



Does the Introduction of N₂-Fixing Trees in Forest Plantations on Tropical Soils Ameliorate Low Fertility and Enhance Carbon Sequestration *via* Interactions Between Biota and Nutrient Availability? Case Studies From Central Africa and South America

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Plant and/or crop growth rely on nutrient dynamics driven by specific soil biota in different environments. This mini-review aims to provide an overview of interactions between soil organisms, nutrient dynamics, and C sequestration. To this end, we investigated published results from three forest plantations (eucalyptus monocultures and mixed plantations with N₂-fixing acacia) on tropical nutrient-poor soils. One case study is located in Central Africa (Congolesse coastal plains) and two others in South America (Southeastern Brazil). Overall, the studies showed that soil biota activity exerted positive effects on (i) C accretion, as both soil carbon and belowground and aboveground biomass are driven and enhanced by soil biota; and (ii) on nutrient dynamics and biogeochemical cycles in nutrient-poor soil of tropical ecosystems, which are boosted following C accumulation. On the other hand, the pedoclimatic environment may potentially impact soil functioning of mixed-species plantations through its influence on the composition and activity of bacterial communities. Regardless of the potential risk of acacia invasiveness, benefits such as pulp, fuelwood, electric pole and non-timber products supply, have been reported in Central Africa. We, therefore, conclude that including N₂ fixing trees in forestry plantations as reported in this mini-review helps strengthen the links between soil biota, nutrient and SOC dynamics in mixed-species plantations on tropical nutrient-poor soils.

Keywords: soil biota, soil nutrients, soil carbon sequestration, crop/plant growth, climate change mitigation

INTRODUCTION

Ecosystem services of forest plantations especially when intercropping with N₂-fixing trees have been evaluated in Central Africa (1). They may benefit both rural and urban populations (i.e., pulp, fuelwood, non-timber products supply and poles for electricity network), and indirectly be linked to land restoration, environmental services, and conservation of natural forests (1–3). Preference of native species to exotic ones must be considered to avoid the risk of invasiveness, and loss of biodiversity (2, 4).

The introduction of N₂-fixing trees in forest plantations was also found to impact soil biota and nutrient dynamic and, therefore, ecosystem functioning and soil carbon sequestration. Interactions among soil biota, nutrient cycling and carbon sequestration have been investigated for decades in different geo-climatic zones (5–7). Soil biota, microbial biomass, community structure and function play a critical role in sustaining the fitness, development, and productivity of plants (8, 9). They regulate ecosystem processes involved in plant litter decomposition, soil organic matter (SOM) turnover, associated nutrient mineralization (10) and soil biodiversity (11). Numerous studies have already been conducted on soil biota and nutrient dynamics in the rhizosphere of acacia and eucalyptus forest plantations, (12–20).

Investigations on the relation of SOC to SOM dynamic on N and P cycles and their connections to soil organic carbon (SOC) sequestration have been performed (21, 22). Stoichiometric limitations (23, 24) for SOM stabilization processes in different ecosystems (3, 25–27) were observed. In highly weathered tropical soils, P availability is especially limited due to strong adsorption of this nutrient to the mineral phase (Al and Fe oxides). However, P availability may be enhanced by intercropping N₂-fixing *Acacia mangium* with *Eucalyptus grandis*, due to the stimulation of the root colonization by arbuscular mycorrhizal fungi (AMF) and phosphatase activity in the soil (28). Nevertheless, there are still some gaps that need to be filled to better understand the strong link between biota and nutrient dynamics, boosting C sequestration in the mixed-species forest plantations on nutrient-poor tropical soils.

In particular, it is unclear how soil biota drives nutrient dynamics and SOC sequestration in mixed-species plantations on tropical nutrient-poor soils. Recently, it was suggested that soil biota may boost soil C sequestration in forest plantations intercropped with N₂-fixing trees by enhancing above and belowground C allocations (29–31) and also reducing old C loss within the ecosystem (32). In general, in mixed plantations with N₂ fixing trees, stimulated changes in microbial community activities have been observed (16, 20, 33, 34). This could lead to C and N accumulation (35) in litter and soil by creating distinct microbial communities for respective monocultures and benefitting soil P and nitrate content (33), while P cycling and P nutrition is enhanced by arbuscular mycorrhizal fungi (AMF) colonization and phosphatase activities (28). It also involves a positive balance of nutrients since N₂-fixation from acacia benefits eucalyptus (30, 36, 37).

In this mini-review, three case-studies have been selected to give a detailed overview of the role of soil biota for nutrient dynamics and carbon sequestration on nutrient-poor tropical soils of acacia and eucalyptus forest plantations. To this end, we reviewed results from one study in Central Africa (Congolese coastal plains, Republic of the Congo), and two studies in South America (Itatinga, Southeastern Brazil). The first case-study reports the link between bacterial communities, nutrient dynamics and environment in the Congolese coastal plains (Central Africa). The two other case studies from Southeastern Brazil (South America) deal with bacterial, archaeal, and fungal communities related to nutrient cycling on the one hand, and soil faunal communities related to soil quality on the other hand. The three case-studies are characterized by the same experimental design of acacia and eucalyptus [*E. urophilla* x *grandis* (Congo) and *E. grandis* (Brazil)] plantations and different pedoclimatic conditions and forest management. Three main questions arise from the revision of the literature regarding the results of the three selected case-studies:

- How do N₂-fixing trees influence the interaction between microbial communities and their impact on SOC and nutrient dynamics in mixed-species forest plantations?
- How are these interactions impacted by soil properties and pedoclimatic conditions?

How can N₂-fixing trees be used to benefit other tropical forest plantations?

We hypothesize that based on similarities, differences and benefits (Table 1) of the practice introducing acacia in eucalyptus plantations in the three case-studies will strongly depend on soil pedoclimatic conditions but also on forest management.

PRESENTATION OF CASE STUDIES

In Brazil, the largest eucalyptus producer in the world, eucalyptus plantations are often implemented on very nutrient-poor soils as monocultures, needing the continuous application of mineral fertilizers. A possible solution is the co-cultivation of eucalyptus and N₂-fixing trees in mixed systems to provide an additional supply of N and P for eucalyptus (38, 39) and to create more heterogeneous systems i.e., higher microbial diversity, and supporting an efficient selection of beneficial microorganisms in the rhizosphere (19, 28).

Without neglecting the potential risk of threatening savanna ecosystems (40–42), afforestation of natural savannas on inherently nutrient-poor soils using eucalyptus started in the 1950s in the Congolese coastal plains, [Makany, 1964 cited in (43)]. This has been made to use unsuitable soils for agriculture, provide pulpwood for the industry, and fulfill the important production and consumption of fuelwood energy by the local populations i.e., preserving natural forests and halting the deforestation (1, 3). Since productivity of forest plantations declines after successive rotations and harvests (44), N₂-fixing trees have been introduced in the 1990s to restore soil fertility, and improve and sustain forest productivity (12, 30, 45).

TABLE 1 | Main characteristics of the two locations of the selected case studies.

| | Congolese coastal plains (Tchissoko, Republic of the Congo, Central Africa) | State of São Paulo (Itatinga, Southeastern Brazil, South America) |
|---|---|---|
| Similarities | | |
| - Former Project (Intens&Fix Project (ANR-2010-STRA-004-03) | + | + |
| - Experimental design | + | + |
| - Purpose | Industry & fuel wood energy | Industry |
| *Differences | | |
| - Latitude | 4°44'S | 23°02'S |
| - Longitude | 12°01'E | 48°38'W |
| - Elevation (m) | 100 | 860 |
| - Annual precipitation (mm) | 1430 | 1370 |
| - Average daily mean temperature (°C) | 25.7 | 19.0 |
| - Soil (WRB classification) | Ferralsols | Ferralsols |
| - Clay: silt:sand (%) | 3:6:91 | 13:3:84 |
| - C (g kg ⁻¹) | 6.9 | 17.6 |
| - N (g kg ⁻¹) | 0.4 | 0.9 |
| -Species | <i>E. urophilla x grandis</i> (clone 18-52) <i>A mangium</i> (collected in Congo) | <i>E. grandis</i> <i>A. mangium</i> (collected from Amazonia) |
| - Tree density | 800 | 1111 |
| - Fertilization (kg ha ⁻¹) | N(43, ammonitrate) | Dolomite limestone (2000), (44, superphosphate), K (potassium chloride, dud in hole at 20 cm from plants), [Fe (7), B (3), Zn (3), Mn (1), K (75, applied at 6, 12 and 18 months after planting)] |
| Age at harvest (years) | 7 | 6 |
| Studies conducted | | |
| -Soil biota | | |
| - Macrofauna | - Cockroaches (acacia litter) & ants (eucalyptus) (<i>Bernhard-Reversat, 1993</i>) | NA |
| - Mesofauna | NA | - Leguminous trees increase mesofaunal abundance and diversity - Positive correlations between soil mesofaunal attributes and microbial attributes (<i>Zagatto et al., 2019, a, b</i>). |
| - Fungal community | NA | - Increase the soil quality.- Increase fungal and bacterial diversity, mainly in litter layer (<i>Santana et al., 2021</i>) - Increase functional gene abundance (<i>nifH</i>) (<i>Pereira et al., 2019</i>) |
| - Bacterial community | <i>Prevalence of Firmicutes</i> (acacia stands), and <i>Proteobacteria</i> (eucalyptus stands), <i>Prevalence of Actinobacteria</i> (all stands) probably due to H ₂ S deposition from oil exploitation (<i>Koutika et al., 2020b</i>) | - Increase root colonization (<i>Bini et al. 2018</i>) - Increase enzymes activity(<i>Bini et al. 2018</i>) |
| - Archaeal community | NA | Abundance of <i>Thaumarchaeota</i> (<i>Santana et al., 2021</i>) |
| - Nutrient dynamics | | |
| - C stocks | - Increase (<i>Koutika, 2021</i>) | - Increase C and N labile fractions |
| - N status | - Increase (<i>Tchichelle et al. 2017, Koutika et al., 2017</i>) | - Increase total nitrogen in litter and soil (<i>Voigtlaender et al., 2019</i>) |
| - P availability | - Decrease (<i>Koutika et al. 2016</i>) but increase relative to natural savannas (<i>Koutika & Mareschal, 2017</i>) | - Reduced C/N ratio in litter (<i>Pereira et al., 2017</i>) |
| - S concentrations | - Increase (H ₂ S deposition, <i>Koutika et al., 2020b</i>) | NA |
| - Ecosystems services | | |
| -Non-timber products | Available (<i>Shure et al., 2012</i>) | NA |
| - Fuel wood energy | -Available (<i>Shure et al., 2012</i>) | NA |
| - Regularising deforestation of natural forests | -9% of households use fuel wood energy mainly from forest plantations (<i>Shure et al., 2012</i>) | |

* From (30).

NA, Not analyzed; +, shows the similarities.

To the best of our knowledge, very few studies addressed soil biodiversity (bacterial, fungal and faunal) in the mixed-species plantations in the Congolese coastal plains. Bernhard-Reversat, (12) reported an enhanced activity of edaphic macroarthropod communities i.e., the dominance of cockroaches in acacia litter as opposed to ants in eucalyptus. In general, few investigations have been carried out in tropical environments and especially in sub-Saharan Africa. On the contrary, within the two case-studies in Southeastern Brazil, studies have been conducted on archaeal (20), fungal (35) and faunal communities (46), in addition to investigations on microbial activity, microbial communities, rhizosphere and or root AMF colonization and soil phosphatase activity (19, 28, 34, 35).

How Do N₂-Fixing Trees Influence the Interaction Between Microbial Communities and Their Impact on Soc and Nutrient Dynamics in Mixed-Species Forest Plantations?

Bacterial communities structure in soil and litter layers was found to be related to the soil nutrient pools in the first case study at Itatinga (Southeastern Brazil). Indeed, in 27- and 39-months old acacia forest plantations, increased C and N contents in the organic soil fractions (including microbial biomass), bacterial diversity and richness (soil and litter), and *nifH* gene (related to nitrogen fixation) abundance was observed (34). Furthermore, *Rhizobium*, *Bradyrhizobium* and *Sphingomonas* showed a positive correlation with *nifH* and total soil N. Additional evidence shows that change in the soil microbial community composition in mixed acacia and eucalyptus plantations is correlated with increased C and N cycling (19).

Archaeal communities are also important contributors to nutrient cycling in mixed-species forest ecosystems. Santana et al. (20) reported that pure stands type influenced the archaeal community structure of the litter layer, as archaeal richness, diversity, and the relative abundance of *Thaumarchaeota* increased in 27- and 39-months old acacia plantations in Southeastern Brazil. It has also been found that archaeal structure responded to stand types in the litter layer, in which NH₄⁺, total-N and the C/N ratio were the most important attributes for community groups differentiation. Young mixed plantations exert a low effect on soil microbial community structure, but archaeal communities may have an important role in nutrient cycling in the litter interface, especially related to the N cycle in the initial stages of tree development (20).

Acacia stimulates the soil phosphatase activity, thereby increasing root AMF colonization and, consequently, P nutrition to the surrounding trees in the same system (28). Pereira et al. (19) showed that the soil organic fraction, phosphorus inorganic fraction, total-P and acid phosphatase activity, were significantly higher in pure stands containing acacia at Itatinga (Southeastern Brazil). Total P, richness, and Shannon diversity of the fungi in the litter was significantly higher in these stands with an intermediate structure

between the two pure stands. Also, mixed systems strongly correlated with P dynamics, particularly in the litter layer. Co-occurrence networks of fungal taxa became simpler in pure eucalyptus stands, whereas mixed counterparts showed a more connected and complex network. This result evidenced that mixed forest plantations promote positive responses in the fungal community connections, which are closely related to P availability in the system, prominently in the litter layer.

The second case-study in Southeastern Brazil reported an improvement in soil quality in stands containing acacia compared to pure eucalyptus stands due to their soil mesofaunal and microbial attributes (46). In these planted forests, chemical attributes (especially N, low C/N ratio and macronutrients) are strongly related to different mesofaunal orders in the litter layers (47). A higher diversity of mesofaunal orders in acacia monoculture and mixed-species stands than eucalyptus monoculture is probably due to the higher quality of the litter in stands containing acacia than in pure eucalyptus counterparts (34, 37).

Seasonality is another important factor for the organisms that inhabit the soil (48). Higher mesofauna density in soil during drought periods relative to mesofauna density in the litter at the same period in forest plantations of eucalyptus and acacia highlighted the soil's importance as a refuge for the invertebrate community in periods of water scarcity in Southeastern Brazil (47). Forest plantations presented higher mesofauna diversity, but a lower mesofauna density in litter when compared to no-tillage (15) once secondary forests in regeneration accumulate organic matter of higher quality and present higher niche diversity than agricultural systems.

In Central Africa (Congolese coastal plains), probably due to stimulated microbial activity (16) and enhanced P cycling, AMF colonization, phosphatase activities (28) and nutrient dynamics (N and P) were stimulated in acacia and eucalyptus plantations in the afforested ecosystems compared with native tropical savannas (49). An enhanced N dynamics was also reported in stands containing acacia relative to eucalyptus monocultures (50, 51). In addition, nuclear magnetic resonance (solid state ¹³C CPMAS and NMR and ³¹P-NMR) spectroscopy reported higher amounts of extractable inorganic P (litter and soil) in the stands containing acacia (43), probably due to high mineralization rate and the lack of soluble leaching during the drought period. This is probably related to greater biological activity (28), which would prevent the P losses in the soil and may indicate a mechanism able to sustain forest plantation through P demand (19, 25).

Further effects have been observed through increased C stocks in stands containing acacia in the Congolese coastal plains. As in other ecosystems within the world (24, 38, 39), carbon sequestration in biomass and soil does occur in acacia and eucalyptus plantations (30, 52). Greater soil carbon stock increments were estimated in pure acacia and mixed-species stands with 0.8 t ha⁻¹ and 1.9 t ha⁻¹, respectively, relative to eucalyptus stands (53). This potentially may contribute to climate change mitigation, and adaptation and resilience by creating healthier soils rich in C and other nutrients (3, 53).

How Are These Interactions Impacted by Soil Properties and Pedoclimatic Conditions?

Although the three case-studies showed similar design (Table 1), there are differences in main site characteristics such as latitude, longitude, annual precipitation, soil classification, tree density, and fertilization (30). From this mini-review, it is apparent that forest management, soil type and geo-climatic zone affect the links between soil biota and nutrient and SOC dynamics. Mixed plantations on poorest soils and poor forest management i.e., those of the Congolese coastal plains responded better to the introduction of *Acacia mangium* relative to the control (eucalyptus), as they showed more improved soil N status (50, 51), C stocks (52, 53), and stand wood biomass (30, 45) than the trials in Southeastern Brazil.

This may illustrate the potential impact of the environment on soil functioning and productivity in forest plantations. Sustaining forest plantations strongly relies on interactions among nutrient cycling, microbial communities and environment (54). Using meta-barcoding of the 16S rRNA bacterial genes, the predominance of *Actinobacteria* phylum, strongly correlated to sulfur (S) at all classes, has been observed in different stands of monoculture and mixed-species plantations in the Congolese coastal plains (55). This may be due to the potential impact of H₂S deposition from oil exploration activities (from the end of the 1960s) on the environment i.e., the bacterial communities (Koutika, personal communication). It was previously observed that sulfur (S) has a potential to stimulate the growth of Gram-positive bacteria, fungi and *Actinobacteria* in subtropical forest soil (56), while the prevalence of hydrogen sulfide (H₂S) depositions from industrial areas does increase the growth of *Actinobacteria* alone (57).

How Can the Introduction of N₂-Fixing Trees Be Used to Benefit Other Tropical Forest Plantations?

In addition to above mentioned positive effects on soil microbial functioning, other benefits of the intercropping with N₂-fixing trees include its impact on ecosystem services. Most of our knowledge on the effects of N₂-fixing trees on ecosystem services derives from local or regional studies, with a great influence of the environmental conditions, history and cultural background of each region on these effects (58). Therefore, it is fundamental to identify synergies (like among soil fertility, soil formation and climate regulation) and trade-offs among the effects of N₂-fixing trees on different ecosystem services. For example, the introduction of N₂-fixing trees was found to affect the SOC stock, and the recalcitrant carbon chemical composition in *Eucalyptus urophylla* plantation in subtropical China (59). N₂-fixing trees may attain a higher production, especially in infertile or degraded soils, explaining their contribution to soil formation, land restoration and erosion control and water regulation (58). Also, mixed forest plantations provide a wide range of social and environmental services by mitigating future wood shortage problems and producing a huge proportion of world industrial

wood and other forest products (60). When compared with monospecific plantations, mixed forest plantations have been found to give more benefits in biodiversity, economy, forest health and occasionally in productivity, producing more pulp, fuelwood and non-timber products supply (1, 2). The mixed-species forest tree stands can be beneficial for both trees and ecosystems in many regions. Therefore, we could apply findings reported in this mini-review to other similar tropical forest ecosystems in Central Africa (3, 61), and or elsewhere in the world.

CONCLUDING REMARKS

This mini-review reports how soil biota drives and enhances nutrient dynamics and C sequestration in the mixed-species acacia and eucalyptus plantations on tropical nutrient-poor soils in three case-studies in Central Africa and South America. Soil properties and pedoclimatic conditions drive this interaction. However, enhanced nutrient dynamics and C sequestration induced by the swift change in microbial communities in the acacia-eucalyptus mixed forest plantations reported in the Brazilian case-studies, may explain enhanced soil C sequestration (all case-studies), C allocation in belowground (South America), and stand wood biomass (all case-studies). The mini-review also reports other ecosystem services of the practice directly or indirectly linked to the local populations (Central Africa) such as fuelwood energy, pole for electricity network and non-timber products. Finally, the mini-review highlights the effects of anthropogenic activities and environment on soil biota of forest plantations with further benefit on soil fertility improvement, land restoration and potentiality to resilience and adaptation to climate change.

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All authors listed have made a substantial, direct, and intellectual contribution to the work and approved it for publication.

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