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REGULAR ARTICLE

Tree mixture effects on aboveground nutrient pools of trees in an experimental plantation in Panama

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Abstract Mixed plantations might contribute to sustainable land use because of complementary nutrient use. Our objective was to assess the nutrient economy of five native tree species and their response to different neighbor trees in an experimental plantation in Panama. In our study, *H. crepitans* was the least nutrient efficient tree species. *H. crepitans* produced less biomass in mixtures than in monocultures while *Cedrela odorata* – the most nutrient efficient species – produced more biomass independent of stem growth rates because they acquired more nutrients in mixtures than in monocultures.Three-species mixtures had increased mean Ca concentrations in branches and stems and increased N, P, K, Ca, and Mg storage in aboveground biomass compared to monocultures suggesting complementary resource uptake. Our results highlight the need to properly consider species-specific nutrient requirements and species interactions when designing tree mixtures for afforestation.

Keywords Tree nutrient storage · Tree diversity · Overyielding · Sardinilla Project

Abbreviations

A. exc.	*Anacardium excelsum* (Bert. & Balb. Ex Kunth) Skeels
BA	basal area
BM	biomass
C. odo.	*Cedrela odorata* L.
DBH	diameter at breast height
D_{MAX}	deviation from expected biomass production or nutrient storage based on best performance of corresponding monocultures
H. cre.	*Hura crepitans* L.
HT	height
L. see.	*Luehea seemannii* Triana & Planch
NF	neighborhood factor
NW	neighborhood weighted
T. ros.	*Tabebuia rosea* (Bertol.) DC

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Introduction

In the tropics, concern over biodiversity loss and the need to reforest degraded land led to a debate on the use of species mixtures in plantation forestry (Kelty 2006). Particularly in the tropics, plantations are often established with exotic tree species (Parrotta 1999; Binkley et al. 2003). Because of negative effects on long-term ecosystem stability i.e., decreased water tables and increased damage by herbivores, this plantation practice was criticized (Leopold et al. 2001). Alternatively, mixtures of native tree species are beginning to be used successfully for reforestation in the tropics (Redondo-Brenes and Montagnini 2006; Weber et al. 2008) which might be a better substitute for naturally occuring forests than mixtures of exotic tree species. Although many probable beneficial effects of mixed native-tree plantations on ecosystem functioning in the tropics were proposed (Leopold et al. 2001; Evans and Turnbull 2004; and references therein) experimental validations remain scarce.

Little is known about the effects of planting monocultures or combinations of native tropical trees on the nutrient cycle of the resulting forest ecosystems (Montagnini 2000). The design of mixed plantations is generally based on complementarity of traits among tree species (position in a stratified canopy) or on facilitation among species (additional N supply by N_2 fixing species; Kelty 2006, Piotto 2008). At the community level, plant species can use available nutrients in a complementary way. The reason is that strong competition in diverse systems promotes niche differentiation in space or time, resulting in more effective community resource use compared to less diverse systems (Hooper et al. 2005). In grassland manipulation experiments, several authors reported a positive relationship between plant diversity and productivity (Naeem et al. 1996; Tilman et al. 1996; Tilman et al. 2001; van Ruijven and Berendse 2003; Spehn et al. 2005). In forestry, studies of mixture effects on productivity date back to the 18th century in temperate regions (Pretzsch 2005). Positive effects of mixtures compared to monoculture stands were reported for stem wood production and nutrient cycling (Rothe and Binkley 2001, Pretzsch 2005). These studies focused primarily on interactions of two tree species. Based on a meta-analysis of literature, Piotto (2008) found that mixtures containing up to seven tree species increased productivity across tropical and temperate plantations.

Another important knowledge gap pertains to site-specific adaptation. Because of the large number of tropical tree species, knowledge of site conditions such as soil nutrient availability, soil water regime or microclimate required for successful establishment is scarce (Mackensen et al. 2000; Hiremath et al. 2002; Binkley et al. 2003). Some mixed forest stands stored more nutrients in aboveground biomass than expected from summing up the nutrient storages of corresponding monocultures (Montagnini 2000), which could be explained by increased nutrient uptake through increased biomass. However, opposite effects of mixtures on biomass and nutrient storage were also observed, highlighting the importance of both species identity and local site conditions (Pretzsch 2005).

Competition with neighbor trees of another species might either increase (“overyielding”) or decrease (“underyielding”) the biomass production of a particular species in mixtures compared to monocultures, because of differing intra- and interspecific competitiveness (Hector et al. 2002). The different biomass production of mixtures and monocultures also affects the associated nutrient storage of plant species (Palmborg et al. 2005). The biomass production of a plant species in mixture might be related to nutrient use efficiency because a more nutrient efficient plant species should be more competitive in mixtures and consequently result in overyielding (Vitousek 1982; Hiremath and Ewel 2001). One indicator of nutrient use efficiency is the inverse of N concentrations in aboveground litterfall (Vitousek 1982), that should be determined simultaneously to studying diversity effects in mixtures to control for effects of successional stages (Ingestad and Ågren 1992). It has to be kept in mind that this measure of N use efficiency does not include the coarse litter fall and retranslocation of N prior to the abscission of leaves possibly also associated with the production of new biomass (Vitousek 1982).

So far, species identity or species diversity have not been explicitly included in concepts of ecosystem element cycling (Groffman et al. 2004), nor in models like CENTURY, Biome-BGC, and TEM (Running and Coughlan 1988; Raich et al. 1991; Parton et al. 1993). In a recently developed model, Bunker et al. (2005) related carbon storage in a tropical forest with extinction of species. In their model, Bunker et al. (2005) accounted for species identity and plant functional traits. However, they were not able to represent the interactions of neighboring trees in their model because no information was available. As species interactions are important drivers of plant community performance (Kelty 2006), the response of individual trees to various neighboring tree species needs to be known in order to address species-specific effects in modeling efforts of biogeochemical cycles (Fujinuma et al. 2005).

Using the site of the Sardinilla Project in Panama, an experimental tree plantation in which diverse tree mixtures were planted in a randomized block design in 2001, our objective was to assess possible differences in nutrient economy (concentrations, storages, and nutrient use efficiencies) and their response to diverse environments of five tree species (*Luehea seemannii* Triana & Planch, *Anacardium excelsum* (Bert. & Balb. Ex Kunth) Skeels, *Hura crepitans* L., *Cedrela odorata* L., and *Tabebuia rosea* (Bertol.) DC.). We hypothesized that (1) nutrient concentrations in plant compartments of individual trees are independent of the kind and number of neighboring species because nutrient uptake is driven by biomass production, and (2) biomass production of individual trees depends on kind and number of neighboring species which is related to species-specific nutrient use efficiency.

Material and methods

Study site

Our study was conducted in the *Sardinilla Project*, a permanent large-scale facility maintained by the Smithsonian Tropical Research Institute (STRI) in Panama, Central America. The study site is located in Sardinilla (9°19′30″N, 79°38′00″W) ca. 50 km north of Panama City (Wilsey et al. 2002). The elevation of the site is 70 m.a.s.l. with slightly undulating topography. Parent material consists of Tertiary limestone and other sedimentary rocks. The soil type is a Vertic Luvisol shifting to a Gleyic Luvisol in depressions (FAO 1998). The thickness of the organic layer is less than 0.01 m. Mean annual rainfall at nearby Buena Vista is 2,351 mm with 25–50 mm per month during the dry season (January to March) and 250 mm per month during the rainy season (May to November). Daily and seasonal temperatures are relatively constant ranging from a daily maximum of 32.3°C in November and 34.3°C in April to a minimum of 21.1°C in January and 22.4°C in May. Mean values are based on weather records of STRI between appr. 1972 and 2001 (personal communication Steve Paton, STRI).

The plantation was set up in July 2001. On an area of 9 ha, 24 plots were planted with six native tree species. These tree species were chosen based on their relative growth rate: two fast growing species (*Luehea seemannii* Triana & Planch [Tiliaceae], *Cordia alliodora* (Ruiz & Pavon) Oken [Boraginaceae]), two intermediate species (*Anacardium excelsum* (Bert. & Balb. Ex Kunth) Skeels [Anacardiaceae], *Hura crepitans* L. [Euphorbiaceae]), and two slowly growing species (*Cedrela odorata* L. [Meliaceae], *Tabebuia rosea* (Bertol.) DC. [Bignoniaceae], Potvin and Gotelli 2008). Saplings of approximately 0.5 m height were planted diagonally within the square plots in rows with 3 m spacing. Each of the 24 plots has an area of 2025 m² resulting in 225 trees per plot. Survival of saplings was variable across species with *C. alliodora* failing to establish in monoculture (Potvin and Gotelli 2008). Therefore, we did not use this species in our study. The experiment comprises plots of three diversity levels: i) monoculture of each tree species replicated twice (n=10), ii) three-species mixture plots drawn randomly from the species pool with every growth class (fast, intermediate, slow) present in the mixture (n=6, six differing three-species mixtures were established without replication), iii) six-species mixtures replicated six times (n=6). To allow a balanced design, replicates of monoculture plots were set up to be able to chose the best performing monoculture of each species according to Hector et al. (2002). The layout of the plots followed a completely randomized block design (random allocation of species mixtures or monoculture in the field) while within one plot, individual species position followed a latin-square pattern (Scherer-Lorenzen et al. 2007a; Potvin and Gotelli 2008). Further details on the particular species mixtures can be found in Scherer-Lorenzen et al. (2007a).

To study the effect of tree diversity on nutrient concentrations and storage, we chose an individual-tree approach as was also done by Fujinuma et al.

(2005). Former grassland experiments mainly focused on the effect of plant diversity on community or plant species performance with restricted power of conclusions on underlying mechanisms, because competition as the main driving force of plant performance occurs among plant individuals (Scherer-Lorenzen et al. 2007b). Therefore, the individual tree approach improves the mechanistic understanding of plant diversity effects and can serve as a prerequisite for modeling the influence of individual species on biogeochemical cycles of tree mixtures. In each experimental treatment (monoculture, three-species mixture, six-species mixture) we selected four replicate trees of each of the five species (altogether 60 trees, 5 species x 3 treatments x 4 replicates). Individual trees were selected on one monoculture plot per species (n=5), four three-species mixtures and four six-species mixtures of the complete design. All selected trees were located near an even-levelled ridge through the experimental area. We chose ridge positions because adjacent depressions showed waterlogging in soil during the rainy season resulting in decreased plant growth. The selected trees cover the range of height and diameter at breast height (DBH) observed for the stands of the respective species in mixtures and monocultures at the same topographic position in 2007 (mean±standard deviation; height: *A. excelsum* 5.4±2.1 m, *C. odorata* 7.4±3.4 m, *H. crepitans* 4.2±2.0 m, *L. seemannii* 6.5±2.6 m, *T. rosea* 5.3±1.7 m; DBH: *A. excelsum* 0.101±0.063 m, *C. odorata* 0.089±0.048 m, *H. crepitans* 0.066±0.043 m, *L. seemannii* 0.128±0.084 m, *T. ros.* 0.081±0.036 m; own unpublished data). Given these variations in height and DBH in this even-aged plantation, we considered four individual trees an adequate number to address biomass production and nutrient storage of individual trees with differing neighbors. To include interactions among as many tree species as possible, we had to include mixtures containing *C. alliodora*. In these mixtures, however, our individual trees were selected in a way that *C. alliodora* was never a direct neighbor to our study trees.

Soil sampling

Three soil cores (diameter 0.01 m) randomly located in the canopy drip line of each tree (1.5 m from base of tree) were taken at a depth of 0 to 0.3 m to comprehensively sample the main root zone of the study trees and pooled together in April 2007. This depth was chosen because even after six years of growth the main rooting zone is between 0 and appr. 0.3 m because of the periodically high groundwater levels (Coll et al. 2008; Healy et al. 2008). Soil samples were air-dried and sieved to <2 mm.

Tree properties and sampling

Six years after establishment, tree basal diameter (0.1 m from the ground, BD) and diameter at breast height (DBH) were determined using a circumference chain. Tree height was measured with a hypsometer (Vertex III, Haglöf, Sweden). These two measurements were done for all study trees and their direct neighbors (n=8 for each study tree) from the last week of December 2006 until the end of January 2007.

To determine biomass allocation ten trees per species per diversity treatment (n=150) were harvested. Of course, these harvested trees were neither our individual trees nor neighbors. To select trees representative of the size range in each species-treatment group we ranked all trees by height, and divided them into three equal size classes (small, medium and large). Three trees were then chosen randomly from the respective size classes, and one chosen randomly within all size classes. Trees were cut at the base and the primary trunk was separated in three equal sections. Using a 20 kg capacity scale, we weighed separately the primary trunk, the branches, the secondary (tertiary, and subsequent) trunks. We took a sub-sample of two branches from each of the three height categories of the primary trunk. We weighed these branches, removed all leaves, and then weighed again to determine the mean fresh weight of leaves. We then dried the segments in a drying oven and reweighed to determine their dry weight.

At the end of the dry season, in March 2007, we sampled leaves of two randomly selected branches per tree. We were not able to include more branches because of the probable effect on sapflow and throughfall fluxes that were determined subsequently (not objective of this manuscript). Nevertheless, we harvested 372±SE 51 g (fresh weight) leaves per tree. We sampled leaves of the lower crown only representing shade leaves. Because only one tree individual of *C. odorata* and two tree individuals of

H. crepitans had leaves in March 2007, we took one and two composite samples of leaves, respectively, for these species. Six parts of the two branches (approximate length 0.08 m) were bulked to one twig sample per tree. We collected composite stem samples (bark, sapwood, heartwood) with a portable driller at approximately breast height. Because the variability of height of the even-aged plantation is small (coefficient of variation of 40% of all trees in the plantation, own unpublished data), we assume that we sampled the same relative heights including minimum interferences of ontological and physiological differences among trees and tree species.

Biomass samples (leaves, branches, and stem) were dried at 60°C. Leaf and branch samples were homogenized using a chipper (SM 2000, Retsch, Germany). Stem material was already sufficiently fine because of the sampling procedure.

Chemical analyses

The pH of soil was measured with a H^+-sensitive electrode (MultiCal, WTW Weilheim, Germany) in a soil: 1 M KCl suspension (1:2.5 v/v). Cation exchange capacity (CEC) of soil was assessed according to Sumner and Miller (1996) using NH_4NO_3 instead of NH_4Cl as extraction solution. Nitrogen concentrations in soil, leaves, branches and stem were determined by an Elemental Analyzer (EA, Vario EL III, Elementar, Germany). To analyze P, K, Ca, and Mg in plant material, samples were digested with HNO_3 at 200°C using a microwave system (MARS5Xpress, CEM, Germany). In soil extracts and plant digests, concentrations of K, Ca, Mg, and Al were determined by Atomic Absorption Spectrometry (AAS 240 FS, Varian, Germany). After irradiation with UV and oxidation with $K_2S_2O_8$, we measured PO_4^{3-} concentrations in plant digests photometrically with a Continuous Flow Analyzer (AutoAnalyzer, Bran&Luebbe, Germany) (Kuo 1996).

Calculations and statistics

Aboveground biomass was calculated for each tree using species-specific allometric equations derived in 2006/07 from the harvesting of 10 trees per species per diversity treatment ($n=5\times10\times3=150$). Equations 1 to 5 represent best fits of models (generalized linear modeling [LM]) using five different basic allometric equations models of Chave et al. (2005), Brown et al. (1989), Ketterings et al. (2001), and Overman et al. (1994). Tenfold cross-validation (Breiman and Spector 1992), a resampling method, was used resulting in the cross-validation relative error (CVRE, sum of squares between predicted and real value on sum of squares of those same values around the general mean) to select the most appropriately approximating model (Ouellette and Potvin, personal communication):

Anacardium excelsum (R^2=0.97):

$$\ln \mathrm{BM} = 0.74 - 7.33 \ln \mathrm{BD} - 4.02(\ln \mathrm{BD})^2 - 0.49(\ln \mathrm{BD})^3 \tag{1}$$

Luehea seemannii (R^2=0.88):

$$\ln \mathrm{BM} = 0.23 + 2.16 \ \ln \mathrm{HT} + 0.61 \ln \mathrm{DBH} \tag{2}$$

Cedrela odorata (R^2=0.77):

$$\ln \mathrm{BM} = -1.33 - 10.28 \ln \mathrm{BD} - 5.52\,(\ln \mathrm{BD})^2 - 0.76\,(\ln \mathrm{BD})^3 \tag{3}$$

Hura crepitans (R^2=0.88):

$$\ln \mathrm{BM} = 2.02 + 1.87 \ln \mathrm{HT} + 1.00 \ln \mathrm{DBH} \tag{4}$$

Tabebuia rosea (R^2=0.86):

$$\ln \mathrm{BM} = 6.21 + 1.13 \ln \left(0.54\, \mathrm{BD}^2\ \mathrm{HT}\right) \tag{5}$$

with biomass (BM) in kg; BD, height (HT), and DBH in m.

We accounted for the influence of neighboring trees on our individual trees by introducing a neighborhood factor (NF, similar to neighborhood analyses by Kennedy et al. 2002). High NF reflect strong competition or facilitation by high biomass or close distance of the neighbor trees. Therefore, we accounted for the distance (DI_{NT}) and the biomass (BM_{NT}) of trees that were neighbors of the individual trees (IT=individual tree; NT=neighboring trees; Eq. 6).

$$\mathrm{NF}_{\mathrm{IT}} = \sum_{n=1}^{8} (\mathrm{BM}_{\mathrm{NT}}/\mathrm{DI}_{\mathrm{NT}})/100 \tag{6}$$

Biomass of our individual trees was then multiplied by the neighborhood factors of each individual tree resulting in neighborhood-weighted (NW) biomass.

Based on aboveground biomass, stem biomass growth rates (= stem growth rates) were calculated as the species-specific proportional mass of stem wood (Table 1) divided by six – the age of the trees in years.

Nutrient storage of individual trees was calculated as the sum of the product of biomass and nutrient concentrations of the respective tree compartments (leaves, branches, stem). Because nutrient concentrations in leaves did not significantly differ among diversity levels, we calculated nutrient storage for each individual tree of *C. odorata* and *H. crepitans* based on nutrient concentrations of leaves of one or two individual tree(s) of these two species. Although this assumption might introduce an error in our calculations, we can assume that it is negligible because branches and stems contribute 95% to total tree biomass of these two species (Table 1). Furthermore, nutrient concentrations in leaves are about three times higher than in branches and stems (Fig. 1), but total nutrient storage is dominated by stems and branches because of the twentyfold greater biomass in stems/branches than in leaves. Analogous to biomass, nutrient storage of each indidual tree was neighborhood weighted by using the NF based on distance and biomass of neighboring trees.

Hector et al. (2002) suggested a method to calculate "overyielding" based on the deviation of realized biomass production of a diverse community from the calculated community biomass production derived from the corresponding monoculture biomass production. We applied this approach to nutrient storage in aboveground biomass of whole trees. The result is interpreted as an indication of complementary effects among species in mixtures. We did not determine community nutrient storages because of our individual tree-based approach. Instead, "nutrient overyielding" of a species was calculated using the mean nutrient storage of a tree species in a given mixture as observed nutrient storage (O_T) and the highest nutrient storage in monoculture as the expected nutrient storage (E_{MAX}). Deviation from expected nutrient storage (D_{MAX}="nutrient overyielding or underyielding") is then calculated according to Eq. 7.

$$D_{MAX} = (O_T - E_{MAX})/E_{MAX} \tag{7}$$

According to the deviation approach, we postulate that an individual of a particular tree species not influenced by mixing with other tree species will show the same biomass production/nutrient storage in monoculture of any of the component species and mixtures of different tree species ($D_{MAX}\approx 0$). Complementary effects will be indicated by $D_{MAX}>0$, whereas competition would lead to $D_{MAX}<0$. Including the highest biomass production of a monoculture of a particular tree species as a reference (=E_{MAX}) is generally referred to as transgressive overyielding ($D_{MAX;}$ Hector et al. 2002; Scherer-Lorenzen et al. 2007a). Throughout the manuscript, overyielding refers to transgressive overyielding. We used the deviation approach because it is more conservative than e.g., relative yield calculations (RY=biomass production of a given species in mixture divided by that in monoculture, Harper 1977) and to allow direct comparisons with the results of other diversity experiments in forests and grasslands from which overyielding is frequently reported (e.g., Scherer-Lorenzen et al. 2007a, Tilman et al. 2006, Caldeira et al. 2005).

All statistical analyses were conducted with the SPSS software package (SPSS 14.0 SPSS Inc., Chicago, IL, USA,). Significance for all statistical analyses was set at $p<0.05$ if not otherwise stated in the text. To compare nutrient concentrations among tree compartments, we used a non-parametric test for connected samples (Friedman). We used a General Linear Model (GLM, Type I) and a post-hoc test (Least Square Differences [LSD]) to elucidate the effects of tree species and tree diversity in mixtures (hierarchical approach fitting tree species before tree

Table 1 Mean contribution (%) of tree compartments to total tree biomass of the five studied tree species

Tree compartment	*A. exc.*	*L. see.*	*C. odo.*	*H. crep.*	*T. ros.*
Leaves	15	7	5	5	14
Branches	38	36	33	51	38
Stem	47	57	62	44	48

A. exc. = Anacardium excelsum, C. odo. = Cedrela odorata, H. cre. = Hura crepitans, L. see. = Luehea seemannii, T. ros. = Tabebuia rosea

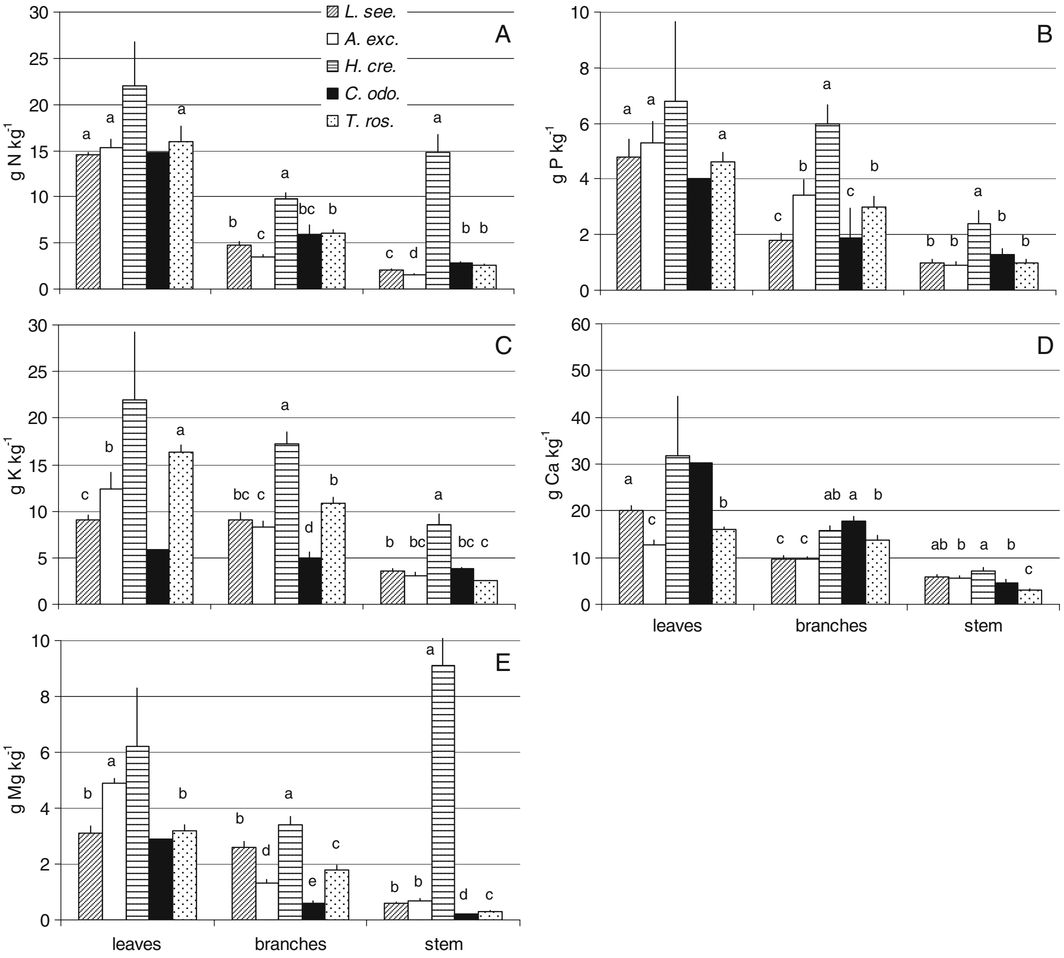

Fig. 1 Mean Nitrogen (A), P (B), K (C), Ca (D), and Mg (E) concentrations of tree compartments (leaves, branches, and stem) of all individuals of the five studied tree species irrespectively of tree diversity. Whiskers indicate the standard error (SE). Differing letters depict significant differences ($p<0.05$) of nutrient concentrations of the respective compartment among the five tree species. Note that we had too few replicates of leaves of *Cedrela odorata* (*C. odo.*) and *Hura crepitans* (*H. cre.*) for statistical analyses. *A. exc.* = *Anacardium excelsum*, *L. see.* = *Luehea seemannii*, *T. ros.* = *Tabebuia rosea*

diversity). In cases of heteroscedacity of variances, we transformed the data and if transformation still did not result in homogeneous variances we used a post-hoc test that does not require homogeneous variances (Games Howell). Stem growth rates and nutrient concentrations in the respective tree compartments were transformed (logarithmic, or reciprocal, or square root) if data did not show homogeneity of variances (leaves excluding *C. odorata* and *H. crepitans*: P, Ca, K; branches: P, K; stem: K). For some nutrient concentrations (leaves: N; branches: N, stem: N, P, Mg), transformations did not result in homogeneous variances. The same was true for storage of N, P, K, and Mg in trees.

Results

Soil and plant nutrient concentrations

Soil properties had a coefficient of variation (CV) of 3 to 33% except for pH and concentrations of exchangeable Al (Table 2). These variations were smaller than the variations in nutrient concentrations of leaves, branches, and stems of the studied trees (CV 25 to 173%). There were no effects of the nature of tree mixtures on soil properties.

All nutrient concentrations in tree compartments significantly decreased in the order, leaves> branches>stem (Fig. 1, Friedman Chi² 50.7 to

Table 2 Summary of soil properties

	Mean	SE	CV(%)
C (g kg^{-1})	34	0.7	15
N (g kg^{-1})	3.2	0.1	18
C/N	11	0.1	5.7
pH	3.9^{a}	n.a.	n.a.
CEC (mmol$_c$ kg^{-1})	335	7.5	17
K (mmol$_c$ kg^{-1})	6.5	0.3	33
Ca (mmol$_c$ kg^{-1})	290	8.1	22
Mg (mmol$_c$ kg^{-1})	32	1.0	24
Na (mmol$_c$ kg^{-1})	2.8	0.1	18
Al (mmol$_c$ kg^{-1})	4.0	0.9	166
BS (%)	98	0.4	3.1

[a] calculated based on measured H^{+} activities

CEC = Cation Exchange Capacity, BS = Base Saturation i.e., contribution of "base" cations (K, Ca, Mg, Na) to the CEC. n.a. = not applicable

70.2, $p<0.0001$). Independent of the number of mixed tree species, tree species significantly differed in mean nutrient concentrations (Fig. 1, Table 3). In branches and stems, *H. crepitans* had significantly higher nutrient concentrations than all other species. Although statistically not testable because we only had one composite leaves sample of this species, this trend was also obvious for nutrient concentrations in leaves of *H. crepitans* (Fig. 1). There were only few exceptions from this general pattern. Potassium concentrations in leaves of *T. rosea* were similar to those of *H. crepitans*. The branches of *T. rosea* had the second highest K concentrations (Fig. 1C). *Cedrela odorata* had similarly high Ca concentrations in branches and leaves as *H. crepitans* (Fig. 1D).

Except for Ca concentrations in branches and stems, kind and number of tree species in mixtures did not influence nutrient concentrations in leaves, branches, or stems of all studied tree species (Table 3). In branches, Ca concentrations were significantly higher in three-species mixtures than in monocultures (LSD, $p<0.05$). In stems, six-species mixtures had significantly lower Ca concentrations than monocultures and three-species mixtures (LSD, $p<0.01$). In contrast to all other species (Ca concentrations in monocultures < three-species mixtures), Ca concentrations in branches of *A. excelsum* were higher in monocultures than in three-species mixtures.

Table 3 Results of a univariate ANOVA (Type I) of nutrient concentrations in leaves (excluding *C. odorata* and *H. crepitans*), branches, and stems

Source		**N**		**P**		**K**		**Ca**		**Mg**	
	df	SS (%)	p	SS (%)	p	SS (%)	p	SS (%)	p	SS (%)	p
Leaves											
Species	2	2.5	0.649	0.5	0.921	53.5	**<0.001**	45.7	**<0.001**	56.2	**<0.001**
Tree Diversity in Mixture	2	12.0	0.145	5.7	0.408	1.9	0.538	3.9	0.341	0.2	0.929
Species x Tree Diversity in Mix.	4	7.4	0.641	10.8	0.490	3.5	0.679	3.4	0.748	3.9	0.627
Residual	28	78.1		83.0		41.0		47.0		39.7	
Branches											
Species	4	51.4	**<0.001**	46.8	**<0.001**	69.5	**<0.001**	51.5	**<0.001**	74.8	**<0.001**
Tree Diversity in Mixture	2	1.8	0.380	0.4	0.797	0.8	0.471	4.6	**0.035**	0.3	0.664
Species x Tree Diversity in Mix.	8	5.7	0.621	12.9	0.097	6.9	0.126	15.2	**0.009**	6.1	0.095
Residual	46	41.1		39.8		22.8		28.7		18.7	
Stem											
Species	4	85.8	**<0.001**	31.0	**<0.001**	61.7	**<0.001**	38.6	**<0.001**	83.0	**<0.001**
Tree Diversity in Mixture	2	0.4	0.468	4.7	0.184	0.1	0.939	8.3	**0.011**	0.7	0.320
Species x Tree Diversity in Mix.	8	2.3	0.357	4.5	0.903	7.0	0.288	15.9	**0.030**	2.6	0.412
Residual	46	11.5		59.9		31.2		37.2		13.7	

Significant p values (<0.05) are given in bold. SS% = explained proportion of total of Sum of Squares; Mix. = Mixtures

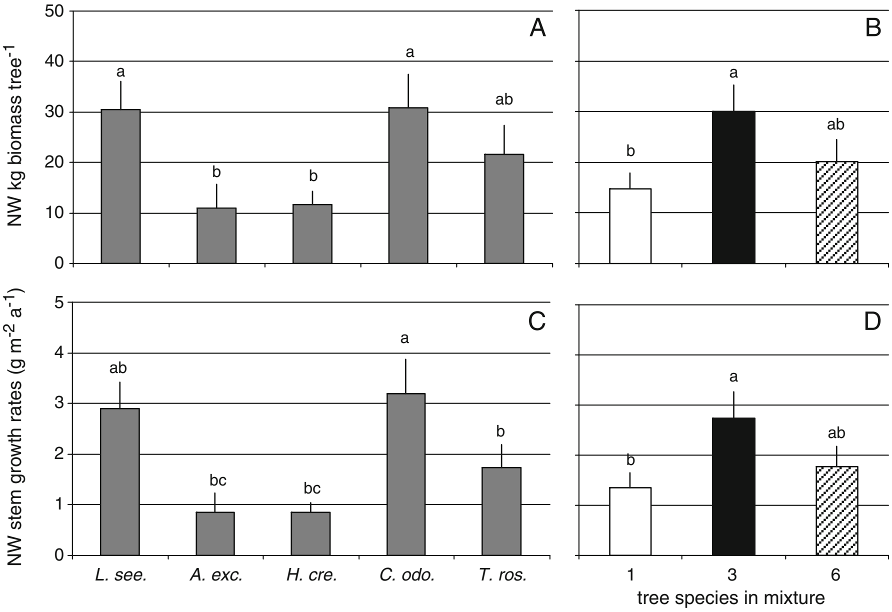

Fig. 2 Neighborhood-weighted (NW) mean aboveground biomass of trees (A, B) and stem growth rates (C, D) depending on (A, C) tree species - averaged across tree diversity levels, and (B, D) tree diversity in mixtures. Whiskers indicate the standard error (SE). Differing letters depict significant differences ($p<0.05$) of nutrient storage of either tree species or tree diversity in mixtures. *A. exc.* = *Anacardium excelsum*, *C. odo.* = *Cedrela odorata*, *H. cre.* = *Hura crepitans*, *L. see.* = *Luehea seemannii*, *T. ros.* = *Tabebuia rosea*

Aboveground biomass and nutrient storages

Neighborhood factors as an indicator of competition of the individual trees with their neighbors varied with tree species. The number of neighboring trees was not significantly different among tree species: on average, one or no neighbor of the individual trees has died since the establishment of the experiment. Neighborhood factors did not significantly differ among tree species.

Anacardium excelsum stored significantly less nutrients in aboveground biomass (NW) than all other studied tree species (Fig. 3). Furthermore, stems of *A. excelsum* grew slower than stems of all other species except *H. crepitans* (Fig. 2C). Concerning biomass production and nutrient storage, *C. odorata* did not significantly differ from the other species while stem growth rates of *C. odorata* were significantly higher than those of the other species (Fig. 2C).

Neighborhood factors were not significantly different among diversity levels. In three-species mixtures, NW aboveground biomass production, NW stem growth rates, and storage of N, P, K, Ca, and Mg in aboveground biomass of all five tree species was significantly larger than in monocultures (Figs. 2, 3). The effect of tree diversity in mixtures on NW biomass and nutrient storages of the studied tree species varied depending on tree species as indicated by species-specific over- or underyielding (Table 4). *Cedrela odorata* stored significantly more nutrients when grown together with two other tree species (overyielding, Table 4). *Luehea seemannii* stored less nutrients (underyielding) in six-species mixtures compared to monoculture (Table 4).

Discussion

High concentrations of exchangeable Ca in soil (Table 2) were related to Tertiary limestone as the substrate for pedogenesis (Potvin et al. 2004). At first sight, the low pH in soil contradicts high exchangeable Ca concentrations. However, the low pH in soil is probably attributable to the sieving of soil before measurement removing carbonatic soil skeleton. For example, sieving had a significant effect on pH in waterlogged soil in the study of Elberling and Matthiesen (2007). Carbonate-rich remains of the Tertiary limestone (that can even be found as blocks with equivalent diameters >0.5 m on the soil surface in the field) obviously lead to continuous release of Ca^{2+} and Mg^{2+} ions as indicated by the high base saturation. Our study site in Panama is located near the Carribean Sea (straight-line distance 30 km) and the Pacific Ocean (straight-line distance 50 km) and therefore another source of Ca, K, and Mg might be input by sea spray (Reimann et al. 2007). Yavitt and Wright (1996) also found high exchangeable Ca and

Fig. 3 Neighborhood-weighted (NW) mean storage of nitrogen (A, B), phosphorus (C, D), potassium (E, F), calcium (G, H), and magnesium (I, J) in trees. Figures A, C, E, G, I, and K show mean nutrient storages of all 12 individual trees per species irrespectively of the tree diversity. Figures B, D, F, H, J, and L show mean nutrient storages of all trees in the differently diverse mixtures. Whiskers indicate the standard error (SE). Differing letters depict significant differences ($p<0.05$) of nutrient storage of either tree species or tree diversity in mixtures. *A. exc. = Anacardium excelsum*, *C. odo. = Cedrela odorata*, *H. cre. = Hura crepitans*, *L. see. = Luehea seemannii*, *T. ros. = Tabebuia rosea*

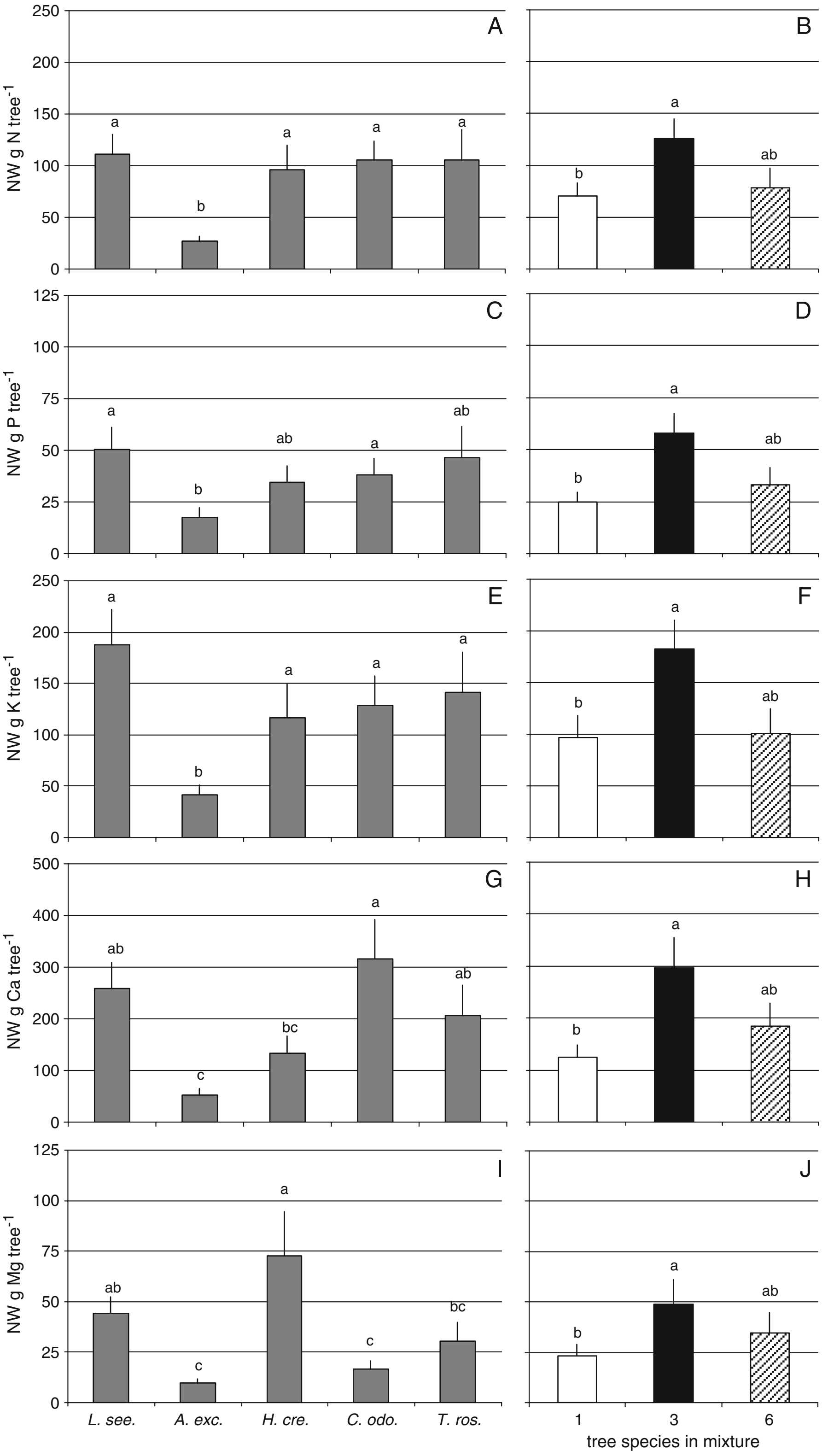

Table 4 Deviation from expected biomass production or nutrient storage of the five tree species based on the best monoculture performance (D_{MAX})

Species	Biomass	N	P	K	Ca	Mg
Deviation from expected biomass production or nutrient storage (D_{MAX})						
3-species mixtures						
L. see.	-0.18	0.01	**0.16**	0.04	0.17	0.20
A. exc.	3.48	-0.21	-0.43	-0.34	-0.04	-0.22
H.cre.	-0.25	-0.43	-0.22	-0.56	-0.28	-0.09
C. odo.	**1.79**	*0.56*	**1.61**	**2.20**	**2.74**	*1.66*
T. ros.	0.27	-0.46	-0.55	-0.42	-0.49	-0.43
6-species mixtures						
L. see.	**-0.81**	**-0.75**	**-0.82**	**-0.80**	**-0.76**	*-0.67*
A. exc.	0.71	-0.04	0.17	*0.30*	0.73	0.52
H. cre.	-0.12	-0.69	-0.63	-0.74	-0.42	-0.21
C. odo.	0.87	*0.52*	*0.90*	**0.77**	0.89	0.53
T. ros.	1.02	-0.47	-0.53	-0.28	-0.07	0.19

Significant ($p<0.05$) and marginally significant ($p<0.1$) differences between monocultures and mixtures are given in bold and italics, respectively. *A. exc.* = *Anacardium excelsum*, *C. odo.* = *Cedrela odorata*, *H. cre.* = *Hura crepitans*, *L. see.* = *Luehea seemannii*, *T. ros.* = *Tabebuia rosea*

Mg concentrations despite low pH in soils of Barro Colorado Island in Panama near to our study site. The low exchangeable Al concentrations in spite of the low pH are a consequence of the competition with base metal cations released by the limestone fragments. Generally, nutrient availability in soil was high because of the nutrient-rich parent material and additional input by sea spray. As a consequence nutrient concentrations in trees were higher than at many other tropical sites.

Except for Ca, genetic differences among species rather than nutrient availability of the study site were suggested to mainly control nutrient concentrations and nutrient storage in trees (Hagen-Thorn et al. 2004). *Hura crepitans* showed exceptionally high nutrient concentrations in leaves, branches, and stems and, thus, low N use efficiency (inverse of N concentrations in litterfall 55 g litterfall $[\text{g N}]^{-1}$; Scherer-Lorenzen et al. 2007a). High nutritional value of seeds and leaves of *H. crepitans* were also reported by Fowomola and Akindahunsi (2007) and Rincon and Martinez (2006). High Ca concentrations in leaves of *C. odorata* based on one bulk sample in our study (Fig. 1D) were in line with the study of Craven et al. (species-specific values: personal communication D. Craven 2007; *C. odorata* 5.5±0.2 g Ca kg^{-1}, *T. rosea* 3.7±0.2 g Ca kg^{-1}, *L. seemannii* 2.0±0.1 g Ca kg^{-1}). *Anacardium excelsum* and *C. odorata* generally had lower nutrient concentrations in tree compartments than the three other tree species (Fig. 1). Scherer-Lorenzen et al. (2007a) showed that *A. excelsum* and *C. odorata* had lower litter quality resulting in lower litter turnover rates and the highest N use efficiency (inverse of N concentrations in litterfall 99 g litterfall $[\text{g N}]^{-1}$ and 78 g litterfall $[\text{g N}]^{-1}$ respectively) compared to the other three tree species at our study site. Generally, N use efficiencies of the studied tree species were at the lower end of literature values in the tropics (40–239 g litterfall $[\text{g N}]^{-1}$; Vitousek 1984; Cuevas and Medina 1986; Smith et al. 1998). In summary, the studied tree species differed with respect to nutrient concentrations. High nutrient concentrations in tree compartments (correspondingly low nutrient use efficiency) of *H. crepitans* and low nutrient concentrations (correspondingly high nutrient use efficiency) of *A. excelsum* and *C. odorata* in our study confirmed trends observed in other studies.

In three- and six-species mixtures, *C. odorata* produced more biomass and stored more nutrients than in monoculture (Table 4). This species was most efficient in acquiring nutrients which obviously resulted in an advantage if competing for nutrients with other tree species in mixtures. The underlying mechanisms remain unclear, because we do not have information on spatial (species-specific rooting depth) or temporal (time-series) patterns of nutrient uptake. However, the consistent overyielding supports the hypothesis of complementary resource use of *C. odorata* in mixture. We observed maximum stem growth rates for this species (Fig. 2C). Thus, stem growth rates might be related to overyielding of *C. odorata*. *Hura crepitans* and *L. seemannii* produced less biomass or acquired less nutrients in three- or six-species mixtures than in monoculture (Table 4). Underyielding of these two species indicates competition with other tree species in mixtures. Particularly *H. crepitans*, very likely is not competitive neither in monoculture nor in mixture on nutrient-poor soils in the tropics. Species-specific nutrient storage depends on tree diversity and must be considered if designing tree species mixtures for sustainable forestry. Tree species with high nutrient use efficiency and higher biomass production in mixture such as *C. odorata*, probably preserve plant-available soil nutrient resources.

Tree species and tree diversity had a significant effect on Ca concentrations in branches and stems and on stem growth rates, biomass production, and nutrient storage in aboveground biomass of the studied tree species (Table 3, Figs. 2 and 3) indicating that faster growth of trees in three-species mixtures resulted in increased biomass production and nutrient storage. As nutrient concentrations in soil showed only small variations in response to different neighbors (Table 2), increased nutrient storage when growing in three-species mixtures might be interpreted as a result of complementary nutrient uptake. A possible mechanism might be the exploitation of nutrients by roots at different depths in the soil profile (spatial niche) or the timing of nutrient uptake by different tree species (temporal niche). However, high nutrient availability in soil of our study site might reduce competition for nutrients, thereby also reducing the need of tree species to occupy niches. Thus, high nutrient availability in soil might reduce an effect of tree diversity in mixtures. On the other hand, high resource availability generally increases aboveground biomass production probably associated with more space to be explored above- and belowground (Hector et al. 1999). Our findings are in line with the observations of Fridley (2003) that aboveground biomass production increased with increasing diversity of grassland species at a site with high resource availability.

The pronounced effect of three tree species mixtures on biomass production, stem growth rates, and nutrient storages in tree compartments compared to a minor effect of six tree species in mixtures cannot be resolved completely. We can rule out a sampling effect of one particular tree species, because all species were equally present in the mixtures (every species planted in three out of six mixtures). One explanation might be that greater intra-specific competition in the three species mixtures may optimize resource use better than greater inter-specific competition in the six species mixtures. However, no other tropical diversity experiment based on a complete statistical design (i.e., all tree species present in all diversity levels) including more than two species exists to confirm our speculation. This explanation might be restricted to plantations where seedlings are established at a high number per area with neighbors of the same species close by. In native tropical rainforests, numbers of tree species are much higher (e.g., 227 tree species on Barro Colorado Island, Panama; Bunker et al. 2005) whereas the distance to neighbors of the same species is much greater than in our study.

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