

Is tree diversity an important driver for phosphorus and nitrogen acquisition of a young tropical plantation?

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ABSTRACT

Many tropical plantations in Central America are monocultures of fast growing, mostly exotic species such as a teak, eucalypts and pines. This has been perceived as a problem for ecosystem stability, pest control, local biodiversity and long-term nutrient availability. In our study, we followed the effects of increasing tree diversity (1, 3 and 6 native species) on aboveground nitrogen (N) and phosphorus (P) pools in a young experimental biodiversity plantation (central Panama) over two subsequent years. Our results show a positive but not consistent net effect of biodiversity on the N and P pools, mainly explained by the complementarity effect. N and P use efficiencies strongly varied among the investigated tree species and the species richness gradient. *Anacardium excelsum* and *Luehea seemannii* were associated with higher N and P use efficiencies while *Hura crepitans* and *Tabebuia rosea* were less efficient in aboveground biomass production per unit N or P. Tree species tended to have lower P use efficiencies in the intermediate diversity level compared to monocultures and six-species mixtures. Although the environmental conditions explained a large part of the variation in the N and P pools (58%) in our experiment, we argue that incorporating tree mixtures in the management can bring additional benefits and improve tree growth and nutrient uptake as compared to the monocultures.

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1. Introduction

As the cover of natural tropical forests has declined over the last decades and the demand for wood products continues to grow, tree plantations have become increasingly important. The conversion of grasslands into forest plantations is currently a wide-spread land use in tropical regions and contributes to the production of timber, fuelwood and could serve as carbon-sinks under the Clean Development Mechanisms (UNEP, 2008) within the Kyoto Protocol. According to FAO (2005), the area of forest plantations increased at a rate of 2.8 million ha yr⁻¹ between 2000 and 2005. However, many of the tropical plantations are monocultures of fast growing, mostly exotic species as teak (*Tectona grandis*), eucalypts or pines. This has been seen as a problem for system stability, long-term nutrient availability and associated biodiversity (Aweto, 2001; Haggard et al., 1998; Piotto et al., 2003; Spangenberg et al., 1996 and references in Hartley, 2002).

Thus, both the tremendous loss of biodiversity due to disappearance of the tropical rainforest and the predominance of monocultures in plantation forestry have raised concerns about the significance of tree diversity for ecosystem functioning and the delivery of goods and services (Millennium Ecosystem Assessment, 2005). Although some of the experimental and observational studies from the tropics suggested positive effects of mixed plantations on tree growth and productivity (Erskine et al., 2006; Potvin and Gotelli, 2008; Petit and Montagnini, 2004; Piotto et al., 2004; Redondo-Brenes and Montagnini, 2006), tree regeneration (Carnevale and Montagnini, 2002) and nutrient storage (Montagnini, 2000), no or negative effects were found for litter decomposition (Scherer-Lorenzen et al., 2007), soil nutrient concentrations (Firn et al., 2007; Stanley and Montagnini, 1999) and woody understorey diversity (Butler et al., 2008). As a result, several of these studies highlighted the importance of tree species identities in mixed stands rather than species richness per se. Positive effects of diversity were often observed in mixtures including N₂-fixing tree species. This has led to intensive research on facilitative tree interactions (cf. Forrester et al., 2006; Kelty, 2006). In contrast, less information is available about other positive plant interactions such as complementary resource use. Two important aspects of complementary resource use in tropical managed systems are

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light partitioning through canopy stratification and water and/or nutrient partitioning, e.g. through root stratification. While there is substantial evidence from plantation forestry on the first aspect (Ewel and Mazzarino, 2008; Menalled et al., 1998), information on belowground mechanisms largely comes from tropical agroforestry studies (e.g. Dinkelmeier et al., 2003; Rowe et al., 2001; Schroth et al., 2001). Nevertheless, the implications for tree nutrition and hence tree productivity are large, if species with complementary resource use can be identified for plantation purposes (Richards et al., 2010).

A possible way to statistically assess the importance of tree species complementarity in mixtures is by applying the additive partitioning method of Loreau and Hector (2001). This method allows to partition the net effect of biodiversity (NE) into a complementarity effect (CE) and a selection effect (SE). SE represents the changes in resource uptake and/or biomass production of a mixture due to the dominance of a particular species with a disproportionate effect on these traits (also referred to as sampling effect). In contrast, CE represents the changes in NE which cannot be attributed to any single species in the mixture and is often interpreted as evidence for niche separation of facilitative species interactions. However, Cardinale et al. (2007) concluded in their study that CE rather includes all forms of resource partitioning, i.e. also indirect and non additive species interactions, thus making it impossible to identify a single biological mechanism for positive mixture effects. Nevertheless, applying the additive partitioning method in plantation forestry still could be useful to identify combinations of tree species resulting in a positive biodiversity effect through multiple species processes. In addition, site characteristics such as soil nutrient availability and topographical heterogeneity must be included in studies on diversity effects as they can have a strong influence on tree nutrition and may enhance or hide effects of species richness (Healy et al., 2008; Hiremath and Ewel, 2001).

The quantification of nutrients stocks in the aboveground biomass is an important issue in sustainable plantation management. Depending on rotation length and harvest practices, the amount of nutrients lost through biomass removal can crucially determine the future success of productive plantations (Montagnini and Jordan, 2005). Nutrient use efficiency, i.e. the amount of biomass produced per unit of a certain macro- or micronutrient, is a useful measure to assess the nutrient demand and the productivity of a tree species on a site. Especially, the use efficiencies of the two macronutrients nitrogen (N) and phosphorus (P) by different tree species need to be considered for sustainable site management, since the two nutrients are pivotal in many metabolic plant processes and are known to limit plant growth (Metzner, 1995; Niklas, 2008).

The Sardinilla plantation in Panama is a tree biodiversity experiment designed to test the relationship between biodiversity and ecosystem functioning. In contrast to many other research plantations in the tropics, its experimental setup does not include N_2 -fixing tree species due to their known and strong effects in mixed forest experiments. Therefore, the design allows to address other, more subtle mechanisms than N_2 -fixation, as for example complementary soil resource use or changes in nutrient use efficiencies (Richards et al., 2010). The aim of this study was to address the importance of tree diversity for acquisition of P and N by the trees in a native tree species plantation. By estimating the amount of the two macronutrients stored in the standing biomass, henceforth referred as N and P pools, we intended to answer the following questions:

1. Does species richness and species composition affect the size of N and P pools in the trees and if so, is this caused by selection or complementarity?

2. To what extent do the environmental variables contribute to the explanation of the N and P pool patterns in the plantation?
3. Are N and P use efficiencies affected by the tree species and/or the species richness?

2. Materials and methods

2.1. Study site

The study was conducted during 2006 and 2007 in an experimental tree plantation in Sardinilla (9°19'30"N, 79°38'00"W), central Panama, approximately 50 km north of Panama City. The study site has an elevation of 70 m a.s.l. and extends over a slightly undulated terrain. Mean annual precipitation is around 2350 mm with a prominent dry season from January to March, and mean annual temperature is 25.1 °C with a daily minimum of 21.7 °C and a maximum of 33.1 °C. The soils belong to the order of Alfisol with Typic Tropudalfs on the ridges shifting to Aquic Tropudalfs in the depressions. They contain a high content of expanding clays (up to 65%), causing deep cracks during the dry season. The bedrock is composed of Tertiary limestone and other sedimentary rocks (Potvin et al., 2004). The site was originally covered with semideciduous tropical lowland forest until it was logged in 1952/53, subsequently used for cropping (2–3 years) and eventually converted into a pasture. The plantation was established in 2001; it consists of 24 plots (45 × 45 m), each divided into 4 subplots of equal size (Healy et al., 2008), with an initial tree density of 1111 trees ha⁻¹. The six tree species planted are all native to Panama and include two fast-growing species *Luehea seemanii* (Tiliaceae) and *Cordia alliodora* (Boragniaceae), two moderately fast growing species *Anacardium excelsum* (Anacardiaceae) and *Hura crepitans* (Euphorbiaceae) and two slow growing species *Cedrela odorata* (Meliaceae) and *Tabebuia rosea* (Bignoniaceae). The design included 12 monocultures (2 replicate plots per species), six replicates of three-species and six replicates of six-species mixture plots (see Fig. A.1 in the supplementary). Three-species mixtures differed in their species composition, whereas six-species mixtures did originally include all six tree species and were thus identical in composition (Scherer-Lorenzen et al., 2007). *Cordia alliodora* suffered such high mortality rates after planting that it almost completely failed to establish in the plantation. The two monoculture plots of *C. alliodora* had to be abandoned. Therefore, we excluded this species from the analyses. In extension to a previous study by Oelmann et al. (2010) that used an individual tree approach, our investigation expanded over 2 years and included the collection of plant and soil samples in all relevant plots of the experimental design. In particular, the terrain elevation differences and information on the slope inclination were integrated in the analyses.

2.2. Sampling

At the end of the growing season (December to January) in 2006 and 2007, every tree in the plantation was measured in order to estimate aboveground tree biomass. Tree height was assessed using a hypsometer (Vertex III, Haglö, Sweden). Tree basal diameter (BD), taken at 10 cm aboveground, and tree diameter at breast height (DBH) were measured with a circumference chain.

For the determination of nitrogen and phosphorus concentrations, leaves and branches were collected during the rainy season between 4 and 7 July 2006 and 2 and 6 July 2007. In each plot, 3 individuals (within ±2 m of mean tree height) were semi-randomly selected for each species. Border trees were omitted to avoid edge effects. From each tree, 5–10 sun and shade leaves each, and 3 terminal branches were collected. From each of the branches, one disc of about 1 cm thickness, including both bark and wood, was

processed. All samples were dried for 3 days at 65 °C to constant mass and ground. Nutrient data of stems were kindly provided by Oelmann et al. (2010).

Soil samples for the quantification of pH, total, organic and microbial phosphorus concentrations were collected at the early rainy season in June 2007. Soil samples were collected at 4 equally distributed locations per subplot at a depth of 0–10 cm and pooled to one sample per subplot. Samples were taken with an soil core sampler (\varnothing 2 cm, Eijkelkamp Agrisearch Equipment, The Netherlands). Coarse plant debris and stones were manually removed from the samples since the moist soil was too sticky to pass through any sieve.

For the analysis of total soil C and N, inorganic N (nitrate and ammonium) and plant available P concentrations, soil samples were collected in a second sampling campaign during the wet season between the 9 and 27 August 2007. Samples were taken from six locations per subplot with the constraint that all species were represented equally near the sampling locations. We collected soil from 3 different soil depths: 0–5, 5–15 and 25–35 cm. The six soil samples from a subplot were pooled to one sample per subplot per depth, resulting in 12 samples per plot (4 subplots \times 3 depths).

N mineralization rates (ammonification and nitrification) in the field were estimated using *in situ* aerobic incubation (Hart et al., 1994). The first incubation experiment was done during the transition from the dry to the wet season (15–23 May 2007), the second campaign was carried out in the wet season (15–23 August 2007). In one subplot per plot, we randomly chose two locations in monocultures, 3 locations in 3-species mixtures and 6 locations in the six-species mixtures (locations were equally distributed to the different tree species). Two plastic tubes with a diameter of 7.5 cm were inserted 15 cm into the soil at each location. One cylinder was removed immediately and taken to the laboratory for analysis. The other tube was capped with a styrofoam cover permitting gas exchange with the atmosphere and remained in the field for a period of 8 days. In addition, we visually estimated the cover of the herbaceous understorey in the area, where tubes were inserted.

All soil samples were divided into different subsamples. One subsample was dried at 105 °C for 48 h to determine water content gravimetrically. Another subsample was dried at 65 °C for 72 h and pulverized in a ball mill for nutrient analyses. For the determination of inorganic N, field-moist soils were kept in cool darkness and were processed within 2 days after the field sampling.

2.3. Chemical analyses

Total C and N concentrations in plant and soil samples were measured with an elemental analyzer (Euro EA, HEKAtech GmbH, Germany). P concentrations in plant samples were determined according to Ohno and Zibiliske (1991). In brief, 100 mg of plant material were incinerated for 8 h at 550 °C, ashes dissolved in 2 ml HNO₃ (65%), filtered through a paper filter (Whatman No. 40) and made up to 25 ml. Soil microbial P and plant available P was extracted from soil by anion exchange resin adsorption according to Kouno et al. (1995) and Saggari et al. (1990), organic and total P in the soils were assessed after ignition according to Saunders and Williams (1955). The concentration of P in the soil extracts was measured colorimetrically using malachite green according to Ohno and Zibiliske (1991). Mineral N (NO₃⁻ and NH₄⁺) was extracted from soils according to Faithfull (2002), filtered and kept frozen at -20 °C until analysis. Extracts were then analyzed photometrically using a Flow Injection Analyzer (San⁺, SKALAR Analytical B.V., The Netherlands). Soil pH was measured with an Orion pH meter (720A) in water extracts (1:5; w:v).

2.4. Calculations and statistical analyses

Aboveground tree biomass was estimated by species-specific allometric equations based on tree height, BD and/or DBH (Oelmann et al., 2010). For each species, the allometric equation was derived from the data of 10 trees per diversity level harvested during December 2006 and January 2007. Further, this data was used to define the biomass allocation to different aboveground plant compartments (leaves, branches and stems) for each species separately. We applied the same set of allometric equations and allocation patterns for both years of our study as species-specific allometric equations were not available for 2007.

Aboveground tree biomass in Mg ha⁻¹ at the plot-level was calculated by summing across all individuals of all species measured in the plot.

N and P pools (kg N or P ha⁻¹) at the stand level were calculated as the sum of products of mean nutrient concentrations in leaves, branches and stems times the plot biomass of each compartment (leaves, branches or stems). Biomass and pool calculations were done for each species, diversity level and year separately.

As a measure of nutrient use efficiencies, we determined the amount of tree biomass produced per unit of aboveground N or P (NUE and PUE, respectively, in kg DM kg⁻¹ N or P) of each tree species for both years.

Soil nutrient concentrations were averaged over the different soil depths and subplots resulting in a mean concentration per plot.

N mineralization rates were calculated according to Hart et al. (1994):

$$N_{\text{Min}} = \frac{(\text{NH}_4^+ + \text{NO}_3^-)_{t_1} - (\text{NH}_4^+ + \text{NO}_3^-)_{t_0}}{\Delta t} \quad (1)$$

where N_{Min} is the net mineralization rate (mg N kg_{soil}⁻¹ day⁻¹), NH₄⁺ and NO₃⁻ are the ammonium and nitrate concentrations (mg N kg_{soil}⁻¹), respectively, at the beginning (t_0) and the end (t_1) of the incubation period Δt (8 days).

To compare the productivity of the different tree species, we tested the effects of diversity, species and time on the aboveground biomass normalized for species richness. Therefore, we applied a linear mixed effect model with repeated measurements (year), where planted diversity (=species richness 1, 3 or 6), species and sampling years were defined as fixed effects and species within plots was defined as random effect. We chose mixed effect because they are recommended for unbalanced datasets (Pinheiro and Bates, 2000). In our design, the imbalance is the number of replicates per diversity level. Estimates of variance parameters were calculated by Restricted Maximum Likelihood, which takes into account the degrees of freedom for fixed effects. Effect of the different treatments on aboveground biomass, N and P pools in the different plant compartments and on N and P use efficiencies were tested with similar models. Where necessary, data were log-transformed for analysis. Linear mixed effect models were fitted using the nlme package (Pinheiro et al., 2008) of R version 2.8 (R Development Core Team 2007).

As a second approach to determine effects of tree diversity on aboveground N and P pools, we applied the additive partitioning method of Loreau and Hector (2001) to the nutrient pool data to unravel any biodiversity effect. This method defines an overall net effect (NE) of biodiversity composed of two additive components: a selection effect (SE) and a complementarity effect (CE). Therefore, we calculated ΔRY_i , which is the deviation of the observed from the expected relative N or P pool of species i in the mixture, according to the following equation:

$$\Delta RY_i = RY_{O_i} - RY_{E_i} \quad (2)$$

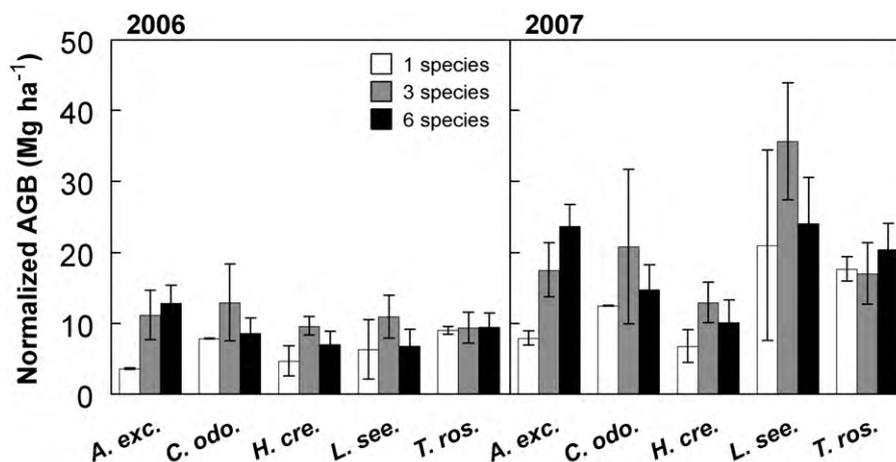


Fig. 1. Normalized aboveground biomass (AGB) in Mg ha^{-1} for each species across the species richness gradient. Values are means \pm standard errors. Species had no effect on AGB in 2006 but in 2007 with $A.\text{exc.} > H.\text{cre.}$; $L.\text{see.} > C.\text{odo.}$; $L.\text{see.} > H.\text{cre.}$ and $T.\text{ros.} > H.\text{cre.}$. Species richness had no significant effect on normalized AGB in none of the 2 years. Species abbreviations are given in Table 2.

where RY_{0i} is the observed N or P pool of species i in the mixture divided by the N or P pool of its monoculture (mean of two monoculture plots) and RY_{Ei} is the expected relative N or P pool, which corresponds to the proportion of the species i planted in the mixture. Tree species, which are not affected by other species in mixtures, will show $\Delta RY_i \approx 0$. Effects of competition on the N and P pool size would lead to $\Delta RY_i < 0$, whereas complementarity effects will be indicated by $\Delta RY_i > 0$ according to Loreau and Hector (2001).

Similar to Healy et al. (2008), we performed a partial redundancy analysis (RDA) to evaluate the influence of soil nutrient parameters on the variability of the N and P pools in the plants. We reduced the set of environmental variables by conducting stepwise regression (forward selection) of the following fourteen parameters: Total soil C and N, nitrate, ammonium, plant available phosphate, microbial, organic and total P concentrations, soil pH, N mineralization rates in May and August 2007, herbaceous understorey cover, plot elevation and slope inclination. Variables used were those statistically significant at the 10% level (Monte Carlo permutation test, $n = 999$). The reduced set of environmental variables was then used for unraveling the interaction between plant and soil data. The response matrix consisted of N and P pools in the trees at the plot-level, whereas the diversity matrix included the species richness and the realized species composition of each plot. Response and explanatory variables were centered and standardized for the analysis. In a first step, we employed RDA to estimate the total variation in the response data by both the diversity and environment variables. In a second step, we conducted a RDA for each of the two explanatory matrices solely with no covariables. In a third step, RDA was done with the environment matrix as explanatory variable and including the diversity matrix as a covariable and vice versa. As a result, total variation was decomposed into the pure effects of each one of the explanatory matrices and their joint effect (Legendre and Legendre, 1998). The significance of pure effects were tested by the Monte Carlo permutations ($n = 999$). For the multivariate analysis, the software application CANOCO Version 4.5 (ter Braak and Smilauer, 2002) was used.

3. Results

3.1. Aboveground biomass, nitrogen and phosphorus pools

Comparing the productivity of the different species, trees species had no effect on the normalized aboveground biomass in 2006 but in 2007 (species \times year, $F_{4,40} = 35.3$, $P < 0.0001$, Fig. 1).

In 2007, *A. excelsum*, *L. seemannii* and *T. rosea* had more standing biomass than *H. crepitans*. Differences between the species across diversity were not significant (diversity \times species, $F_{8,21} = 1.14$, $P = 0.127$).

From 2006 to 2007, average standing biomass at the stand level nearly doubled from 7.47 to 15.1 Mg ha^{-1} (see Fig. 2a and b), which proved highly significant (Table 1). The largest fraction of freshly produced biomass appeared in the stems of trees (4.08 Mg ha^{-1}), followed by branches (2.86 Mg ha^{-1}) and leaves (2.17 Mg ha^{-1}). Species richness had no significant effect on any of the three plant compartments (Table 1). In both years, three-species mixtures tended to have higher standing biomass (9.15 and 17.5 Mg ha^{-1} for 2006 and 2007, respectively) than six-species mixtures (7.58 and 15.7 Mg ha^{-1}) or monocultures (6.41 and 13.3 Mg ha^{-1}), but the effect of species richness was not significant ($F_{2,19} = 0.83$, $P = 0.449$, Fig. 2a and b).

The total N pool in the standing biomass significantly increased by $35.9 \text{ kg N ha}^{-1}$ from 2006 to 2007. Most of the N taken up or remobilized was stored in the leaves (42%), whereas the proportions in stems and branches were similar, 32% and 26%, respectively (see Fig. 2c and d). Again, there was no significant effect of species richness on either the stem, branch or leaf compartment (Table 1).

P pools in the standing biomass increased from 10.6 ± 1.29 to $16.8 \pm 1.93 \text{ kg P ha}^{-1}$ between 2006 and 2007 with a significant increase in the stem and leaf compartments (see Fig. 2e and f, Table 1). The largest fraction of P was allocated to stems (70.9%) and leaves (22.5%) and only a small fraction was stored in the branches (6.5%). Species richness had a marginally significant effect on the P pools in stems ($F_{2,19} = 2.74$, $P = 0.090$, Table 1), but not on the P pool in branches or leaves. In addition, interactions between species richness and years were not significant for any of the three plant compartments.

The additive partitioning of the aboveground N pools revealed a marginally significant net effect of species richness in 2006 and 2007 for the three-species mixtures (2006: $P = 0.052$; 2007: $P = 0.052$), but not for the six-species mixtures (Fig. 3, left panels). The net effect was actually not different between the three-species and six-species mixtures for any of the 2 years (species richness: % SS = 0.15, $P = 0.857$; Year: % SS = 1.65, $P = 0.558$). In 2007, the negative selection effect in the six-species mixtures was significantly different from zero.

Tree diversity had a significantly positive net effect on the aboveground P pools in the three-species mixtures in both measured years, but not in the six-species mixtures (Fig. 3, right panels,

Table 1
Linear mixed effect model for effects of species richness and sampling years on standing biomass, nitrogen pools and phosphorus pools in three compartments.

Variable ^a	Effect	Stem			Branch			Leaf			
		df	F	P	Mean (±SE)	F	P	Mean (±SE)	F	P	Mean (±SE)
Standing biomass (Mg ha ⁻¹)	Species richness (SR)	2; 19	0.77	0.476		0.85	0.443		1.25	0.310	
	1				5.23 ± 0.94			3.70 ± 0.58			60.94 ± 0.18
	3				7.09 ± 1.35			5.03 ± 0.84			1.22 ± 0.24
	6				6.00 ± 1.10			4.41 ± 0.80			1.21 ± 0.20
	Year	1; 19	193	<0.0001		190	<0.0001		187	<0.0001	
	2006				3.91 ± 0.45 ^b			2.84 ± 0.30 ^b			0.72 ± 0.01 ^b
Nitrogen pool (kg ha ⁻¹)	2007				7.99 ± 1.02 ^a			5.70 ± 0.64 ^a			1.45 ± 0.19 ^a
	SR × Year	2; 19	0.40	0.673		0.39	0.684		0.48	0.627	
	Species richness	2; 19	0.04	0.959		0.82	0.457		1.15	0.339	
	1				19.2 ± 3.82			22.4 ± 3.68			19.8 ± 4.11
	3				23.2 ± 4.28			28.2 ± 3.77			25.7 ± 4.93
	6				21.8 ± 4.21			28.3 ± 5.03			24.5 ± 4.19
Phosphorus pool (kg ha ⁻¹)	Year	1; 19	158	<0.0001		30	<0.0001		172	<0.0001	
	2006				15.3 ± 2.50 ^b			20.9 ± 2.74 ^b			15.2 ± 2.09 ^b
	2007				26.8 ± 3.62 ^a			30.2 ± 3.70 ^a			30.2 ± 4.10 ^a
	SR × Year	2; 19	0.81	0.459		0.01	0.992		0.95	0.405	
	Species richness	2; 19	2.74	0.090		0.81	0.459		0.95	0.405	
	1				5.32 ± 0.75			3.67 ± 0.47			2.07 ± 0.47
Phosphorus pool (kg ha ⁻¹)	3				10.7 ± 1.96			5.29 ± 0.86			2.66 ± 0.53
	6				6.25 ± 1.16			4.61 ± 0.80			2.22 ± 0.39
	Year	1; 19	182	<0.0001		1.20	0.287		124	<0.0001	
	2006				4.82 ± 0.67 ^b			4.16 ± 0.57			1.57 ± 0.23 ^b
	2007				9.26 ± 1.24 ^a			4.57 ± 0.54			2.98 ± 0.46 ^a
	SR × Year	2; 19	0.32	0.727		0.26	0.770		0.74	0.490	

^a Data were log-transformed for analysis, except the P pool in branches. Within-group means ± standard errors are presented for categorical variables. Values for the three plant compartments are averages of the two sampling years. Different letters denote significantly different means according to Tukey–Kramer multiple comparison test. $n=22$.

7.96 ± 2.65 vs. 3.15 ± 2.56 in 2006 and 10.9 ± 3.90 vs. 4.57 ± 3.49 in 2007). The difference between the two mixture types were only marginally significant (% SS = 13.0, $P=0.088$). The selection effect on the P uptake was negligible.

Analysis of the deviation from the expected relative nutrient pools showed that though the N and P pools of the five tree species were mostly positively affected in the three-species mixtures on average ($\Delta RY > 0$), e.g. *A. excelsum*, *C. odorata*, *H. crepitans* and *L. seemannii*, none of the deviations were actually significantly different from zero (see Table A.1 in the supplementary). Only the six-species mixtures showed a synergistic effect on the N and P pools of *A. excelsum* ($P < 0.05$), whereas the nutrient pools of the other four tree species did not differ from the respective monocultures.

3.2. Soil characteristics

We applied partial RDA to separate the variation in aboveground N and P pools into percentages explained by the environmental growing conditions vs. the tree diversity. By forward selection, we reduced the set of fourteen environmental variables (Table A.2 in the supplementary) to a set of five variables, consisting of elevation (m a.s.l.), slope inclination (°), soil NO₃⁻ and NH₄⁺ concentrations (mg N kg soil⁻¹) and plant available PO₄³⁻ concentration (mg P kg soil⁻¹) (Fig. 4). The five most productive plots, in terms of aboveground biomass, N and P pools (Ls1, T2, T4, A3 and A4), were located on the top of the small ridges and on the adjacent slopes facing the north-west direction, while the least productive

Table 2
Linear mixed effects model for effects of species richness, species and sampling years on nitrogen (NUE) and phosphorus use efficiencies (PUE).

Effect	df	NUE			PUE		
		F	P	Mean (±SE)	F	P	Mean (±SE)
Species richness (SR)	2; 19	0.48	0.627		17.4	0.001	
1				171 ± 13.1			870 ± 59.9 ^a
3				170 ± 8.61			710 ± 35.9 ^b
6				167 ± 7.47			881 ± 32.8 ^a
Species	4; 21	157	<0.0001		90.8	<0.0001	
<i>A. exc.</i>				203 ± 3.66 ^a			983 ± 52.5 ^a
<i>C. odo.</i>				206 ± 8.20 ^a			798 ± 46.9 ^b
<i>H. cre.</i>				83.9 ± 3.86 ^c			570 ± 22.7 ^c
<i>L. see.</i>				210 ± 4.31 ^a			1066 ± 34.6 ^a
<i>T. ros.</i>				139 ± 2.47 ^b			746 ± 31.0 ^b
Year	1; 40	26.6	<0.0001		28.8	<0.0001	
2006				160 ± 6.93 ^b			757 ± 32.2 ^b
2007				177 ± 7.71 ^a			908 ± 33.0 ^a
SR × Species	8; 21	2.87	0.025		10.5	<0.0001	
SR × Year	2; 40	0.12	0.884		0.43	0.657	
Species × Year	4; 40	2.21	0.085		0.25	0.907	
SR × Species × Year	8; 40	0.70	0.687		0.68	0.707	

Within-group means ± standard errors are presented for categorical variables, different letters denote different means according to a Tukey–Kramer multiple comparison test. $n=55$. Species abbreviations are *A.exc.* = *Anacardium excelsum*, *C.odo.* = *Cedrela odorata*, *H.cre.* = *Hura crepitans*, *L.see.* = *Luehea seemannii*, *T.ros.* = *Tabebuia rosea*.

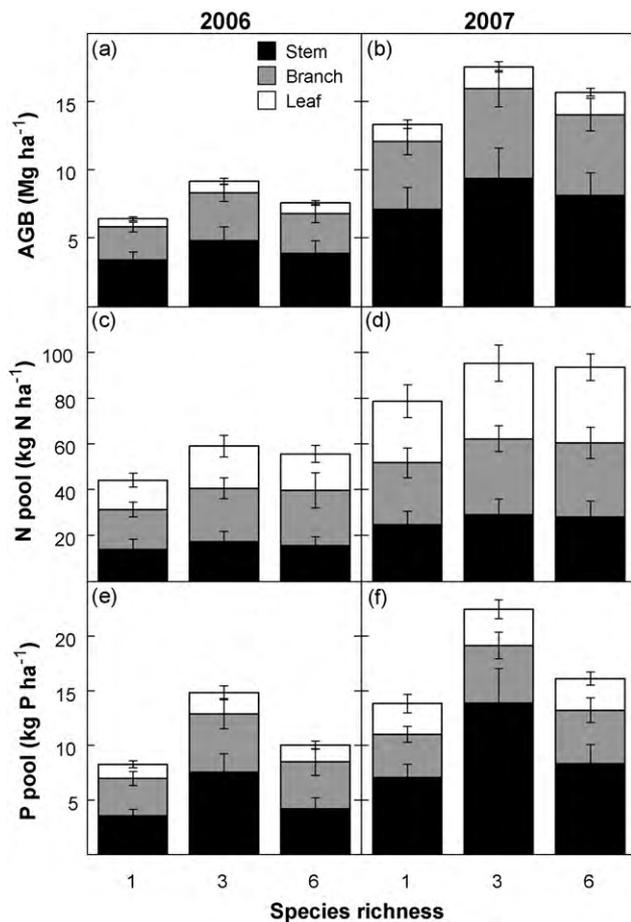


Fig. 2. Aboveground biomass (AGB), N and P pools in stems, branches and leaves along the species richness gradient at the treatment level. Values are means \pm standard errors with $n=10$ for monocultures and $n=6$ for three-species and six-species mixtures.

plots (Ae1, Hc1, Ls2, T6 and A2) were found on less steep slopes close to the depressions (see Fig. A.1 in the supplementary). P pools in trees depended on plant available P concentration (Fig. 5a), whereas N pools correlated significantly with the soil NO_3^- concentration (Fig. 5b), but not with the NH_4^+ concentration (Fig. 5c). Slope inclination was positively correlated with the tree P pools ($r=0.48$, $P<0.05$) but no relationship was found between slope and plant available P ($r=0.02$, $P=0.46$). However, the different soil nutrient concentrations were not significantly affected by diversity (Fig. 5).

As resulted from the partial RDA, this set of environmental variables and the tree species diversity explained 88.5% of the variance in the N and P pool data (Monte Carlo permutation test, $F=82.2$, significance of the first canonical axis $P=0.001$). The pure effect of the environmental variables covered 57.5% ($F=71.2$, $P=0.001$), tree diversity alone explained 17.3% of the total variance ($F=20.2$, $P=0.004$). The part of variation shared by the environmental variables and tree diversity was 13.7%. The explained variation by tree diversity was only significant after removing the effect of the environment, but the effect explained by environment was significant both with and without tree diversity as covariate.

3.3. Nitrogen and phosphorus use efficiencies

Nitrogen use efficiencies (NUE) of the five tree species were significantly affected by species richness (SR \times species interaction, Table 2 and Fig. 6a). Trees of *A. excelsum*, *L. seemannii* and

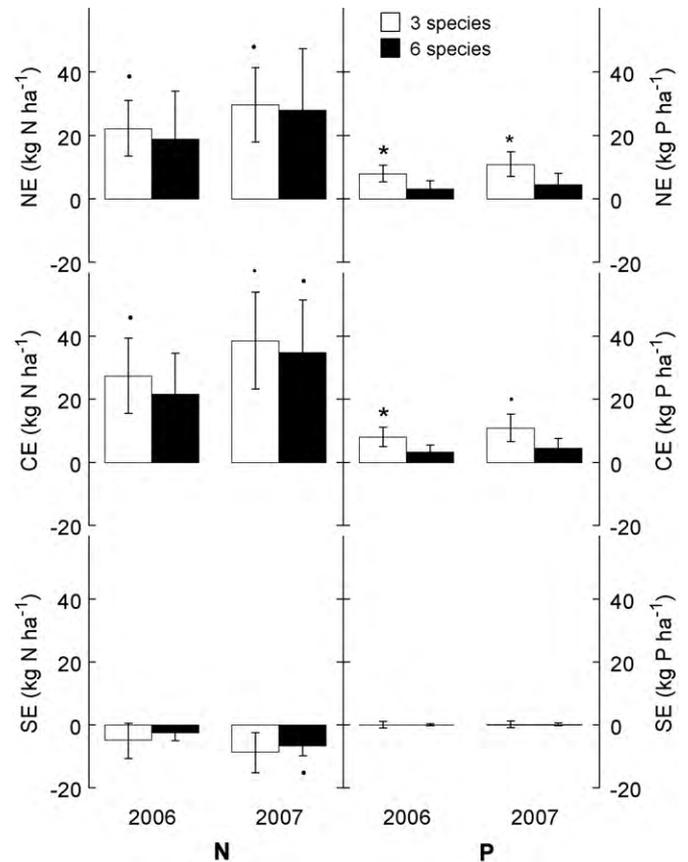


Fig. 3. Additive partitioning of nitrogen pool (left) and phosphorus pool (right) by species richness, calculated for each year separately. The net effect (NE) is the sum of the complementarity effect (CE) and the selection effect (SE). Means \pm standard errors are given ($n=6$). All effects in all diversity treatments and years were tested against zero (Student's t -test). Significant effects are indicated as followed: $\cdot P<0.1$; $*P<0.05$.

T. rosea showed no change in NUE along the species richness gradient, whereas *C. odorata* had significantly higher NUE in monocultures and six-species mixtures compared to the three-species mixture. The opposite pattern was observed for *H. crepitans*, which showed a significant increase in NUE in the intermediate diversity plots. Within the monoculture and six-species mixtures, *A. excelsum*, *C. odorata* and *L. seemannii* were significantly more efficient in terms of biomass production per unit N than *T. rosea* and *H. crepitans*, the latter being the least efficient tree species. NUE significantly increased from 2006 to 2007 (160 vs. 177 kg DM kg^{-1} N (Table 2).

The general linear mixed effect model also revealed a significant effect of species richness on the phosphorus use efficiencies (PUE) of our five species (SR \times species interaction, Table 2 and Fig. 6b). No significant changes in PUE along the species richness gradient were observed for *H. crepitans* and *T. rosea*. However, *A. excelsum* showed a significant linear increase in PUE with increasing species richness, whereas *C. odorata* and *L. seemannii* had significantly lower biomass production per unit P stored in the three-species mixtures compared to the six-species plots and corresponding monocultures. When planted with conspecific neighbours, *C. odorata* and *L. seemannii* were significantly more efficient than *A. excelsum*, *H. crepitans* and *T. rosea*. At the intermediate and high diversity level, the species patterns for PUE were similar. *A. excelsum* and *L. seemannii* showed the highest PUE, while *C. odorata* and *H. crepitans* were the least efficient species. Again, PUE increased over time from 757 to 908 (kg DM kg^{-1} P) between 2006 and 2007, respec-

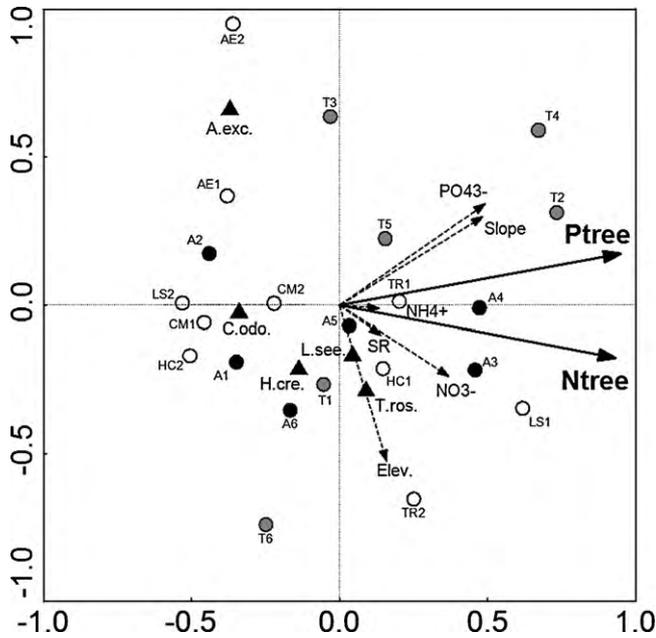


Fig. 4. Effect of soil nutrient availability and tree diversity on the aboveground nitrogen and phosphorus pools. Bold arrows represent response variables, dashed vectors represent explanatory variables, nominal variables are given as filled triangle, circles are given for the different plots. Vector are labeled as follows: Npool = N pool in standing biomass, Ppool = P pool in standing biomass, NO₃⁻ = soil nitrate concentration, NH₄⁺ = soil ammonium concentration, PO₄³⁻ = plant available phosphorus, Elev. = plot elevation, Slope = Slope inclination of a plot, A.exc. = *Anacardium excelsum*, C.odo. = *Cedrela odorata*, H.cre. = *Hura crepitans*, L.see. = *L. uehea seemannii*, T.ros. = *Tabebuia rosea*, SR = species richness.

tively, revealing no significant interactions with species or species richness (Table 2).

4. Discussion

4.1. Tree diversity effects on standing biomass and N and P pools

This research attempted to assess the importance of tree species diversity on aboveground biomass production and N and P acquisition on a per hectare basis. We originally assumed that higher tree diversity leads to an increase of the standing biomass and the N and P pools therein, based on either local deterministic mechanisms such as niche differentiation or complementary resource use (Loreau et al., 2001) or on local/regional stochastic processes such as the sampling or selection effect (Huston, 1997; Tilman et al., 1997).

When accounting for differences in tree density and tree age, standing biomass and macronutrient pools were within values reported from other tropical plantations (Hiremath et al., 2002; Lugo, 1992; Montagnini, 2000; Parrotta, 1999). The two approaches applied to detect possible effects of species richness on the N and P pools revealed, however, no linear or increasing relationship. This supports some other studies on the relationship between biodiversity and ecosystem functioning (Cardinale et al., 2006; Potvin and Gotelli, 2008). In our first analysis, species richness had only a marginally positive effect on the P pools in the stem compartment of the three-species mixtures. Since the P concentrations in stems did not differ within the different diversity levels (Oelmann et al., 2010), the increase in the P pools within the three-species mixtures was probably due to slightly higher biomass allocation to the stems and significantly lower PUE in three of the five three species.

In contrast to absence of clear effects in the first analysis, interesting results were obtained by the additive partitioning method

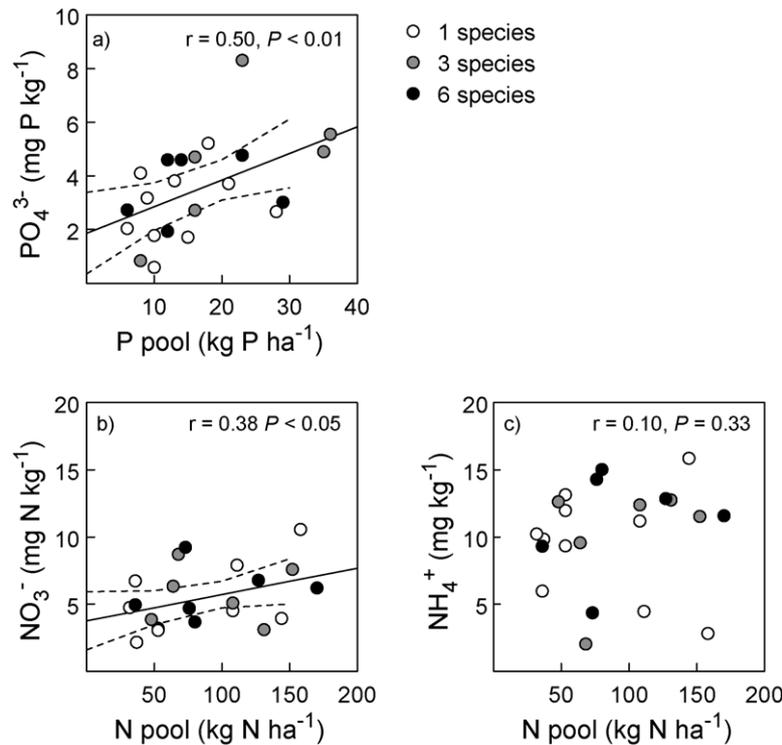


Fig. 5. Correlation between aboveground nutrient pools and soil nutrient concentrations. Different symbols indicate different diversity treatments. Species richness had no significant effect on plant available phosphorus ($F_{2,19} = 1.66, P = 0.22$), soil nitrate concentrations ($F_{2,19} = 0.37, P > 0.5$) and soil ammonium concentrations ($F_{2,19} = 0.36, P > 0.5$).

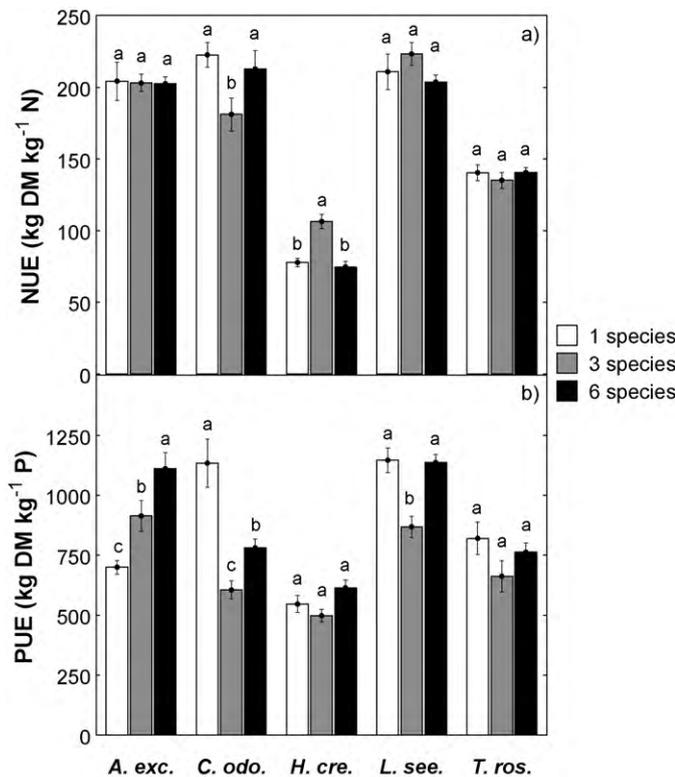


Fig. 6. Nitrogen and phosphorus use efficiencies (NUE and PUE, respectively) in monocultures, three-species and six-species mixtures for the five tree species. Given are means \pm standard errors for the 2 years combined. Letters denote significant differences between diversity treatments for each individual species. The two study years were significantly different from each for both NUE ($F_{1,40} = 26.6$, $P < 0.0001$) and PUE ($F_{1,40} = 28.8$, $P < 0.0001$). Species abbreviations are given in Table 2.

(Loreau and Hector, 2001). We found a distinct positive net effect of biodiversity (NE), due to complementarity (CE), on the above-ground P pools in the three-species mixtures (Fig. 3). Similarly, we found a positive trend for NE and CE on the N pools in the three-species mixtures, although the results were not as obvious as for the P pools. However, we were not able to assign this effect to some specific tree species although one species, *A. excelsum* had higher than expected N and P pools in most mixtures (see Table A.1 in the supplementary). Obviously, some species performed well in particular three-species combinations but not in others. It strengthens the observations made in other studies that not only species richness but also the species identity is crucial for the type of species interaction and the performance in the mixture (Potvin and Gotelli, 2008; Redondo-Brenes and Montagnini, 2006; Scherer-Lorenzen et al., 2007). Further, it is worth noting that we found an increasing negative selection effect (SE) over time in the partitioning of the N pools, suggesting the dominance of a species with small N pools in monocultures. From the comparison between monoculture and mixture performance (ΔRY_i), *A. excelsum* was the only species with significantly higher N and P pools in species rich plots than in pure stands. We ascribe this finding to the position of the two pure stands of *A. excelsum* in waterlogged areas of the plantation (Fig. A.1 in the supplementary), where tree growth was probably suppressed. Healy et al. (2008) in their study also observed low productivity and high mortality rates for *A. excelsum* in the Sardinilla plantation but were not able to relate it to a specific cause. However, the example of *A. excelsum* points out the difficulty in interpreting the effect size calculated by the additive partitioning method. According to the method of Loreau and Hector (2001), the ability of a species to compete in a mixture is predicted on its performance in monoculture. As in the case of *A. excelsum*, however, the

monoculture of a species might not necessarily be a good reference point for such a prediction (Schmid et al., 2008).

4.2. Tree diversity and environmental effects on NUE and PUE

The nutrient use efficiencies calculated for our five tree species were within the range reported for other tropical tree species (Hiremath et al., 2002; Wang et al., 1991), although our calculation did not account for the amount of N and P in the litter and belowground biomass. In contrast to the findings of van Ruijven and Berendse (2005), we did not detect an increasing relationship between diversity and NUE and PUE. In their experiment with four grasses and four dicot species, they showed an increase of NUE with increasing species richness for five of their eight species. They argue that, in their N-limited system, this effect was a result of changes in the biomass allocation and represents another important mechanism contributing to the often observed positive relationship between diversity and productivity. A recent review by Richards et al. (2010) also showed that in 65% of tree mixture studies, where resource use efficiencies could be calculated, trees growing in mixtures had different use efficiencies than in monoculture. However, both increases and decreases in these efficiencies were observed, and a variety of potential mechanisms for such changes have been discussed. In our study, changes in NUE were not consistent with increasing biodiversity. This goes in line with the fact that there are yet no general diversity effects on ecosystem processes in the Sardinilla plantation. For specific species mixtures, especially at the three-species level, some positive effects of mixing species have been documented, e.g. on biomass production, litter fall and nutrient pools (Potvin and Gotelli, 2008; Scherer-Lorenzen et al., 2007; Oelmann et al., 2010) as discussed below.

Interestingly, we observed significantly lower PUE in the three-species mixtures compared to monoculture or the high diverse plots, which is counter intuitive giving the above mentioned positive diversity effects at this diversity level. Richards et al. (2010) in their review reported that 47% of the studies where shifts in P use efficiency could be calculated showed a decrease of >10% for species grown in mixtures compared to monocultures. In some of those studies, productivity of the plantation increased although NUE and PUE of individual species decreased. As discussed in Richards et al. (2010), the productivity in mixed stands may not necessarily be determined by the use efficiency of a single nutrient but rather how the individual species use all limiting above- and belowground resources.

Further, lower nutrient use efficiencies have often been related to higher nutrient availabilities (Aerts, 1990; Boerner, 1984; Hidaka and Kitayama, 2009; Silver, 1994; Vitousek, 1982). For example, values given by Hiremath et al. (2002) for *C. odorata* were lower (145 and 469, for NUE and PUE, respectively) than in our study (206 and 798), which might be due to the relatively nutrient rich soils at La Selva Biological Station in Costa Rica compared to our site. Other authors suggested that mixed species stands have higher nutrient availabilities than monocultures, even in the absence of N₂-fixing species (Rothe and Binkley, 2001; Binkley and Giardina, 1998). Likewise, we found a linkage between resource use efficiency, diversity and nutrient availability in the Sardinilla experiment. On the one hand, there was for both N and P, respectively, a positive relationship between nutrient availability and the corresponding nutrient pools in the trees but no effect of diversity on the N or P availability (Fig. 5). On the other hand, tree nutrient pools themselves tended to be higher in three-species mixtures as shown with the additive partitioning method, supporting previous results by Oelmann et al. (2010). Although nutrient availability is an important determinant of tree nutrient pools, some patterns can apparently only be explained by species interactions. This suggestion is confirmed by the decomposition of variation in the N and P pool data by the

RDA. Soil nutrient availability, scale and topographic heterogeneity have often been mentioned to mask or enhance biodiversity effects (Vila et al., 2005; Mittelbach et al., 2001). In our study, the part of variation explained by the environment was three times larger than the explanatory power of tree diversity. This finding is in good agreement with the results of a previous study of Healy et al. (2008) on the effect of environmental heterogeneity on tree growth and mortality. The effects of tree diversity became only significant after the effect of the environment was removed, indicating that the influence of diversity was hidden by the effect of environment. However, to examine the feedback mechanisms of tree diversity and tree species on soil nutrient availability and vice versa, repeated measures of soil nutrient availability soil would be needed on the long-term. Nevertheless, the significant increase in N and P use efficiencies from 2006 to 2007 in the Sardinilla plantation could indicate that N and P availability in the soil is gradually decreasing.

Other researchers in the Sardinilla project reported similar prominent effects of the three-species mixture. For example, Scherer-Lorenzen et al. (2007) found higher litter production in plots of intermediate diversity as compared to monocultures and six-species mixtures, 5 years after planting, and Potvin and Gotelli (2008) found significant over-yielding of three-species mixtures in that year. Oelmann et al. (2010), following an individual tree approach, found also increased N and P storage in the tree biomass in 2007 in the intermediate diversity treatment. In our study, two out of the six three-species mixture plots showed transgressive overyielding in N acquisition and even four out of the six three-species mixtures had higher P acquisition than expected from their best monoculture in both years (see Table A.3 in the supplementary), but only one six-species mixture out-performed the respective monoculture. Since the three-species mixtures all differed in their species composition, there was not a particular set of species causing this effect. The observed pattern might perhaps be explained by a combination of positive species interactions and small scale heterogeneity in nutrient availability, that eventually resulted in resource use complementarity. Furthermore, we suppose that positive species effects found in certain three-species combinations were “diluted” in the highest diversity level. In the six-species mixtures, species with similar growth rates (Scherer-Lorenzen et al., 2005) were planted in direct adjacencies. This probably led to an adverse increase in interspecific competition (Scherer-Lorenzen et al., 2007; Oelmann et al., 2010). In addition, the lower inter- and intraspecific competition and the increased P acquisition in the three-species mixture could also be related to association with mycorrhizal fungi. As Klironomos et al. (2000) found in an old grassland field, the presence of arbuscular mycorrhizal fungi led to a positive but asymptotic response curve between plant species richness and productivity, reaching the maximum biomass not at the highest species richness level but at a lower to intermediate level of species richness.

5. Conclusion

The Sardinilla plantation is still at an early stage of development. Large amounts of N and P are being taken up by the trees from the soil every year. We expect that effects of tree diversity on ecosystem processes, such as nutrient accumulation, will change over the time course as it has been shown for other tropical plantations (Ewel and Mazzarino, 2008). Though the outcome of a plantation might indeed depend predominantly on the given environmental conditions, our data clearly indicate that incorporating tree mixtures, and particularly the selection of matching tree species in the tropical forest management, has the potential to bring additional benefits as compared to monocultures and improve tree

growth and nutrient uptake per unit of land surface. Further, information on aboveground nutrient pools and nutrient use efficiencies might also help selecting tree species for restoration of degraded lands. Planting species with high nutrient demands and low nutrient use efficiencies (e.g. *H. crepitans* and *T. rosea*) might result in adverse effects on soil fertility on the long run. Under such circumstances, sustainable management should include less nutrient demanding species, which are able to increase their nutrient use efficiencies when grown in mixtures (e.g. *A. excelsum*).

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.foreco.2010.07.020.

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