



Biomass production, nitrogen accumulation and symbiotic nitrogen fixation in a mixed-species plantation of eucalypt and acacia on a nutrient-poor tropical soil



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ABSTRACT

The success of mixed-species tree plantations depends on the balance between positive and negative interactions. Mixtures of *Acacia mangium* and *Eucalyptus urophylla* × *grandis* out-yield their respective monocultures in term of wood production on the Congolese coastal plain, suggesting that facilitation and/or competitive reduction surpass interspecific competition. We investigated how these interactions affected biomass production and N accumulation during the early growth stage of a second rotation of a mixed-species stand of these two species. We used the ¹⁵N dilution method to estimate symbiotic nitrogen fixation and its contribution to N accumulation in acacia monoculture and mixture, and we assessed how much N derived from the atmosphere is transferred to the eucalypt trees in the mixed-species stand. Eucalypts grew taller and acacias grew larger in the mixture compared to the monocultures. N mineralomass was greater in the mixture relative to the average values in the two monocultures, with both species contributing to this enhanced N mineralomass. The amount of N derived from the atmosphere in the mixture was 60% higher than that expected given the amount found in acacia monoculture, and 16% of the nitrogen accumulated in eucalypt trees and aboveground eucalypt litterfall was derived from the atmosphere. Reduced competition for light and soil water also contributed to the increased growth of acacias in the mixture, showing that both species benefit from growing in a mixed stand.

1. Introduction

Soil nitrogen (N) is thought to be non-limiting for tree growth in tropical forests where the rate of biological N fixation is high (Hedin et al., 2009; Martinelli et al., 1999). However, this may not be the case in fast-growing tropical tree plantations on nutrient-poor sandy soils when large amounts of N are regularly exported from the site at the end of each rotation (Gonçalves et al., 2008; Laclau et al., 2010). In this context, the introduction of N-fixing tree species in forest plantations may be a valuable option to sustain wood production (Binkley, 1992; Binkley et al., 2003; Bouillet et al., 2013; DeBell et al., 1989; Forrester et al., 2006; Khanna, 1997).

High rates of biological N fixation, up to 20 g N m⁻² yr⁻¹ have been reported in mixed-species stands including a N-fixing species, where more than 90% of N in N-fixing trees may be derived from the atmosphere (Binkley, 1992; Bouillet et al., 2008; Nygren et al., 2012; Parrotta et al., 1996). N derived from the atmosphere is first mobilized

within N-fixing trees before becoming available for the non-fixing species, mainly after the decomposition of both aboveground and belowground (fine roots, mycorrhizal hyphae, nodules) litter and of harvest or pruning residues (Binkley, 1992; Forrester et al., 2006; Khanna, 1997; Nygren et al., 2000). N derived from the atmosphere can even become more rapidly available to non-fixing species through root exudation (Fustec et al., 2010; Paula et al., 2015; Wacquand et al., 1989; Wichern et al., 2008) or by direct transfer through common mycorrhizal networks (Frey and Schüepp, 1993; He et al., 2009; Li et al., 2009; Nygren and Leblanc, 2015; Paula et al., 2015).

Moreover, at equal stand density (replacement series design), a more efficient capture of limiting resources may alleviate competition and thereby contribute to enhanced productivity in the mixed stand (Forrester et al., 2006; Kelty, 2006). Stratification of the canopy in mixed-species stands may increase light interception compared with monocultures (Bauhus et al., 2004; Binkley et al., 1992; le Maire et al., 2013). Evidence of root stratification in mixed-species stands has also

Abbreviations: Ndfa, percentage of nitrogen derived from the atmosphere; Nfix, amount of fixed nitrogen; x^f, excess atom fraction

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been reported, but its effect on water and nutrient acquisition remains unclear (Khanna, 1997; Laclau et al., 2013). In addition to spatial complementarity, competition is reduced when the species of a mixture use different forms of a limiting resource, such as nitrate, ammonium or amino acids for nitrogen (McKane et al., 2002). The N-fixing tree species of a mixed-species stand may mainly rely on N derived from the atmosphere, thus reducing competition for soil N for the non-fixing species (Forrester et al., 2006).

Previous results obtained on a nutrient-poor sandy soil of the Congolese coastal plain indicate that introducing *Acacia mangium* Willd. in eucalypt plantations leads to a 30% increase in wood biomass at harvest due to decreased belowground allocation of net primary production (Epron et al., 2013). This coincided with an increase in soil N content (Koutika et al., 2014), but it remains unclear whether this increase in soil N resulted from N fixation and whether it fully accounted for the higher aboveground biomass production in mixtures compared to monocultures, or whether the acquisition of another limiting resource was also improved. The objective of the present study was to investigate how interactions between *A. mangium* and *Eucalyptus urograndis* (*E. urophylla* S.T. Blake × *E. grandis* W. Hill ex Maiden) trees affect biomass production and N accumulation during the early growth stage of a second rotation of a mixture of these two species. We estimated the contribution of symbiotic N fixation to N accumulation in both acacia monoculture and mixture and assessed how much N derived from the atmosphere is transferred to the eucalypt trees when the two species are grown together.

2. Materials and methods

2.1. Site description

The studied site is located in the Republic of the Congo, on a plateau close to Tchissoko village (4°44'41"S; 12°01'51"E; 100 m alt.) on a deep Ferralic Arenosol characterized by a sand content above 90% and a cation exchange capacity below 0.5 cmol kg⁻¹ (Mareschal et al., 2011). These soils are acidic with low C and N content, with topsoil N and C concentrations typically under 0.05% and 0.9%, respectively, and pH below 4.6 (Koutika et al., 2014). The climate is subequatorial with a cool dry season extending from June to September. The original vegetation was native tropical savanna dominated by the Poaceae *Loudetia arundinacea* (Hochst.) Steud.

The area studied was afforested in 1984 with eucalypt hybrids. In May 2004, an experimental plantation was established as a completely randomized block design with five replicates (Epron et al., 2013). It comprised monocultures of acacia (*A. mangium* Willd, seeds from the PH482 provenance from Papua New Guinea, grown in a local trial, 100A), monocultures of hybrid eucalypt (*E. urophylla* S.T. Blake from Flores Island × *E. grandis* Hill ex Maid from northern Queensland, Australia, 100E), and mixed stands of the two species in a proportion of 1:1 (50 A:50E). Each plot covered 1250 m² comprising 100 trees (10 plantation lines of 10 trees each) with an inner zone comprising 36 trees (6 × 6). Stocking density was 800 trees ha⁻¹. The first trial was harvested in January 2012 and a new trial was planted following the same design in March 2012. In all blocks, each treatment was planted at the same location as it was for the first rotation. Only the de-barked commercial-sized boles were removed. Harvest residues (bark, top-ends with diameter below 2 cm, branches and leaves) that remained on the forest floor were 11.3, 11.6 and 7.7 Mg ha⁻¹ in 100A, 50A50E and 100E respectively (Tchichelle et al., 2016).

Rainfall (tipping bucket rain gauge ARG100, Campbell Scientific Inc., Logan, UT, USA) and air temperature (HMP45C, Campbell Scientific Inc.) were measured in an open area in the vicinity of the field trial. The volumetric soil water content (CS215-L, Campbell Scientific Inc.) was monitored in one block at depths of 0.15, 0.5, 1, 2 and 4 m (two vertical profiles in each plot). Data were collected every 30 s and measurements were stored half-hourly on data loggers (CR1000,

Campbell Scientific Inc.) powered by solar panels. Discontinuities in the data were mainly due to energy supply problems (failure of batteries or solar panel components). 13% of air temperature and rainfall data, and 23% of soil water content data, were missing.

2.2. ¹⁵N labelling of soil in pure and mixed-species stands

One year after planting (March 2013), two blocks were labelled with a ¹⁵N-enriched solution, the other three blocks being used as a reference. The ¹⁵N was applied in the form of ammonium sulphate (99% of ¹⁵N) and supplied to the soil at the rate of 0.02 g of ¹⁵N per m² in the inner zone of each labelled plot. The aboveground litter was carefully removed before labelling in order to prevent the ¹⁵N from being trapped, and it was reinstalled immediately after application of the tracer. The inner zone of each plot was divided into a gridwork of 36 grid cells of 12.5 m² in order to apply the labelled solution as evenly as possible. Ten liters of labelled solution were applied in each cell, equivalent to a rain pulse of 0.8 mm.

2.3. Tree census, harvest and litterfall

Tree height (H, m) and circumference at 1.3 m height were measured once a year on the 36 trees of the inner zones at ages 12, 24 and 36 months. For multi-stem acacia trees, the circumference of all the stems was measured and the basal area of all the stems was cumulated for each tree.

In April 2014, two years after planting and one year after labelling, 10 trees of each species were harvested both in the pure and in the mixed-species plots. Six of these trees were selected in the inner zone of plots in the blocks that had been ¹⁵N-labelled, and four in plots of the unlabelled blocks. They were chosen so as to reflect the observed distribution of basal areas. One or two trees were selected in each class depending on the class frequency, and then harvested. Felled trees were separated into stem wood, stem bark, living branches and foliage.

Root biomass was measured on unlabelled trees only, in order to avoid disturbing the inner zone of the labelled plots. Samples of coarse, medium and fine roots of each labelled tree were nevertheless collected by digging a small trench close to the tree. All the coarse roots (diameter above 10 mm) of each unlabelled tree, including the stump, were excavated. Medium roots (diameter between 2 and 10 mm) were extracted to the depth of 1 m in one-fourth of the Voronoï polygon, defined as the elementary space delimited by the half-way distances to the sampled tree's neighbours (Levillain et al., 2011). Before the excavation for coarse and medium roots, nine cores (8 cm diameter) were collected to a depth of 1 m, and fine roots (diameter below 2 mm) were sorted. In mixed-species stands, roots of the two species were distinguished by their colour and their branching pattern (Laclau et al., 2008).

Fresh mass was measured in the field and subsamples of known fresh weight were oven-dried at 65 °C in the laboratory, weighed, grinded and stored before analysis, except for fine roots which have all been oven-dried. The leaf subsamples (60 leaves per tree) were scanned using a desktop scanner before drying to estimate specific leaf area and to convert leaf biomass per tree into leaf area per tree (Nouvellon et al., 2010).

Litter fall was collected weekly from June 2013 (beginning of leaf fall) to March 2014 in 75 × 75 cm traps. Four traps were installed in each monoculture plot and eight in each mixed-species plot of the five blocks. Half of the traps were located at the base of a tree and the other half at the centre of the area delimited by four trees. Litter was sorted per species, pooled by plots, oven-dried at 65 °C, weighed and grinded. Composite samples were stored before analysis.

2.4. Chemical and isotopic analyses

All samples were analysed for total N concentration and ¹⁵N composition using an elemental analyser (CE, Milan, Italy) coupled to a

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