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Functional identity explains carbon sequestration in a 77-year-old experimental tropical plantation

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Abstract. Planting forests is an important practice for climate change mitigation, especially in the tropics where the carbon (C) sequestration potential is high. Successful implementation of this mitigation practice requires knowledge of the role of species identity and diversity on carbon accrual of plantations. Despite this need, solid data on the long-term development of forest plantations are still very scarce. Monospecific and two species mixture plots of a 77-year-old tree diversity experiment in Yangambi in the Congo basin were fully inventoried. We calculated above-ground C stocks using allometric equations, and soil C stocks by analyzing soil samples at multiple depths. Linear mixed effects models were used to analyze the effect of taxonomic and functional identity and diversity on the aboveground and soil carbon stocks. A high variability in aboveground C stocks across tree species combinations was observed. Apart from a species identity effect, the proportion of planted species in the total stand basal area (BA_{pl}) and effective species richness were identified as compositional parameters with a significant effect on the aboveground carbon (AGC), with BA_{pl} being more important. Both AGC and BA_{pl} were coupled to the functional identity of the planted species; the planting of short-lived pioneers led to low AGC. We found no clear benefits, but also no drawbacks, for AGC of two species mixture plots over monospecific plots or including nitrogen fixing species in the plantation scheme. However, the latter was the only compositional parameter with a significant positive effect on the soil carbon stock up to 1 m depth. We conclude that the different plantation configurations gave rise to a wide range in carbon stocks. This was predominantly caused by large differences in AGC sequestration over the past 77 years. Altogether, short-lived pioneer species had a low BA_{pl} resulting in low carbon sequestration, while partial shade tolerant species achieved the highest AGC stocks. Tolerating spontaneous ingrowth during the plantation development can further increase the AGC stock, given that the appropriate functional type is planted.

Key words: carbon sequestration; Democratic Republic of Congo; forest plantations; functional biodiversity; identity effect; linear mixed effects models; tree diversity experiments; tropics.

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INTRODUCTION

Forest ecosystems contain 45% of the terrestrial carbon (C) stock and are directly interacting with the atmosphere through C sequestration, deforestation and forest degradation (Bonan 2008). The latter two processes give rise to 95% of the C emissions in the tropics, which equals nearly 10% of the global fossil fuel emissions (Achard 2004, Houghton et al. 2012, Le Quéré et al. 2015). This stresses the importance of carbon offset projects in the tropics, such as afforestation or reforestation, as currently traded in the voluntary carbon market or, to a lesser extent, financed by the Clean Development Mechanism (Canadell and Raupach 2008, Jindal et al. 2008, Cerbu et al. 2011). However, implementation of such programs frequently results in plantations of fast growing monocultures of non-native species (Cossalter and Pye-Smith 2003). While this approach guarantees high carbon sequestration rates, it ignores other important co-benefits of reforestation in the tropics, such as natural forest restoration and biodiversity recovery, for which native species are better suited (Lamb et al. 2005, Greve et al. 2013). But the combination of a bigger species pool, along with the lack of knowledge on the species in the tropics, makes the selection of appropriate species difficult and hazardous for the success of a carbon-offset project (van Breugel et al. 2011).There is a clear need for results of long-term experiments to create a set of management guidelines for selection of suited native species.

Research efforts in biodiversity and ecosystem functioning have pointed out that both biodiversity and species identity have an important effect on a variety of ecosystem processes, such as ecosystem productivity and carbon sequestration (Loreau et al. 2001, Hooper et al. 2005, Cardinale et al. 2012). However, most of the published studies focus on short-lived grassland ecosystems (Tilman et al. 2006), from which the results are not directly transferable to structurally more complex ecosystems with longer turnover times such as forests (Hillebrand and Matthiessen 2009). The emphasis of biodiversity and ecosystem functioning research has therefore recently shifted to these long-lived ecosystems, resulting in e.g., tree diversity experiments (Scherer-Lorenzen et al. 2005). These experiments intend to have an orthogonal design, which avoids the risk that differences in management or soil conditions mask the link between tree diversity and ecosystem processes (Scherer-Lorenzen et al. 2005). Yet, most of these manipulative experiments have been installed during the last decade and were setup in the temperate regions (Verheyen et al. 2015), leaving tropical ecosystems understudied. Moreover, results of plantation studies are predominantly derived from experiments with fast growing, non-native tree species (e.g., Forrester et al. 2006).

The Yangambi reserve, in the center of the Democratic Republic of Congo (DRC), holds a tree diversity experiment, set up by the Belgian colonials. It provides us with information on 77 years of experimental forest development in the tropics. This study is the first to bring results on this experiment, where we analyze the long-term effects of tree species identity and admixture effects on carbon sequestration, which is highly relevant for the development of carbon plantations in the tropics.

METHODS

Study area and experimental set-up

This study was performed in a 77-year-old tree diversity experiment, in the surrounding of the Yangambi Man and Biosphere Reserve (00′47° N; 24′30° E), in the DRC. Yangambi is situated approximately 100 km downstream of Kisangani, on the northern bank of the Congo River. The region has a tropical rainforest climate, Af-type according to the Köppen climate classification (Peel et al. 2007), with an annual rainfall of 1750 mm, one short dry season from January to February, and a temperature of 24.5°C throughout the year. The site has a gentle topography and soils are ferralsols (Van Ranst et al. 2010).

The experiment was established in 1938 by the colonial Belgians, which held a large tropical agriculture and forest research center at this site. Information on the setup and the initial follow-up of the experiment could be tracked in the Belgian State Archive, until the decolonization in 1960. Since then, the experimental sites have been under the protection of the INERA (Institut National pour l'Etude et la Recherche Agronomique), the Congolese national institute for agricultural research, which means that there

Table 1. Experimental design table showing the different configurations that were assessed in this study. We separated the target species (upper part of the table) and the admixed species (lower part). Full names for the abbreviations in the column header can be found in the first column. The diagonal in the upper part of the table shows the monocultures of the target species that are present.

	Target species												
Species	*A.c.*	*E.a.*	*E.c.*	*G.c.*	*L.t.*	*M.a.*	*M.e.*	*P.t.*	*P.o.*	*P.m.*	*P.e.*	*P.s.*	*S.t.*
Autranella congolensis	x												
Entandrophragma angolense		x	x										
Entandrophragma cylindricum		x	x										
Guarea cedrata				x	x						x		
Lovoa trichilioides				x	x								
Mammea africana						x							
Milicia excelsa							x						
Pachyelasma tessmannii								x					
Panda oleosa									x		x		
Pentaclethra macrophylla										x			
Pericopsis elata				x					x		x		x
Pterocarpus soyauxii												x	
Strombosiopsis tetrandra											x		x
Antrocaryon nannanii			x										
Blighia welwitschii											x		
Carapa procera										x			
Chrysophyllum africanum								x					
Drypetes likwa	x												
Khaya anthotheca					x								
Phyllanthus spec.							x						
Strombosia grandifolia						x							
Treculia africana												x	
Zanthoxylum gilletii										x			

have been no logging activities until today. The total experimental plantation holds more than 50 ha of experimental plots. These were planted with a wide variety of tree species in different tree species diversity levels (ranging from monospecific plots up to mixtures of six species). The total planted species pool consisted of 23 tree species, listed in Table 1. However, the majority of the plots contained only one or two planted tree species. Almost no repetitions of the different configurations were planted. The experiment contains plots of both 60 × 60 m (0.36 ha) and 40 × 40 m (0.16 ha). All plots were nursed and kept clear of spontaneous ingrowth, for ten years after planting, except those where *Pericopsis elata* [(Harms) Meeuwen] was planted, which were nursed for 20 years. After that, the plots were deliberately left unmanaged, so spontaneously in-growing species now accompany the planted species, augmenting the total realized species pool to 143 tree species in all plots.

For this study, we wanted to assess both the tree species identity and admixture effects, i.e., the effect of adding one other species in the monoculture, on the long-term carbon sequestration. We therefore selected 13 target tree species, i.e., the species which were planted in at least one monospecific and one two-species mixture, as shown in Table 1. We grouped the plots in 13 groups, each time consisting of the monoculture(s) and admixture(s) of the target species with the admixed species. Remark that in some cases, the admixed species is also a target tree species, and thus also found as a monoculture in the plantation. We inventoried a total of 29 plots, consisting of 14 monocultures and 15 two-species mixtures. Each plot was subdivided in either 4 (for the 0.16 ha plots) or 9 subplots of 20 × 20 m (for the 0.36 ha plots), resulting in a total dataset of 201 subplots.

Data collection

An international standardized protocol for tropical forest inventories (RAINFOR; Malhi et al. 2002) was used. We considered both the planted tree species (one or two) and the species that spontaneously established in the subplots. In each subplot, the diameter of all live stems with a diameter larger than 10 cm was measured at 1.3 m height and the trees were identified to species level. Tree height was measured on 20% of all individuals in each plot, selected across all the diameter classes, using a hypsometer (Vertex III, Haglöf, Sweden). We use abbreviations of the planted species, of which the full scientific name can be found in the Appendix: Table A1. Extra parameters were assigned to each plot to indicate the nursing treatment (group of *P.elata* was kept clear of spontaneous ingrowth for a longer time) and the inclusion of nitrogen fixing tree species in the plantation scheme. We treated all *Fabaceae* members as potential nitrogen fixers (see Appendix: Table A1).

At five different places within every plot, soil samples were taken at five depth increments (0–10, 10–20, 20–30, 30–50 and 50–100 cm) and these samples were pooled per depth increment. All samples were dried for 48 hours at 60°C. Carbon and nitrogen content were analyzed using an elemental analyzer (Automated Nitrogen Carbon Analyser, interfaced with a Sercon 20–20 IRMS; SerCon, Cheshire, UK). In addition, spread over the whole study area, seven soil pits to 1 m depth were dug, and bulk density was measured in the wall of these pits at different depths (20, 40 and 80 cm) using container rings of known volume (Eijkelkamp Agrisearch Equipment, Giesbeek, The Netherlands). We determined the bulk density for the upper soil layer (0–10 cm) at three locations within each plot using container rings.

Data analysis

For the calculation of the aboveground carbon stock (AGC) in the trees, we used the formula of Chave et al. (2005), including wood density and tree height. First, we fitted different diameter-height relationships from literature (see Appendix: Table A2) by non-linear least-squares estimations for every plot, using the actual tree height measurements from the field. The best fit for every plot was selected based on the Akaike's information criterion (AIC) and the residual variation. Broken and strongly leaning trees were measured separately and were not included in the fitting process. The best fit was then used to estimate the unknown tree heights. We used wood density data that were collected in the surrounding natural forest by taking $5 \times 5 \times 5$ cm^3 wood samples from under the bark (Kearsley et al. 2013). If no species data was available from this dataset, we used species averages from the DRYAD global wood density database (Chave et al. 2009, Zanne et al. 2009) or genus averages from both databases to assign wood densities to the individual trees. We assumed a carbon content of 50% in the woody biomass for the final carbon stock calculations.

For the soil organic carbon stock (SOC) down to one meter depth, the averages of the bulk density measurements from the soil pits were used in combination with the specific carbon content from the plot-level composite samples for the bottom four increment layers. Because of the higher variation of the bulk density of the topsoil and the high contribution of this soil layer to the total SOC stock to 1 m depth, we used the plot-specific bulk density and C measurements for the topsoil.

Based on the results of the inventory, we derived subplot-level planted tree species richness (monospecific or two species mixture), effective tree species richness (planted tree species as well as spontaneous ingrowth), effective Simpson diversity, and the proportion of planted species in the stand basal area (BA_{pl}). In a second stage, we replaced the taxonomic target species group as a fixed effect with functional types that summarized the functional role of the planted species (*functional type*). For that purpose, we compiled a simple trait matrix with information on wood density and shade tolerance of all the planted tree species. Wood density is an important trait, strongly linked to the functional ecology of tree species (e.g., Chave et al. 2009), while shade tolerance is a crucial life-history trait, associated with a wide range of physical and chemical plant traits (Valladares and Niinemets 2008). Information on shade tolerance was derived from literature (Lebrun and Gilbert 1954, Hawthorne 1995, Hubau et al. 2012), giving priority to the publication of Lebrun and Gilbert (1954), who based their classification on field observations of seedlings in natural forest in Yangambi. They used three classes—light-demanding, shade-tolerant and shade species—with increasing tolerance to shade. Based on this trait matrix, we performed a hierarchical clustering on the different tree species, and divided them in functional types. We choose four functional types, since there were two distinct groups of light-demanding species

Table 2. Functional traits and included tree species for each type; short-lived pioneers (SLP), long-lived pioneers (LLP), partially shade tolerant (PST) and shade tolerant (ST) trees. The average wood density (WD) was calculated by using the average wood density of the tree species present in each class (averages ± the standard deviations). Shade tolerance was classified based on two literature sources (Lebrun and Gilbert 1954, Hawthorne 1995) using three classes (light-demanding, tolerant to shade, shade).

Class	WD (g cm^{-3})	Light strategy	Species
Short-lived pioneers (SLP)	0.50 ± 0.02	Light-demanding	*Antrocaryon nannanii, Entandrophragma angolense, Entandrophragma cylindricum, Khaya anthotheca, Lovoa trichilioides, Milicia excelsa, Treculia africana*
Long-lived pioneers (LLP)	0.71 ± 0.08	Light-demanding	*Blighia welwitschii, Pentaclethra macrophylla, Pericopsis elata, Phyllanthus* spec., *Pterocarpus soyauxii, Zanthoxylum gilletii*
Partial shade-tolerant (PST)	0.68 ± 0.05	Tolerant	*Autranella congolensis, Chrysophyllum africanum, Drypetes likwa, Mammea africana, Pachyelasma tessmannii*
Shade-tolerant (ST)	0.61 ± 0.06	Shade	*Carapa procera, Guarea cedrata, Panda oleosa, Strombosia grandifolia, Strombosiopsis tetrandra*

with differing wood density properties (Table 2). We tested the differences in wood densities between the types using a non-parametric Kruskal-Wallis test, and the significant association of the shade tolerance with the types using a non-parametric chi-square test.

To analyze the influence of tree species diversity and composition on subplot-level AGC ($n = 201$), we applied linear mixed effects models. Plot was set as random intercept and AGC was log-transformed. We started off with a model containing all calculated compositional parameters for the subplots as fixed effects (i.e., the target species group, planted tree species richness, effective species richness, effective Simpson diversity, the BA_{pl}, the presence/absence of nitrogen fixers among the planted species and the nursing treatment). The non-categorical variables were standardized to make the parameter estimates of the fixed effects comparable. First, we tested the random structure, keeping the fixed effects structure constant (with parameter estimation via restricted maximum likelihood). Once the optimal random structure was found, the fixed effects were backwards selected, based on the AIC and likelihood ratio tests using maximum likelihood estimations. Finally, the marginal and conditional R^2 were calculated for the final model, which indicate the proportion of the variance that is explained by the fixed structure, respectively the fixed and random structures together (Nakagawa and Schielzeth 2013). We additionally checked Spearman correlations in the pooled dataset ($n = 201$) between BA_{pl}, effective species richness and AGC, to increase the interpretability of the mixed effects model results.

Subsequently, we used the functional types to replace the taxonomic target species groups as a fixed effect in the model. Both final models were compared using likelihood ratio tests and AIC. To gain insight in how BA_{pl}, as an important fixed effect, was linked to the functional identity of the planted species, ANOVA was additionally done, with BA_{pl} as dependent variable and the functional types as independent variable on the plot level ($n = 29$).

Finally, we checked whether the SOC stock (to 1 m depth) was correlated to AGC on the plot level, by calculating Spearman correlation coefficients. Subsequently, we repeated the modelling steps on the plot-level for the SOC with all the compositional parameters in the first model as fixed effects.

All statistical analyses were conducted with R version 3.1.1 (R Core Team 2014). We used the 'nmle' package for the mixed effects modeling (Pinheiro et al. 2013).

RESULTS

The overall AGC and SOC is 212 ± 106 Mg C ha^{-1}, respectively 83 ± 16 Mg C ha^{-1} (Fig. 1), with the standard deviations calculated on the plot-level averages, resulting in coefficients of variation of 0.50 (AGC) and 0.19 (SOC). The subplot-level AGC stocks in the complete dataset ($n = 201$)

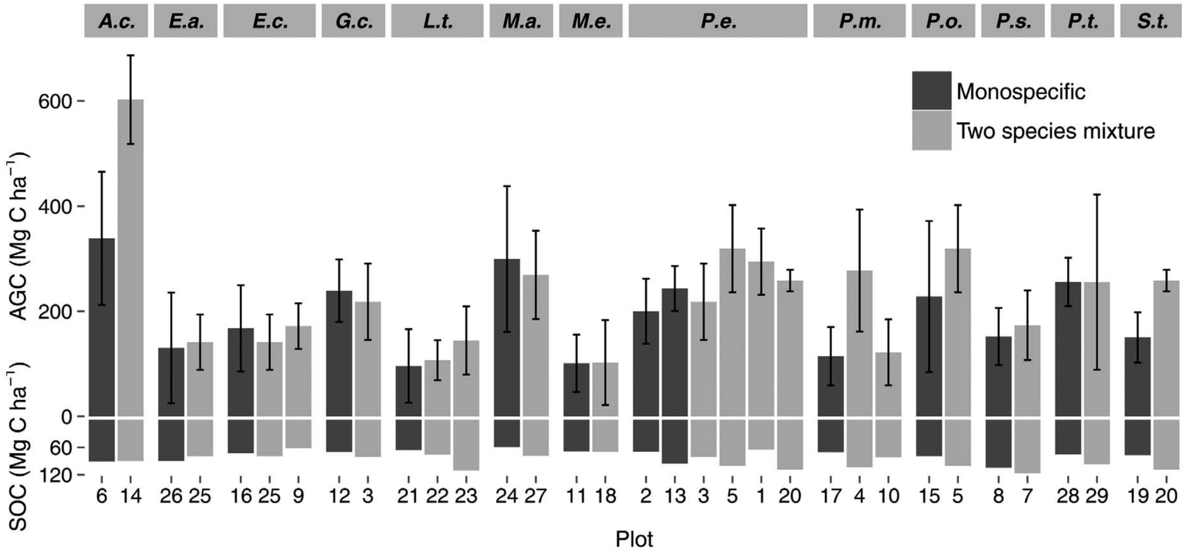

Fig. 1. Aboveground carbon (AGC; Mg C ha^{-1}) and soil organic carbon (SOC; Mg C ha^{-1}) stocks in the different plots. Plots (x-axis) were grouped based on the target tree species they share (indicated with abbreviations on top), hence some two-species mixtures appear twice in the graph. The AGC are averages based on the AGC of the subplots, and the error bars indicate the standard deviation on the subplot averages. The SOC stock values are calculated using composite samples from the whole plot, and thus have no error bars. The full scientific names for the abbreviations of the target tree species are listed in Appendix: Table A1.

range from 31 Mg C ha^{-1} to 731 Mg C ha^{-1}. The average plot-level compositional characteristics per plot are given in Appendix: Table A3.

The functional clustering resulted in four distinct types (Table 2); two light demanding types with different wood densities (further called short-lived pioneers (SLP) and long-lived pioneers (LLP)), a class with high wood density and mediate shade tolerance (partial shade-tolerant species (PST)) and a high-wood density class with high shade tolerance (shade-tolerant species (ST)). The wood densities and shade tolerance significantly differed between the types ($p = 0.003$, respectively $p = 0.001$).

The optimal model structure for the taxonomical approach contained plot as a random intercept. The backward selection of fixed effects resulted in a model with three significant effects: the BA_{pl}, the effective species richness and the target species groups (significant, $p < 0.1$, for four groups), with the parameter estimates and significance shown in Table 3. This resulted in a final model with a marginal and conditional R^2 of respectively 0.51 and 0.55 (Table 3). Simple Spearman-correlations in the dataset ($n = 201$) show a significant positive correlation between BA_{pl} and AGC, a significant negative correlation between effective species richness and BA_{pl}, and a weak correlation between effective species richness and AGC (Fig. 2). The parameter estimates of the functional types in the model (Table 3) pointed out that planting species of type PST (Table 2) had a positive effect on AGC, in contrast with LLP, ST and especially SLP.

Fixed effects selection resulted in the same model as the first model, with functional types replacing the target tree species groups, and the differences in nursing as an additional significant, positive fixed effect. The optimal taxonomical and functional model performed equally well.

The ANOVA analysis revealed a significant negative effect of the presence of the SLP class in the plantation scheme on the BA_{pl} ($p = 0.004$).

The top soil layer (0–10 cm) held on average 33% of the total SOC stock to 1 m depth. The coefficient of variation of the bulk densities decreased with increasing soil depth; 0.16 (5 cm), 0.15 (20 cm), 0.07 (40 cm) to 0.03 (80 cm).

Table 3. Model specifications for the linear mixed effects models of the above-ground carbon (AGC) stocks ($n = 201$). The random structure of each of the models in the table consists of the plot as a random intercept. Model 1 shows the parameters for the taxonomical-approach model, including the target tree species groups as fixed effects (full scientific names for the abbreviations of the target species are given in the Appendix: Table A1). Model 2 shows the results for the functional-approach, with introduction of four functional types (short-lived pioneers (SLP), long-lived pioneers (LLP), partial shade tolerant (PST) and shade tolerant (ST) trees for the target tree species; with specifications in Table 2). BA_{pl} is the ratio of basal area of the planted species to the total stand basal area in the plot (including spontaneous ingrowth). ESR is effective species richness and equals the number of occurring tree species (planted species and spontaneous ingrowth) in the subplot. AIC stands for Akaike's information criterion, which was used as selection criterion. R^2_{marg} and R^2_{cond}, indicate the proportion of variance explained by the fixed structure, and the fixed and random structure together, respectively (Nakagawa and Schielzeth 2013).

Fixed effects	AIC	R^2_{marg}	R^2_{cond}	p	Parameter estimate
Model 1: taxonomical approach	259	0.51	0.55		
BA_{pl}				<0.001	0.26 ± 0.04
ESR				<0.001	0.18 ± 0.04
Groups					
A.c.				0.001	0.63 ± 0.28
E.a.				0.240	−0.24 ± 0.23
E.c.				0.375	−0.22 ± 0.24
G.c.				0.200	−0.19 ± 0.23
L.t.				0.003	−0.51 ± 0.26
M.a.				0.760	0.07 ± 0.28
M.e.				0.144	−0.47 ± 0.27
P.e.				0.069	0.19 ± 0.20
P.m.				0.875	−0.21 ± 0.26
P.o.				0.476	0.21 ± 0.25
P.s.				0.769	−0.22 ± 0.28
P.t.				0.060	0.43 ± 0.28
S.t.				0.280	−0.14 ± 0.25
Model 2: functional approach	257	0.54	0.55		
BA_{pl}				<0.001	0.26 ± 0.04
ESR				<0.001	0.20 ± 0.04
Nursing				0.03	0.30 ± 0.12
Functional class					
SLP				0.02	−0.35 ± 0.14
LLP				0.55	−0.07 ± 0.13
PST				0.01	0.40 ± 0.15
ST				0.24	−0.12 ± 0.10

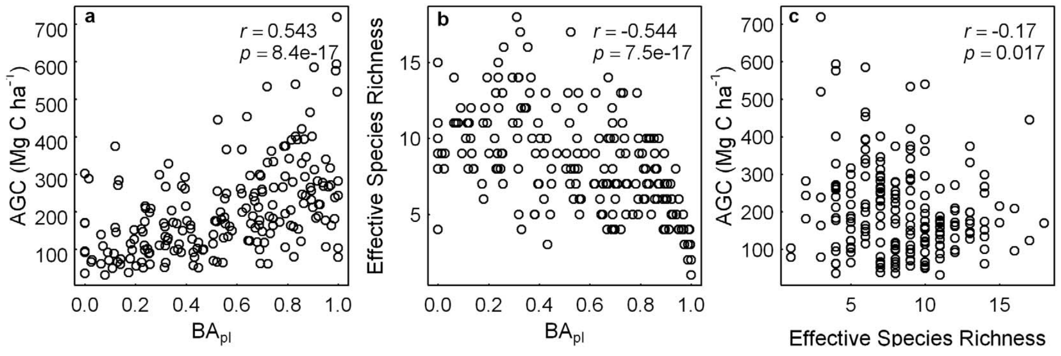

Fig. 2. Interrelationships between aboveground carbon (AGC), BA_{pl} and effective species richness in the different subplots ($n = 201$). AGC stands for above ground carbon in the woody biomass of the subplots. BA_{pl} is the ratio of basal area of the planted species to the total stand basal area in the plot (including spontaneous ingrowth). The effective species richness is the number of tree species with a DBH > 10 cm that were present in the subplot. The r values are Spearman correlation coefficients, along with their p value.

There was no significant correlation between AGC and SOC to 1 m depth on plot-level. Including N-fixers in the plantation scheme was the only significant, positive, effect on SOC stocks ($r^2 = 0.11$ and $p = 0.03$).

Discussion

Both the average and the coefficient of variation of the AGC stocks were considerably higher than SOC stocks. This shows that the impact of the management choices of tropical plantations have a relatively higher impact on AGC in terms of absolute C sequestration compared to SOC stocks. Although soils are an important carbon stock globally, we target management guidelines for carbon sequestration in tropical plantations, so devote more attention to AGC (Houghton 2005). Remark that we did not assess carbon stocks related to the below-ground biomass.

The classification of the functional groups was done using only shade tolerance and wood density, which is consistent with previous work (e.g., Poorter et al. 2006). We stress that these functional types should also be mainly interpreted in terms of shade tolerance and wood density. Tree species in functional types SLP and LLP have a high light requirement, but differ in their allocation to mechanical stability or growth rate (Selaya and Anten 2008). PST species can establish in low light conditions but need gaps to grow, while the ST species can grow in the low light conditions (Poorter et al. 2006).

Tree composition effects on above-ground carbon stocks

Setting the plot factor as a random intercept allowed us to quantify unwanted local differences in e.g., soil conditions. The effect of the target species groups is an identity effect that is to be expected from this type of experiment, and has been observed in similar contexts (e.g., Balvanera et al. 2006, Redondo-Brenes 2007, Ruiz-Jaen and Potvin 2011). In terms of AGC, two species mixtures did not outperform the monocultures of the target species (Fig. 1). This shows that other processes, such as the species identity effect and spontaneous ingrowth of tree species, were more important in the long-term development of these plantations. In the target species group of *A.congolensis* (A.c. in Fig. 1), the AGC increase in the mixture with *D. likwa* compared to the monoculture is remarkable. However, it is important to be cautious with the interpretation of the results; in case there is no monoculture of the admixed species, a positive or negative mixing effect could be falsely reported using only this dataset (Hulvey et al. 2013). BA_{pl} and effective species richness both have a significant positive effect on the AGC and SOC of this plantation. In the pooled dataset ($n = 201$), however, these two predictors are negatively correlated to one another and the positive effect of effective species richness is masked (small negative correlation with AGC; Fig. 2). Based on these combined observations, we conclude that BA_{pl} has a more important effect than species number. We state that, given a high BA_{pl}, the species that manage to grow into the stand spontaneously are probably using different niches than the planted species. This way, spontaneous ingrowth can enlarge the resource use of the stand (Loreau and Hector 2001). Considering a low BA_{pl}, spontaneous ingrowth is of large importance to compensate for the failure of the planted species to establish. In this case, effective species richness reflects the success of spontaneous species to establish, and augment the carbon storage. Hence within each configuration, both parameters show a positive effect on the AGC (Table 3), although the BA_{pl} is the dominant driver (Fig. 2), and should thus be priority in tropical plantation design.

The lack of a significant difference in model performance when summarizing the 13 taxonomic groups into 4 functional groups proofs that the species identity effect is strongly linked to the functional life-history of species. From the final model results, we conclude that planting with species of class PST, has a bigger carbon storage potential in the long-term, while using SLP is clearly not a good practice. *P. elata* was the only target species which was nursed for ten years longer in all plots (two species mixture and monospecific). This is a light demanding species, belonging to class LLP (Table 2), and performed in general better than the other, functionally equal species. We cannot safely generalize this observation of a positive effect of extra nursing, since only one functional class and one species had this treatment. In this case, however, keeping the plantation free of spontaneous ingrowth for a longer time, did not only affect the BA_{pl}, but also the AGC in the plantations with light-demanding species. Through the significant negative effect of SLP trees in the plantation scheme on the BA_{pl}, it is shown that SLP are not successful in carbon sequestration through a failure in BA_{pl}.

The inclusion of N-fixers in the plantation scheme did not significantly contribute to the AGC, although it has been shown that the effect of N-fixers strongly depends on site conditions and complementarity with the other planted species (Forrester et al. 2006). Additionally, tropical old-growth forests are generally considered N-rich leading to a down-regulation of symbiotic N-fixation (Batterman et al. 2013). In the case of the Yangambi experiment, N-fixers may have been actively fixing in the early stand development, but its effect may have been masked by growth-effects in the long-term.

Tree composition effects on soil carbon stocks

Including N-fixers in the plantation scheme was the only compositional parameter with a significant, positive effect on the SOC stock, which is known from other reforestation sites in the tropics (e.g., Resh et al. 2002). The plots with higher AGC were not associated with high SOC stocks. Although literature reports a positive correlation of aboveground productivity with root allocation (Raich et al. 2014), total SOC stock development after land use change is more complex and less understood (Laganière et al. 2010). Initial carbon content and tree species have been identified as key determinants for the soil carbon processes following afforestation (Laganière et al. 2010, Shi et al. 2013). As we have no baseline data on the initial SOC stocks, we cannot quantify actual changes in soil carbon stock. However, taking into account the relative importance of spontaneous ingrowth, we assume that in this case the effective species composition rather than the planted species determines the changes in this stock. This augments the complexity of disentangling the role of tree species composition in the SOC stock formation, as the effective species pool rises to 143 tree species in the total study area, rather than only considering the 23 planted species. For the long-term development of tropical plantations, we state that changes in the absolute SOC stock, following afforestation, are small compared to the sequestration in AGC. This observation, combined with the far higher variability of the AGC stock and the complexity of predicting the SOC changes when considering processes like spontaneous ingrowth, leads to the suggestion that plantation managers should focus on aboveground C sequestration.

Management implications

BA_{pl} is an important driver of carbon stocks in tropical plantations, and is linked to the functional identity of the planted species. This identity should thus be a primordial consideration for reforestation projects in the tropics, which aim at both the re-establishment of native forest and successful carbon sequestration. The species identity can be translated and generalized into very basic functional types, where low wood-density short-lived pioneers had a clear negative impact on both the BA_{pl} and carbon accrual in the long run. Given a high BA_{pl} of planted species, spontaneous ingrowth positively affects the carbon sequestration. In this study, we found no clear positive effect of admixing species (but not a negative one either). Including nitrogen fixers in the plantation did not lead to higher above ground carbon stocks, although these plots showed a higher soil carbon stock.

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SUPPLEMENTAL MATERIAL

ECOLOGICAL ARCHIVES

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