The long-term performance of 35 tree species of sudanian West Africa in pure and mixed plantings

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Abstract

The rapidly growing human population in sudanian West Africa has generated increasing demand for agricultural land and forest products so that most of the original vegetation cover has disappeared and the remainder is highly degraded, meaning that it is urgent to draw up a long-term assessment of the potential of local species to be promoted in pure and mixed plantings as contribution to global forest restoration efforts. We inventoried the survival and growth of 5817 trees belonging to 35 species planted more than 25 years ago in pure and mixed plantings. For a subset of individuals, we estimated heights and volumes of standing timber. We found that (i) the long-term survival (from 50 to 99%.yr^{-1}) and diameter growth (from 1 to 10mm.yr^{-1}) are highly diverse between species and not correlated to each other, (ii) the annual increase in biomass per tree averages 2.22kg while the annual increase in stand biomass may be over 6 Mg. ha^{-1} for three highly-productive species (*Khaya senegalensis*, *Pterocarpus erinaceus* and *Anogeissus leiocarpa*) (iii) the effect of mixture on annual growth is significantly positive with an across-species gain of 0.7mm.yr^{-1} while there is no effect on the survival probability. Considering a potential volume productivity of 10m^3 per hectare at 30 years, 13 species have been retained in the list of woody species of interest for planting in the Sudanese zone of West Africa.

Introduction

In West Africa, the forest-savanna mosaic forms a transitional vegetation zone between the Sudanian savannas in the north and the Guinean forests in the south. In this mosaic, the forest patches have historically been subject to very high rates of deforestation linked to the development of cash crops, particularly Cotton cultivation (historically 40-50% of cultivated land was sown to Cotton in *e.g.* Ivory Coast). Once abandoned, formerly cropped areas tend to be colonized quickly by weedy vegetation and secondary succession progressively develops. These secondary ecosystems are intensively exploited to provide wood energy both for local needs and for the needs of southern cities. Indeed, the Guinean forests located further south are highly degraded and are no longer sufficient to supply domestic markets (Sulaiman et al., 2017). At present, these secondary vegetations are also subject to conversion to Cashewnuts plantations (Temudo and Abrantes, 2014; Tessmann, 2017). Despite their large extent and still existing benefits, abandoned areas are mostly overlooked in forest management while the international attention is focused on the threatened primary forests. The increasing area of secondary ecosystems following cash-crop cultivation abandonment call for the development of integrative land-use and management strategies that can provide important environmental benefits, contribute to the country's social stability and poverty alleviation, and reduce the pressure on the few remaining areas of primary forest.

With that in mind, countries have engaged in large-scale international reforestation initiatives such as AFR100, the African Forest Landscape Restoration Initiative (Bond et al., 2019). For instance, the Ivorian State plans to restore 5 million hectares of forest ecosystems by 2030 and, within this framework, to reforest 100,000 hectares per year over the next 10 years. However, the number of species used for reforestation is currently very limited and mainly dominated by exotic species. Reforestation cannot be carried out using only exotic species to the detriment of native species, some of which are of great technological, commercial and environmental value (Ahoba et al., 1995). Moreover, indigenous species have many non-timber uses for the populations of the sudanian West Africa. For these species to be widely adopted, their long-term potential, including productivity need to be assessed.

The trade of African tropical timber to industrialized countries is declining sharply due to the scarcity or disappearance of valuable species (Assa, 2017). There is therefore an urgent need to reverse this trend. Mixed plantations of native tree species are part of the solution to these problems (Verheyen et al., 2015). A mixed plantation consists of at least two tree species whose requirements for light, water and mineral elements are compatible. Such a plantation have been proved to (i) make better use of the productive potential of the environment, (ii) be more resistant to hazards such as climate change (Schnabel et al., 2019). Increasing the range of indigenous timber species by planting them in a mixture would thus make it possible (i) to increase the productivity of planted forests by taking advantage of synergies between species (Schmitt et al., 2020) and (ii) to sustainably meet the future needs of the West African industry for quality wood and energy wood for the populations, while (iii) restoring forest ecosystems and the biodiversity potential of planted forests (harvesting of various products: pharmacopoeia, gastropods, mushrooms, forest seeds, etc.).

In this context, it is necessary to draw up a long-term assessment of the potential of local species and mixed plantations in the different climatic zones of West Africa. As far as the Sudanian zone is concerned, few long-term experiments are still in place. Fortunately, the Lataha experiment (Northern Ivory Coast), set up in the 1980s, has been protected to date and allows us to answer many questions about the potential of these plantations : (i) What is the long-term demographic performance (growth and survival) of the 35 studied species? (ii) What biomass storage can be obtained by planting them? (iii) Is there a positive effect of mixed plantings on the growth survival and biomass storage? (iv) Which species to recommend for pure and mixed plantations in the Sudanian West Africa?

Materials & Methods

The taxonomic nomenclature used in this article follows PROTA, Plant Resources for Tropical Africa (https://www.prota4u.org/database/).

Site description

The Kamonon Diabaté forestry research station (5°57' N, 5°54' W) near Korhogo in Côte d'Ivoire is fairly representative of the Sudanese region. It is located at an altitude of between 360 and 390m. The station (100ha) is dominated by an outcropping granite dome surrounded by superficial gravelly soils, then, and further away, by deep gravelly soils with a heavy texture (sandy loamy clay) to sandy silt at the bottom of the slope. The pH is close to 6. They are poor in organic matter (former cropland), highly desaturated, poor in calcium, magnesium, potassium and phosphorus and at the limit of deficiency for boron (Louppe and Ouattara, 1996).

The climate is tropical with a rainy season (april to october) and a dry season. At the time of planting (1988-1995), evapotranspiration averaged 1,764 mm.yr^{-1} and rainfall 1216 mm.yr^{-1}. Only the months of June to September were in water surplus. Rainfall was highly variable from one year to the next, both in abundance (817 mm in 1990 and 1,494 mm in 1991) and seasonal distribution (431 mm in August 1991 and 140 mm in 1992). Atmospheric humidity was high from April to October (over 70%). There were 2,270 h of insolation per year and the average annual temperature was 26.6°C (Louppe and Ouattara, 1996). In 30 years, the climate has generally dried up and average temperatures have increased (+0.09°C/decade on the warmest days), linked to local land use changes and global climate change (Barry et al., 2018). However, following the political crisis that affected the country in the 2000s, there is no longer any meteorological monitoring in the station.

In the studied area, the natural vegetation was open forest (with species such as *Isoberlinia doka*, *Afzelia africana*, *Anogeissus leïocarpa*, *Terminalia spp.*), even dense dry forests (of which the sacred forests are the only relics). Most of the station was farmed until 1987 but some patches of the ancient vegetation formations remain on soils too shallow to be cultivated. The vegetation was then shaped by many parks with *Vitellaria paradoxa* (shea) and *Parkia biglobosa* (nere). The station has been under strict protection since 1988.

Setting up the plantations

Between 1988 and 1995, 5817 individuals belonging to 35 local species (Table 1) were planted on 9 plots in pure stand or mixed stands (Table 2). Plots ranged in size from 1040 to 22008 m^2. Three planting densities were used: 400 individuals.ha^{-1} for 1 plot, 924 individuals.ha^{-1} for 3 plots and 1400 individuals.ha^{-1} for the remaining 5.

All species came from seeds collected in the vicinity of the station or near Korhogo except *Afzelia africana*, of which 180 plants out of 224 came from seeds collected in Burkina Faso at Bobo-Dioulasso and Péni for *Balanites sp* (large-fruited variety consumed). Seedlings were grown in plastic pots of 8 cm in diameter and 16cm in height filled with soil from the station. Seeds with high dormancy were treated with 95% concentrated sulphuric acid before being sown directly into the pots at a rate of 2 or 3 seeds per pot. Only *Anogeissus leïocarpa* was sown as a germinate (because only 1-5% maximum of the seeds are viable) and then transplanted into pots. After a stay under shade during the germination period, the seedlings were put in full sun. The pots were moved every 15 days to prevent the roots from penetrating the soil, which increases the root hair inside the pot. Seedlings were kept growing in the nursery for 4 to 5 month except *Vitellaria paradoxa* that grew in the nursery for a year before being planted in the field.

To date, the stands have been protected from outside intrusion as the station is surrounded by a barbed wire fence. Maintenance was done three times a year with a disc sprayer between the planting lines and manually on the planting lines until July 1999. Thereafter, scientific monitoring was stopped (and therefore no pruning or depressing was carried out) due to the political crisis in Côte d'Ivoire. At that time, only the technical staff remained, who protected the site with the help of the surrounding village chiefs. There was no illegal exploitation of the planted plots. The 2019 measurement campaign is the first scientific work since 1999.

Data collection

Data were collected between 10 and 20 November 2019 by a single team. Each tree was spatialized, permanently numbered and its DBH was measured with a forest tape. For a sub-sample of randomly selected individuals, the Bitterlich relascope was used to measure (i) total height, (ii) bole height and (iii) bole volume (Table 1).

Data analysis

All models were written in stan language (Carpenter et al., 2017), implemented in R with the rstan package. All model codes are provided in Supp Mat 1.

Demographic performance

We analyzed two aspects of demographic performance: (i) survival and (ii) the growth of surviving individuals.

For survival, we have developed and parameterized a binary process model (Aubry-Kientz et al., 2013) where the response variable is the 2019 *Status* (dead or alive) of tree i of species s in plot p that follows a Bernoulli likelihood given that the response is either 0 or 1.

$$Status_{i,s,p} \sim Bernoulli\left(\left(\theta_s^S + \theta_p^S + \theta^S \times C_i\right)^{t_i}\right) \quad \text{(eqn 1)}$$

with θ_s^S the annual probability of survival, θ_p^S the annual plot random effect $\left(\theta_p^S \sim \mathcal{N}(0\ ,\ \sigma_{Sp}^2)\right)$ and θ^S the annual effect of changing the initial plantation density C. The overall annual probability $\left(\theta_s^S + \theta_p^S + \theta^S \times C_i\right)$ is set to the power t, where t corresponds to the number of years since planting.

For growth, we have developed and parameterized a model where the response variable is the 2019 DBH of tree i of species s in plot p that follows a lognormal likelihood given that the response is always positive (Hérault et al., 2011) .

$$DBH_{i,s,p} \sim log\mathcal{N}\left(\left(\theta_s^G + \theta_p^G + \theta^G \times C_i\right) \times t_i \ , \ \sigma_G^2\right) \qquad \text{(eqn 2)}$$

with θ_s^G the annual growth rate, θ_p^G the annual plot random effect $\left(\theta_p^G \sim \mathcal{N}(0 \ , \ \sigma_{Gp}^2)\right)$, θ^G the annual effect of changing the initial plantation density C and σ_G the model standard error. The overall annual growth rate $\left(\theta_s^G + \theta_p^G + \theta^G \times C_i\right)$ is multiplied by t, where t corresponds to the number of years since planting.

To synthesize the average performances in 4 explicit groups (Figure 1), we have chosen two thresholds: (i) a 30-year survival threshold of 16% which corresponds on average to about 200 residual trees per hectare (in our experience, this density corresponds to what is commonly practiced in the region at the end of the rotation) and (ii) an average DBH of 10cm at 30 years which corresponds to a tree having reached a standard size in forest inventories (in our experience, below 10cm the trees are not at all exploitable by the local formal or informal timber market).

Biomass stock

Given that total heights were measured on a subset of individuals, we first modeled total height Ht as a function of DBH with the following Michaelis-Menten species-specific model form (Molto et al., 2014) where the response variable is the 2019 Ht of tree i of species s that follows a lognormal likelihood given that the response is always positive.

$$Ht_{i,s} \sim log\mathcal{N}\left(\frac{\theta_s^H \times DBHi}{\gamma + DBHi} \ , \ \sigma_H^2\right) \qquad \text{(eqn 3)}$$

with θ_s^H the asymptotic value (*i.e.* the maximal height) of the Michaelis-Menten model for each species s, γ the model parameter that modifies the rate with which the asymptote is reached and σ_H the model standard error.

Using the predicted $\widehat{Ht_{i,s}}$, individual tree biomasses, the measured DBH_i and the wood density database of the BIOMASS package (Réjou-Méchain et al., 2017), aboveground biomasses were estimated both at the tree and hectare level with the function *computeAGB()*. To calculate biomasses per hectare and per species, individuals planted in a mixed stand were assigned an area proportional to their relative density.

Mixed *vs* pure plantings

In order to test for a positive effect of mixed plantings on the growth survival and biomass storage, we first classified the trees into two groups: "pure" or "mixed". A tree is assigned to the "pure" group if all its immediate neighbours belong to the same species. Conversely, a tree is assigned to the "mixed" group if at least 1 of its immediate neighbours is of a different species. We did so to benefit from the specific experimental design: 2 plots in pure plantings, 1 plot with a tree-by-tree mixture and 6 plots with a mixture of subplots. For the 6 plots that are mixtures of subplots, the spacing between subplots was exactly the same as the spacing between trees within a subplot. Therefore, we chose to use the particular position of the trees that are in mixture (in contact between two subplots) or not (inside the subplot) to analyze the effect of the mixture. We are aware that treating mixture as a binary variable is a crude classification but we did not have the statistical power to make a more refined classification. Trees at the plot boundary were excluded from this analysis in order to avoid edge effect.

Based on equations 2 and 3, we added a mixture variable to test the influence of planting in mixture on the 30-year survival and growth of the trees studied.

$$Status_{i,s,p} \sim Bernoulli\left(\left(\theta_s^S + \theta_p^S + \theta^S \times C_i + \theta_s^{SM} \times M_i\right)^{t_i}\right) \quad \text{(eqn 4)}$$

$$DBH_{i,s,p} \sim log\mathcal{N}\left(\left(\theta_s^G + \theta_p^G + \theta^G \times C_i + \theta_s^{GM} \times M_i\right) \times t_i \ , \ \sigma_{GM}^2\right) \quad \text{(eqn 5)}$$

with θ_s^{SM} the random $\left(\theta_s^{SM} \sim \mathcal{N}(0 \ , \ \sigma_{Sm}^2)\right)$ per species mixture effect on the yearly survival, θ_s^{GM} the random $\left(\theta_s^{GM} \sim \mathcal{N}(0 \ , \ \sigma_{Gm}^2)\right)$ per species mixture effect on the annual growth rate and σ_{GM} the growth model standard error.

Practical recommendations

To select the species that we recommend for planting, we applied the following procedure.

First, building on the subsample of randomly selected individuals for which we estimated bole volumes using the Bitterlich relascope, we modeled *Bole* as a function of DBH with a power function where the response variable is the 2019 *Bole* of tree i of species s that follows a lognormal likelihood given that the response is always positive.

$$Bole_{i,s} \sim log\mathcal{N}\left(\theta_s^B \times (DBH_i)^{\beta}, \sigma_B^2\right) \quad \text{(eqn 6)}$$

with θ_s^B the species-specific link between *Bole* and *DBH*, β the power exponent and σ_B the model standard error. We then predicted $\widehat{Bole_{i,s}}$ for all individual trees of our database and we divided it by the number of years each tree was planted to obtain an annual volumetric growth value.

Second, we selected, by species, the 20 individuals with the highest volumetric growth. We then hypothesized that, with the application of real silviculture rules, these individuals could give us an idea of the production of a one-hectare plot on which 200 individuals (an average density at the end of rotation in the Sudanian zone) of the same population would be planted. From the 20 individuals selected per species, we calculated the values of volume, biomass and average diameter that could be expected on a 200-tree-plot at 30 years. The species retained in our final list of species to be promoted are those that obtain at least $10m^3.ha^{-1}$ at the end of the 30 years of plantation.

Results

Among the 35 species inventoried, four species had completely disappeared: *Acacia polyacantha*, *Balanites aegyptiacus*, *Cordia abyssinica* and *Swartzia madagascariensis*. Globally, the survival rate is 40.7% which means that we have gone from an average planting density of about 1250 $trees.ha^{-1}$ to about 500 $trees.ha^{-1}$ 30 years later. The average growth of the surviving individuals was 4.35 $mm.yr^{-1}$. Behind these global values, there was a very high diversity of species behaviors (Figure 1).

Demographic performance

The probability of annual survival (θ_s^S) varied from less than 50% (*Acacia polyacantha*, *Balanites aegyptiacus*, *Cordia abyssinica* and *Swartzia madagascariensis* that have completely disappeared after 30 years, *i.e.* their probability of survival would be less than 0.5^{30}) to more than 99% (*Cola cordifolia*, *Khaya senegalensis*, *Anogeissus leiocarpa*, *Isoberlinia doka*, *Lannea barteri*) with an average of 89.4%. At the 30-year horizon, 11 of the 35 species had survival rates above 50%, 12 between 20 and 50% and the remaining 12 (4 of which have completely disappeared) below 20%.

The specific average annual diametric growth rate (θ_s^G) of individuals that have survived was always greater than 1mm.yr^{-1} but never exceeded 1cm.yr^{-1}. Four species had very low growth rates below 2mm.yr^{-1} (*Strychnos spinosa*, *Vitellaria paradoxa*, *Faidherbia albida*, *Daniallia oliveri*) while four others have growth rates above 5mm.yr^{-1} (*Ceiba pentandra*, *Khaya senegalensis*, *Pterocarpus erinaceus*, *Albizia zygia*).

There is no significant correlation between annual survival rate and average annual growth ($\rho_{spearman} = 0.03$, P=0.85). Considering the two thresholds of 16% survival and 10cm DBH at 30 years, 15 species are part of the group "*Reasonable Growth - Reasonable Survival*" (Figure 1).

Biomass stock

The average annual increase in biomass per tree, all species considered, was 2.22kg. This average increase hided a very high variability between species which vary from 0.14kg (*Strychnos spinosa*) to 7.44kg (*Pterocarpus erinaceus*). Biomass storage at plot scale was relatively related to individual storage but was balanced by survival rate (Figure 2). For example, *Bombax costatum* had a fairly high individual storage (3.95kg per year) but, because of its low survival rate (Figure 1), showed low plot-scale storage (1.68Mg per year). Conversely, *Isoberlinia doka* had a relatively low individual storage (1.64kg per year) but, due to its high survival rate (Figure 1), showed a plot-scale storage that was good (2.04Mg per year). Overall, three species showed remarkable performance at both the individual and plot scales (Figure 2): *Anogeissus leiocarpa*, *Khaya senegalensis* and *Pterocarpus erinaceus.*

Mixed *vs* pure plantings

Overall, the effect of mixture on performance depends on demographic rates. The average effect of mixture on annual growth was positive with an across-species average gain of 0.7mm per year while the average effect on the annual probability of survival was zero.

In terms of growth (Figure 3), nine species showed annual growth gains (θ_s^{GM}) significantly higher in mixed stand compared to pure stand. Among the most notable are *Khaya senegalensis* (+2.21mm.yr^{-1}), *Anogeissus leiocarpa* (+1.87mm.yr^{-1}), *Parkia biglobosa* (+1.92mm.yr^{-1}) and *Entada africana* (+2.30mm.yr^{-1}). Only one species showed significantly lower growth in mixed plantings: *Daniellia oliveri* (-0.54mm.yr^{-1}).

Regarding annual survival rates (Figure 4), there were few differences significantly related to stand type. Three species had slightly, but significantly lower annual survival (θ_s^{SM}) in mixed plantings: *Khaya senegalensis* (-0.17%), *Detarium microcarpum* and *Daniellia oliveri* (-0.70%). Three species had slightly, but significantly better survival in mixed plantings: *Sterculia setigera* (+0.49%), *Vitellaria paradoxa* (+0.30%) and *Tamarindus indica* (+0.83%).

Potential species for plantation establishment

Considering a volume productivity threshold of 10m^3 per hectare at 30 years, thirteen species have been retained in the list of forest species of interest for planting in the Sudanese zone of West Africa (Table 2). Some species such as *Khaya senegalensis*, *Anogeissus leiocarpa*, *Bombax costatum* and *Pterocarpus erinaceus* showed very high productivity at 30 years with expected volumes exceeding 40 m^3.ha^{-1} and expected average diameters exceeding 25cm. Their biomass stocks were also very high, except for *Bombax costatum* which has a very low wood density (0.374g.cm^{-3}). From a silvicultural point of view, combining the previous results on growth (Figure 3) and mortality (Figure 4) of the mixture effects, it appears that 6 of the 13 can be alternatively managed in pure and/or mixed plantings. For 7 of these species, however, there was a real gain in planting them in a mixed stand, mainly due to improved growth (Figure 3).

Discussion

The dry forests of the Sudanese zone are fragile ecosystems, but very much used by the local populations for their daily subsistence (energy wood, service wood, pharmacopoeia, food resources etc. . .) (Amahowe et al., 2018; Zizka et al., 2015). The aim of the experimentation at the Kanomon

Diabaté site in northern Côte d'Ivoire was to select high-performance species to meet the needs of populations and the challenges of the fight against climate change. The species tested are endemic to the Sudanian and Sudano-Guinean zones with a broad ecological spectrum (Spichiger, 2010). Our results showed a very wide range of survival and growth performance in plantations (Figure 1) despite the fact that all the species tested are species that occur locally in the wild. Planting in mixture had generally a positive effect on productivity. The top-performing (fast growth and high survival) species are also the species that most benefited from the positive effect of mixture (Figure 3). The later show very good carbon storage capacities (Figure 2) and are therefore good candidates for carbon sequestration projects in the region. These results lead us to promote 13 species for forest plantations in the area (Table 3). More than half of these 13 species perform better in mixed plantings than in pure plantings.

Demographic performance

Survival and growth are not significantly correlated (Figure 1): a species may have rapid growth and low survival (e.g. *Ceiba pentandra*) and vice versa (e.g. *Vitellaria paradoxa*). This result calls into question the applicability in tree plantations of the classical growth-survival tradeoff. The growth-survival tradeoff is a central concept for understanding the coexistence strategies of faster-growing acquisition species and slower-growing conservative species (Meira-Neto et al., 2019). Understanding the inter-species functional characteristics that contribute to the growth-survival trade-off is a key to imagining the functioning of a tree plantation with very different ecological strategies and to deciding on initial plantation densities (Fayolle et al., 2015). The analysis of the demographic performances recorded on the Lataha station has made it possible to classify the species into four groups according to their survival and growth rates. Fifteen species stand out with reasonable demographic rates (Figure 1). These are species that appear to be well adapted to both (i) environmental conditions and (ii) plantation life. In this group 6 species show survival rates of more than 50% after 30 years (*Khaya senegalensis*, *Anogeissus leiocarpa*, *Isoberlinia doka*, *Lannea barteri*, *Pterocarpus erinaceus*, *Terminalia glaucescens*). These results corroborate the analyses previously carried out after a few years of planting (Louppe and Ouattara, 1996). The best performing species is, without a doubt, *Khaya senegalensis*, whose deep root system gives it access to subsoil water and great resistance to water stress (Ouédraogo-Koné et al., 2007). Apart from these 15 species, the other species have either very low growth or survival rates. There are two possible causes of this behaviour: (i) an ecology of the species that is poorly adapted to planting or (ii) inadequate environmental conditions. For (i) this seems to be the case of *e.g. Cordia africana*, which is never found in pure assemblage in the wild (Yadessa et al., 2009). As another example, *Faidherbia albida* does not seem to be able to withstand competition because of its need to regenerate close to termite mound-rich soils (Sileshi et al., 2010) and of its inverse phenology (Roupsard et al., 1999). Trees of this species are leafy, growing and fruiting during the dry season, while the leaves fall after the first rains and growth does not really resume until the end of the rainy season. This phenology is advantageous for agroforestry management (Sida et al., 2018), because competition with associated crops growing in the wet season is minimized but is very disadvantageous for dedicated stand management where competition in the dry season is strong. For (ii), it seems, for example, that *Acacia polyacantha*, which is a species found on cool, rich soils, wet stations and colonizes forest galleries close to watercourses (Sharam et al., 2009) cannot perform well outside this particular ecological niche. In the Lataha trials, *Acacia polyacantha* showed very rapid initial growth by behaving like a pioneer species (Louppe and Ouattara, 1996). Soon the seedlings outside old termite mounds declined, while those on termite mounds showed very strong growth until at least eight years, after which all the trees eventually died (Louppe and Ouattara, 1996).

Biomass stock

Biomass storage differed markedly among species both at the tree level and stand level. One group of three species (*Khaya senegalensis*, *Pterocarpus erinaceus* and *Anogeissus leiocarpa*) shows a biomass production between 6 and 8 Mg. ha^{-1} .yr^{-1}. This figure should be put in relation to the values retained by the IPCC for natural forests in the area, which are 2.9 Mg. ha^{-1} .yr^{-1} for secondary forests less than 20 years old, and 0.9 Mg. ha^{-1} .yr^{-1} for secondary forests more than 20 years old (Suarez et al., 2019). Thus, plantations of these three tree species would be more efficient, in terms of biomass storage, than reconstitution by natural regeneration of all species combined.

Even more surprisingly, the rates of carbon storage would be even higher than those of the semi-deciduous zone located further south under more favourable climatic conditions (N'Guessan et al., 2019). These three species are therefore very good candidates for carbon storage projects in the area (Olsson and Ouattara, 2013; Jindal et al., 2008) while producing high quality lumber over the long term (Ahoba et al., 1995). A second group consists of *Diospyros mespiliformis, Prosopis africana, Terminalia schimperiana* , *Afzelia africana, Cassia sieberiana* and *Isobelinia doka* with a biomass production of 2 to 4 Mg. ha^{-1} .yr^{-1} . This good result is mainly due to a fairly high tree growth except for *Isoberlinia doka*, which is efficient due to its 30-year survival rates of more than 80%.

Mixed *vs* pure plantings

After three decades, the generally positive effect of mixed planting on the performance of trees (Figure 3) can be explained by different characteristics of the species studied.

- In the Sudano-Guinean natural formations, among the 35 species studied, only *Anogeissus leïocarpa* and *Acacia polyacantha*, which are pioneer species, and *Isoberlinia doka* grow naturally in monospecific communities. Assuming that the classic monodominance in tropical forests is reached in old-growth forests when the species is found under conditions of low exogenous disturbance (Peh et al., 2011), it is not surprising that these situations do not occur in the Sudanian zone of West Africa, where the sources of stress are multiple: water stress, human disturbance, fires, exploitation, etc.. Indeed, species such as *Afzelia africana, Pterocarpus erinaceus, Parkia biglobosa, Bombax costatum, Prosopis africana, Diospyros mespiliformis* and *Anogeissus leiocarpa* are known to regenerate and grow naturally in mixtures of species in dense dry forests. *Faidherbia albida*, *Parkia biglobosa* and *Vitellaria paradoxa* are species favoured by human activity: they are essentially agroforestry park species (Brenan and Schnell, 1978). As observed in other parts of the world, local species thus thrive best in mixedwood plantings (Piotto et al., 2004)
- More than 45% (16/35) of the species studied belong to the families of nitrogen-fixing trees (Fabaceae). In mixed plantings including nitrogen-fixing trees, it was observed that foliar

N concentrations of non-fixing species increased significantly, compared to a monospecific stand. As a result, higher levels of photosynthesis and greater efficiency in resource use are very often observed with a positive effect on the diameter growth of non-fixing species (Richards et al., 2010). Nitrogen-fixing trees improve overall soil quality and, for this reason, intercropping of nitrogen-fixing trees is a widely used silvicultural option to stimulate growth (Piotto, 2008).

- Some species tested (e.g. *Khaya senegalensis*, *Pterocarpus erinaceus* and *Prosopis africana*) are known to be very sensitive to parasites (rodents, insects and other ruminants) during their development. During the experiment, plots were protected against ruminants and systemic insecticides against *Hypsipyla robusta* were applied in the first year of planting (Louppe and Ouattara, 1996). These species known to be sensitive are nevertheless found in the species whose growth benefits most from mixing, confirming the added value on the pest resistance potential of mixed plantations (Verheyen et al., 2015).

While mixed plantings bring positive direct impacts on the overall productivity of the stand, very positive indirect impacts are also expected, such as, for example, better management of the water cycle (Forrester et al., 2010).

Potential species for plantation establishment

Khaya senegalensis, *Pterocarpus erinaceus*, and *Anogeissus leïocarpa* are the three high-value wood species (Ahoba et al., 1995) that showed the best growth both individually and in stands (Table 3). These species can be recommended for open ground plantings because, due to their dense canopy, they eliminate undergrowth including herbaceous plants that could compete with them and propagate fires.

- *Khaya senegalensis*, planted in a mixture, shows better growth in diameter than in a pure stand, which could be explained by fewer attacks of *Hypsipila robusta*, a terminal bud borer that is most prevalent in the early years, delays growth and causes low forks (Ofori et al., 2007).
- *Pterocarpus erinaceus* is a species highly prized by foresters (Dumenu, 2019). Its productivity

has probably been somewhat underestimated because there has been a wild exploitation of a few individuals (less than 10) from the inventoried stands. This species has a relatively slow initial growth rate in non-natural situations (Jurisch et al., 2012) but then shows an acceleration and can therefore be recommended for full planting. On the other hand the growth of the first years is weak, which can discourage the planters (Louppe and Ouattara, 1996).

- *Anogeissus* (Assogbadjo et al., 2009). Its growth is rapid and its only constraint is the low rate of viable seeds in the fruit, about 1-5%, but these are produced in abundance (Some et al., 1989). It is the only species that naturally forms monospecific even-aged forests (Assogbadjo et al., 2009) and can therefore safely be planted for this purpose.

The other species selected have less interesting performances than the three above-mentioned, but make it possible to build diversified plantation strategies in mixed stands:

- Bombax costatum is a species whose propagation in nurseries is particularly difficult and for which propagation by suckering has been recommended in Burkina Faso (Ouédraogo and Thiombiano, 2012). The species could nevertheless be multiplied in village terroirs for its various productions other than wood and in particular its much appreciated flowers (Ouédraogo et al., 2014). Its thick, corky bark protects it from fire (Nyg and Elfving, 2000). Bombax costatum is naturally associated with *Pterocarpus erinaceus*, *Daniellia oliveri*, *Terminalia macroptera* and *Prosopis africana* and is therefore ideal for mixed plantations (Frederiksen and Lawesson, 1992).
- *Isoberlinia doka* is a species of the original dry dense forest of which it is the dominant species (Bationo et al., 2005). In plantations its growth is slow but it compensates by a very high survival of the individuals (Table 4). In the station, it has naturally recolonized some plots with good growth rates, probably because these trees sucker and resprout abundantly (Louppe and Ouattara, 1996).
- *Afzelia africana* had a difficult start in the plantations because it was heavily overrun by cattle entering the station (Louppe and Ouattara, 1996). Once the terminal bud was no

longer accessible, growth accelerated and the mixed plantations that had got off to the worst start overtook the monospecific plantations. Because of the high value of its wood, *Afzelia africana* deserves to be planted in mixtures with species that are not easily eaten by livestock.

- *Prosopis africana* is a valuable species with practically rot-proof wood (Agboola, 2004). Characteristic species of the dry dense forest, it settles quickly in the fallows but without being gregarious (Houètchégnon et al., 2015). I t shows good survival and fairly rapid growth in mixed plantings and could be associated with *Diospyros*, a species with which it cohabits very well (pers. obs.).
- *Diospyros mespiliformis* is a species found in undergrowth and which, despite its weak initial growth, takes the place of the species that preceded it because it has a long lifespan (Swaine et al., 1990). Our results show that, in the long term, this is a very productive species that can, due to its temperament, be installed in mixture with faster growing species.
- *Parkia biglobosa* is an open field fruit tree, which may account for its poor growth in dense stands overgrown with weedy vegetation (Kater et al., 1992). The species is prone to borer attacks (Sétamou et al., 2000) and is therefore not intended to be planted as a pure stand but as a mixed stand and/or individual trees in agroforestry systems.
- *Blighia sapida* is a medicinal and fruit-growing species whose arils are consumed and which also produces quality wood and is preserved near villages (Ekue et al., 2010). It showed good recovery at planting and good initial growth, quickly forming a very dense canopy (Louppe and Ouattara, 1996). However, it exhibited 65% mortality afterwards, possibly due to its requirements for deep, fertile soil (Swaine, 1996). Its extensive use by local populations would justify a dedicated research program for its domestication. (Ekue et al., 2010).
- *Terminalia schimperiana* would be at the northern limit of its range but shows good recovery at planting and good growth: at 5.5 years of age it was the species with the best growth immediately following *Anogeissus* and *Prosopis* (Louppe and Ouattara, 1996). This species, which grows naturally in forest galleries, also easily colonizes fallow land (Azihou et al., 2013). Its plantation can be considered for the production of energy and service wood.
- *Sterculia setigera* is also a species with dry tops (pers. obs.) that affect the majority of

individuals despite good survival. This species, whose only interest is the production of a food gum (Aspinall et al., 1965) does not seem to be suitable for dense plantings.

- *Lannea barteri* shows good recovery at planting (Louppe and Ouattara, 1996) and grows best in mixed plantings.

Beyond their capacity for growth and survival, the importance of these species in the lives of the people living in this Sudanian zone is remarkable, even vital. Many species are used for soil fertility restoration needs (*Pterocarpus erinaceus, Prosopis africana, etc.)*, livestock feed (*Pterocarpus erinaceus, Khaya senegalensis*), the production of wood energy (*Terminalia glaucescens Khaya senegalensis*, *Pterocarpus erinaceus*, *Prosopis africana* et *Anogeissus leïocarpa)* or their medicinal properties (Yaoitcha et al., 2015; Oyewole and Carsky, 2001).

Perspectives

In the Sudanian zone of West Africa, the strong anthropogenic pressure, combined with climate change, slow growth of forest trees and their destruction by grazing, agriculture and wood energy needs means that naturally mixed forest formations are very rare and are only found in sites protected from fire, agriculture and/or pastoralism (Houehanou et al., 2013). Our results show the great potential of local species for plantations. The mix of species has a positive effect on productivity and some species have very good carbon storage capacities. Thirteen species are selected for plantations in the Sudanian zone with a clear advantage of including more than half of these species in a mixture.

In all the experimental plots measured, there is natural regeneration of many native species, similar to what has already been observed elsewhere in Africa (Yirdaw, 2001). Additional studies should be carried out specifically to estimate the potential of this natural regeneration and to set up technical reforestation itineraries taking advantage of these spontaneous recruits (Sansevero et al., 2011). The differences in natural regeneration observed in situ in each of the inventoried stands indicate that the performance of plantations as a pure restoration strategy for a complex and multi-species forest may also differ, depending on the initial species composition, plantation density and site conditions. Finally, if the results presented in this work were obtained under the climatic conditions of the last 30 years, during which the climate has generally dried up and average temperatures have risen (Barry et al., 2018), there appears to be a need to investigate the adaptive capacity of selected species to current climate changes (Claeys et al., 2019; Schongart et al., 2006), including the effects of the current rise in temperatures (Aubry-Kientz et al., 2019).

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Tables

Species	Family	Year	N	Alive	Height	Volume	Mixed	Vegetation
Acacia polyacantha Willd.	Fabaceae	1990	224	0	0	0	42	Riverine Forest
Acacia sieberiana DC.	Fabaceae	1990	224	5	5	5	53	Riverine Forest
Afzelia africana Sm. Ex Pers.	Fabaceae	1990	302	160	20	20	131	Dense Dry Forest
Albizia zygia (DC.) J.F.Macbr.	Fabaceae	1990	224	6	6	5	42	Secondary Forest
Anogeissus leiocarpa (DC.) Guill. & Perr.	Combretaceae	1988	378	350	31	31	48	Dense Dry Forest
Antiaris toxicaria Lesch.	Moraceae	1992	112	3	3	3	27	Dense Dry Forest
Balanites aegyptiaca (L.) Delile	Zygophyllaceae	1990	28	0	0	0	14	Woody Savannas
Blighia sapida K.D.Koenig	Sapindaceae	1990	224	78	21	15	53	Dense Dry Forest
Bobgunnia madagascariensis (Desv.) J.H.Kirkbr. & Wiersema	Fabaceae	1991	63	0	0	0	63	Open Dry Forest
Bombax costatum Pellegre. & Vuillet	Malvaceae	1992	112	31	20	16	27	Woody Savannas
Cassia sieberiana DC.	Fabaceae	1991	68	41	20	20	68	Woody Savannas
Ceiba pentandra (L.) Gaertn.	Malvaceae	1990	224	14	10	1	53	Secondary Forest
Cola cordifolia (Cav.) R.Br.	Malvaceae	1990	112	105	20	20	13	Gallery Forest
Cordia africana Lam.	Boraginaceae	1992	112	0	0	0	27	Open Dry Forest
Daniellia oliveri (Rolfe) Hutch. & Dalziel	Fabaceae	1990	171	60	19	2	90	Woody Savannas
Detarium microcarpum Guill. & Perr.	Fabaceae	1990	224	112	20	20	42	Woody Savannas
Diospyros mespiliformis Hochst. Ex A.DC.	Ebenaceae	1991	74	40	19	19	74	Woody Savannas
Entada africana Guill. & Perr.	Fabaceae	1995	182	41	13	13	96	Woody Savannas
Faidherbia albida (Delile) A.Chev.	Fabaceae	1988	150	8	2	2	85	Field Crops
Isoberlinia doka Craib & Stapf	Fabaceae	1992	224	181	19	19	61	Open Dry Forest
Khaya senegalensis (Desr.) A.Juss.	Meliaceae	1988	166	152	30	29	8	Open Dry Forest
Lannea barteri (Oliv.) Engl.	Anacardiaceae	1992	112	89	20	20	20	Woody Savannas
Parkia biglobosa (Jacq.) R.Br. Ex G.Don	Fabaceae	1990	390	154	34	34	149	Field Crops
Pericopsis laxiflora (Benth.) Meeuwen	Fabaceae	1990	112	66	20	17	27	Woody Savannas
Prosopis africana (Guill. & Perr.) Taub.	Fabaceae	1995	187	116	18	18	114	Open Dry Forest
Pterocarpus erinaceus Poir.	Fabaceae	1990	104	59	20	20	25	Woody Savannas
Spondias mombin L.	Anacardiaceae	1990	144	4	4	4	22	Fruit Tree
Sterculia setigera Delile	Malvaceae	1990	224	119	20	19	41	Woody Savannas
Strychnos spinosa Lam.	Loganiaceae	1991	61	10	10	8	61	Woody Savannas
Syzygium guineense (Willd.) DC.	Myrtaceae	1992	112	34	20	17	27	Open Dry Forest
Tamarindus indica L.	Fabaceae	1990	304	95	21	21	139	Disseminated
Terminalia macroptera Guill. & Perr.	Combretaceae	1990	140	42	20	19	27	Riverine Forest
Terminalia schimperiana Hochst.	Combretaceae	1990	48	29	20	18	24	Open Dry Forest
Vitellaria paradoxa C.F.Gaertn.	Sapotaceae	1991	169	137	19	19	103	Field Crops
Vitex doniana Sweet	Lamiaceae	1990	112	28	20	19	27	Riverine Forest

Table 1: Description of the 35 species studied: Scientific name, botanical family, median year of planting (Year), number of individuals planted (N), number of individuals living in 2019 (Alive), number of individuals with total and bole height measurement (Height), number of individuals cubed (Volume), number of individuals in mixed plantings (Mixed), optimum vegetation in the area (Vegetation)

Plot	Area	N subplots	Planting Year	Spacing	Type
88-2	1155	1	1988	3×3.5	pure
88-3	6000	3	1988	5×5	subplot mixture
88-4	1040	1	1988	3×3.5	pure
88-9	1837	1	1988	3×3.5	subplot mixture
90-1	22008	21	1990	2×3.5	subplot mixture
91-8	1568	1	1991	2×3.5	subplot mixture
91-12	6552	1	1991	2×3.5	tree mixture
92-1	4312	6	1992	2×3.5	subplot mixture
95-3	1456	2	1995	2×3.5	subplot mixture

Table 2: List of plots studied: Plot Number, Plot Area in m^2, Number of Subplots, Planting Year, Tree Spacing, Plantation Type

Species	Commercial Name	Volume	Diameter	Biomass	Silviculture
Khaya senegalensis	Dry-zone mahogany	78.58	36.89	160.26	pure / mixed
Anogeissus leiocarpa	African birch	53.7	28.06	157.31	mixed
Bombax costatum	Red-flowered silk-cotton tree	43.68	27.72	36.01	pure / mixed
Pterocarpus erinaceus	African rosewood	40.95	27.32	97.37	pure / mixed
Isoberlinia doka	Doka	33.9	21.78	33.1	mixed
Afzelia africana	Lingue	32.77	26.32	73.48	mixed
Prosopis africana	African mesquite	20.13	25.04	62.61	mixed
Diospyros mespiliformis	African ebony	16.95	21.76	41.07	pure / mixed
Parkia biglobosa	African locust bean	16.2	32.52	75.86	mixed
Blighia sapida	Akee apple	15.77	18.22	21.55	pure / mixed
Terminalia schimperiana	/	14.59	16.07	24.92	pure / mixed
Sterculia setigera	Sterculia	13.62	15.68	10.14	mixed
Lannea barteri	/	10.82	18.52	12.94	mixed

Table 3: The ranked 13 selected species for plantations in the Sudanian West Africa: Botanical Names, Commercial Names, 30 years expected volumes ($m^3.ha^{-1}$), 30 years expected mean DBH (cm), 30 years expected aboveground biomass ($Mg.ha^{-1}$), plantation type for best performance

Figures

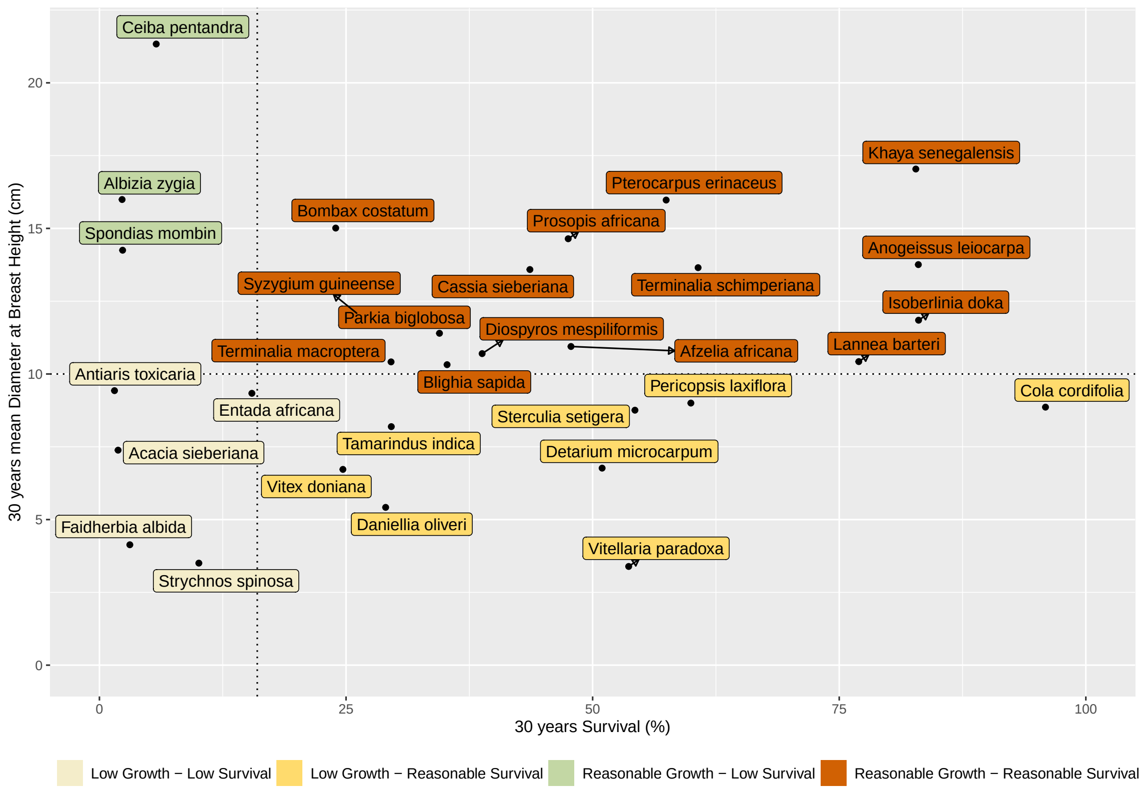

Figure 1: The long-term demographic performance of 35 sudanian species of West Africa. The thresholds for group classification are 16% survival (corresponding, on average, to a density of 200 trees.ha^{-1} at 30 years) and 10 cm of average Diameter al Breast Height in 30 years.

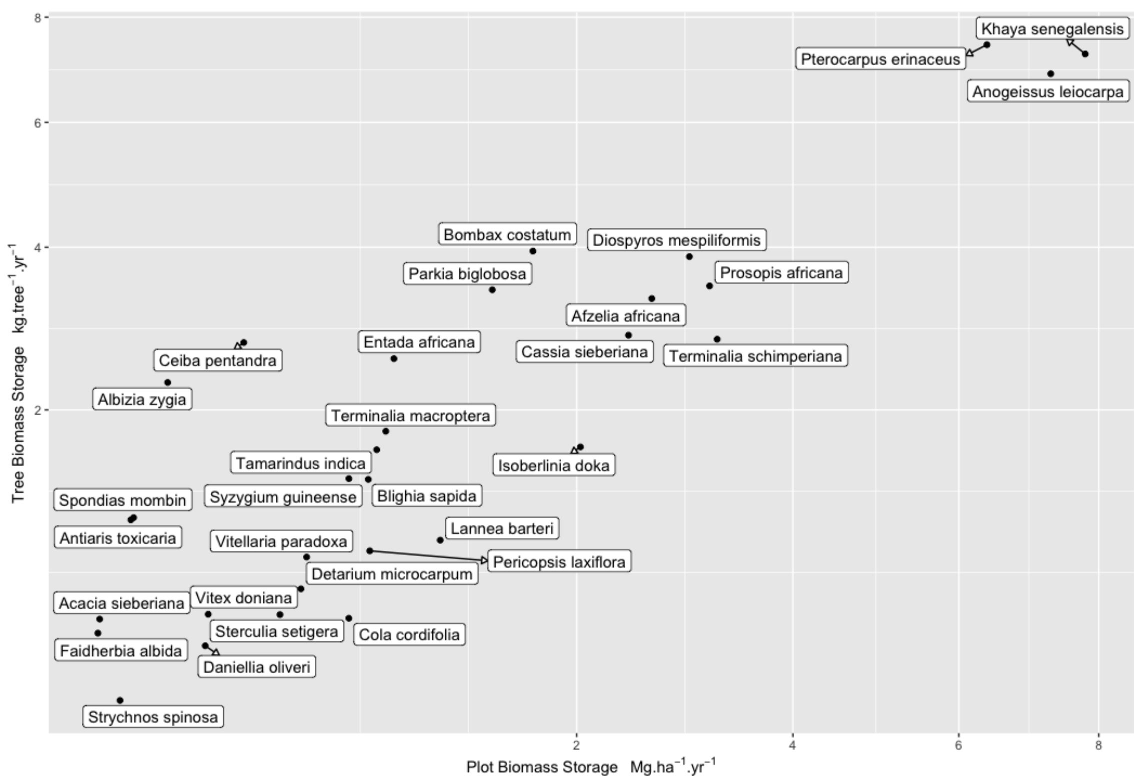

Figure 2: The biomass storage capacity of 35 West African sudanian species. Estimates are the annual biomass fluxes provided on a surface (plot, x axis) and on a individual (tree, y axis) basis. Axis are root-squared transformed for better readibility.

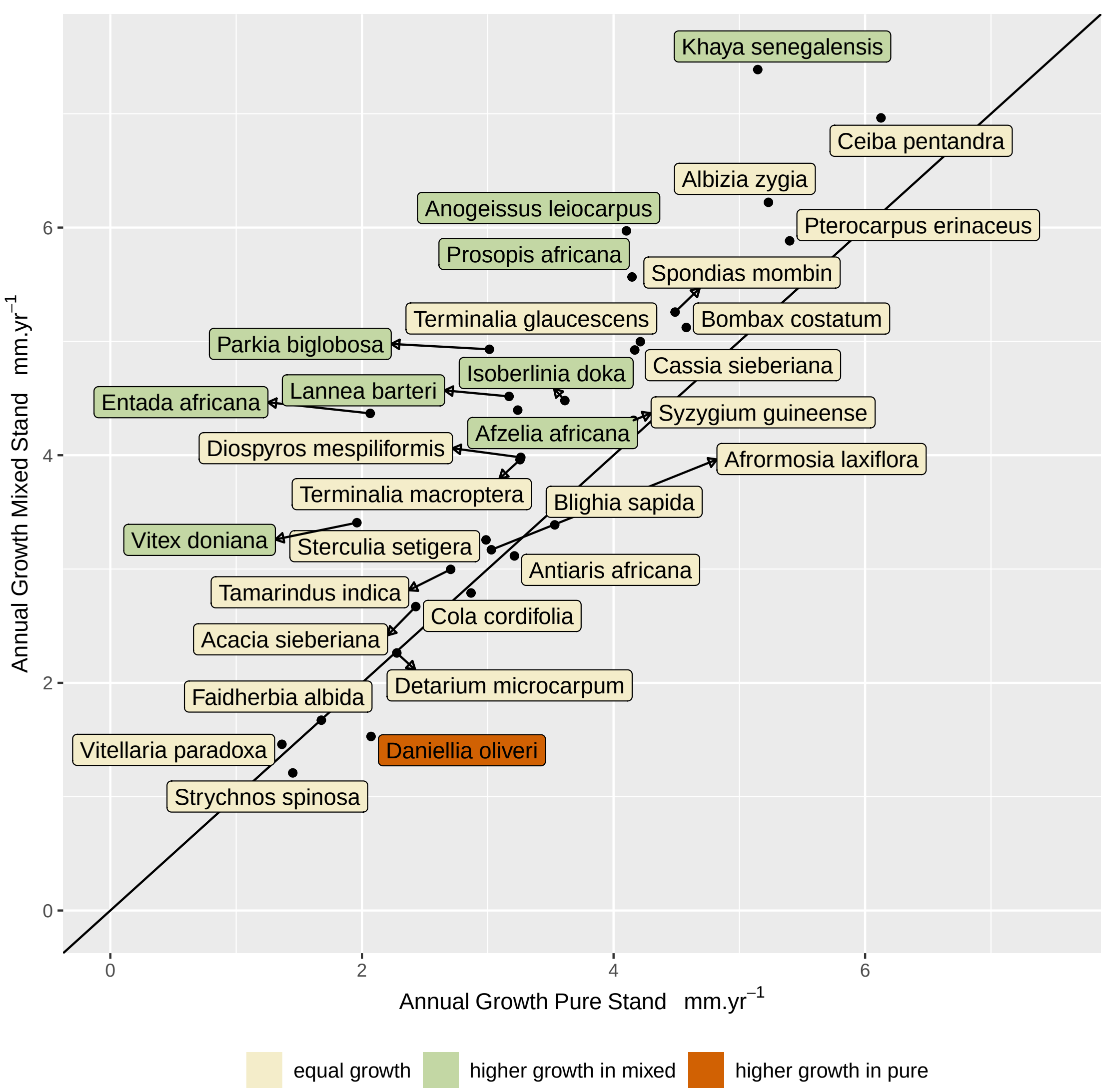

Figure 3: The growth performance of 35 sudanian species in mixed (y axis) versus pure (x axis) plantings. Colors refer to the species best performance in mixed (green), pure (orange) plantings or to equal performance (yellow). The oblique line indicates a strictly identical performance.

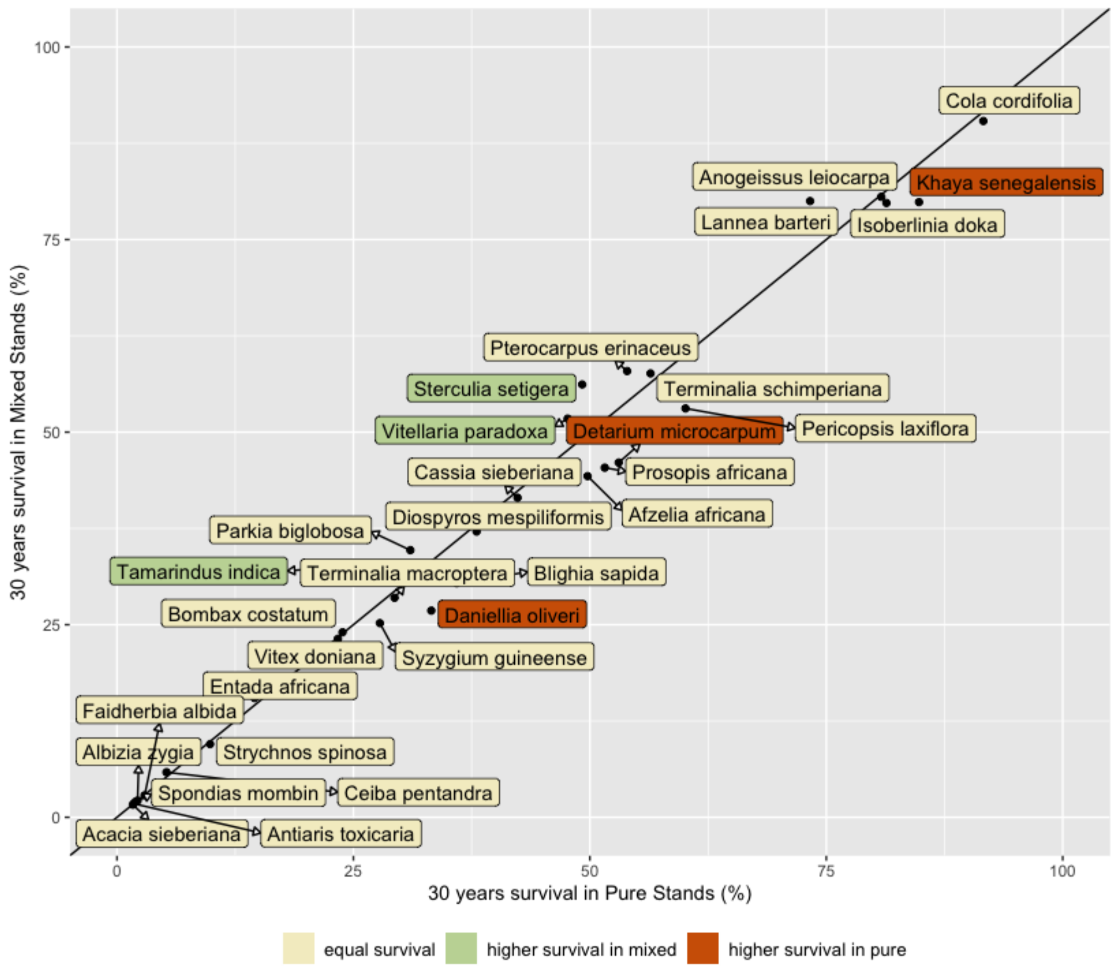

Figure 4: The survival performance of 35 sudanian species in mixed (y axis) versus pure (x axis) plantings. Colors refer to the best performance in mixed (green), pure (orange) plantings or to equal performance (yellow). The oblique line indicates a strictly identical performance.

Supplementary Materials

S1 - Stan models

eqn 1 - Survival model

```
data {
  int<lower=0> n_obs;
  int<lower=0> n_species;
  int<lower=0> n_plot;
  int<lower=1, upper=n_species> species[n_obs];
  int<lower=1, upper=n_plot> plot[n_obs];
  int<lower=0,upper=1> survival[n_obs];
  int<lower=0> t[n_obs];
  vector[n_obs] C;
}
parameters {
  vector <lower=0,upper=1> [n_species] theta_s;
  vector <lower=-0.02,upper=0.02> [n_plot] theta_p;
  real<lower=0> sigma_p;
  real <lower=-0.9> theta_c;
}
model {
  theta_s ~ beta(1,1);
  for (i in 1:n_obs)
  {
    survival[i] ~ bernoulli(pow((theta_s[species[i]] + theta_p[plot[i]] + theta_c*C[i]),t[i]));
  }
  theta_p ~ normal(0, sigma_p);
}
```

eqn 2 - Growth model

```
data {
  int<lower=0> n_obs;
  int<lower=0> n_plot;
```

```
  int<lower=0> n_species;
  int<lower=1, upper=n_plot> plot[n_obs];
  int<lower=1, upper=n_species> species[n_obs];
  vector[n_obs] dbh;
  vector[n_obs] t;
  vector[n_obs] C;
}
parameters {
  real<lower=0> sigma;
  vector <lower=1.0> [n_species] theta_s;
  vector <lower=-1, upper=1> [n_plot] theta_p;
  real<lower=0> sigma_p;
  real <lower=-0.9> theta_c;
}
model {
  real mu[n_obs];
  for (i in 1:n_obs)
  {
    mu[i]= (theta_s[species[i]] + theta_p[plot[i]] + theta_c*C[i]) *t[i];
  }
  dbh ~ lognormal(log(mu), sigma);
  theta_p ~ normal(0, sigma_p);
}
```

eqn 3 - Height model

```
data {
  int<lower=0> n_obs;
  int<lower=0> n_species;
  int<lower=1, upper=n_species> species[n_obs];
  vector[n_obs] dbh;
  vector[n_obs] height;
}
```

```
parameters {
  real<lower=0> sigma;
  real<lower=0> gamma;
  real<lower=0, upper=50> alpha;
  vector <lower=1.0, upper=70> [n_species] theta_s;
  real<lower=0> sigma_s;
}
model {
  real mu[n_obs];
  for (i in 1:n_obs)
  {
    mu[i]= (theta_s[species[i]] * dbh[i]) / (gamma + dbh[i]);
  }
  height ~ lognormal(log(mu), sigma);
  theta_s ~ normal(alpha, sigma_s);
}
```

eqn 4 - Survival model with mixture effect

```
data {
  int<lower=0> n_obs;
  int<lower=0> n_species;
  int<lower=0> n_plot;
  int<lower=1, upper=n_species> species[n_obs];
  int<lower=1, upper=n_plot> plot[n_obs];
  int<lower=0,upper=1> survival[n_obs];
  int<lower=0> t[n_obs];
  vector[n_obs] C;
  vector[n_obs] mixed;
}
parameters {
  vector <lower=0.8,upper=0.998> [n_species] theta_s;
  vector <lower=-0.01,upper=0.01> [n_plot] theta_p;
```

```
  real<lower=0> sigma_p;
  vector <lower=-0.01,upper=0.01> [n_species] theta_m;
  real <lower=-0.003,upper=0.005> theta_m_mu;
  real<lower=0> sigma_m;
  real <lower=-0.007 , upper=0> theta_c;
}
model {
  theta_s ~ beta(1,1);
  sigma_p ~ normal(0, 1);
  sigma_m ~ normal(0, 1);
  for (i in 1:n_obs)
  {
    survival[i] ~ bernoulli(pow((theta_s[species[i]] + theta_p[plot[i]] + theta_m[species[i]]*mixed[i] +
theta_c*C[i]),t[i]));
  }
  theta_p ~ normal(0, sigma_p);
  theta_m ~ normal(theta_m_mu, sigma_m);
}
```

eqn 5 - Growth model with mixture effect

```
data {
  int<lower=0> n_obs;
  int<lower=0> n_plot;
  int<lower=0> n_species;
  int<lower=1, upper=n_plot> plot[n_obs];
  int<lower=1, upper=n_species> species[n_obs];
  vector[n_obs] dbh;
  vector[n_obs] t;
  vector[n_obs] C;
  vector[n_obs] mixed;
}
parameters {
```

```
  real<lower=0> sigma;
  vector <lower=1.0> [n_species] theta_s;
  vector <lower=-1, upper=1> [n_plot] theta_p;
  vector <lower=-1, upper=10> [n_species] theta_m;
  real <lower=-0.3, upper=2> theta_m_mu;
  real<lower=0> sigma_p;
  real <lower=-0.9> theta_c;
  real<lower=0> sigma_m;
}
model {
  real mu[n_obs];
  for (i in 1:n_obs)
  {
    mu[i]= (theta_s[species[i]] + theta_p[plot[i]] + theta_m[species[i]]*mixed[i] + theta_c*C[i]) *t[i];
  }
  dbh ~ lognormal(log(mu), sigma);
  theta_p ~ normal(0, sigma_p);
  theta_m ~ normal(theta_m_mu, sigma_m);
}
```

eqn 6 - Bole model

```
data {
  int<lower=0> n_obs;
  int<lower=0> n_species;
  int<lower=1, upper=n_species> species[n_obs];
  vector[n_obs] dbh;
  vector[n_obs] vol;
}
parameters {
  real<lower=0> sigma;
  real<lower=0> gamma;
  real<lower=0, upper=50> alpha;
```

```
  vector <lower=0, upper=70> [n_species] theta_s;
  real<lower=0> sigma_s;
}
model {
  real mu[n_obs];
  for (i in 1:n_obs)
  {
    mu[i]= (theta_s[species[i]] * pow(dbh[i], gamma));
  }
  vol ~ lognormal(log(mu), sigma);
  theta_s ~ lognormal(log(alpha), sigma_s);
}
```

S2 - Plot Random Effects

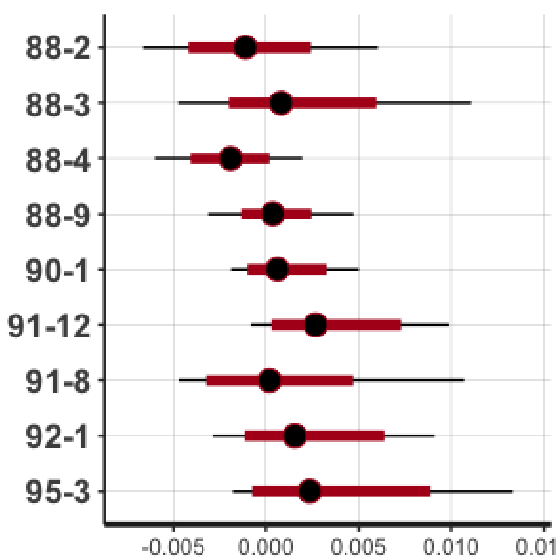

Figure 5: Plot random effects (θ_p^S) on Survival probability (eqn 1)

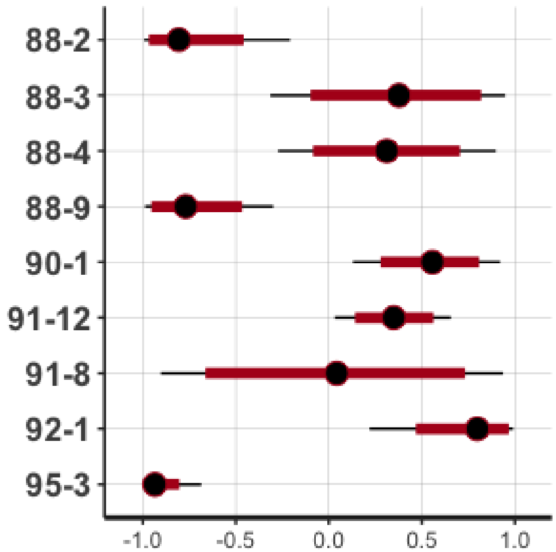

Figure 6: Plot random effects (θ_p^G) on Growth (eqn 2)

S3 - Detailed Maps

See attached file.