

# Tree species identity and interactions with neighbors determine nutrient leaching in model tropical forests

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**Abstract** An ecosystem containing a mixture of species that differ in phenology, morphology, and physiology might be expected to resist leaching of soil nutrients to a greater extent than one composed of a single species. We tested the effects of species identity and plant-life-form richness on nutrient leaching at a lowland tropical site where deep infiltration averages  $>2$  m year<sup>-1</sup>. Three indigenous tree species with contrasting leafing phenologies (evergreen, dry-season deciduous, and wet-season deciduous) were grown in monoculture and together with two other life-forms with which they commonly occur in tropical forests: a palm and a giant, perennial herb. To calculate nutrient leaching over an 11-year period, concentrations of nutrients in soil water were multiplied by drainage rates estimated from a water balance. The effect of plant-life-form richness on retention differed according to tree species identity and nutrient. Nitrate retention was greater in polycultures of the dry-season deciduous tree species (mean of 7.4 kg ha<sup>-1</sup> year<sup>-1</sup> of NO<sub>3</sub>-N lost compared to 12.7 in monoculture), and calcium and magnesium retention were greater in polycultures of the evergreen and wet-season deciduous tree species. Complementary use of light led to intensification of soil exploitation by roots, the main agent responsible for enhanced nutrient retention in some polycultures. Other mechanisms included differences

in nutrient demand among species, and avoidance of catastrophic failure due to episodic weather events or pest outbreaks. Even unrealistically simple multi-life-form mimics of tropical forest can safeguard a site's nutrient capital if careful attention is paid to species' characteristics and temporal changes in interspecific interactions.

**Keywords** Complementarity · Ecosystem functioning · Life-form richness · Nutrient retention · Phenology

## Introduction

Of all the services rendered to society by terrestrial ecosystems, perhaps none are of greater long-term importance than maintenance of soil fertility and water quality. Vegetation protects soil by reducing erosion and retaining nutrients that might otherwise be lost via deep infiltration. This process is of particular importance in the humid tropics, where heavy rainfall can lead to rapid loss of nutrient capital, especially after disturbance (Parker 1985; Williams and Melack 1997; Bigelow et al. 2004; Markewitz et al. 2006). Some species-rich systems have been observed to resist leaching better than species-poor systems (Ewel et al. 1991; Tilman et al. 1996), but the predictability and magnitude of plant identity and diversity effects on nutrient retention are poorly quantified. Here, we compare nutrient retention over an 11-year period among tree monocultures and mixtures of life-forms in a wet tropical climate, and we explore some of the mechanisms and processes that account for differences observed.

Confirmation of early findings of a positive, asymptotic relationship between plant species richness and nutrient retention (Tilman et al. 1996) has been elusive. Hooper and Vitousek (1998), working with plants representing four

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functional groups, did not detect differences in  $\text{NO}_3$  losses between diverse and simple treatments. Scherer-Lorenzen et al. (2003) measured  $\text{NO}_3$  losses from random assemblages of up to 16 species (grasses and forbs) and found that increased species richness decreased leaching primarily in the presence of N-fixing legumes. And Erickson et al. (2008), who compared post-fertilization N losses from fast-growing, monospecific turf and assemblages of 12 slower-growing species, found that the diverse systems lost significantly more N than did the turf. Clearly, there is weak ability to predict when enhanced plant species richness may augment nutrient retention, but the prevalence of such effects on another ecosystem functional property, productivity (Hooper et al. 2005), suggests that such effects exist.

Root systems are an obvious if technically challenging place to seek attributes that may be linked to effects of plants on nutrient retention. As a rule, increased root biomass is associated with increased nutrient retention (Scherer-Lorenzen et al. 2003), but spatial placement of roots is also likely to be important, and uptake of nutrients from different places in the soil profile results in complementarity (McKane et al. 1990; Mamolos et al. 1995; Fargione and Tilman 2005). Other root-related mechanisms include seasonal differences in timing of nutrient uptake (Stevens and Carson 2001), or use of different chemical forms of an essential nutrient (McKane et al. 2002). Some measure of root attributes is likely to enter into any useful predictive scheme for plant composition and nutrient retention.

Few studies of plant species or life-form diversity and nutrient retention, whether employing randomly assembled or intentionally contrived mixtures, have measured rates of nutrient loss (Schlöpfer and Schmid 1999). Among leaching studies on microcosms (Naeem et al. 1995), semi-natural grasslands (Tilman et al. 1996; Hooper and Vitousek 1998; Scherer-Lorenzen et al. 2003), crop simulation models (Schlöpfer and Erikson 2001), and turf (Erickson et al. 2008), only the grassland study by Scherer-Lorenzen et al. (2003) included estimates of rates of downward flux of water. Leaching estimates in the other papers were based on concentrations of nutrients in capillary soil water or collection of leachate beneath roots or in pots. Estimates of nutrient loss obtained in this way involve considerable assumptions and large uncertainty. Direct measurement of nutrient fluxes is essential for rigorous assessment of the ecosystem services of water quality and soil fertility maintenance (Balvanera et al. 2006).

Species that differ in gross morphology and physiology (i.e., in life-form) are more likely to occupy distinct fundamental niches, and hence use resources in complementary ways, than are species that are similar to one another (Lavorel and Garnier 2002). Tropical forests offer a rich array of potentially complementary plant life-forms, and

may serve as a model for ecosystem construction (Ewel 1986). We report here the results of a long-term experiment in a wet tropical forest environment in which we grew monocultures of a dominant life-form and assemblages of three potentially complementary plant life-forms. The broad objectives of this experiment were to determine the degree to which (1) ecosystem functioning might be enhanced by growing a dominant life-form together with two potentially complementary life-forms, and (2) identity of the dominant life-form influenced functioning of both monocultures and multi-life-form systems. The floristic simplicity of these constructed ecosystems lent itself to understanding processes and mechanisms, while fertile soil and a warm, wet climate led to fast, continuous growth, so results were evident in a few years that would not have been visible for decades in a less benign environment. The species chosen for the experimental communities were not selected at random from the hundreds of potential candidates in the local flora, but instead were assembled to combine life-forms of proven evolutionary success, as evidenced by their diversity and abundance in the local forest. The three life-forms selected were canopy tree, palm, and giant perennial herb. The locally dominant life-form, canopy tree, was grown in monospecific stands and together with the other two life-forms in polycultures.

The focus of this study is on leaching of the macronutrients  $\text{NO}_3$ , Ca, Mg, and K. We predicted that nutrient retention would increase with richness of life-forms (from 1 to 3) and, based on previous results from these plots, that identity of the dominant tree species would exert a measurable influence on leaching (Hiremath et al. 2002; Bigelow et al. 2004; Russell et al. 2004; Ewel 2006; Ewel and Mazzarino 2008). By conducting the study continuously for 11 years, we were able to examine the temporal dynamics of nutrient loss as life-forms waxed and waned in dominance. Unique aspects of the research included its use of large stature perennial plants, its long duration, and its incorporation of water flux, which provided a means to go beyond concentrations and estimate rates of nutrient loss.

## Materials and methods

The study took place at La Selva Biological Station, Sarapiquí Province, Costa Rica. The site is on an alluvial terrace at the junction of the Puerto Viejo and the Sarapiquí rivers (10°26'N, 83°59'W, 41 m above sea level). The study site soil is a Eutric Hapludand (Weitz et al. 1997), a volcanic ash soil characterized by amorphous allophane clays that bind organic matter strongly (Sollins et al. 1994). Surface soil bulk density is low ( $\sim 0.7 \text{ Mg m}^{-3}$ ), and pH ( $\sim 5.5\text{--}6.5$ ) and cation exchange capacity ( $\sim 20\text{--}35 \text{ cmol}_c \text{ kg}^{-1}$ , dominated by variable charge) are relatively high, in

comparison with most soils of the wet tropics. The soil profile reflects fluvial deposition with minimal weathering. The A and AB horizons, which extend to 0.1 and 0.3 m, respectively, are sandy clay loams. Depths of deeper features vary with location in the 8-ha research site but include a coarse sand lens starting at depths from 0.6 to 0.9 m, and a buried A horizon, with slight mottling in a 2-cm-thick layer above it, beginning at depths from 0.7 to 1.5 m.

Dicotyledonous canopy trees, the dominant life-form of wet tropical forests everywhere, were the main group of interest. To ensure that findings were not due to choice of species alone, the experiment was conducted with three tree species. The tree species chosen, all of which occur locally, were known to grow well on the site and to be manageable in the nursery; seed sources of known provenance were available for each of them (Haggar and Ewel 1995). Species capable of N fixation were intentionally excluded because their distinct mode of N acquisition puts them in a different functional group. The tree species were selected because they differed greatly in crown architecture and leafing behavior, but many other differences of ecological importance were revealed over the ensuing 13 years of research: root system architecture (Haggar and Ewel 1997), water relations (Gutiérrez-Soto and Ewel 2008), nutrient use efficiency (Hiremath et al. 2002), defenses and responses to herbivores (Trager and Bruna 2006), and N mineralization (Ewel 2006), among others.

*Hyeronima alchorneoides* Alemão (Euphorbiaceae), an evergreen species, has leaves that are huge when the tree is young ( $\sim 280 \text{ cm}^2$ ) but diminish to one-quarter their former size as the tree ages. In dense, young plantations its canopy is very effective at capturing almost all incoming light. (After first mention, species are referred to by genus.) *Cedrela odorata* L. (Meliaceae) is semi-deciduous when young, but after about age 5 years becomes dry-season deciduous, although there is substantial variation in leafing behavior among individuals. It has long (up to 1 m) compound leaves of 20–40 leaflets (ca.  $40 \text{ cm}^2$  each) and moderately open crown architecture. *Cordia alliodora* (R. & P.) Cham. (Boraginaceae) has simple leaves (ca.  $30 \text{ cm}^2$ ) and tiered branching, with successive tiers separated by long ( $>1 \text{ m}$ ) internodes on fast-growing individuals. The result is an open crown architecture that allows high light transmittance. In the wet climate of La Selva, this species of *Cordia* is evergreen in youth and wet-season deciduous as a reproductive adult ( $\sim 7$  years).

Two contrasting species were planted with each tree species, producing three life-form polycultures. The larger of the two non-tree life-forms was a palm, *Euterpe oleracea* Mart. (Arecaceae), a native of Amazonia that has a native congener (*E. macrospadix*) in the local forest. *Euterpe* forms clumps containing up to 20 shoots and, with a single bud at the apex of each stem, attains a height of

25 m. Its pinnate leaves are  $\sim 3 \text{ m}$  long and have 40–80 leaf segments, each  $\sim 1 \text{ m}$  long. Densely planted *Euterpe* therefore achieve extremely high leaf area and allow little light transmittance to the understory. The third life-form was a giant perennial herb, *Heliconia imbricata* (Kuntze) Baker (Heliconiaceae). Like *Euterpe*, *Heliconia* is a large-leaved monocot (reminiscent of a short-stemmed banana plant), but it differs from the palm in that its meristem is basal, so its height growth is biomechanically limited. *Heliconia* forms clumps of monocarpic shoots up to 6 m tall. Its leaf blades are large, 0.3 m wide by 2 m long, and oriented vertically. Like *Euterpe*, it attains high leaf area and allows little light transmittance.

Experimental plantations were established in June 1991, after 8 ha of an abandoned cacao plantation (not known to have been fertilized or limed) were felled and the resulting slash had dried and then been burned in situ. The experimental design devoted three blocks to each of the three tree species. Trees were planted at 2.0 m on center ( $2,887 \text{ trees ha}^{-1}$ ) in plots of 60 by 40 m. This high planting density was used to ensure rapid and near-complete use resources by the trees; an interplanted life-form that thrived would presumably be using resources in complementary ways. The other two life-forms were planted additively within the same half of each plot, with *Euterpe* at one-quarter the tree density and *Heliconia*, a year later, at one-half the tree density. The polyculture half of each plot was separated from the tree monoculture by root barrier cloth buried vertically to a depth of 1 m, and all plots were surrounded by buffer rows of the same tree species, which in turn were buffered by secondary vegetation of stature similar to that of the plantations. The resulting layout comprised three monocultures and three polycultures of each of three tree species, or 18 plots of  $30 \times 40 \text{ m}$ . The monocultures, particularly those of *Cedrela* and *Cordia*, required weeding (first by machete, later by string-line trimmers, still later by annual application of 1% glyphosate) to keep them free of colonists. Glyphosate added  $<0.12 \text{ kg ha}^{-1} \text{ year}^{-1}$  of N, an amount well below our error of measurement. To prevent stand stagnation while sustaining maximum use of resources, the monocultures were lightly thinned from below every 3–4 years. No dominant tree crown was ever exposed by removing more than one neighboring canopy tree.

#### Water balance

Daily water drainage rates were estimated from the water balance, i.e.,

$$Dr = P - I - ET - \Delta w,$$

where  $Dr$  is drainage,  $P$  is precipitation,  $I$  is interception,  $ET$  is evapotranspiration, and  $\Delta w$  is the change in water

storage in the uppermost 1 m of soil. Methods used are described in Bigelow et al. (2004). A single-species ET model (Bigelow 2001) was extended for use in the multi-species stands by altering the canopy-conductance coefficient to incorporate stomatal and leaf-boundary-layer conductances of monocots in parallel with the conductances of the accompanying trees. Aerodynamic conductances were modeled as a function of the height of the tallest plants within each plot regardless of plant life-form.

Leaf area index, an important input to the canopy conductance formula, was obtained from allometric equations (Cole and Ewel 2006, plus unpublished equations for *Heliconia*). The equations predicted individual plant leaf area from height and stem diameter (stem number for the monocots plus leaf counts of *Euterpe*), and were scaled up to plot area with data from annual censuses of every plant.

Net radiation ( $R_n$ ) data, a critical input for ET models, came from direct measurement above the experimental plantations with net radiometers supplemented by modeling from total solar radiation data measured at the Organization for Tropical Studies' meteorological station  $\sim 1$  km distant from the study site. Net radiometers were the Q\*7 and Q\*6 (Radiation and Energy Balance Systems; Seattle, WA, USA). About 15% of the data were measured directly, the rest were modeled. Modeled  $R_n$  was based on a daily total solar radiation ( $S_t$ ) dataset that had been proofed and gap-filled. After testing several models against measured data, the relationship between hourly  $S_t$  and daily  $S_t$  was established by modeling total intercepted  $S_t$  as a sine curve.

Storage of water in the upper 1 m of soil on a daily interval was estimated with the SWAP93 soil water model (van den Broek et al. 1994). Site-specific hydraulic conductivity parameters for this model were obtained using the suction crust infiltrometer method (Booltink et al. 1991).

#### Measurement of nutrient leaching

Soil water nutrient concentration measurements began 1 year after tree planting. Nutrient leaching was measured by multiplying concentrations of  $\text{NO}_3$ , Ca, Mg, and K in drainage water (linearly interpolated between successive sampling dates) with the daily rate at which water drained past the 1-m depth (Lord and Shepherd 1993). Draining water was sampled with tension lysimeters consisting of 1.3-m PVC tubes sealed with a porous ceramic cup (Soil Moisture Equipment, Santa Barbara, CA, USA) at the bottom, and a rubber bung with an access tube at the top. There were three lysimeters in the central  $10 \times 30$  portion of each plot, an area reserved for non-destructive sampling. The lysimeters were randomly located on a grid that was offset from planting positions. After 20 mm of rain had fallen within 3 days, air was pumped from the tube to

create a light vacuum ( $-16$  kPa); after 24 h, the soil water that had collected was extracted by placing suction on a narrow polyethylene tube that was passed through the access tube to the bottom of the ceramic cup. Lysimeters were routinely sampled every 3 months except during periods of intensive sampling which tracked individual rainfall events. On any given sampling date, all lysimeters were sampled in all plots, and the water from the three lysimeters in each plot was combined into a single sample prior to analysis.

The water was preserved by adding 0.05 ml of chloroform and refrigerating at  $4^\circ\text{C}$ . Nutrient analyses were done at La Selva Biological Station (subset of  $\text{NO}_3$  only); the University of Florida, Institute of Food and Agricultural Sciences, Analytical Research Laboratory (Gainesville, FL, USA); the Universidad de Costa Rica, Centro de Investigaciones Agronómicas (San José, Costa Rica); the Institute for Ecosystem Studies (Millbrook, NY, USA); and the Centro Agronómico Tropical de Investigación y Enseñanza (Turrialba, Costa Rica). Each of these laboratories except La Selva participates in a sample exchange network for cross-laboratory verification of analyses.

#### Root sampling

Fine roots ( $< 2$  mm diameter) were sampled annually at eight randomly determined points in each plot. Cores were extracted in 0.10-m increments, to 0.5 m in the first year and thereafter to 1.1 m, i.e., below the depth of the porous-cup lysimeters used to sample leachate. Cores from the eight points were combined according to depth interval. Fine roots were separated from soil using air-pressurized water, then sorted by species and diameter class. Root length was estimated using the line intersect method (Tennant 1975) and converted to length density (cm of root per  $\text{cm}^3$  of soil).

#### Statistical analysis

Comparisons of mean nutrient concentration values, without regard to block or date of sampling, were carried out separately for each tree species using life-form richness (monoculture or polyculture) as the treatment effect. The frequency distribution of  $\text{NO}_3$  concentrations was highly right-skewed, with many values at the lower detection limit ( $0.04 \text{ mg L}^{-1}$ ). Means and variances were therefore estimated with maximum likelihood based on the gamma distribution adjusted for left-censored data (Newman et al. 1989); means comparisons were done with the  $z$  statistic. Analysis of Ca, Mg, and K concentration values was done with analysis of variance (Proc GLM; SAS Institute 1999), and  $\alpha < 0.05$  was used for the acceptable probability of type I error.

Daily leaching estimates were summed by the hydrological year beginning May 1 (i.e., slightly before the usual beginning of the wet season) and ending April 30. Hydrological year 2, the first year reported here, runs from May 1, 1992 to April 30, 1993. Because of fluctuations in year-to-year leaching imposed by varying precipitation, annual leaching was analyzed by modeling the differences between treatments. The analysis made three sets of comparisons: each monoculture of a tree species with its corresponding three life-form system (mono vs. poly); monocultures of tree species with one another (mono vs. mono); and polycultures dominated by each tree species with one another (poly vs. poly). These differences were analyzed for temporal trends using a simple linear function of time, leaching difference =  $a + b \cdot \text{time}$ , and a quadratic polynomial function of time, leaching difference =  $a + b \cdot \text{time} + c \cdot \text{time}^2$ . Analyses were done using Proc Mixed (SAS Institute 1999). Repeated-measures analysis was carried out using a first-order autoregressive correlation structure to account for covariance of successive measurements in the same location. When  $b$  or  $c$  parameters were significant at  $\alpha < 0.05$ , this was accepted as evidence for a significant effect. When parameters for both linear and quadratic statistical models were significant, the model with the lowest AIC<sub>c</sub> value was identified as being better if the AIC<sub>c</sub> difference was  $>2$ .

## Results

### Stand development

Leaf area index of monospecific *Hyeronima* plantations reached 4 within 2 years of planting and increased slowly thereafter to a maximum of 5.2 (Fig. 1). *Cedrela* reached a maximum LAI of 5.8 in monoculture, but *Cordia* LAI was lower, attaining a maximum of 3.7. The tree species' leaf area developed differently in polyculture compared to monoculture, and the palm and giant herb leaf area developed differently according to the tree species with which they were paired. Grown with the dense-canopied *Hyeronima*, *Heliconia* never thrived and *Euterpe* produced very little leaf area for the first 5 years, after which it grew at rates comparable to those observed in other polycultures years earlier. The *Hyeronima* trees suffered no reduction in leaf area as a result of the palm growth. When grown with the deciduous tree species *Cedrela* and *Cordia*, *Heliconia* and then *Euterpe* grew rapidly in succession; the palms eventually reached a very high LAI of up to 10.7, while the leaf area of the accompanying tree declined markedly.

Patterns of fine root length density (RLD) in response to presence of the palm and giant herb were even more

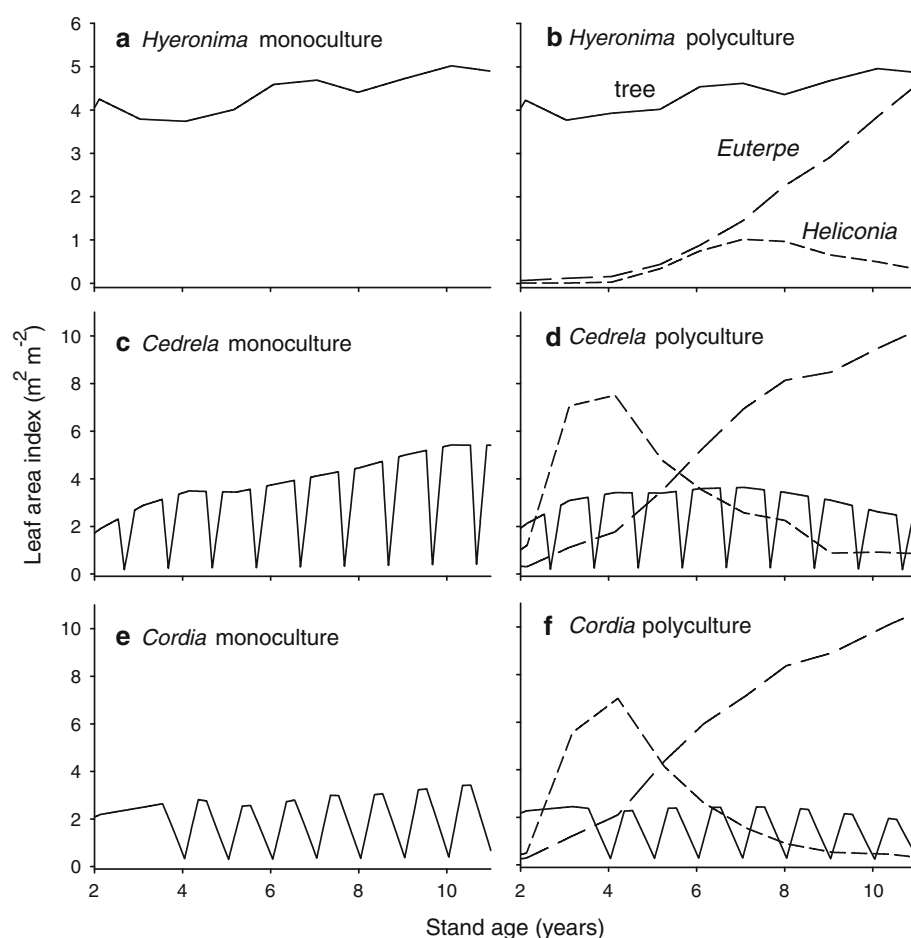
dramatic than the above-ground responses (Fig. 2). The identity of the tree species had a large impact on the response. The least sensitive of the three tree species was *Hyeronima*, whose RLD did not change discernibly in response to the monocots. During the first 8 years, palm RLD in *Hyeronima* stands lagged behind that of the accompanying trees, but eventually palm and *Hyeronima* RLD became approximately equal at all depths in the soil profile. Maximum RLD in the surface soil (mean of three blocks, 0–0.1 m depth) was 3.0 (palm) and 3.4  $\text{cm cm}^{-3}$  (tree). Tree RLD in *Cordia* and *Cedrela* polycultures, in contrast, declined markedly compared to monocultures. By year 6, *Cordia* RLD in polyculture was less than in monoculture; and the same occurred in *Cedrela* stands by 10 years of growth. Nevertheless, the declines in RLD of those two tree species was more than compensated for by explosive growth of palm roots. Maximum RLD of the palms was high, 14.7  $\text{cm cm}^{-3}$  at its peak in the 10th year of growth in the *Cedrela* and *Cordia* stands.

### Water fluxes

Estimated ET from polycultures exceeded that from monocultures (Fig. 3), mainly as a result of higher canopy conductances ( $g_c$ ). Canopy conductances closely tracked LAI; monoculture  $g_c$  reached from 1.4 (*Hyeronima*) to 2.7  $\text{mol m}^{-2} \text{s}^{-1}$  (*Cedrela*), but polyculture  $g_c$  became as high as 5.6  $\text{mol m}^{-2} \text{s}^{-1}$ . (Aerodynamic conductances differed little between monoculture and polycultures, approaching an asymptote of 2.4  $\text{mol m}^{-2} \text{s}^{-1}$ .) For *Hyeronima*, the differences in ET between monocultures and polycultures were small at first, gradually increasing with increments in *Euterpe* leaf area. Polyculture ET in *Hyeronima* stands exceeded monoculture ET by an average of 114  $\text{mm year}^{-1}$  (1,504 vs. 1,390  $\text{mm year}^{-1}$ ). Mean annual ET in monoculture *Cedrela* stands was 83 mm greater than in *Cordia* stands (1,244 vs. 1,161  $\text{mm year}^{-1}$ ), but annual ET of polycultures of the two tree species was virtually identical (mean of 1,436 vs. 1,429 mm).

Differences in drainage among treatments and stands, on an annual basis, were nearly identical to the respective differences in ET, as increased ET translated to decreased drainage. Precipitation exceeds evapotranspiration by a factor of three in this wet tropical forest environment, so absolute differences in drainage among treatments were modest in comparison with total water fluxes. Nevertheless, on a relative basis, the differential was important to drainage and therefore to nutrient leaching. There was an average 4% reduction in drainage from *Hyeronima* polycultures compared to monocultures, and 7 and 9% from *Cedrela* and *Cordia* polycultures, respectively.

**Fig. 1** Leaf area index during stand development of monocultures of three tropical trees (**a, c, e**), and stands of the same trees grown with the palm *Euterpe oleracea* and the giant herb *Heliconia imbricata* (**b, d, f**). Note expanded vertical axis in (**a**) and (**b**)

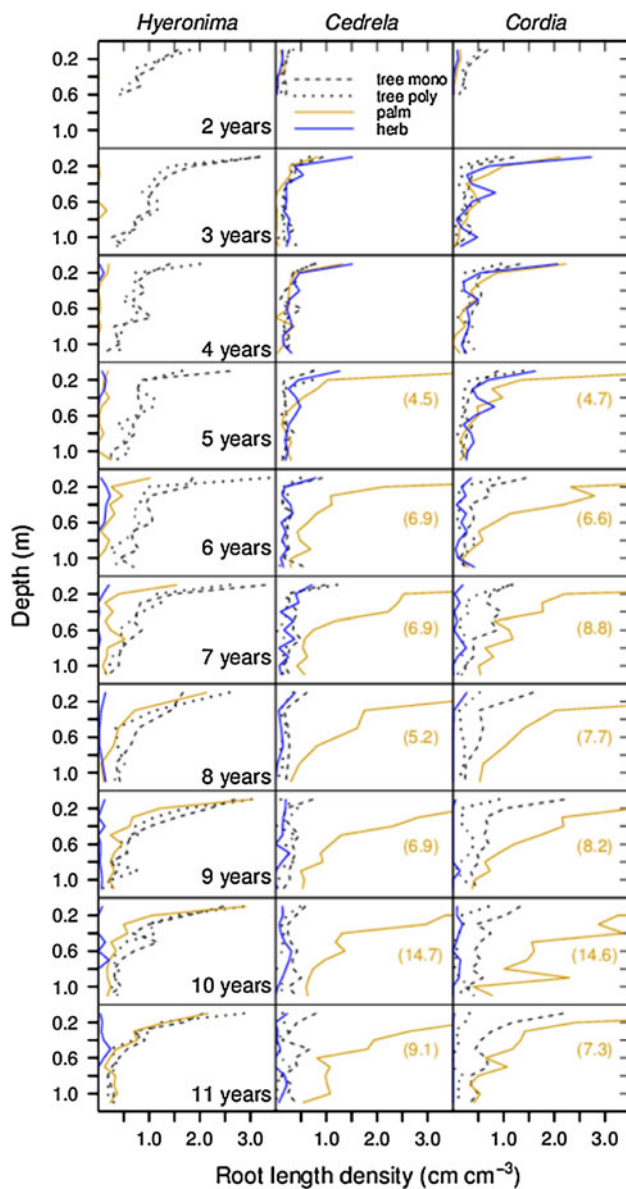


### Nutrient leaching

Concentrations of  $\text{NO}_3\text{-N}$  in leachate were low (Fig. 4). The overall mean of 1,327 measurements was  $0.38 \text{ mg L}^{-1}$ , and even when 561 values  $\leq 0.04 \text{ mg L}^{-1}$  (the lower reliable limit of detection) were excluded, the mean rose only to  $0.66 \text{ mg L}^{-1}$ . Nevertheless,  $\text{NO}_3$  concentrations  $> 2.0 \text{ mg L}^{-1}$  were common in all treatments, although much less frequent under *Cordia* than under stands of the other two tree species.  $\text{NO}_3$  concentrations were more than double in monocultures than polycultures dominated by *Cedrela* ( $0.30$  vs.  $0.65 \text{ mg L}^{-1}$ ,  $P < 0.001$ ) and higher in *Cordia* monocultures than polycultures ( $0.36$  vs.  $0.24 \text{ mg L}^{-1}$ ,  $P < 0.05$ ). Ca concentrations in leachate were high (mean of 880 values =  $10.5 \text{ mg L}^{-1}$ ), which is not surprising because the study site soil is high in Ca (typical extractable values are  $10 \text{ cmol}_c \text{ kg}^{-1}$ ). Mean Ca concentrations in leachate from *Hyeronima* monocultures ( $12.7 \text{ mg L}^{-1}$ ) were higher than in polycultures ( $10.7 \text{ mg L}^{-1}$ ,  $P < 0.001$ ); the reverse was true for *Cedrela* ( $10.2$  vs.  $11.7 \text{ mg L}^{-1}$ ,  $P < 0.01$ ). Concentrations of Mg in leachate averaged  $2.3 \text{ mg L}^{-1}$  across the 1,063 measurements from all treatments, and monoculture and polyculture

concentrations did not differ significantly with any tree species. Average concentrations of K in leachate were low (mean of 1,028 values =  $2.2 \text{ mg L}^{-1}$ ), but much higher concentrations were measured moderately frequently. In *Hyeronima* polycultures, K concentrations were slightly higher than those in monocultures ( $P = 0.04$ ), while in *Cedrela* stands, K concentrations were substantially higher in monocultures than in polycultures ( $2.3$  vs.  $1.9 \text{ mg L}^{-1}$ ,  $P = 0.001$ ).

Fifteen of 72 comparisons of annual leaching losses (18 for each of four nutrients) had significant coefficients, 10 fitting model 1 and 5 fitting model 2 (Table 1). Several differences were visible between monocultures and polycultures with time (Fig. 5). Most notably, there was rapid loss of  $\text{NO}_3$  from *Cedrela* monocultures during the last 5 years of the study (mean of  $18 \text{ kg ha}^{-1} \text{ year}^{-1}$ ), which resulted in significantly greater losses than from *Cedrela* polycultures ( $P = 0.012$ ) or from monocultures of the other two tree species. *Hyeronima* stands, both monocultures and polycultures, lost substantial amounts of  $\text{NO}_3$  during the first 3 years, while *Cordia* stands were comparatively retentive of  $\text{NO}_3$  throughout. *Cordia* polycultures were initially more retentive of  $\text{NO}_3$  due to larger



**Fig. 2** Fine-root length density (RLD) of three trees grown in single-species stands (*dashed lines*), and in polyculture (*dotted lines*) with a palm, *Euterpe* (*solid, light colored lines*) and a giant herb, *Heliconia* (*solid, dark colored lines*). Horizontal axis is truncated so that only values  $0.1 < \text{RLD} \leq 3.5$  are displayed; values  $> 3.5$  are in *parentheses*. Stand age (denoted in *Hyeronima* panels) increases from 2 years (*top row*) to 11 years (*bottom row*)

losses from corresponding monocultures early in stand establishment, but differences in leaching losses between monocultures and polycultures were indistinguishable from zero for the middle years of the experiment. *Cordia* monocultures and polycultures both showed a renewed tendency to elevated  $\text{NO}_3$  leaching losses in the final year of the experiment (increasing from 0.3 to 1.5 and 0.1 to  $1.3 \text{ g m}^{-2}$  in the monoculture and polyculture, respectively), but the confidence intervals for the difference between them overlapped zero (Fig. 6e).

Leaching of Ca and Mg followed parallel trends which differed from those of  $\text{NO}_3$ . The largest losses of Ca occurred in *Hyeronima* monocultures (significantly more so than from monocultures of *Cedreia* or *Cordia*) during the latter half of the study (Fig. 5), and those losses accelerated with time, as shown by a significant positive coefficient of the quadratic term in model 2 (Table 1; Fig. 6b). Losses of Mg, like those of Ca, were greater from *Hyeronima* monocultures than polycultures during the latter half of the study, but unlike Ca those losses did not accelerate with time. Thus, the monoculture–polyculture difference increased linearly (model 1 significant). Polynomials with positive linear and negative quadratic coefficients proved the best models for the difference in Ca and Mg leaching from *Cordia* polycultures and monocultures. Maximum retention of Ca and Mg occurred around years 6–7, after which the difference between *Cordia* polycultures and monocultures grew smaller, practically disappearing (in the case of Ca) by the last 2 years of the study (Fig. 6). Neither Ca nor Mg losses differed significantly between *Cedreia* monocultures and polycultures.

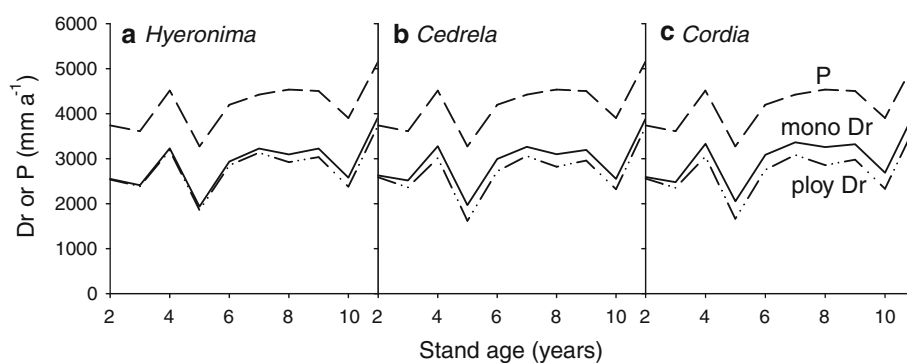
Trends in K leaching were weaker than for  $\text{NO}_3$  and the divalent cations; no significant differences were detected in K loss from monocultures and polycultures (Table 1). In the closest case ( $P = 0.05$ , model 1), loss of K from *Cedreia* monocultures exceeded loss from polycultures in 8 of 11 hydrologic years, amounting to an average difference of  $1.3 \text{ g m}^{-2} \text{ year}^{-1}$  over the course of the study.

## Discussion

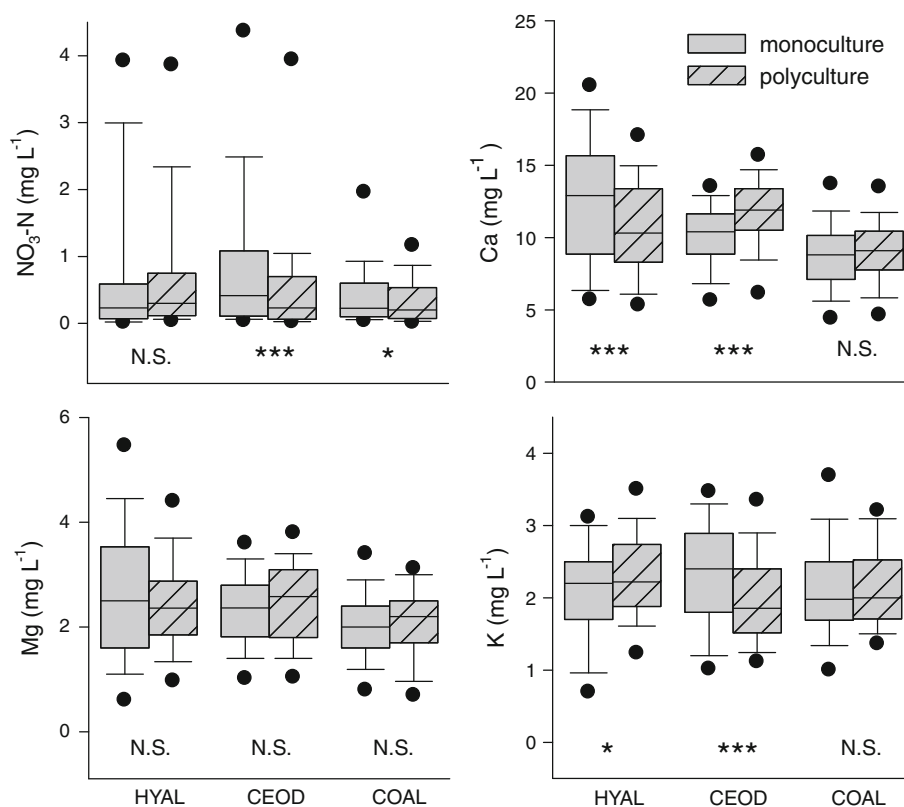
Effects of life-form richness on nutrient leaching, like other ecosystem processes, can be due to complementarity, selection effects, or insurance effects. Complementarity among plant species results from niche differentiation in time or space, from requirements for nutrients in different forms or ratios, or from facilitation (Trenbath 1974; Fridley 2001), while selection effects indicate the presence of a dominant species or functional group that has strong influence on ecosystem functioning (Aarssen 1997; Huston 1997; Loreau and Hector 2001). Selection effects can lead to a single-winner outcome in nutrient competition models in which one member is a superior competitor (Tilman 1988; Tilman et al. 1997; Loreau 1998). The insurance effect (Lawton and Brown 1993; Yachi and Loreau 1999) refers to reduced risk of impaired ecosystem functioning in the event of species loss.

Our relatively long-term experiment involving perennial plants yielded substantial evidence that systems containing three life-forms often experience lower leaching losses than systems composed solely of the life-form that dominates most tropical forests: dicotyledonous trees. Nevertheless,

**Fig. 3** Estimated drainage ( $D_r$ ) from stands of three tropical tree species grown in single-species stands (solid line) or multispecies stands with a palm (*Euterpe*) and a giant herb (*Heliconia*) (dot-dash line). Precipitation ( $P$ ) is shown by the upper, dashed line; evapotranspiration is approximately equal to the difference between precipitation and drainage



**Fig. 4** Quartile distributions of concentrations of nutrients in leachate over 11 years from single- and multi-species plots. Tree species are designated HYAL (*Hyeronima alchorneoides*), CEOD (*Cedrela odorata*), and COAL (*Cordia alliodora*). Lower and upper dots respectively represent 5th and 95th percentiles. N.S. Not significant at  $P \geq 0.05$ ; \* $P < 0.05$ ; \*\*\* $P \leq 0.001$



the constraints of our design (i.e., no study-long measurements of leaching losses from monocultures of the two monocots) preclude unequivocal assertions regarding the role of diversity per se in nutrient retention. With that caveat, it is useful to examine a broad overview of the findings among the six kinds of plant communities.

Polycultures lost significantly lower amounts of nutrients than did their corresponding tree monocultures in 6 of 12 comparisons (4 nutrients  $\times$  3 tree species; Table 1). Polycultures and monocultures did not differ significantly in the other 6 comparisons, and in no instance did a polyculture lose significantly more than its corresponding tree monoculture. When cumulative losses of each of the four nutrients over 11 hydrologic years are compared (a non-statistical comparison; Fig. 5), in two out of every

three cases it was a polyculture that lost the least and a monoculture that lost the most. Thus, our data support the contention that systems composed of more life-forms tend to be at least as retentive of nutrients, and often more so, than monocultures.

#### Three tree species, two outcomes

In *Cordia* and *Cedrela* polycultures, all three life-forms thrived during the middle years of the study. *Hyeronima* polycultures, in contrast, developed more slowly due to rapid, near-complete, and uninterrupted light capture by the tree. This led to nutrient retention outcomes of different magnitude among polycultures containing different tree species. In general, leaching losses were lowest, and the



**Table 1** Probability of Type 1 error for coefficients of linear and non-linear models of leaching comparisons: monoculture–polyculture, monoculture–monoculture, and polyculture–polyculture

Nutrient	Model <sup>a</sup>	Sp.	Mono. versus poly.		Comparison	Mono. versus mono.		Poly. versus poly.	
			p(b) <sup>b</sup>	p(c)		p(b)	p(c)	p(b)	p(c)
NO <sub>3</sub>	1	Hyal	0.072		Hyal–Ceod	<b>0.001</b>		<b>0.021</b>	
NO <sub>3</sub>	1	Ceod	<b>0.012</b>		Hyal–Coal	<b>0.005</b>		<b>0.0002</b>	
NO <sub>3</sub>	1	Coal	0.189		Ceod–Coal	<b>0.002</b>		0.094	
NO <sub>3</sub>	2	Hyal	0.128	0.267	Hyal–Ceod	0.063	0.217	0.0474	0.1324
NO <sub>3</sub>	2	Ceod	0.338	0.645	Hyal–Coal	0.820	0.829	0.0001 <sup>c</sup>	0.0015 <sup>c</sup>
NO <sub>3</sub>	2	Coal	<b>0.013</b>	<b>0.023</b>	Ceod–Coal	0.372	0.746	0.0842	0.1522
Ca	1	Hyal	0.0001 <sup>d</sup>		Hyal–Ceod	<b>0.017</b>		0.5062	
Ca	1	Ceod	0.466		Hyal–Coal	0.0001 <sup>c</sup>		0.8744	
Ca	1	Coal	0.878		Ceod–Coal	0.874		0.4025	
Ca	2	Hyal	0.218	<b>0.007</b>	Hyal–Ceod	0.943	0.547	0.1334	0.0961
Ca	2	Ceod	0.642	0.533	Hyal–Coal	0.200	<b>0.028</b>	0.1078	0.1048
Ca	2	Coal	<b>0.007</b>	<b>0.007</b>	Ceod–Coal	0.219	0.198	0.7400	0.8606
Mg	1	Hyal	<b>0.0001</b>		Hyal–Ceod	<b>0.0005</b>		0.3376	
Mg	1	Ceod	0.092		Hyal–Coal	<b>0.0001</b>		0.9158	
Mg	1	Coal	0.984		Ceod–Coal	0.773		0.0701	
Mg	2	Hyal	0.458	0.520	Hyal–Ceod	0.595	0.769	0.5011	0.3755
Mg	2	Ceod	0.816	0.903	Hyal–Coal	0.768	0.163	0.1124	0.1078
Mg	2	Coal	<b>0.007</b>	<b>0.006</b>	Ceod–Coal	0.265	0.280	0.0500	0.1103
K	1	Hyal	0.941		Hyal–Ceod	0.357		0.3050	
K	1	Ceod	0.343		Hyal–Coal	0.417		0.7627	
K	1	Coal	0.050		Ceod–Coal	0.197		0.8409	
K	2	Hyal	0.820	0.829	Hyal–Ceod	0.245	0.120	0.2992	0.3893
K	2	Ceod	0.881	0.925	Hyal–Coal	0.205	0.115	0.6217	0.5707
K	2	Coal	0.474	0.257	Ceod–Coal	0.788	0.977	0.2622	0.2679

Bold font indicates significance at  $P < 0.05$ ; where both models are significant, the model with lower  $AIC_c$  is highlighted

*Hyal Hyeronima alchorneoides*, *Ceod Cedrela odorata*, *Coal Cordia alliodora*

<sup>a</sup> Model 1 is a linear function of time ( $a + b \cdot \text{year}$ ), Model 2 is a second-order polynomial function of time ( $a + b \cdot \text{year} + c \cdot \text{year}^2$ )

<sup>b</sup>  $p(b)$  is probability of significance for the coefficient of the first-order term in linear or polynomial model;  $p(c)$  is probability of significance of second-order term in polynomial model

<sup>c</sup>  $AIC_c$  model 1 is 66.3,  $AIC_c$  model 2 is 70.6

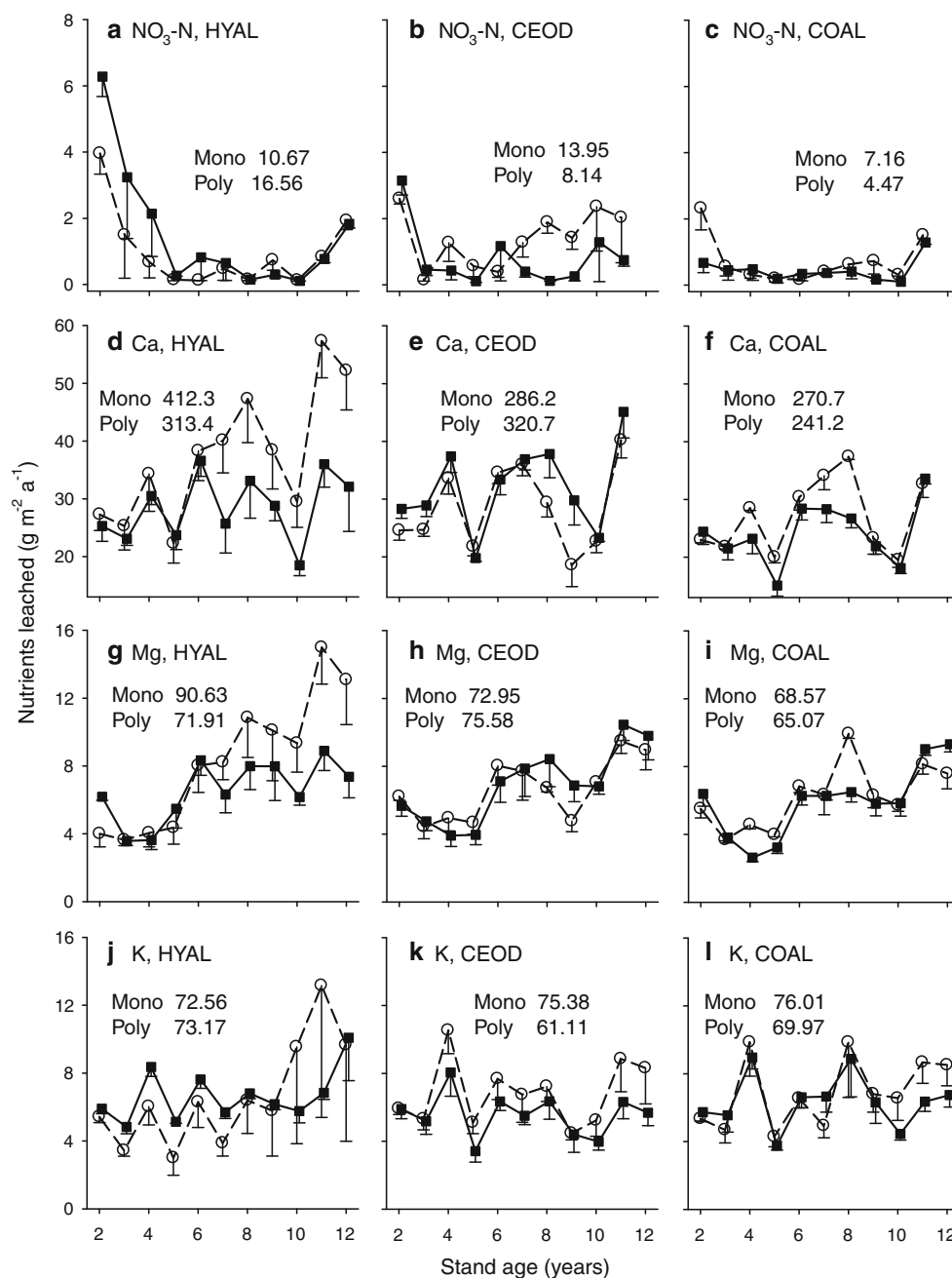
<sup>d</sup>  $AIC_c$  model 1 is 214,  $AIC_c$  model 2 is 210.7

<sup>e</sup>  $AIC_c$  model 1 is 202.0,  $AIC_c$  model 2 is 199.1

impact of added life-forms was most pronounced, in polycultures containing *Cordia* and *Cedrela*. But despite its effective dominance of the site, *Hyeronima* likewise had lower leaching from polycultures than monocultures. In this case, however, the response occurred later in stand development, and the mechanism was different.

Polycultures containing either of the two deciduous tree species (*Cedrela* or *Cordia*) typically underwent five developmental stages during the course of the study: (1) tree dominated, (2) tree plus herb, (3) tree plus herb plus palm, (4) tree plus palm, and finally (5) palm dominated. Stands in which the palm eventually dominated were analogous to the single-winner prediction of competition

for nutrients (Tilman 1988; Tilman et al. 1997; Loreau 1998). In this case, however, the resource was light not nutrients: the palm prevailed by invading the tree canopy from below, compressing the space available to tree crowns and thereby limiting their light capturing potential (Ewel and Mazzarino 2008). Nevertheless, it was not only the final outcome but the intervening temporal dynamic that is of interest. For example, the superiority of *Cordia* polycultures in retaining divalent cations was most accentuated during Stage 3, when all three life-forms flourished (Fig. 6c, d), and *Cedrela* polycultures retained  $\sim 8 \text{ kg ha}^{-1} \text{ year}^{-1}$  more N during Stage 3 than did monocultures.

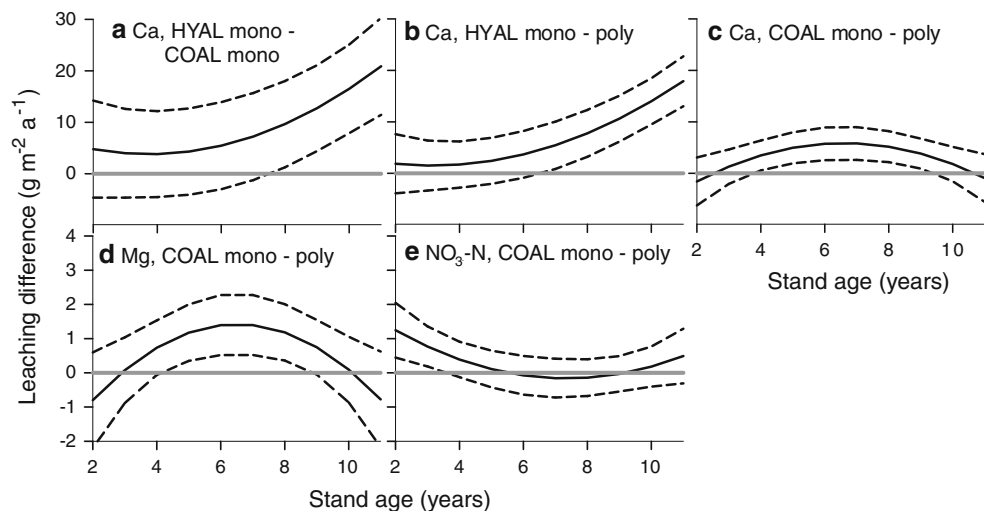


**Fig. 5** Time courses of nutrient leaching (means and standard errors of three blocks) from tropical tree monocultures (Mono, open circles) and diverse plots containing a palm (*Euterpe*) and a giant herb (*Heliconia*) in addition to a tree species (Poly, filled squares); **a**, **d**, **g**,

**j** are from plots with the tree *Hyeronima alchorneoides* (HYAL), **b**, **e**, **h**, **k** with *Cedrela odorata* (CEOD), and **c**, **f**, **i**, **l** with *Cordia alliodora* (COAL). Values labeled Mono or Poly are 11-year totals ( $\text{g m}^{-2}$ ) of annual means from three blocks

We propose that two mechanisms were responsible for reduced leaching when two or three life-forms thrived simultaneously. One mechanism was an increase in intensity of soil exploitation (and not complementarity resulting from a spatial or temporal partitioning by roots). The trees were tightly packed from the start (2 m between individuals), and both crowns and root systems closed in less than

3 years (Haggard and Ewel 1995). Furthermore, RLD for both deciduous tree species was low (Fig. 2). Why did the trees not simply develop denser root systems to make full use of nutrients available in the soil? Because their growth was not nutrient limited (at least not because of N or P scarcity; Hiremath 2000), but light limited. And given the trees' inability to add more light-gathering foliage, there



**Fig. 6** Modeled difference (with 95% confidence intervals) in annual leaching from stands of tropical trees, showing contrasts in which best model was nonlinear (Table 1). **a** Ca, *Hyeronima* monoculture minus *Cordia* monoculture. **b** Ca, *Hyeronima* monoculture minus

polyculture. **c** Ca, *Cordia* monoculture minus polyculture. **d** Mg, *Cordia* monoculture minus polyculture. **e**  $\text{NO}_3\text{-N}$ , *Cordia* monoculture minus polyculture

was no physiological stimulus to add more nutrient-gathering roots; the tree species alone were incapable of fully exploiting available soil resources. This left an opportunity for complementary use of light by plants having very different foliage displays, the palm and giant herb. With their huge, vertically subtended, evergreen leaves, the monocots captured light missed seasonally and spatially by the deciduous tree species. Given the monocots' ability to obtain light in these dense stands, they were able to exploit the soil more completely than the trees alone, thereby reducing leaching losses. Thus, the increased intensity of rooting that retarded nutrient loss was a product of complementarity in light utilization.

The second mechanism involved higher ET in polycultures due to the palm, *Euterpe*. In the model used to calculate ET, canopy conductance ( $g_c$ ) was the most important parameter (Bigelow 2001). Polycultures containing deciduous trees had  $g_c$  values of  $3 \text{ mol m}^{-2} \text{ s}^{-1}$  by age 3–4 years, ultimately reaching 5 because of the high leaf area of the palm. In comparison, nearby natural forest had maximum  $g_c$  of 3 (Loescher et al. 2005). The resulting 4–9% decrease in soil water drainage from polycultures translated into equivalent decreases in nutrient leaching.

The evergreen *Hyeronima* had attributes that led to different results. *Hyeronima* developed nearly twice as much leaf area (Fig. 2), and had cumulative photosynthetic nutrient use efficiency (N and P) at least twice as high as either *Cedrela* or *Cordia* (Hiremath 2000). *Hyeronima* also formed a denser network of roots than the other two tree species (Hagggar and Ewel 1997; Russell et al. 2004). Unlike the stands containing the deciduous tree species, *Hyeronima* polycultures underwent only two developmental stages:

tree-dominated followed after about 5 years by tree plus palm-dominated. During the two-life-form stage, the elevated Ca and Mg leaching observed in *Hyeronima* monocultures disappeared. By that stage, both tree and palm had developed similar RLD ( $2\text{--}3 \text{ cm cm}^{-3}$  in the 0–0.1 m soil-depth layer), and the growth rate of tree roots did not diminish in the presence of the palms (Russell et al. 2004). It was likely the relatively low demand of *Hyeronima* for divalent cations that led to enhanced retention by the combination of life-forms. Foliar concentrations of Ca and Mg in *Hyeronima* ( $\sim 1$  and  $0.3\%$ , respectively) were only about one-third those in *Cordia*, for example, and the additional uptake provided by the palm led to greater overall retention in *Hyeronima* polycultures. There was value in an additional life-form, even in the presence of a dominant species such as *Hyeronima* that approaches the status of ecosystem engineer.

Although *Hyeronima* has relatively low demand for Ca and Mg, this does not explain the delay of about 6 years before an upsurge in cation leaching was observed in its monocultures. Nitrification-induced leaching is ruled out because N mineralization and nitrification are suppressed in *Hyeronima* monocultures (Ewel 2006). Time courses of pH show no signs of acidification; pH ranged from about 5.8 to 6.6 throughout the study period, varying somewhat among soil depths. We conjecture that *Hyeronima* may accelerate cation leaching by producing large amounts of organic acids from root exudation (Jones 1998), but we only have the observation that the anions bicarbonate, chloride, and  $\text{NO}_3$  balance less than half the positive charge from Ca, Mg and other cations in the soil solution (Bigelow et al. 2004). Nevertheless, the cation losses from *Hyeronima* stands do

demonstrate that high productivity does not necessarily translate to full utilization of resources.

One of the mechanisms discussed above—increased intensity of rooting—is an admittedly indirect measure of nutrient uptake. It is not possible to assess leaching as a function of uptake (as measured by accrual in biomass) because both variables employ leaf area in their calculation; thus, they are not independent. And although nutrient concentration in leachate can be treated as an independent variable, preliminary analyses did not reveal straightforward relationships between it and N mineralization (no significant differences between monocultures and polycultures; Ewel 2006), sequestration in biomass (4 years of N data; Hiremath and Ewel 2001), or leafless periods of *Cedrela* and *Cordia* (not shown). Although unraveling the direct mechanisms awaits additional analysis of soil, plants, and the cycling between the two, it is reasonably clear that the mechanisms proposed—increased intensity of rooting; complementary, if ephemeral, use of light by trees and monocots; elevated transpiration by the palm—are all implicated in retarding nutrient leaching.

#### Unexpected non-imprint of *Heliconia* on potassium loss

*Heliconia* (a phylogenetic neighbor of banana) takes up prodigious quantities of K; at our site, its leaves and stems had average concentrations of 2.5 and 5.1%, respectively. We therefore anticipated that this uptake would manifest itself in reduced K loss from the *Cedrela* and *Cordia* polycultures where *Heliconia* thrived, followed by a pulse of leaching when the *Heliconia* began to die after about 4 or 5 years once it was overtopped by *Euterpe*. Nevertheless, neither increased retention nor increased loss of K were discernible in the data, and leaching losses of K from polycultures dominated by *Hyeronima* (where *Heliconia* never prospered) did not differ from those of the other tree species.

The explanation for the lack of *Heliconia* effects on K leaching may lie in the chemistry and mineralogy of the soils at the study site. Soils developed from volcanic parent material often retain K preferentially over Ca, in contrast to the usual rapid leaching of K because of its low charge density (Schalscha et al. 1975; Parfitt 1992). This selective K retention is attributed to the secondary clay mineral halloysite (Fontaine et al. 1989; Espino-Mesa and Hernandez-Moreno 1994), a weathering product of allophane which characterizes soils at the study site (Sollins et al. 1994; Nieuwenhuys and van Breemen 1997; Kleber et al. 2007). Such K retention may well have obscured differences among our experimental treatments, but this remains a hypothesis absent further work on the chemistry and mineralogy of these soils.

#### Insurance effects

Whereas temporal complementarity typically arises as a result of semi-predictable pulses in resource use related to phenology or succession, the insurance effect is a response to a stochastic event that harms a particular species. Although not a primary objective of the design, the study's long-term nature yielded two unanticipated examples of risk reduction related to nutrient leaching.

In 1999, a block of pure *Hyeronima* was struck by lightning. A year later, K concentrations in leachate more than doubled, to values as high as 10–13 mg L<sup>-1</sup>; a pulse of N loss also followed the strike (Ewel 2006). The converse occurred in polycultures, where lightning strikes twice killed several *Cordia* trees but left the monocots unscathed. The gap caused by tree death was quickly filled by growth of the surrounding herbs and palms, and the leaching data revealed no change in nutrient losses due to the tree death. Biological agents provided a second example of the insurance effect. *Cedrela* is vulnerable to *Hypsipyla* shoot borer attack (Gara et al. 1972), which stunted or killed some trees in all plots, and *Fusarium* root rot (Arguedas 2007), which killed >20% of the trees in one monoculture block. *Cedrela* death caused by either agent was associated with increased NO<sub>3</sub> leaching in monoculture, but roots of the palm and herb were available in polyculture to take up the flush of NO<sub>3</sub>. Catastrophes of the sort we observed commonly target individual species, not all members of a community, and any species that survives and continues to take up nutrients reduces the risk of nutrient loss.

#### Conclusions

Our ecosystem-level measurements of nutrient losses to deep infiltration show that enhanced life-form richness, even at very low levels, can help preserve nutrient capital. This is accomplished through a variety of processes: sometimes additional life-forms increase total roots; sometimes an added life-form increases ET, thereby reducing deep infiltration; sometimes uptake by additional life-forms compensates for low nutrient demand by an ecosystem dominant; and sometimes additional species provide the functional redundancy required to compensate for catastrophic loss. Species identity is important in understanding the specific mechanisms involved.

Simple, multi-life-form ecosystems can safeguard the ecosystem functional property of nutrient retention, making them important tools in restoration, agroforestry, and agronomy. Additional functional properties require more species (Hector and Bagchi 2007; Gamfeldt et al. 2008), and landscape-scale multifunctionality can require an

array of communities, each of different composition (Zavaleta et al. 2010). Sustaining even one ecosystem service, such as reduced rates of leaching, is a challenge in light of shifts in competitive balance among life-forms that sometimes lead to increasing simplicity. This is especially true when ecosystems are closed to colonization, where processes enhanced through complementary use of resources at one stage sometimes deteriorate as complementarity gives way to dominance by a superior competitor. Managers need to expect, tolerate, and even foster change in composition if they wish to sustain ecosystem services.

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