



# Is tree diversity an important driver for phosphorus and nitrogen acquisition of a young tropical plantation?

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## ABSTRACT

Many tropical plantations in Central America are monocultures of fast growing, mostly exotic species such as a teak, eucalypts and pines. This has been perceived as a problem for ecosystem stability, pest control, local biodiversity and long-term nutrient availability. In our study, we followed the effects of increasing tree diversity (1, 3 and 6 native species) on aboveground nitrogen (N) and phosphorus (P) pools in a young experimental biodiversity plantation (central Panama) over two subsequent years. Our results show a positive but not consistent net effect of biodiversity on the N and P pools, mainly explained by the complementarity effect. N and P use efficiencies strongly varied among the investigated tree species and the species richness gradient. *Anacardium excelsum* and *Luehea seemannii* were associated with higher N and P use efficiencies while *Hura crepitans* and *Tabebuia rosea* were less efficient in aboveground biomass production per unit N or P. Tree species tended to have lower P use efficiencies in the intermediate diversity level compared to monocultures and six-species mixtures. Although the environmental conditions explained a large part of the variation in the N and P pools (58%) in our experiment, we argue that incorporating tree mixtures in the management can bring additional benefits and improve tree growth and nutrient uptake as compared to the monocultures.

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## 1. Introduction

As the cover of natural tropical forests has declined over the last decades and the demand for wood products continues to grow, tree plantations have become increasingly important. The conversion of grasslands into forest plantations is currently a wide-spread land use in tropical regions and contributes to the production of timber, fuelwood and could serve as carbon-sinks under the Clean Development Mechanisms (UNEP, 2008) within the Kyoto Protocol. According to FAO (2005), the area of forest plantations increased at a rate of 2.8 million ha yr<sup>-1</sup> between 2000 and 2005. However, many of the tropical plantations are monocultures of fast growing, mostly exotic species as teak (*Tectona grandis*), eucalypts or pines. This has been seen as a problem for system stability, long-term nutrient availability and associated biodiversity (Aweto, 2001; Haggard et al., 1998; Piotto et al., 2003; Spangenberg et al., 1996 and references in Hartley, 2002).

Thus, both the tremendous loss of biodiversity due to disappearance of the tropical rainforest and the predominance of monocultures in plantation forestry have raised concerns about the significance of tree diversity for ecosystem functioning and the delivery of goods and services (Millennium Ecosystem Assessment, 2005). Although some of the experimental and observational studies from the tropics suggested positive effects of mixed plantations on tree growth and productivity (Erskine et al., 2006; Potvin and Gotelli, 2008; Petit and Montagnini, 2004; Piotto et al., 2004; Redondo-Brenes and Montagnini, 2006), tree regeneration (Carnevale and Montagnini, 2002) and nutrient storage (Montagnini, 2000), no or negative effects were found for litter decomposition (Scherer-Lorenzen et al., 2007), soil nutrient concentrations (Firn et al., 2007; Stanley and Montagnini, 1999) and woody understorey diversity (Butler et al., 2008). As a result, several of these studies highlighted the importance of tree species identities in mixed stands rather than species richness per se. Positive effects of diversity were often observed in mixtures including N<sub>2</sub>-fixing tree species. This has led to intensive research on facilitative tree interactions (cf. Forrester et al., 2006; Kelty, 2006). In contrast, less information is available about other positive plant interactions such as complementary resource use. Two important aspects of complementary resource use in tropical managed systems are

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light partitioning through canopy stratification and water and/or nutrient partitioning, e.g. through root stratification. While there is substantial evidence from plantation forestry on the first aspect (Ewel and Mazzarino, 2008; Menalled et al., 1998), information on belowground mechanisms largely comes from tropical agroforestry studies (e.g. Dinkelmeier et al., 2003; Rowe et al., 2001; Schroth et al., 2001). Nevertheless, the implications for tree nutrition and hence tree productivity are large, if species with complementary resource use can be identified for plantation purposes (Richards et al., 2010).

A possible way to statistically assess the importance of tree species complementarity in mixtures is by applying the additive partitioning method of Loreau and Hector (2001). This method allows to partition the net effect of biodiversity (NE) into a complementarity effect (CE) and a selection effect (SE). SE represents the changes in resource uptake and/or biomass production of a mixture due to the dominance of a particular species with a disproportionate effect on these traits (also referred to as sampling effect). In contrast, CE represents the changes in NE which cannot be attributed to any single species in the mixture and is often interpreted as evidence for niche separation of facilitative species interactions. However, Cardinale et al. (2007) concluded in their study that CE rather includes all forms of resource partitioning, i.e. also indirect and non additive species interactions, thus making it impossible to identify a single biological mechanism for positive mixture effects. Nevertheless, applying the additive partitioning method in plantation forestry still could be useful to identify combinations of tree species resulting in a positive biodiversity effect through multiple species processes. In addition, site characteristics such as soil nutrient availability and topographical heterogeneity must be included in studies on diversity effects as they can have a strong influence on tree nutrition and may enhance or hide effects of species richness (Healy et al., 2008; Hiremath and Ewel, 2001).

The quantification of nutrients stocks in the aboveground biomass is an important issue in sustainable plantation management. Depending on rotation length and harvest practices, the amount of nutrients lost through biomass removal can crucially determine the future success of productive plantations (Montagnini and Jordan, 2005). Nutrient use efficiency, i.e. the amount of biomass produced per unit of a certain macro- or micronutrient, is a useful measure to assess the nutrient demand and the productivity of a tree species on a site. Especially, the use efficiencies of the two macronutrients nitrogen (N) and phosphorus (P) by different tree species need to be considered for sustainable site management, since the two nutrients are pivotal in many metabolic plant processes and are known to limit plant growth (Metzner, 1995; Niklas, 2008).

The Sardinilla plantation in Panama is a tree biodiversity experiment designed to test the relationship between biodiversity and ecosystem functioning. In contrast to many other research plantations in the tropics, its experimental setup does not include  $N_2$ -fixing tree species due to their known and strong effects in mixed forest experiments. Therefore, the design allows to address other, more subtle mechanisms than  $N_2$ -fixation, as for example complementary soil resource use or changes in nutrient use efficiencies (Richards et al., 2010). The aim of this study was to address the importance of tree diversity for acquisition of P and N by the trees in a native tree species plantation. By estimating the amount of the two macronutrients stored in the standing biomass, henceforth referred as N and P pools, we intended to answer the following questions:

1. Does species richness and species composition affect the size of N and P pools in the trees and if so, is this caused by selection or complementarity?

2. To what extent do the environmental variables contribute to the explanation of the N and P pool patterns in the plantation?
3. Are N and P use efficiencies affected by the tree species and/or the species richness?

## 2. Materials and methods

### 2.1. Study site

The study was conducted during 2006 and 2007 in an experimental tree plantation in Sardinilla (9°19'30"N, 79°38'00"W), central Panama, approximately 50 km north of Panama City. The study site has an elevation of 70 m a.s.l. and extends over a slightly undulated terrain. Mean annual precipitation is around 2350 mm with a prominent dry season from January to March, and mean annual temperature is 25.1 °C with a daily minimum of 21.7 °C and a maximum of 33.1 °C. The soils belong to the order of Alfisol with Typic Tropudalfs on the ridges shifting to Aquic Tropudalfs in the depressions. They contain a high content of expanding clays (up to 65%), causing deep cracks during the dry season. The bedrock is composed of Tertiary limestone and other sedimentary rocks (Potvin et al., 2004). The site was originally covered with semideciduous tropical lowland forest until it was logged in 1952/53, subsequently used for cropping (2–3 years) and eventually converted into a pasture. The plantation was established in 2001; it consists of 24 plots (45 × 45 m), each divided into 4 subplots of equal size (Healy et al., 2008), with an initial tree density of 1111 trees ha<sup>-1</sup>. The six tree species planted are all native to Panama and include two fast-growing species *Luehea seemanii* (Tiliaceae) and *Cordia alliodora* (Boragniaceae), two moderately fast growing species *Anacardium excelsum* (Anacardiaceae) and *Hura crepitans* (Euphorbiaceae) and two slow growing species *Cedrela odorata* (Meliaceae) and *Tabebuia rosea* (Bignoniaceae). The design included 12 monocultures (2 replicate plots per species), six replicates of three-species and six replicates of six-species mixture plots (see Fig. A.1 in the supplementary). Three-species mixtures differed in their species composition, whereas six-species mixtures did originally include all six tree species and were thus identical in composition (Scherer-Lorenzen et al., 2007). *Cordia alliodora* suffered such high mortality rates after planting that it almost completely failed to establish in the plantation. The two monoculture plots of *C. alliodora* had to be abandoned. Therefore, we excluded this species from the analyses. In extension to a previous study by Oelmann et al. (2010) that used an individual tree approach, our investigation expanded over 2 years and included the collection of plant and soil samples in all relevant plots of the experimental design. In particular, the terrain elevation differences and information on the slope inclination were integrated in the analyses.

### 2.2. Sampling

At the end of the growing season (December to January) in 2006 and 2007, every tree in the plantation was measured in order to estimate aboveground tree biomass. Tree height was assessed using a hypsometer (Vertex III, Haglö, Sweden). Tree basal diameter (BD), taken at 10 cm aboveground, and tree diameter at breast height (DBH) were measured with a circumference chain.

For the determination of nitrogen and phosphorus concentrations, leaves and branches were collected during the rainy season between 4 and 7 July 2006 and 2 and 6 July 2007. In each plot, 3 individuals (within ±2 m of mean tree height) were semi-randomly selected for each species. Border trees were omitted to avoid edge effects. From each tree, 5–10 sun and shade leaves each, and 3 terminal branches were collected. From each of the branches, one disc of about 1 cm thickness, including both bark and wood, was

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