

Changes in N and C concentrations, soil acidity and P availability in tropical mixed acacia and eucalypt plantations on a nutrient-poor sandy soil

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Abstract

Background and aims The introduction of *Acacia mangium* in *Eucalyptus urophylla* x *grandis* stands improves wood production on poor sandy soils of coastal plains of the Congo. We assessed the impact of *A. mangium* plantations in pure stands and in mixture with eucalypt trees on the physico-chemical properties of the soil after one rotation.

Methods Bulk densities, N, C, available P and pH were determined on soil sampled in the pure acacia (100A), pure eucalypt (100E) and mixed-species (50A:50E) stands. N and P were determined in aboveground litters and in leaves, bark and wood of trees.

Results N and C concentrations were higher in 50A:50E than in 100A and 100E in the top soil layer. The pH was lower in 100A and higher in 100E than in 50A:50E. The available P was lower in 50A:50E than in 100A and 100E. Leaf N was lower in 50A:50E than in 100A for acacia, and higher than in 100E for eucalypt. Leaf P was similar for acacia but higher for eucalypt in 50A:50E than in 100E. In contrast to P, the amount of N in aboveground litterfall increased with the proportion of acacia in the stand.

Conclusions The introduction of acacia trees in eucalypt plantations increased C and N contents of the soil but decreased the available P content in the mixed-species stand. This may be related to a higher uptake of P needed to maintain the N:P stoichiometry in eucalypt leaves.

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and N concentrations · Eucalyptus

Abbreviations

SOM Soil organic matter
C Carbon
P Phosphorus
N Nitrogen
NFS Nitrogen fixing species

Introduction

Afforestation is an option to sequester atmospheric CO₂ (Resh et al. 2002; Mao et al. 2010; Li et al. 2012) and to provide biomass energy to curb the use of fossil fuel. The use of nitrogen fixing species (NFS), alone or in mixture in forest plantations may be a good strategy for future carbon sequestration through forest management intensification and reforestation programs (Zhang et al. 2012). Nowadays, NFS are increasingly used in cropping systems or in forestry because of their beneficial effects on ecosystems through soil fertility improvement and C sequestration (Binkley 1992; Kaye et al. 2000; Resh et al. 2002; Mao et al. 2010; Inagaki et al. 2011). The NFS introduction in forest plantations leads to an improvement in soil nutrient status, mainly through N fixation from the atmosphere (Rothe and Binkley 2001) but also through a potential increase in the rate of phosphorus (P) cycling (Binkley 1992). However, an increase in N availability may also involve a decrease in P availability (Kaye et al. 2000), as N₂ fixing species generally need more P for sustaining symbiotic root nodules and N₂ fixation processes (Inagaki et al. 2011). In addition, the introduction of NFS may also induce soil acidification (Binkley 1992; Yamashita et al. 2008).

Besides N, P availability is one of main soil fertility constraints to crop production in many tropical soils as these soils are highly weathered and have a high ability to fix P (Sanchez and Uehara 1980). Clay particles, Fe and Al oxides or free Fe and Al ions react readily with soluble phosphate ions released through mineralisation or from fertilizers to form less soluble Al and Fe phosphates (Vitousek 1984). Al and Fe phosphates can be released by the effect of organic acids exuded by roots which compete with inorganic P for the same sorption sites or solubilized through ligand promoted mineral dissolution (Otani et al. 1996; Hinsinger et al. 2011). P supply to plant roots is not only determined by P in soil solution but also by P quantity (P buffer capacity, Syers et al. 2008). Some NFS might efficiently mobilize P from soils with both low and high P availability (Nuruzzaman et al. 2006; Wang et al. 2012). Some NFS increase P availability due to a better soil exploration and high capacities to mobilize insoluble mineral P but also organic forms (Forrester et al. 2006; Gunes et al. 2007). Sitters et al. (2013) showed that soil organic P pools increased with increasing density of acacia and argued that this was due to an ability of acacia to access

P from deeper soil layers and perhaps also to utilize organic forms more efficiently through the production of phosphatase enzymes. This production of phosphatase enzymes was compulsory (Criquet et al. 2004; Kohler et al. 2007). An improvement in the soil P status under the mixed species of eucalypts with a N₂-fixing species is observed through the recycled and accumulated P in roots and leaves of NFS (Forrester et al. 2006). However, other studies have shown a decrease in available P with the increase in N availability in mixed forest plantations (Binkley 1992; Kaye et al. 2000; Inagaki et al. 2011).

An increase in soil acidity is often observed in the forest plantations where NFS have been introduced (Binkley 1992; Yamashita et al. 2008; Kasongo et al. 2009). Leaching of nitrate was thought to be the main cause of soil acidification under legume crop cultivation (Tang et al. 1999). An increased translocation of base cations from soil to plant biomass to sustain high growth rates of acacia trees caused a decrease in exchangeable cations leading to soil acidification (Yamashita et al. 2008). Moreover, roots may release protons in the rhizosphere to balance a larger uptake of cations than anions (Hinsinger et al. 2003). Consequently, the pH of the rhizosphere differs when compared to the bulk soil mainly because of the ionic form of nitrogen taken up. Higher biomass production may also increase soil carbon (C) through an enhanced production of litter (Forrester et al. 2013) and humification processes can therefore be an additional cause of soil acidification under NFS plantations (Kasongo et al. 2009).

Acacia mangium Wild is a tropical N₂ fixing legume tree species that has a good growth potential on infertile soils (Bernhard-Reversat et al. 1993; Cole et al. 1996) and that is largely planted in monoculture, especially in South East Asia (Khanna 1998). Acacia mangium trees have been introduced in experimental eucalypt plantations in several tropical areas as an attractive option to increase the yield of eucalypt plantations without resorting to inorganic fertilizers (Bouillet et al. 2013). Replacing half of eucalypt trees by *A. mangium* trees had a positive effect on stand wood production in coastal Congo related to a shift in biomass partitioning from belowground to aboveground (Epron et al. 2013) and putative complementarity for light and soil resource capture between the two species (Bouillet et al. 2013). The acid sandy soils in this area are poor in nutrients, especially in N (Nzila et al. 2002; Laclau et al. 2010). This shift in partitioning resulted mainly from an improvement in N availability related to a facilitation

interaction through N₂ fixation and transfer to eucalypt trees (Epron et al. 2013). However, the impact of acacia trees on soil carbon, nitrogen and available phosphorus (P), that are important factors for the long-term sustainability of the forest plantations in this area, has not yet been evaluated.

This study examined the impact of *A. mangium* plantations pure stands and in mixture with eucalypt trees on chemical and physico-chemical properties of the soil (C and N concentrations, soil acidity and P availability) after one rotation (7 years). The following hypotheses were tested: (1) soil N increases in both pure acacia and mixed-species stands compared to a pure eucalypt stand; (2) soil C is higher in the mixed-species stand as a result of the higher stand productivity and we further evaluated (3) if the introduction of *A. mangium* causes soil acidification and whether (4) its enhances the amount of soil available P or decreases it as a result of greater P uptake by the trees.

Materials and methods

Site description

The studied site is located at about 35 km of Pointe-Noire city on a plateau close to Kissoko village in Congo (4°S, 12°E, 100 Alt.) on a deep Ferralic Arenosol laying on a geological bedrock composed of thick detritic layers of continental origin dated from plio-pleistocene. Soils in this area are characterized by a low CEC (< 0.5 cmolc kg⁻¹), a high sand content (> 90 % of the mineral soil), very low clay and silt content (6 and 2 % respectively) and low iron oxides content (< 1.5 % of the bulk soil, Mareschal et al. 2011). In brief, climate is subequatorial with a cool dry season extending from June to September. The original vegetation was native tropical savanna dominated by the C₄ poaceae *Loudetia arundinacea* (Hochst.) Steud. The studied area was afforested in 1984 with eucalypt hybrids. A complete randomized block design was established in May 2004 with 5 blocks. The soils (0–0.20 m layer) of the 5 blocks (3 replicates per block) contained low N (0.026 %±0.003) and C (0.40 %±0.05) concentrations with a C/N ratio of 15.7 (± 1.1) prior to the trial setup. The difference between blocks was not significant (one way ANOVA, *p*<0.05). The trial was planted with an *Eucalyptus urophylla* × *grandis* hybrid (18–52) and *Acacia mangium* with a starter fertilization (ammonitrate, 43 kg ha⁻¹ of N). A pure acacia plot (100A), a mixed-

species plot with 50 % acacia and 50 % eucalypt trees (50A:50E) and a pure eucalypt plot (100E) were established within each block at a stocking density given in Table 1. Each plot (1,250 m²) consisted of an inner part of 36 trees (6×6) and 2 buffer rows. Tree height and circumference at 1.3 m height were measured each year on these 36 trees per plot and data from age 7 years are given in Table 1. A full description of the experimental site and the partitioning of net primary production in the different stands can be found in Epron et al. (2013, see also Table 1).

Soil sampling

The soil sampling was done in December 2011 in 3 out of the 5 blocks at the end of the rotation (7 years) in the inner part of the plots. Nine soil samples (18 for the 50A:50E stand) were collected in each plot and separated in four layers (0–0.05 m, 0.05–0.10 m, 0.10–0.15 m and 0.15–0.25 m) using 5x5 cm sampling cylinders. In each plot, three transects (six for the 50A:50E) were setup starting at the base of a tree and ending in the centre of the area delimited by four trees. The three samples were separated by 0.7 m from each other on each transect. The total number of sampling points was 27 (9×3 blocks) in both single-species stand and 54 (9×2 species×3 blocks) in the mixed-species stand.

Soil analyses

The soil samples were air-dried, sieved at 2 mm and root fragments were removed. Bulk density was calculated as the ratio between oven-dried soil mass determined from a subsample (dried at 105 °C) and the volume of the sampling cylinders.

The pH (H₂O and 1 M KCl) (sample:liquid ratio, 1:5) was measured using a S47 SevenMulti TM (Mettler Toledo, Switzerland) after the suspensions were shaken for 30 min and equilibrated for one hour. Total C and N concentrations were determined by combustion with an elemental analyser (NCS 2500, Thermoquest, Italy).

Resin-Extractable P was determined only in the 3 first soil layers i.e., 0–0.05 m; 0.05–0.10 m and 0.10–0.15 m. Two anion exchange resin strips (BDH#551642S) each 20 mm×60 mm were added to 0.5 g of dried and sieved soil suspended in 30 ml distilled water. Phosphate adsorbed by the anion exchange resin was recovered in 30 ml of 0.5 M HCl after shaking for 16 h (100 revs min⁻¹) according to method of Tiessen and Moir (1993).

Table 1 Tree sizes, leaf, wood and total net primary production (NPP) and annual aboveground litterfall in pure acacia (100A), pure eucalypt (100E) and mixed-species (50A:50E) stands (mean with standard error, adapted from Epron et al. 2013^a)

	100A	50A:50E		100E
		acacia	eucalypt	
Tree planting density (tree ha ⁻¹)	800	400	400	800
Mean diameter at 1.3 m high (cm)	18.3±0.7a	18.2±0.6a	22.3±0.8b	15.7±0.7a
Mean tree height (m)	20.3±0.5a	19.6±0.3a	28.4±0.5b	23.7±0.7c
Foliage NPP (t ha ⁻¹ year ⁻¹)	5.8±0.2a	6.2±0.4a		5.3±0.0a
Wood NPP (t ha ⁻¹ year ⁻¹)	12.8±0.0a	21.8±2.3b		15.8±3ab
Total NPP (t ha ⁻¹ year ⁻¹)	30.3±0.2a	44.4±5.2b		40.7±0.5b
Aboveground litterfall (t ha ⁻¹ year ⁻¹)	7.0±0.3a	7.0±0.6a		6.2±0.1a

^aDry matter were converted in biomass carbon in Epron et al. (2013) using the carbon content of each component (46 % on average)

Malachite reactive P was determined at 630 nm with a GENESYS 10 UV-Visible spectrophotometer (Cambridge, UK).

N, C and available P concentrations in each soil layer were converted to Mg ha⁻¹, knowing the thickness and the bulk density of each soil layer, and summed to 0.25 m for N and C, and to 0.15 m for P.

Nitrogen and phosphorus in biomass and in fresh litter

Eight trees of each species distributed over the range of tree basal areas were selected and sampled over the three blocks but they were not equally distributed among blocks (2 to 4 individuals per block depending on stands and species). Trees were felled in each stand and the crown was divided into three equal-length sections. All leaves of each section were immediately weighed in the field. An aliquot of 20 randomly-selected leaves of each section were weighed. Their fresh mass was immediately measured. The leaves were dried at 65 °C and ground. The three aliquots of each tree were combined in a single composite sample according to the proportion of leaf fresh mass in each Section. A disk section of the trunk of each tree was cut with a chain saw at 1.3 m of the base of the tree and bark and wood were separated, oven-dried and ground.

Aboveground litterfall was collected every two weeks in litter traps (75 cm×75 cm) in two blocks from January to December 2011. The number of traps was four in the pure acacia and pure eucalypt plots of each block, and six in the mixed-species plot of each block. Litter was separated by species into leaves, bark and branches, weighed, oven-dried at 65 °C and ground. Litters collected over the year were combined in a single annual composite sample according to the biweekly litterfall (Epron et al. 2013).

Total N concentrations were determined as described above for the soil samples. P concentration was measured using the spectrophotometric vanadium phosphomolybdate method (Motsara and Roy 2008) after samples were digested with nitric acid (HNO₃) at 120 °C for six hours. N and P in aboveground litterfall and N and P immobilized in foliage, stem-bark and stem-wood were calculated by multiplying the concentrations with annual above-ground litterfall (Table 1) and with foliage, stem-wood and stem-bark biomasses estimated from allometric relationships applied to tree inventories (Epron et al. 2013).

Statistical analyses

Statistical analyses were performed with R software version 2.13.0 (R Development Core Team, 2012). Mixed-effect models with blocks and sampling place within blocks as random effects were used to estimate the effects of stand (100A, 100E and 50A:50E) and depth (fixed effects) on soil data. Contrasts were used to test relevant differences between stands and between depths when the overall model was significant (a probability level below 0.05). One way analyses of variance followed by Tukey's HSD tests were used to assess differences in N and P concentrations in aboveground biomass and litter compartments for the two species growing either in pure or in mixed-species stands.

Results

Soil N and C concentrations

N concentrations were lower than 0.065 % under all studied stands and decreased with depth. N

concentrations were significantly higher under the mixed-species stand (50A:50E) than under the pure eucalypt (100E) stand in the 0–0.05 m (Fig. 1). As for N, C concentrations of the studied layers also decreased

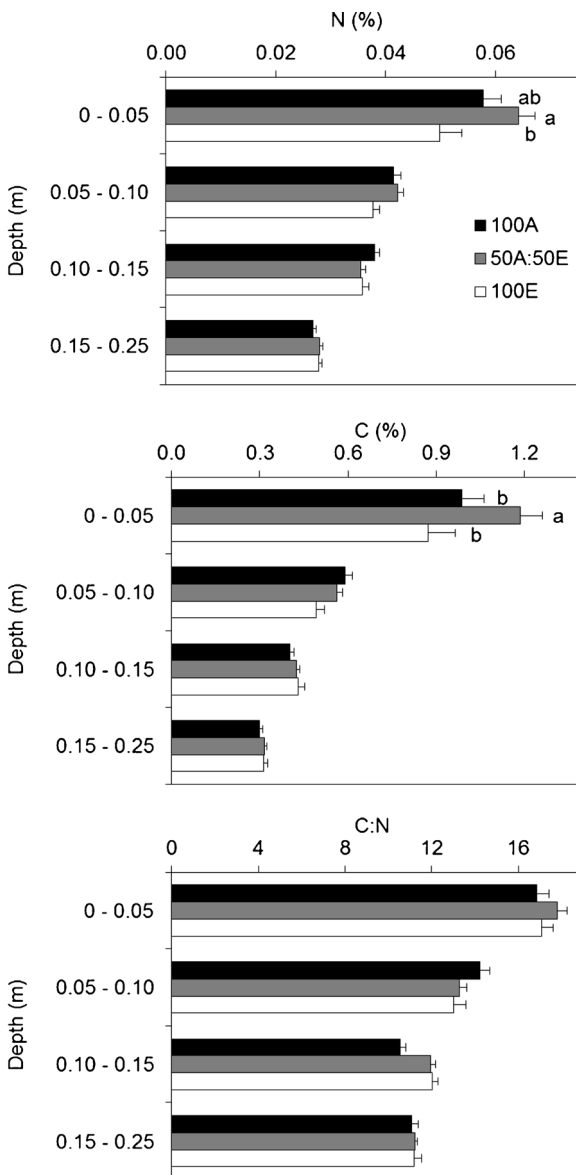


Fig. 1 Vertical profiles of nitrogen concentration (N), carbon concentration (C) and the ratio of carbon to nitrogen (C:N) down to 0.25 m in the three stands: 100A in black; 50A:50E in grey and 100E in white. The differences between stands were significant for N ($p < 0.01$) and C ($p < 0.05$). The differences between depth were significant for N, C and C:N ($p < 0.001$). A significant interaction between stand and depth was observed for C and N ($p < 0.01$), and for C:N ($p < 0.05$). The different letters indicate that means are significantly different between stands ($p < 0.05$) at a given depth. Vertical bars represent standard errors

with depth and were lower than 1.5 %. C concentrations were significantly higher in the 50A:50E than in the 100A and in the 100E stands in the 0–0.05 m depth layer (Fig. 1). C/N ratios decreased with depth in the soils of all studied stands (Fig. 1), and there was no significant difference between stands. We did not observe significant differences in soil N and soil C concentrations between samples collected under acacia trees and under eucalyptus trees in 50A:50E stands (data not shown).

Soil acidity and resin P

The pH (H_2O) values of the four soil layers in all stands were lower than 4.9, while those of pH (KCl) were lower than 4.1, and both increased significantly with depth in all stands (Fig. 2). The pH (H_2O) of the pure acacia was significantly lower than that of the pure eucalypt and the mixed-species stands in all studied layers. The pH (KCl) of the pure acacia stand was significantly lower than that of the mixed-species and pure eucalypt stands at all depths but did not differ significantly between 100E and 50A:50E.

The resin P values increased significantly with soil depth in all stands (Fig. 3). The mean value of resin P in the 0–0.05 m layer of all stands was lower than 9 mg P kg^{-1} , with the lowest value (6.94 mg P kg^{-1}) in 50A:50E. The difference between the mixed-species stands and the two pure stands was significant at all depths.

Bulk densities, N, C and P stocks

The bulk densities increased significantly with depth in all studied stands but did not differ significantly between stands (Table 2). The N stocks down to 0.25 m were significantly higher in 50A:50E (1.28 t ha^{-1}) than in 100E (1.19 t ha^{-1}). The same trend was found with the C stocks, ranging from 15.9 (100E) to 17.8 t ha^{-1} (50A:50E). The stock of available P down to 0.15 m was significantly lower in 50A:50E than in the two pure stands.

N and P in biomass and in litterfall

Nitrogen concentrations were higher in acacia than in eucalypt leaves (Table 3). Leaf N was significantly higher for eucalypt in 50A:50E than in 100E while it was significantly lower in 50A:50E than in 100A for

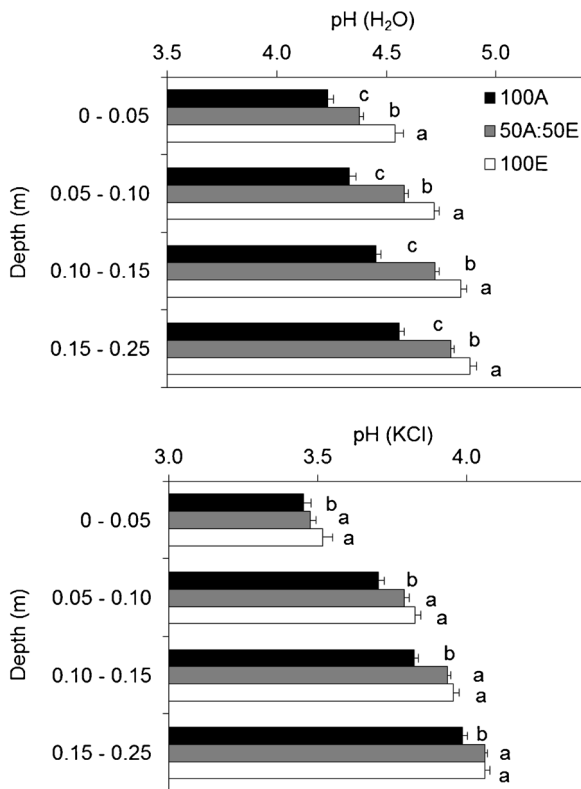


Fig. 2 Vertical profiles of pH (H₂O) and pH (KCl) down to 0.25 m in the three stands: 100A in black; 50A:50E in grey and 100E in white. The differences between stands and between depth were significant for pH (H₂O) and pH (KCl) ($p < 0.001$) with no interaction between stand and depth. The different letters indicate that means are significantly different between stands ($p < 0.05$) at a given depth. Vertical bars represent standard errors

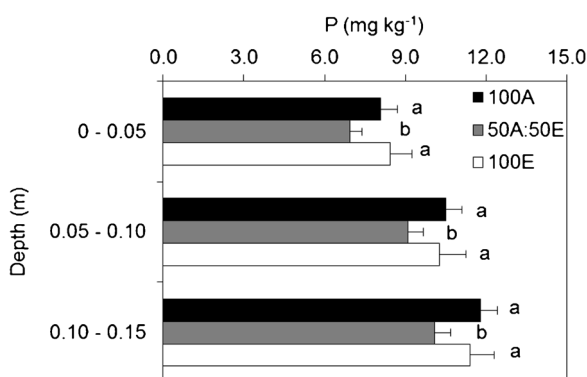


Fig. 3 Vertical profiles of resin available phosphate (P) down to 0.15 m in the three stands: 100A in black; 50A:50E in grey and 100E in white. The differences between stands and between depth were significant ($p < 0.001$) with no interaction between stand and depth. The different letters indicate that means are significantly different between stands ($p < 0.05$) at a given depth. Vertical bars represent standard errors

acacia. Phosphorus concentrations were higher in eucalypt leaves in the mixed-species stand compared to pure eucalypt stand, reaching similar values than acacia leaves. The N:P ratio was higher for acacia than for eucalypt leaves with no significant difference between the mixed-species and the pure stands. Bark and wood of acacia trees contained significantly more N than bark and wood of eucalypt trees while the P content was similar for both species, leading to higher N:P ratio in bark and wood for acacia than for eucalypt. There was no significant difference between trees growing in pure and mixed-species stands for both species.

Fresh leaf litter contained less N than leaves for both species with a stronger remobilization for eucalypts than for acacia, while P concentration exhibited less marked difference between leaves and leaf litter (Table 4). The N:P ratio of fresh leaf litter was thus lower than in leaves, especially for eucalypt. Branch litters of both acacia and eucalypt contained less N and less P than leaf litter. N concentrations in branch litter of acacia were three times higher than in eucalypt branches while their P concentrations were almost similar. Bark litter of eucalypt contained about twice less N and three times less P than leaf litter.

The amount of N and P stored in the foliage biomass was higher in the mixed-species and in the pure acacia than in pure eucalypt stands. The amount of N immobilized in stem-bark was greater in 100A and lower in 100E compared to the mixed-species stand (Table 5). Less N was immobilized in stem-wood in 100E compared to the two other stands. Unlike for P, the amount of N returning to soil through litterfall at the stand level was lower in 100E and higher in 100A compared to 50A:50E (Table 5) despite similar amounts of annual aboveground litterfall (Table 1).

Discussion

Soil nitrogen

Binkley (1992) argued that productivity usually increases in the presence of NFS on N-limited sites. The introduction of *A. mangium* in the eucalypt plantations on inherently poor Arenosols in the coastal plains of the Congo (Nzila et al. 2002; Laclau et al. 2010; Mareschal et al. 2011) led to a one third higher wood biomass at harvest in the mixed-species stand. The amount of C allocated to belowground production was shifted toward

Table 2 Soil bulk densities of the four studied soil layers, N and C stocks down to 0.25 m and available P stocks down to 0.15 m in the three stands: pure acacia (100A), mixed-species (50A:50E) and pure eucalypt (100E). Each value is an average (with standard error) of 27 (9×3 blocks) replicates for the pure stands and 54 replicates (18×3 blocks) for the mixed-species stand. The different letters indicate that means are significantly different between stands ($p<0.05$). There was no difference in bulk densities between stands but bulk density increased significantly with depth ($p<0.001$) in all stands (depth×stand interaction was not significant)

	Depth (m)	100A	50A:50E	100E
Bulk density (t m ⁻³)	0–0.05	1.21±0.02	1.19±0.2	1.22±0.02
	0.05–0.10	1.33±0.01	1.33±0.01	1.36±0.01
	0.10–0.15	1.37±0.01	1.36±0.01	1.40±0.01
	0.15–0.25	1.41±0.01	1.39±0.02	1.39±0.01
N stock (t ha ⁻¹)	0–0.25	1.25±0.02ab	1.28±0.03a	1.19±0.02b
C stock (t ha ⁻¹)	0–0.25	16.7±0.4ab	17.8±0.7a	15.9±0.4b
Available P stock (kg ha ⁻¹)	0–0.15	20.2±1.0a	17.0±1.3b	20.2±1.2a

aboveground production, highlighting positive interactions between species in the mixed-species stands (Epron et al. 2013).

The lack of difference in soil N concentrations under acacia trees and under eucalyptus trees in 50A:50E is not surprising because aboveground litter of both species were well-mixed on the forest floor and fine root of both species spread several meter away from each tree. The N concentrations in the topsoil layers and the soil N

stock were significantly higher in 50A:50E than in 100E, while the N stock of pure acacia stand was not significantly different from that of the mixed species stand. This may reflect a higher immobilisation of soil N in 100A than in 50A:50E due to higher N concentration in the biomass compartment of acacia trees than that of eucalypt trees. Increase in N concentration in the soil under NFS trees in monocultures were reported for a chronosequence of *A. auriculiformis* plantations on similar sandy Arenosols (Kasongo et al. 2009). While an increase in soil N under NFS trees has been reported in several studies either in comparison with non-fixing tree stands (Resh et al. 2002; Inagaki et al. 2011) or native grasslands (Ludwig et al. 2004; Hagos and Smit 2005; Sitters et al. 2013), it was not always the case. The introduction of *A. mangium* in *E. grandis* plantations did not affected soil N concentration in the topsoil on a Ferralsol in Brazil (Voigtlaender et al. 2012).

The effect of NFS trees on soil N may depend on the soil N status of the site that drives the contribution of symbiotic N₂ fixation to the N budget (Khanna 1997). In our site, N input through symbiotic N₂ fixation was estimated at 210 kg per hectare of N per year 2.5 years after planting in the pure acacia stand (Epron et al. 2013). While annual litterfall was found to be similar in the three stands (Epron et al. 2013, Table 1), branch and leaf litters of acacia trees exhibited three time greater N concentration than those of eucalypt trees and return more nitrogen to the soil. Thus, N₂ fixation by acacia and the recycling of N rich litter of acacia probably accounted for an improved soil N availability in our

Table 3 Nitrogen (N) and phosphorus (P) concentrations in leaves, bark and wood (%; $n=8$ trees, mean with standard error) of acacia and eucalypt trees growing in pure (100A) and (100E) and mixed-species (50A:50E) stands. Leaves were collected in the entire tree crowns. Bark and wood were sampled at 1.3 m height. The different letters indicate that means are significantly different between the two species growing either in pure or in mixed-species stands ($p<0.05$)

	100A	50A:50E		100E
		Acacia	Eucalypt	
Leaves				
N (%)	3.11±0.11a	2.74±0.07b	2.20±0.08c	1.62±0.07d
P (%)	0.22±0.01a	0.22±0.02a	0.23±0.01a	0.17±0.01b
N:P	14.6±0.9a	12.9±1.0a	9.9±0.5b	9.4±0.5b
Bark				
N (%)	1.17±0.03a	1.19±0.03a	0.44±0.01b	0.37±0.02b
P (%)	0.11±0.01a	0.13±0.01a	0.10±0.01a	0.13±0.01a
N:P	11.9±1.3a	9.5±0.5a	4.6±0.5b	3.1±0.3b
Wood				
N (%)	0.217±0.004a	0.227±0.009a	0.148±0.004b	0.13±0.005c
P (%)	0.015±0.001a	0.017 ±0.001a	0.015 ±0.001a	0.015 ±0.000a
N:P	15.1±0.8a	13.6±0.8a	10.0±0.6b	8.6±0.4b

Table 4 Nitrogen (N) and phosphorus (P) concentrations in fresh aboveground litter (%; n=2 blocks, mean with standard error) collected over a full year and separated into leaves, bark and branches for acacia and eucalypt trees growing in pure (100A) and (100E) and mixed-species (50A:50E) stands. The different letters indicate that means are significantly different between the two species growing either in pure or in mixed-species stands ($p < 0.1$)

	100A	50A:50E		100E
		Acacia	Eucalypt	
Leaves				
N	1.82±0.14a	1.80±0.01a	0.64±0.02b	0.56±0.02b
P	0.159±0.005a	0.198±0.010b	0.169±0.000a	0.170±0.003a
N:P	11.4±0.4a	9.1±0.4b	3.8±0.1c	3.3±0.2c
Bark*				
N	-	-	0.29±0.02a	0.30±0.02a
P	-	-	0.050±0.004a	0.050±0.007a
N:P	-	-	5.8±0.1a	6.0±0.4a
Branches				
N	0.94±0.02a	0.97±0.02a	0.27±0.01b	0.24±0.01b
P	0.095±0.005a	0.072±0.007b	0.088±0.004ab	0.074±0.001ab
N:P	9.9±0.2a	13.6±1.6a	3.05±0.0b	3.24±0.2b

*only for eucalypt trees

site, highlighting that facilitation is an important process of species interactions on N poor sites (Binkley 1992; Forrester et al. 2006).

Soil carbon

Greater C accumulation under NFS trees compared to non-fixing trees has been widely observed both when grown in monoculture (Paul et al. 2002 and references therein; Resh et al. 2002) or in mixed-species

plantations (Forrester et al. 2013) with few exceptions (Voigtlaender et al. 2012). The C concentrations in the topsoil layers and the soil C stock at our site exhibited a similar trend than soil N, being significantly higher in 50A:50E than in 100E. Such related changes in soil C and soil N are often reported after afforestation (Kaye et al. 2000; Li et al. 2012). As for N, changes in soil C concentration were mainly observed in the topsoil layers after changes in land use (Koutika et al. 1997; d'Annunzio et al. 2008; Epron et al. 2009; Qiu et al. 2010).

Two main mechanisms were proposed to account for an increase in soil C under NFS trees (Resh et al. 2002): an increase in C input (e.g. litterfall) or a decrease in C output (e.g. mineralization of SOM). In Southeast Australia, the increase in soil C under mixed-species stands of *A. mearnsii* and *E. globulus* was related to higher litterfall and higher belowground C flux (Forrester et al. 2013) that was ascribed to a higher productivity than in monocultures. A higher productivity was also observed in the mixed-species stand in our site but it did not translate into a higher aboveground litterfall, a higher total belowground C flux, a higher belowground net primary production or a higher fine root biomass (Epron et al. 2013).

The alternative hypothesis, e.g. a lower SOM mineralization, was observed under N-fixing *Albizia falcata* compared to eucalypt stands (Kaye et al. 2000) and it was ascribed to both a lower turnover of old C and a greater accretion of new C. Resh et al. (2002) found that about 55 % of the greater soil C

Table 5 Nitrogen (N) and phosphorus (P) in aboveground biomass compartments and in annual aboveground litterfall (kg ha^{-1} , n=2 blocks, mean with standard error) in pure acacia (100A), pure eucalypt (100E) and mixed-species (50A:50E) stands. The different letters indicate that means are significantly different between stands ($p < 0.1$)

	100A	50A:50E	100E
Leaves			
N	159±3a	127±13a	51±2b
P	11.3±0.2a	11.9±1.0a	5.3±0.2b
Stem-bark			
N	72±1a	47±9b	17±2c
P	6.8±0.1a	7.1±0.9a	5.9±0.7a
Stem-wood			
N	119±6a	127±13a	78±8b
P	8.1±0.4a	11.4±0.9a	8.9±1.0a
Annual above-ground litterfall			
N	112±12a	63±1b	30±4c
P	10.0±0.2a	10.7±4a	8.8±0.2a

storage under NFS than Eucalyptus species resulted from greater retention of old C_4 -C while 45 % resulted from greater accretion of new C_3 -C. A slowdown of C turnover related to N enrichment was also postulated after NSF tree species encroachment on tropical grassland (Sitters et al. 2013). SOM may be more protected or less prone to priming, e.g. to the rhizosphere-mediated stimulation of SOM decomposition (Fontaine et al. 2003; Kuzyakov 2010). Priming is known to be constrained by high nutrient availability in tropical forests soils (Nottingham et al. 2012) and available N may be an important factor modulating priming (Fontaine et al. 2004; Pausch et al. 2013). In contrast to other reports (Kaye et al. 2000; Voigtlaender et al. 2012; Forrester et al. 2013), the C:N ratio of the soil was not different between the two monocultures and the mixed-species stands despite much lower C:N ratio in above-ground litter of acacia than of eucalypt. This may indicate that soil C is less mineralized in acacia and in mixed-species stands than in pure eucalypt stands due to an increase in N concentrations.

Soil acidification

Soil acidification occurred under the acacias, and to a lesser extent in the mixed-species stands in our site. This is in line with several studies showing a soil acidification under NFS trees (Binkley 1992; Yamashita et al. 2008; Kasongo et al. 2009). The decrease in soil pH observed with the introduction of acacia in our system may be due to the fact that NSF have a higher cation:anion uptake balance, as their uptake of nitrate is smaller. Hence NSF would exude more H^+ and/or less OH^- as counterbalance ions, which would result in an enhanced acidification. Soil acidification after afforestation of Imperata grasslands by acacia in Indonesia was ascribed to a decrease in the amount of exchangeable cations on the exchange complex related to the translocation of base cations from soil to sustain tree growth demand (Yamashita et al. 2008). However, in our site, net primary production was 35 % higher for eucalypt monoculture than for acacia monoculture (40.7 and 30.2 t ha⁻¹ year⁻¹ respectively, Epron et al. 2013). Thus, eucalypt growth would have lowered soil pH more than acacia growth.

Any increase in SOM will increase the size of the exchange complex which would lower soil pH in cation-limited soils (Binkley 1992). In our site, soil C concentration was higher in the mixed-species than in the pure

acacia stands and thus the increase in SOM did not explain the difference in pH between stands (no correlation was found between SOM content and pH).

A significant decrease in pH values was also observed under *A. auriculiformis* fallows (>10 years) compared to virgin savannah mainly composed of *Loudetia arundinacea* and *Hyparrhenia diplandra* in the Arenosols on the Batéké Plateau in the D.R. Congo (Kasongo et al. 2009). The authors argued that this increase in soil acidity was due to humification and nitrification processes. Leaching of nitrate has been identified as a major cause of soil acidification under NFS crops (Tang et al. 1999). Nitrification in acacia monoculture was twice as high as in eucalypt monoculture in Brazil, and N mineralization was well-related to the amount of N returning to the soil in litterfall (Voigtlaender et al. 2012). In our site, much higher N concentration was found in above-ground acacia litter than in eucalypt one, while above-ground litterfall was similar in all stands. This indicates that the amount of N returning to the soil in litterfall was higher in 100A, lower in 100E and intermediate in 50A:50E. Nitrification was not measured in our site at the end of the rotation but preliminary results of N mineralization during the first two years following replantation of our site show higher nitrification in the acacia than in the eucalypt stands, and intermediate rates in the mixed-species stand (Tchichelle et al. unpublished data).

Soil available P

The available P concentrations in 100E (8.5 mg P per kg at 0–0.05 m depth) are in the range of those found in tropical eucalypt plantations (4–19 mg P per kg at 0–0.05 m depth, Laclau et al. 2010). NFS generally need more P for assuring symbiotic N_2 fixation in root nodules (Vitousek 1984; Binkley 1992; Inagaki et al. 2011). According to the soil type, acidification may increase soil P availability in the rhizosphere of NSF (Hinsinger et al. 2003; Shen et al. 2004) but soil acidification may not increase P availability in soils rich in Fe and Al oxides. Indeed, protonation of Fe and Al-oxides promote P adsorption on oxide surfaces and reduce its availability. In the soil of the studied area, the amount of Fe-oxide is very small (1.5 % of the bulk soil) and Al-oxides are not detected by X-Ray diffraction (Mareschal et al. 2011). Therefore, the increase in P adsorption on oxide surfaces linked to a decrease in pH in acacia stand should not be a major process in our soil.

Conversely, it has been demonstrated that roots and root-associated microorganisms of some NFS produce a greater variety and amount of organic acids, complexing organic acids and phosphatases than other plant species (Li et al. 2008; Marra et al. 2012), which may increase soil P availability in the rhizosphere of NFS. These compounds are important factors which control release of P through OM digestion, mineral weathering, and competition for site adsorption on oxide surfaces. All these chemical components exuded in the rhizosphere of NFS contribute to satisfy the P requirement of acacias.

However, lower available P was observed under *Albizia falcata* than under *Eucalyptus saligna* in Hawaii with the mixture of both species being intermediate (Binkley et al. 2000; Kaye et al. 2000). In contrast in our site, available soil P was similar under pure acacia and pure eucalypt stands, but was significantly lower in the mixed-species stand, showing an antagonist response compared to soil N. P concentration was higher in the eucalypt leaves in the mixed-species stand than in the pure eucalypt stand while litter P concentrations were similar. The lower N:P ratio in leaf litter than in green leaves indicated that the two species resorbed N more efficiently than P. This opposite trend to that often observed for tropical forests growing on highly weathered P impoverished soils (Hattenschwiler et al. 2008; Yuan and Chen 2009) highlights that N is more limiting in our site than P. The drop in N:P during senescence was much higher for eucalypt than for acacia, which confirms that acacia remobilized N less efficiently than non-fixing tree species (Inagaki et al. 2011). The N:P stoichiometry was similar in eucalyptus leaves in the pure eucalypt and in the mixed-species stands, highlighting that the improvement of soil N status by the acacia in the mixed-species stand enhanced P requirements of eucalypt trees. The amount of P immobilized in the foliage biomass was greater in the mixed-species stand and in the acacia monoculture than in 100E. Low P availability in the mixed-species stand may thus result from a higher translocation of P from soil into tree biomass which is less replenished than under the pure acacia stand. While similar quantities of P were returned to the soil in above-ground litterfall, slower decomposition rates of eucalypt litter than of acacia litter is however expected (Bernhard-Reversat 1996; Forrester et al. 2005). Alternatively we cannot exclude that in the 50A:50E, the use of N by eucalypt trees reduced N availability for acacia trees which enhanced the N₂ fixation and consequently involved the higher P uptake than in the 100A.

Synthesis

The introduction of *A. mangium* in eucalypt plantations increased the soil N concentration and stock on the acidic sandy and poor soils of the coastal plains at Pointe-Noire in the Congo. This increase was paralleled with a similar increase in soil C concentration and stocks, but understanding the underlying mechanisms requires further studies. This highlights that forest plantations mixed with NFS is a great option to retain the old soil C and may be an important strategy of reforestation or afforestation to offset C emissions. However, higher P uptake related to higher N availability may shift the system from N-limitation to P-limitation after several rotations, with a negative feedback on N₂ fixation. In addition, higher nitrification may induce soil acidification, especially in inherently acidic soils. It raises questions about the sustainability of mixed-species plantations and clearly highlights the need of long term monitoring.

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