION

The pathways of mineral and nutrient fluxes through a forest are complex, and their loss or recycling depends to a large extent on their nutritional value to trees. Nutrients are captured and stored in the biomass of trees and used for biological processes, then released from the tree to be remineralized in the surrounding environment, and eventually used again as part of the biogeochemical nutrient cycle (Jordan 1985). Resorbed nutrients (relative to nutrients lost through litterfall) comprise a significant fraction of available nutrients in forests, but this availability can differ by up to 50% or more among species. This high intraspecific variation in nutrient return indicates that tree species differentially affect stand-level soil quality, as well as overall tree fitness. By documenting temporal patterns of nutrient return in litterfall, researchers can begin to understand interactions between tree species and soils in an evolutionary context (Binkley and Giardina 1998).

In this tree-soil nutrient feedback loop, litterfall is a major pathway for the return of organic matter and nutrients from aerial portions of the forest to the soil surface (Vitousek and Sanford 1986, Tanner et al. 1998a, Vilella and Proctor 1999). Most organisms are directly or indirectly dependent on the nutrients available in plant tissues deposited as litter, which account for 70% of all aboveground litter (Killingbeck 1996). However, nutrients lost in litterfall do not immediately benefit the plant that shed them because the litter must be decomposed, and the nutrients contained in that litter must be remineralized to become available for plant uptake. As these processes are not instantaneous, the

nutrients contained in litterfall must be, at least temporarily, considered as losses to the plant population (Chapin 1980, Jordan 1985, Berendse and Aerts 1987, Aerts and Berendse 1989, Aerts 1996, Killingbeck 1996).

Trees can compensate for these delays by a process called nutrient retranslocation in which nutrients are withdrawn from leaves prior to abscission and redeployed in developing tissues, such as leaves or reproductive structures such as seeds, or stored for later use, thus extending the mean residence time of nutrients in the plant (Wright and Westoby 2003). Retranslocation has been characterized as one of the most important strategies used by trees to conserve nutrients, which consequently influences competition, nutrient uptake, and productivity (Killingbeck 1996). Stored nutrients that become retranslocated are immediately available for plant use, allowing trees to react quickly to changes in their environment and remain productive during nutrient-limiting periods (Helmisaari 1992).

Retranslocation can be quantified in two distinct ways (Killingbeck 1996). Retranslocation “proficiency” is the absolute level to which nutrient concentrations are reduced in senesced leaves or litter. Retranslocation “efficiency” is a different (but complementary) index of nutrient conservation that measures the relative proportion of nutrients resorbed from senesced leaves. Proficiency values are a more definitive and objective measure of the degree to which evolution has acted to minimize nutrient loss, but efficiency values are more useful to measure both nutrient demand (green-leaf nutrient content) and nutrient withdrawal. Their complementary nature suggests that plants use

proficiency and efficiency in combination with one another for optimum nutrient conservation (Killingbeck 1996).

Retranslocation efficiency at a particular growth phase is subject to many variables, even within a species. In general, about 50% of leaf N and P can be recycled via retranslocation (Aerts 1996, Killingbeck 1996), but the retranslocation efficiency varies widely among species (Wright and Westoby 2003). For example, Aerts and Chapin (2000) documented that plants from all habitats can retranslocate <5% to 80% of foliar N, and 0-95% of foliar P. Evergreens have lower litter P concentrations than deciduous species, whereas N₂-fixers have higher litter N concentrations than non-N₂-fixers (Killingbeck 1996). Yet, patterns of retranslocation and their governing factors may be similar among species in the absence of interspecies competition for growth and crown structure, which occurs in mixed species stands (Fife et al. 2008).

The extent to which an element can be retranslocated depends on its physical properties, as well as its importance to the plant's nutrient requirements. Nitrogen, P, and K are relatively mobile, and are important for metabolism and growth, so they retranslocate the most efficiently (Fife et al. 2008). Nitrogen and P are considered limiting in most tropical environments—P is particularly limiting in lowland tropical rain forests (Townsend et al. 2007) and N most limiting in montane tropical forests (Tanner et al. 1998a), whereas K tends to be the most mobile nutrient and easily available relative to concentrations in soils and rainfall. Calcium is an important macronutrient for cell growth and functioning, but it is not easily retranslocated because it becomes immobilized in the cell walls and

other structural components of leaves (Salisbury and Ross 1992, Fife et al. 2008). Other elements such as Na are not biologically active, so they are usually retranslocated in insignificant quantities. In contrast to the other minerals, some elements such as Al are toxic to most plants, which either resist their uptake using physiological mechanisms in their roots and leaves, or reduce toxicity by sequestering them in vacuoles (Delhaize and Ryan 1995).

In addition to retranslocation, plants also use other mechanisms to increase their overall nutrient-use efficiency (Wright and Westoby 2003). Nutrient-use efficiency (NUE) is defined as the ratio of litterfall production per unit nutrient to the litterfall nutrient content (Knops et al. 1997). Evergreen plants increase their NUE by synthesizing leaves with a long leaf life-span, high leaf mass per area, low leaf nutrient concentrations and low photosynthetic capacity (Aerts 1996, Harrington et al. 2001, Wright and Westoby 2003, Fife et al. 2008).

Cloud forests are those that are frequently in direct contact with clouds (or fog), and receive by condensation a significant amount of water in addition to rainfall (Mai 1986). This frequent cloud cover influences the water balance as well as radiation and other climatological, ecological, and soil parameters (Mai 1986). Soils in cloud forests have relatively slow rates of decomposition and nutrient release (Jordan 1985). The slow rate of litter decomposition in cloud forests, relative to rates in tropical lowland forests, also has been attributed to low air and soil temperatures, lack of drying-rewetting cycles, a high degree of sclerophylly, and waterlogged soils (Nadkarni and Matelson 1992). In cloud forests, litter dynamics may be especially important because litterfall is the major

path of flux for macronutrients, and broadleaf evergreens are the dominant growth form (Vitousek and Sanford 1986). Plants are expected to minimize nutrient concentrations in leaves and maximize nutrient retranslocation from leaves before senescence in response to the slow remineralization of nutrients (Veneklaas 1991).

Compared to lowland forests, however, cloud forest trees may support foliage with higher nutrient concentrations due to the larger amounts of nutrients that enter the system via interception of precipitation, especially in the form of wind-blown mist (Nadkarni 1986, Vitousek and Sanford 1986, Clark et al. 1997), and from canopy organic matter from the epiphyte community, which reaches greatest abundance and diversity in cloud forests (Nadkarni 1986, Nadkarni et al. 2004).

To date, there has been extensive ecosystem-level research into forest nutrient cycling in a few cloud forests (e.g., Luquillo National Forest, Puerto Rico (Zou et al. 1995, Thompson et al. 2002)), but fewer ecosystem- or landscape-level studies exist for upper montane cloud forests. The montane forests of Monteverde, Costa Rica, have relatively high regional plant biodiversity within a narrow elevational zonation of habitats along upper mountain slopes, which make them especially interesting for nutrient cycling research. The area is characterized by an abundance of mosses, epiphytes and tree trunk climbers (Haber 2000). Gaps exist in our understanding of how cloud forest tree species react to the complex balance of biotic and abiotic factors in this environment. For example, are trees in this ecosystem nutrient-conservative as a result of nutrient deficiency? Or do they

show nutrient “leakage” that would indicate higher productivity on more fertile soils? In a previous study at Monteverde, the amounts of N, P and K transferred in litterfall to the forest floor were high compared to those reported from other tropical montane forests (Nadkarni and Matelson 1992), and fell more closely within the range reported for forests growing on alfisols and other moderately fertile tropical soils (Vitousek and Sanford 1986). This suggests trees in Monteverde are less conservative and have access to a larger nutrient pool than other trees in cloud forests. If this is true, then the retranslocation efficiency of macronutrients might be relatively lower than that in other cloud forests. This is the first study to observe the interspecies retranslocation variation of dominant trees in Monteverde that can be compared to other cloud forests. This comparison may aid future researchers in understanding the relative importance of roles of cloud forest tree species in nutrient cycling, soil development and tree-soil interactions.

2. OBJECTIVES AND HYPOTHESES

In this study, I investigated the amounts and dynamics of nutrient cycling in the foliage of four species of trees in the upper montane forest of Monteverde, Costa Rica, and how much of that nutrient capital is transferred to the soil via litterfall. The primary objectives of this study were to: i) investigate the retranslocation dynamics of six foliar nutrients in three primary forest tree species, and one secondary forest species; and ii) compare these data to retranslocation studies in other ecosystems. I hypothesize that:

- Foliage and litterfall nutrient content will be relatively higher than those in other cloud forests;
- the nutrients most critical for plant productivity (N, P, K) will be retranslocated most efficiently;
- elements not useful for plant productivity will not be retranslocated;
- the elemental nutrient retranslocation efficiency will occur in the order of $K > P > N > Na > Al > Ca$;
- retranslocation efficiency will be lower than for other cloud forests;
- each tree species observed in this study will exhibit different retranslocation efficiencies;
- seasonality should have an effect on retranslocation efficiency, but to variable degrees in each species.

3. MATERIALS AND METHODS

STUDY SITE—The montane cloud forests of Monteverde are located in the Intertropical Convergence Zone (a zone of low pressure associated with intense solar radiation and heating that follows the seasonal migration of the sun), at an altitude (1460 m) where orographic precipitation and fog play major roles in precipitation, nutrient deposition, and plant productivity. The tropical montane forests at Monteverde are in a relatively narrow altitudinal zone with frequent cloud cover during much of the year. Solar radiation and evapotranspiration are

limiting factors for growth, and precipitation is enhanced by canopy interception of cloud water. Compared to trees in lower altitude tropical moist forests, trees in the tropical montane cloud forests at Monteverde tend to be suppressed by wind and frequent storms, with dense and relatively short, gnarled trunks, compact crowns and small, thick leaves. Epiphytes are abundant and diverse, and soils are frequently wet and highly organic (Nadkarni et al. 2000).

The climate of Monteverde is transitional between lowland and montane sites in terms of ambient air temperature, and between the Caribbean and Pacific sides of Costa Rica in incident solar radiation and amounts and seasonality of precipitation (Clark et al. 2000) (Fig. 1). Mean annual temperature at Monteverde (1460 m) is approximately 18.5° C, with a minimum of 9° C and a maximum of 27° C. From 1956 to 1995, mean annual precipitation depth at 1460 m was 2519 mm, but actual wet deposition is probably much higher because of the prevalence of wind-driven mist and fog that occurs throughout the year (Nadkarni and Matelson 1992).

The climate of Monteverde can be roughly divided into three seasons (Fig. 1). The misty-windy season (November-January) is characterized by advective cloud cover and precipitation dominated by mist borne by the northeast tradewinds. During the dry season (February-April), advective cloud water and mist deposition occur, but measurable precipitation is low; bouts of strong tradewinds abate at the end of this season. The wet season (May-October) is characterized by low windspeeds and convective precipitation, much of which originate in the Pacific-side lowlands.

Field research was conducted from June 19, 1990, to June 25, 1992, in the Puntarenas Province of the Monteverde Cloud Forest Preserve (MCFP) of Costa Rica (10° 18' N, 84° 48' W). This life zone occurs on a restricted area of the upper Pacific slope, extending from the lower part of the MCFP above Monteverde to Las Nubes, including the upper Río Negro and Río Chiquito drainages (Fig. 2). The study area was in tropical lower montane moist forest (1480 m), described as a leeward cloud forest (Lawton and Dryer 1980). The continually moist soils are derived from volcanic rhyolites and are classified as Typic Dystrandept. These volcanically derived soils are considered to be fairly fertile, recently deposited, and share characteristics with other tropical cloud forests at similar elevations (Vance and Nadkarni 1990).

In April 1987, a 4-ha study area was established within the primary forest of the research area of the MCFP (Fig. 3). This forest is composed of trees that are 15-30 m in height, with a well-developed subcanopy. Tree density was 555 ha⁻¹, with a reverse-J diameter distribution. Tree species composition, density, basal area and structural characteristics are reported in Nadkarni et al. (1995). The three most common families of trees in this forest are Moraceae, Lauraceae, Sabiaceae, respectively (Lawton and Dryer 1980). Species from these families include *Ficus tuerckheimii*, *Ocotea tonduzii* and *Meliosma vernicosa*.

In 1989, a 1-ha research plot was established in the adjacent secondary forest, which is also within the research area of the MCFP. In the early 1960s, the area was cleared for cattle pasture, but was left to regrow because the area was too cold and wet to be productive for agriculture. In this study, all trees in the plot

were measured, identified to species, and tagged. This forest is strongly dominated (91%) by a single tree species (*Conostegia oerstediana*, Melastomataceae), with a density of 1,124 trees ha⁻¹ and a size class distribution typical of early successional montane forests (Fig. 4). The forest supports a well-developed understory, with saplings of some of the primary forest trees from the adjacent primary forest present. Additional details about study plots, precipitation, structural characteristics and floristic composition are found in Nadkarni et al. (1995) and in Nadkarni and Wheelwright (2000).

TREE SELECTION—Nine trees in the largest size class (>80 cm dbh) in the primary study plot were randomly chosen for sampling live foliage of primary forest trees. These included three trees for each of the species *Ficus tuerckheimii*, *Ocotea tonduzii* and *Meliosma vernicosa*. Three trees in the secondary forest plot (all *Conostegia oerstediana*) were also sampled. The sample trees were rigged and climbed with single-rope mountain-climbing methods (Perry 1978, Nadkarni 1988).

FOLIAGE—Foliage was collected for foliar analysis from the same 12 sample trees at intervals of 20 to 68 days, generally each month for year 1, and every 2-3 months after that, for a total of 23 collections dates. For each of the four species, three individual trees per species (N=3) were sampled at each harvest. Live foliage was collected from at least three locations within accessible areas of the crowns of the sample trees. Leaves that appeared to have emerged recently were classified as immature, indicated by light green color and proximity to bud,

were not taken. Leaves were bagged separately by tree, dried, processed and analyzed for nutrients as described below.

At the same time, a sample of litterfall leaves (15-35 leaves) was collected from under each of these trees, from mesh surfaces (0.5 m x 0.5 m) installed on the forest floor to differentiate new from old fallen leaves. Any visible frass or detritus was removed from leaf surfaces. Foliage and litterfall were dried at 60° C to constant weight (24 to 48 h), ground, and analyzed. The mean nutrient concentration was calculated by averaging the nutrient concentrations of tissue from the individual sample trees by species for each time interval.

NUTRIENT ANALYSIS—Foliage was analyzed for five macronutrients (K, P, N, Na, Ca) and one micronutrient (Al). Nutrient analysis of plant and soil material was done at Micro-Macro International, Inc. analytical laboratory (Athens, Ga.). Plant tissue was prepared by weighing a 0.5 g sample into a porcelain crucible and ashing at 500° C for four hours. The ash was dissolved in 30% aqua regia, and then the digest assayed by ICP with Cd as an internal standard. A LECO Nitrogen Determinator was used for N in plant tissue. A 0.25 g sample was placed into an induction furnace, and the N was reduced to N₂, which was measured by thermal conductivity. Nutrient content is expressed in mean percent of total leaf dry weight except for the micronutrient Al, which is expressed in parts per million (ppm) because of its low foliar concentrations.

DATA ANALYSIS—Missed collections were treated as an “NA” and made up >4% of the total calculations. Following Veneklaas (1991), retranslocation efficiency was calculated by dividing the difference between elemental

concentrations of live foliage and litterfall by the concentration of that element in live foliage:

$$\text{Retranslocation Efficiency} = [(\text{live foliage-litterfall})/\text{live foliage}] * 100$$

Analysis focused on N, P and K due to their importance to foliage production. Data were confirmed to be normally distributed with a Shapiro-Wilk test. Statistical analyses were performed using R (Free Software Foundation, Boston, Mass., version 2.6.2). Comparisons of retranslocation efficiency among tree species, nutrients, and seasonality used a one-way ANOVA test for assessing differences of means; pair-wise comparisons of species and nutrients used the student t-test (with Bonferroni adjustment) for assessing differences of means; correlation analysis used the Spearman Rank Test.

4. RESULTS

LIVE FOLIAGE AND LITTER CONTENT—significant differences existed in foliar element concentrations between species in green-leaf and litterfall nutrient content, particularly for Na, Ca, and Al (Table 1). The most limiting macronutrients, N and P, however, showed less interspecies variability. Phosphorus and Na showed low nutrient content variability. The high foliar Al concentration of *Conostegia* is characteristic of the family Melastomataceae (Delhaize and Ryan 1995, Jansen et al. 2002). As hypothesized, the values for live foliage and leaf litter for both N and P were in the upper range when compared to other cloud forests (Table 2).

RETRANSLOCATION PROFICIENCY—Species demonstrated varying degrees of nutrient proficiency (Table 3). *Meliosma* had the lowest observed litterfall nutrient content. *Conostegia* consistently showed the lowest mean proficiency, although other species showed a lower absolute nutrient proficiency in litterfall (Table 3).

RETRANSLOCATION EFFICENCY—For all species combined, the order of retranslocation efficiency was $K > P > N > Na > Al > Ca$ (Fig. 5). As hypothesized, elements useful for tree growth were retranslocated with relatively high rates for P and K, whereas all other elements were transferred in the litterfall. Mean retranslocation efficiency differed by element ($p < 0.001$; Fig. 5). The high standard errors for Na and Al (Fig. 5) resulted from isolated pulses of mineral deposition in the litterfall, relative to green-leaf nutrient supply. These outliers were included in the analysis because each data point is an average of multiple leaf samples and not an individual sample susceptible to human input error. The values for the retranslocation efficiency of both N and P were in the lower range when compared to other cloud forests (Table 2).

Mean interspecific retranslocation efficiency was highly variable (Table 4). Among the macronutrients, K was the most variable. Variation was mostly higher for the other elements. *Ficus* exhibited high Na variation; Al variation was consistently high, except for *Conostegia*. Significant interspecific differences existed in N ($p = 0.001$), P ($p < 0.001$), K ($p < 0.001$), Na ($p = 0.002$), but no significant differences existed for Ca and Al.

Species also showed markedly different patterns of mean retranslocation efficiency over time (Fig. 6). There were strong temporal correlations in N, P, and K retranslocation efficiency, with a significant relationship (Spearman $r > 0.5$) between N and P (Spearman $r = 0.64$; $p < 0.001$), and K and P (Spearman $r = 0.80$; $p < 0.001$), but not K and N (Spearman $r = 0.46$; $p < 0.001$).

The effect of seasonality on retranslocation efficiency was negligible when all three samples were combined (Fig. 7) and at the species level (Table 5). There were no significant seasonal differences ($\alpha < 0.05$) in retranslocation efficiency when sampling was combined for N, P, and K, or among any of the tree species in this study. However, retranslocation efficiency did increase from the dry to wet seasons (N, +3.6%; P, +3.7%; K, +1.6%) with the exception of K, which peaked in the misty season and was greater than any other seasonal macronutrient retranslocation.

5. DISCUSSION

At the ecosystem level, this study showed that the minerals most needed for tree nutrient requirements (N, P, K) are those that are most readily retranslocated, while all other minerals are transferred from the tree at higher rates via litterfall. This is because most soil nutrients taken up by trees are used in annual production of foliage, which serves as a reservoir of reusable nutrients (Fife et al. 2008). Potassium is the most mobile nutrient and was the most readily retranslocated. Phosphorus was retranslocated almost as much as K, and

significantly more than N, perhaps indicating P is a limiting nutrient at this site. For all other elements, no retranslocation was observed.

Many studies have suggested P is more limiting than N in tropical environments (Vitousek 1982, 1984, Vitousek and Sanford 1986), but these studies are generalizations based on lowland tropical forests growing on relatively older, highly weathered clay soils, e.g., oxisols and ultisols (Tanner et al. 1998b). In contrast, the montane soils at Monteverde are considered to be mostly alfisols and recently deposited andisols (Vance and Nadkarni 1990). In such soils, N is thought to limit net primary productivity due to an elevationally constrained lower mineralization rate. In contrast, P availability is high as fresh minerals weather, but decreases over time due to leaching, occlusion by secondary minerals, and the formation of recalcitrant soil organic matter (Tanner et al. 1998b, Harrington et al. 2001). I found higher foliar N (a potential index of nutrient availability) than several other sites, although the N:P ratio was not higher than other similar tropical localities (Fassbender and Grimm 1981, Grubb and Edwards 1982, Veneklaas 1991, Nadkarni and Matelson 1992); Table 2). The contradiction between the high P retranslocation efficiency found in this study and potentially high P content in the soil at Monteverde may indicate retranslocation efficiency is not a perfect measure of soil fertility (Killingbeck 1996) and does not differ according to site nutrient status (Delarco et al. 1991, Aerts 1996, Wright and Westoby 2003), thus making it a poor indicator of nutrient availability.

Senesced-leaf nutrient concentrations (retranslocation proficiency) are a much more accurate indicator of site fertility (Killingbeck 1996, Wright and

Westoby 2003). The relatively high values of N and P in this study suggest that trees at this site are relatively nutrient-rich and have access to a larger nutrient supply (partially from allochthonous sources) than other cloud forests (Nadkarni and Matelson 1992, Nadkarni and Solano 2002). These trees are less nutrient-conservative, and as such, nutrients are not held as tightly by the trees. This would allow the nutrients to recirculate into the environment (Harrington et al. 2001, Townsend et al. 2007).

Differences in species retranslocation may have a functional significance that helps determine the present performance, and likely the future species composition, of a community. There exists a two-way connection between the species diversity present in a community and the interactions occurring among those species (Hacker and Gaines 1997). The relatively low overall mean retranslocation rates may indicate trees in this study were not as overall productive as those in other comparable studies. Retranslocation has been linked to enhancing tree productivity by providing nutrient supply to apical growing points in shoot growth, rather than linked to nutrient supply (Nambiar and Fife 1991, Fife et al. 2008). Younger gap-colonizing tree species in rapid production of biomass tend to have higher retranslocation rates than mature forests with competitively suppressed trees (Nambiar and Fife 1991). Although tree age was not measured in this study, trees in the primary plot were all >80 cm dbh and considered mature. In contrast, retranslocation rates of N, P, and K in *Conostegia* were much higher than those in the primary plot (Table 3). The quick-growing *Conostegia* is Monteverde's dominant gap-colonizing tree species at this altitude.

The *Conostegia* trees that were sampled were much younger (<50 years old) than those in the primary plot, and presumably were not as suppressed by competition and limited in productivity by age. This implies that retranslocation efficiency is a better indicator of productivity than nutrient conservation efficiency and may explain differences in site results.

In this study, high variation in leaf nutrient proficiency and retranslocation efficiency over time and between species hindered the detection of uniform temporal patterns of retranslocation. Nutrient retranslocation tended to be greatest during the wet and misty seasons (Fig. 7), but no significant seasonal differences were found when all three samples were combined. No seasonal signal is qualitatively discernable, although there is an apparent coupling between N, P and K (Fig. 6). The lack of a seasonal signal may have been due to the length of this study and short-term variance in weather patterns. However, at least one review study has found seasonal controls on N:P values differing by 25% between wet and dry seasons (Townsend et al. 2007), and that study also concluded that the most striking feature of the 150-tree species data set was high variation at the species level. This study also showed a 25% difference (N:P=0.48 in wet season; N:P=.36 in dry season) between seasons and high interspecific variation, indicating that some seasonal effect may be present but was not statistically significant.

The variance in retranslocation proficiency may be due to multiple constraints in biochemical and biophysical processes during leaf aging, nutrient transformation, and phloem loading (Hattenschwiler et al. 2008). The existence of

high interspecific variation in this study and others also suggest that tree species use a wide range of nutrient-conservation strategies at the levels of green-leaf functioning, plant nutrient acquisition, and nutrient retranslocation physiology, and to overcome environmental constraints (Hattenschwiler et al. 2008). This indicates nutrient retranslocation is but one adaptive strategy of nutrient conservation and can be influenced by other species-specific adaptations that conserve nutrients by other means. This contradicts commonly held generalizations on plant nutrient economies based upon broad functional groups, and indicates that ecosystem-scale selection is of minor relevance for evolution of plant nutrient-use strategies (Hattenschwiler et al. 2008).

Cloud forests are complex in their nutrient cycling regimes and need further study. Relative to other cloud forests, the high contents of nutrients in tree foliage found in this study suggest nutrients at Monteverde may not be as limiting as those in other cloud forests, and the low rate of retranslocation suggests these nutrients are being recycled into the soil. However, the feedback loop between nutrient deposition and site fertility is still not fully understood (Binkley and Giardina 1998, Townsend et al. 2007). Interactions between trees and their soil may increase tree fitness, may indirectly benefit the tree's fitness, or may not optimize a tree's fitness at all. The broad generalizations that often characterize tropical forests as N-rich, P-poor environments still rely upon relatively small amounts of data and may mask critical variation in the extent and nature of nutrient limitation at multiple scales. In the future, longer-term surveys of the

foliage nutrient content and their associated retranslocation patterns of multiple species will be useful.

Nutrient cycling studies have many implications for understanding nutrient dynamics. The observed high variation in litter chemistry implies a highly heterogeneous litter input to the soil at small spatial scales (Hattenshwiler et al. 2008). The wide range of variation in litter (as well as differences in carbon quality) may affect higher trophic levels of the decomposer community with varying constraints, depending on the local species composition of the litter. In the future, broad generalizations that are rooted in sufficient data will result in a more complete understanding of cloud forest nutrient cycling across multiple spatial scales.

6. CONCLUSIONS

In this study, the amounts of nutrients being retranslocated in tree species in Monteverde were complex at multiple scales, but they did follow some predictable patterns. As hypothesized, at the stand level, foliage and litterfall N and P content were higher than those in other cloud forests, indicating Monteverde is a relatively nutrient-rich cloud forest. Nutrients needed for growth were retranslocated, while elements not useful for plant productivity were deposited in litterfall. However, since Monteverde is relatively nutrient-rich, these nutrients were not retranslocated as efficiently as in other cloud forests. At the species level, retranslocation efficiency was highly variable, indicating litterfall nutrient return is variable at small spatial scales. However, seasonality did not

have a great effect as hypothesized. This might be due to the shortness of the study's length or variation at the species level.

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8. TABLES AND FIGURES

Table 1: Mean percent of total leaf dry weight (+/-SE) in live leaves and leaf litter. Al is expressed in ppm because it is a micronutrient. Values were compared by species (vertically) and different letters do differ at alpha=0.05.

		live foliage				
Genre	N	P	K	Na	Ca	Al
<i>Ficus</i>	1.73 (0.09)a	0.15 (0.01)a	2.18 (0.14)a	0.07 (0.01)a	1.57 (0.10)a	130.45 (24.46)a
<i>Meliosma</i>	1.81 (0.10)a	0.12 (0.01)b	0.97 (0.15)b	0.38 (0.03)b	0.77 (0.04)b	65.73 (6.83)b
<i>Ocotea</i>	2.22 (0.03)b	0.12 (0.01)b	1.01 (0.05)b	0.27 (0.01)c	0.77 (0.04)b	83.74 (8.06)b
<i>Conostegia</i>	2.01 (0.06)c	0.14 (0.01)a	1.03 (0.05)b	0.14 (0.01)d	2.02 (0.06)c	7157.91 (227.06)c
		leaf litter				
Genre	N	P	K	Na	Ca	Al
<i>Ficus</i>	1.65 (0.09)a	0.11 (0.01)a	1.27 (0.08)a	0.08 (0.01)a	1.88 (0.06)a	153.18 (35.80)a
<i>Meliosma</i>	1.73 (0.11)a	0.11 (0.01)a	0.82 (0.15)b	0.33 (0.03)b	0.88 (0.03)b	61.64 (12.36)b
<i>Ocotea</i>	2.01 (0.04)b	0.11 (<0.01)a	0.86 (0.04)b	0.25 (0.01)c	0.94 (0.03)c	65.30 (16.51)b
<i>Conostegia</i>	1.59 (0.05)a	0.08 (<0.01)b	0.60 (0.02)c	0.14 (0.01)d	2.13 (0.05)d	6106.26 (95.07)c

Table 2: Cross-study comparison of mean percentage of nutrients in green-leaf and litterfall content for multiple cloud forests; a) Fassbender and Grimm 1981; b) Grubb and Edwards 1982; c) Veneklaas 1991; d) Nadkarni and Matelson 1992; e) the current study.

Site	Elements (%)				Retranslocation efficiency (%)	
	N		P		N	P
	Live foliage	Leaf Litter	Live foliage	Leaf Litter		
a) Venezuela	1.74	1.20	0.08	0.06	31	25
b) Papua New Guinea	1.32	1.30	0.09	0.07	2	22
c) Colombia	1.8	1.10	0.10	0.06	38	40
d) Costa Rica	1.97	1.47	0.14	0.08	25	42
e) This study	1.94	1.75	0.13	0.10	10	25

Table 3: Mean retranslocation proficiency for all sampling dates of tree species (mean) and the lowest observed litterfall nutrient content (low). Standard errors of the nutrient content mean are also provided. Quantities are mean percent of total leaf dry weight.

Genre	N			P			K		
	Mean	Low	SE	Mean	Low	SE	Mean	Low	SE
<i>Ficus</i>	1.65	1.13	0.09	0.11	0.06	0.01	1.27	0.81	0.08
<i>Meliosma</i>	1.73	1.02	0.10	0.11	0.04	0.01	0.82	0.24	0.15
<i>Ocotea</i>	2.01	1.62	0.04	0.11	0.07	<0.01	0.86	0.40	0.04
<i>Conostegia</i>	1.59	1.11	0.05	0.08	0.04	<0.01	0.06	0.040	0.02

Table 4: Mean percent retranslocation efficiency by species (+/- SE) for all sampling dates combined. Values were compared by species (vertically) and same letters do not differ at alpha=0.05.

Genre	N	P	K	Na	Ca	Al
<i>Ficus</i>	4.15 (2.36)a	26.17 (2.22)a	40.30 (2.50)a	-50.66 (23.38)a	-21.62 (3.77)a	-70.63 (39.46)a
<i>Meliosma</i>	4.10 (2.80)a	12.96 (3.31)b	13.13 (5.50)b	11.23 (6.79)b	-16.79 (5.47)a	-9.44 (24.44)a
<i>Ocotea</i>	8.90 (2.08)a	10.52 (4.17)b	10.92 (5.44)b	8.61 (3.44)b	-28.12 (7.7)a	4.17 (27.07)a
<i>Conostegia</i>	19.52 (3.09)b	40.56 (4.06)c	37.74 (4.21)a	1.33 (4.32)c	-7.29 (4.00)a	13.24 (2.42)a

Table 5: Mean retranslocation efficiency (+/- SE) of nutrients grouped by season.

No significant seasonal differences of means were found among species.

Genus		N	P	K
<i>Ficus</i>	W	7.71 (2.52)	28.92 (3.40)	38.33 (3.96)
	M	-0.24 (7.07)	20.57 (4.82)	47.94 (2.75)
	D	-0.04 (5.19)	24.39 (2.81)	39.14 (3.76)
<i>Meliosma</i>	W	9.09 (3.47)	12.72 (4.18)	9.77 (6.96)
	M	-4.71 (11.47)	25.69 (13.75)	45.52 (16.30)
	D	-2.32 (2.10)	7.12 (4.12)	4.23 (5.96)
<i>Ocotea</i>	W	9.39 (3.19)	13.49 (6.15)	14.07 (8.75)
	M	14.19 (4.60)	16.54 (10.77)	17.87 (9.78)
	D	4.30 (1.96)	0.05 (4.41)	-0.53 (5.12)
<i>Conostegia</i>	W	17.27 (4.52)	39.86 (6.24)	38.42 (6.30)
	M	18.92 (5.32)	35.36 (8.04)	23.67 (9.98)
	D	24.81 (6.01)	45.54 (6.38)	45.63 (3.70)

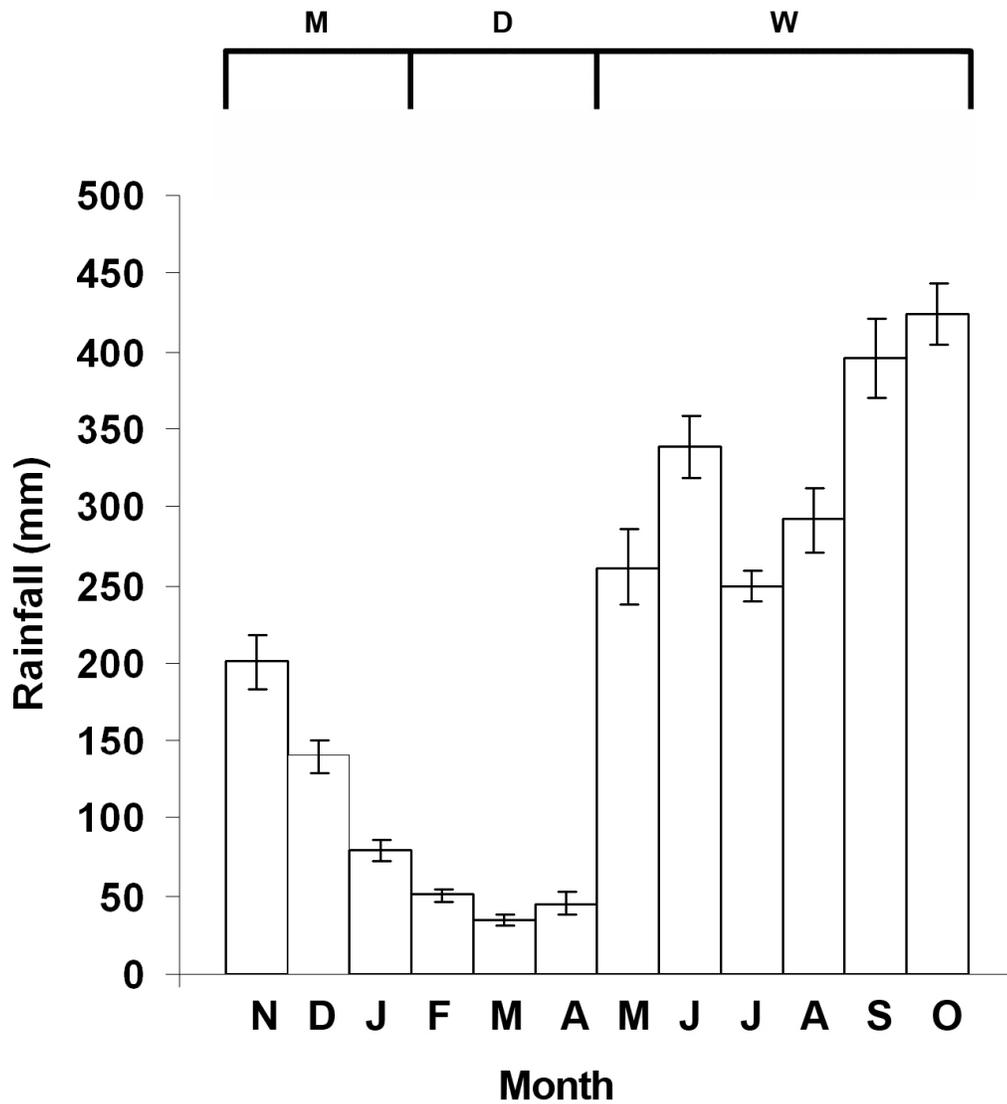


Figure 1. Mean annual rainfall (mm) with standard error margin (SE) at Monteverde Forest Preserve from 1956-1995. Seasons: misty (M), dry (D), wet, (W). Data collected by John Campbell.

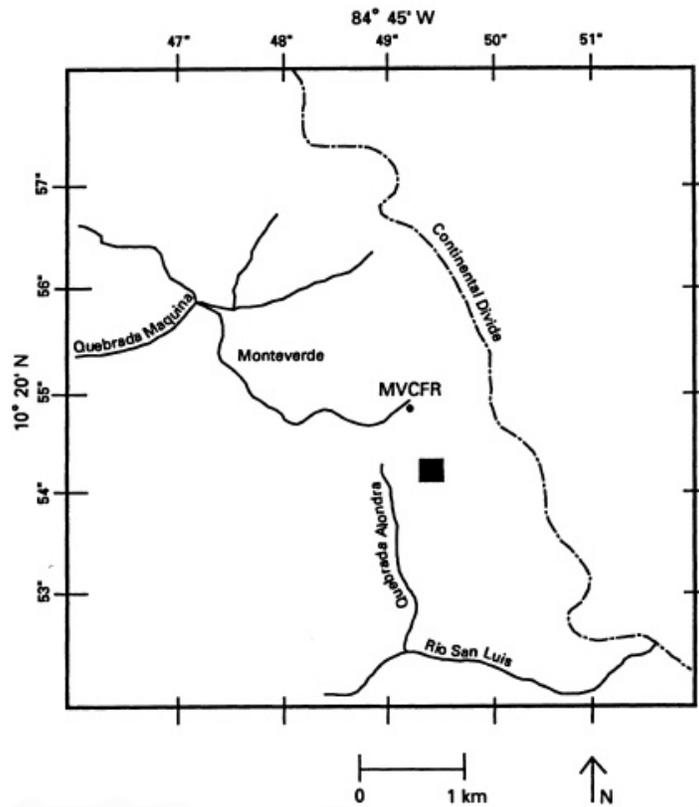


Figure 2: Map of Costa Rica (opposite page) and study site, Monteverde Cloud Forest Reserve (MVCFR). Small circle indicates the field station of the Tropical Science Center. Black square represents the 4-ha study site.



Figure 3: The primary forest research plot located in a tropical lower montane forest (1480 m)



Figure 4: *Conostegia oersediana* in the secondary forest research plot located in tropical lower montane forest.

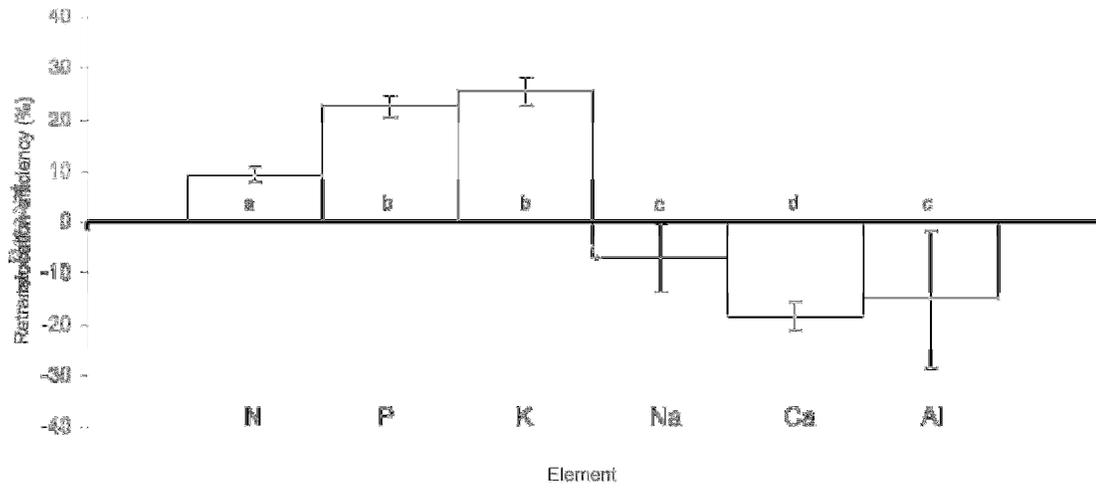


Figure 5: Mean mineral percent retranslocation efficiency (+/- SE) for all tree species and all sample dates combined. Values were compared and same letters do not differ at alpha=0.05.

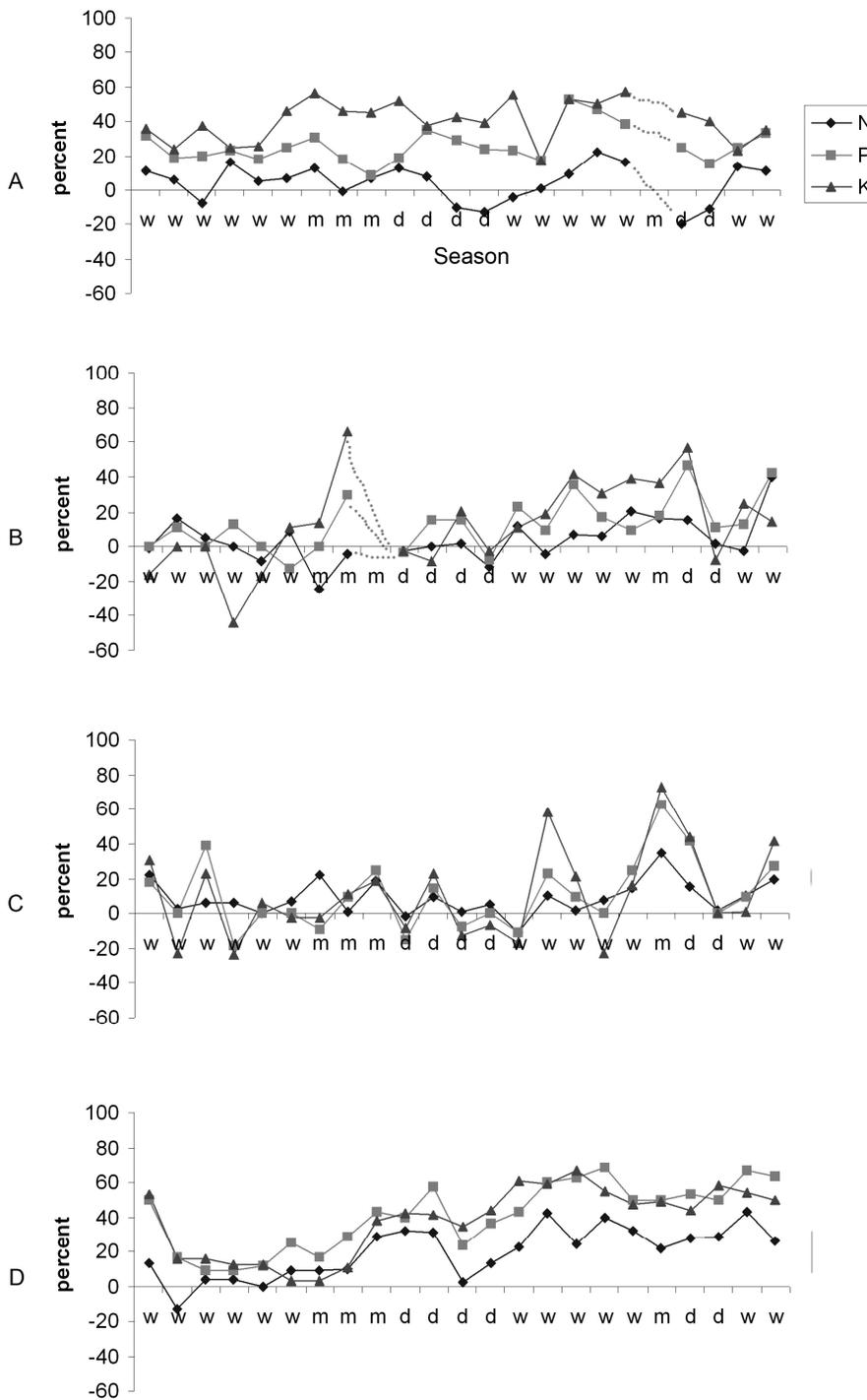


Figure 6: Temporal changes in mean retranslocation efficiency for Nitrogen, Phosphorus, and Potassium for four species A) *Ficus tuerckheimii*, B) *Meliosma vernicosa*, C) *Ocotea tonduzii*, D) *Conostegia oerstediana*; W=wet season, M=misty-windy season, D=dry season.

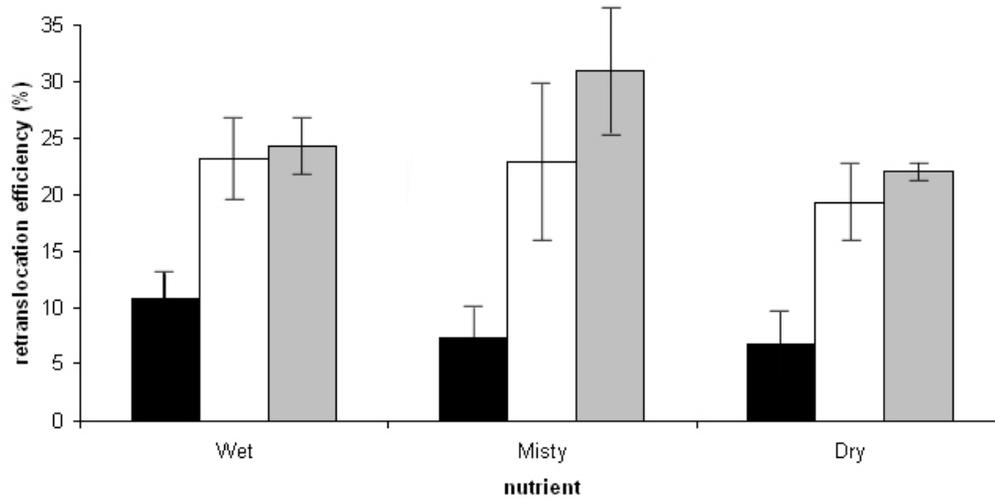


Figure 7: Seasonal efficiency (+/-SE) for all species combined. No significant seasonal differences of means were found among nutrients.