Root distribution of *Adansonia digitata, Faidherbia albida* and *Borassus akeassii* along a climate gradient in Senegal

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Abstract In order to understand the ecophysiology of sub-Sahelian tree species and to optimize their use in agroforestry, studies on tree root distribution are essential. The aim of this study was to investigate the root distribution of three sub-Sahelian tree species, *Adansonia digitata, Faidherbia albida* and *Borassus akeassii,* in three sites along a precipitation and soil gradient in Senegal. Root density maps observed on trench walls and soil-coring methods were used to characterize variations in root density of mature trees. Coarse and fine root distribution was strongly influenced by the site conditions, with root density being highest in the humid site for all tree species. *B. akeassii* had the highest root density compared to the other two species. Fine root biomass was concentrated in the 0–30 cm soil layer for *A. digitata* and from 30 to 60 cm for *B. akeassii* and *F. albida.* Laterally, the fine root biomass decreased substantially with increasing distance from the trees. Understanding the root distribution of sub-Sahelian tree species across climatic conditions could help to reduce competition between crops and perennials in agroforestry parklands.

Keywords Agroforestry · Soil depth · Root density · Climate · Semi-arid regions

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Introduction

Agroforestry systems represent an important strategy for sustainable agriculture in developing countries, creating many benefits in terms of better utilization of soil resources, and yield diversification (Camara et al. 2017; Roupsard et al. 2020). Agroforestry parklands constitute the predominant agroforestry system in semi-arid regions in West Africa (Bazié et al. 2012; Bayala et al. 2015) and provide many services for the populations in ecological and economical terms.

Still, the interactions between components need to be understood to optimize management of the systems. Such interactions can be divided into aboveground (i.e., shade from trees may increase or decrease the yield of associated crops) and belowground processes such as uptake of nutrients and water which may be affected by synergies or competition (Anderson and Sinclair 1993; Bayala and Prieto 2020). Many studies have investigated aboveground processes, despite belowground processes often being at least as important.

Plant growth and development depend on the acquisition of water and soil nutrients and so are closely associated with root architecture, morphology and physiology (Ju et al. 2015). In agroforestry systems (AFS), tree roots play important roles by enriching soil carbon through root exudates and turnover, feeding soil organic matter (SOM), recycling nutrients from the subsoil, reducing nutrient leaching, anchoring of trees and loosening compact soil layers (Schroth and Zech 1995; Jonathan 2019).

Trees and shrubs adapted to semi-arid areas tend to exhibit deep root systems and can cause complementarity or facilitation with associated crops by taking up water from the deep subsoil layers and redistributing it to shallow horizons (Bayala and Prieto 2020). Fine roots are the most dynamic part of the root system and most physiologically involved in water and nutrient uptake, and consequently of great interest in agroforestry (Aanderud and Richards 2009).

However, the association between crops and tree species in AFS can lead to various forms of competition. This can mask or suppress many of the advantages that trees may provide for the long-term sustainability of AFS (van Noordwijk and Purnomoshidi 1995). Trees cast shade, thereby reducing amounts of photosynthetically active radiation available to crops underneath them, and root systems may depress crop yields by root competition for water and nutrients. This may contribute to the economic failure of such land-use systems (Schroth et al. 1995). Root competition depends largely on the spatial distribution of roots, which in turn is modified if competition is high (Mulia and Dupraz 2006). Root distribution is thus an important determinant of tree-crop competition, because it defines the soil volume available and the amounts of soil water and nutrients that are accessible to plants (Mulatya et al. 2002). Water and nutrient uptakes depend not only on the area and length of the roots but also on their distribution in different horizons (Groot et al. 1998). Understanding and predicting ecosystem functioning with respect to nutrient cycling and water fluxes therefore requires an accurate assessment of plant root distribution (Jackson et al. 1996).

Root distribution, activity and turnover are determined by environmental and biological factors, such as climate, soil properties, plant species and microbial composition (Sokalska et al. 2009). Marone (2015) showed that in a semi-arid environment, root distribution varied between tree species, with *Faidherbia albida* identified to having particularly deep roots. Trees with a substantial uptake of nutrients and water from deep soil layers may deplete the topsoil less than those with a shallower root system (Hu et al. 2013).

However, root systems in dry zones are insufficiently characterized to understand tree-crop interactions, and most studies were focused on variation in root mass between species. To our knowledge, no study has yet investigated the variation in root distribution of sub-Sahelian tree species under different climatic conditions. Studies on root systems of different tree species at different sites may help to reconcile the gap in our understanding of not only intraspecific but also interspecific root ecophysiology, which may be important in managing AFS (De Kroon 2007). Therefore, the purpose of this study was to compare the vertical and horizontal root distribution of three sub-Sahelian tree species in three different climate and soil conditions. Our hypotheses were that root systems would be shallower under humid conditions in the southern site compared to northern semi-arid sites, and that responses would be tree species-specific.

Materials and methods

The three tree species considered in this study were a legume from the Fabaceae family, *Faidherbia albida* (Del.), a stem-succulent tree from the Malvacae family, *Adansonia digitata* L. and a massive palm from the Arecaceae family, *Borassus akeassii* Bayton, Ouédraogo & Guinko. All three species commonly occur in West African parklands and are widely used by farmers.

Sites

The study was conducted in three sites along a north–south climatic gradient (Table 1, Fig. S1). The climate is Sahelian in Ndiambe Fall; Soudano-Sahelian in Fandene and Soudano-Guinean in Djifanghor. The climate is bimodal with a dry season lasting 7–8 months and a rainy season ranging from approximately June to October, being shorter towards the north. The annual precipitation in 2019, when the current study was conducted, was 333; 683 and 1233 mm respectively in Ndiambe Fall (north), Fandene (center) and Djifanghor (south) (Senegal, Meteorological Service, unpublished data).

In addition, soil types varied from sandy and relatively nutrient poor in the northern site to loamy sand and slightly more nutrient-rich in the south, with the site in the center being intermediate (Supplementary Information Table S1).

All sites had been cultivated but were left fallow for one year before root sampling took place. Thus, shallow roots would not have been disturbed by recent ploughing. The last crop species cultivated in the sites were pearl millet, peanuts/cowpeas and rice in Ndiambe Fall, Fandene and Djifanghor, respectively.

Sampling

Sampling was carried out between October 1st and October 10th 2019 at the end of the rainy season. The data were collected from a total of 24 trees. In each site, three trees of each species were selected, except in Ndiambe Fall where *B. akeassii* was not present. Within species, we selected trees with comparable diameters and with a distance to neighboring trees of around 50 m. Heights were measured with a Rangefinder (Nikon Forestry Pro) and diameters at breast height and GPS coordinates recorded (Table 2).

Table 1 Characteristics of the three study sites. Precipitation and temperature (1989–2019) are estimates from the Climate Research Unit (CRU) at East Anglia University (Harris et al. 2020). Soil types according to the FAO classification (IUSS Working Group WRB 2015)

Site name	Latitude °N	Longitude °W	Average rainfall (mm)	Temperature (min–max °C)	Soil texture	Soil type (FAO)	Organic matter (%)	C/N-ratio	Dominant woody species
Ndiambe Fall	15.708	16.426	362	19.7 – 33.6	Sand	Arenosol	0.13	3.52	*Faidherbia albida*, *Prosopis africana*, *Adansonia digitata*
Fandene	14.457	16.919	680	20.2 – 33.5	Sand	Ferralic Arenosol	0.32	7.62	*Acacia seyal*, *Adansonia digitata*, *Faidherbia albida*, *Borassus akeassii*
Djifanghor	12.571	16.249	1261	20.7 – 33.3	Loamy sand	Ferric Acrisol	0.70	11.95	*Erythrophlaeum guineense*, *Neocarya macrophylla*, *Khaya senegalensis*, *Ceiba pentandra*, *Pterocarpus erinaceus*

Sites	Tree species	Diameter (cm)	Height (m)
Ndiambe Fall (north)	*Adansonia digitata*	76 ± 9	8.6 ± 2.6
	Faidherbia albida	32 ± 2	6.5 ± 1.2
Fandene (center)	*Adansonia digitata*	75 ± 5	10.1 ± 2.5
	Faidherbia albida	45 ± 9	10.4 ± 1.4
	Borassus akeassii	30 ± 2	9.7 ± 0.8
Djifanghor (south)	*Adansonia digitata*	105 ± 13	15.6 ± 2.9
	Faidherbia albida	39 ± 2	10.1 ± 1.7
	Borassus akeassii	32 ± 2	12.2 ± 2.3

Table 2 Diameter and height for the sampled trees at the three sites

Values are means ± s.d. ($n = 3$)

Root sampling was based on two methods, including trench wall observations near the trunk and the coring method to assess the vertical and horizontal fine root distribution at increasing distances from the tree.

Trench wall profile

For *A. digitata* and *F. albida,* the basal part of the roots at the stem base was excavated in a sphere with a 1 m radius from the trunk to a depth of 1.5 m (Fig. S1). We considered the different root categories for each tree, coarse (D > 10 mm), medium (10 mm < D < 2 mm) and fine (D < 2 mm). The root number on the soil profile facing the tree was counted and converted into Root Intercept Density (RID, roots m^{-2}). All roots were counted in soil depth layers of 0–20 cm; 20–50 cm; 50–100 cm and 100–150 cm, respectively.

For *B. akeassii*, a trench profile was dug at 1 m from the tree in the tangential direction, resulting in a profile towards the tree with a width of 2 m and a depth of 1.5 m. A grid was placed vertically against the pit wall and roots were counted. Only one trench wall of the profile was considered to avoid excessive harm to the root system. In the southern site at Djifanghor we stopped digging at 80 cm having reached the water table.

Soil cores

Soil cores were extracted using an auger inserted manually into the ground to a maximum depth of 90 cm. The cylinder had an inner diameter of 7.2 cm and a length of 30 cm. Soil cores were taken at 1, 2, 4, 5 and 7 m, respectively from the tree trunk until roots were no longer present in the soil cores. Only

samples taken at 1, 2 and 4 m were used in the analyses, for at 5 and 7 m roots were only found at Djifanghor for *A. digitata*. At each distance, three soil cores were extracted at increasing depths, of 0–30 cm, 30–60 cm and 60–90 cm, giving a total of 9 soil cores for each tree. Cores were kept separately, put in plastic bags and stored in a cooler until arrival in the laboratory, where each sample (including roots) was weighed to determine the humid weight. Thereafter, roots were separated manually from the soil with a toothbrush over two sieves of 2 mm and 2.5 mm mesh sizes, discarding organic debris and dead roots. Roots were weighed to obtain the fresh biomass and stored in a cold chamber at 6 °C until further analyses. After sorting, coarse and medium roots were oven-dried at 65 °C for 48 h and weighed. Fine roots were scanned (Epson perfection V700 Photo, Japan), and assessed with WinRHIZO software (Regent Instruments Inc. Regular version, 2012b, Canada) to determine fine root length and average diameter. The fine roots were also oven-dried at 65 °C for 48 h to determine their dry mass. Specific root length (SRL) was calculated by dividing fine-root length by dry weight and the root length density (RLD) was calculated by dividing fine root length by soil volume.

Soil water content (SWC) was assessed in the same soil samples through determination of the fresh weight (FW) while the dry weight (DW) was obtained after drying at 80 °C for 72 h. SWC was calculated as SWC = (FW − DW)/DW × 100%.

Soil analyses

For all trees, we took 5 soil samples from each 20 cm layer to 100 cm depth at two distances (1 and 4 m from the trunk). The samples for each species, distance and depth were pooled for each site,

giving 80 samples in total, that were subjected to analysis of texture and chemical analysis. At ISRA laboratories in Saint Louis, Senegal, the carbon content was measured by the modified Black and Walkley method (Walkley and Black 1934). The percentage of organic matter in the soil was based on the soil carbon content. Total nitrogen was estimated according to the Kjeldahl method. The soil texture was analyzed at the National Center for Agricultural Research in Bambey, Senegal using the Bouyoucos method with a hydrometer.

Statistical analysis

Statistical analyses were performed by linear mixed effects models (*lmer* function in package *lme4*) in R

(version 3.6) and R Studio (version 1.2.5001), to test whether measured variables differed with sites, species, distances and soil depths (R Core Team 2020).

For each response variable (Table 3), a starting statistical model included the fixed effects of site, species, depths, distances and all interactions between these factors. As random effects, tree number and the interaction between tree number and distances were included. Height and diameter of the trees were considered as co-variates, but were not significant ($P > 0.05$) and not considered further.

Model reduction was carried out by comparing the P values of the model using the ANOVA function and sequentially eliminating non-significant interactions, starting with the highest order interactions and those with least significance, until all remaining interactions

Table 3 Results of analyses of variance for the three tree species at three sites

Trench profile

Sources	RID (coarse roots)	RID (fine roots)
	P value	
Sites*Species*Depth	0.3116	0.0014 **
Sites*Species	0.9431	0.0035 **
Sites*Depth	0.7681	0.0022 **
Species*Depth	0.0000***	0.1650
Sites	0.4968	0.0000 ***
Species	0.0000 ***	0.0000 ***
Depth	0.0000 ***	0.0000***

Soil cores

Sources	Dry biomass	RLD	SRL
	P value		
Sites*Species*Depth	0.0002 ***	0.0000 ***	0.8515
Sites*Species*Distance	0.0000 ***	0.0001 ***	0.1254
Sites*Depth*Distance	0.0963	0.4077	0.0360 *
Species*Depth*Distance	0.0337 *	0.1075	0.6106
Sites*Species	0.2254	0.094792	0.0327 *
Sites*Distance	0.0766	0.0063 **	0.0105 *
Sites*Depth	0.0001 ***	0.0416 *	0.3464
Species*Distance	0.0103 *	0.1949	0.0067 **
Species*Depth	0.4908	0.2436	0.2123
Depth*Distance	0.0646	0.4830	0.5401
Sites	0.0000 ***	0.0000 ***	0.0000***
Species	0.0165 *	0.06623	0.0000 ***
Depth	0.0078 **	0.0258*	0.7167
Distance	0.3036	0.0470 *	0.0331 *

Signification codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

were significant. We investigated the selected models via estimated marginal means using the *emmeans* package in R. Assumptions on variance heterogeneity and normality of residuals were validated by residual and quantile plots. For all the variables, a cubic-root transformation was used to achieve a valid model.

Results

Soil moisture and nutrient patterns

The soils differed in moisture and nutrient contents between the three sites. We found that the average SWC in October (all species included) was substantially higher (62%) in the southern site at Djifanghor than in the center site at Fandene (4%) and the northern site at Ndiambe Fall (5%). Likewise, contents of soil organic matter, carbon and nitrogen increased from the northern to the southern site (Table 1 and Table S1). The soil organic matter content in Djifanghor site (0.70%) was double that of Fandene (0.32%) and more than five times that of Ndiambe Fall site (0.13%).

Root distribution and traits

The root types were generally similar from one site to another, but roots tended to be shallower in the south than in the north and the center, respectively (Fig. S2). Fewer roots were observed in the northern site, especially for *F. albida* at the different observed depths limited at 150 cm. Very few roots (mainly taproots) were observed at the depth of 100–150 cm.

Root intercept density (RID)

This variable was assessed from the trench profile set up at 1 m from the trunk of the trees. RID showed interactions between species and depths for coarse and medium roots and between sites, species and depths for fine roots (Table 3, Fig. 1). For fine roots, RID was highest near the topsoil at the Fandene and Djifanghor sites in the center and south for all species except for *B. akeassi* in Djifanghor where RID was highest at 20–50 cm. At the northern site, in Ndiambe

Fall, the maximum RID was observed at 20–50 cm for *A. digitata*, and there were almost no fine roots for *F. albida* at this site (Fig. 1a).

Regarding coarse and medium roots, *A. digitata* and *F. albida* had fewer roots compared to *B. akeassii* at the two sites (Ndiambe Fall and Fandene) where a comparison was made. *A. digitata* and *F. albida* showed almost similar patterns across the three sites, always having a maximum amount of coarse and medium roots at 20–50 cm (Fig. 1b). For *B. akeassii,* the RID of both coarse and fine roots were higher and had maximum depth than for the two other species. For this species (*B. akeassii)*, the highest root density was observed in Djifanghor at 50–100 cm (Fig. 1b).

Root biomass

The distribution of root biomass of the three species varied significantly ($p < 0.001$) among depths and sites at the three distances, and there were several interactions between the factors, showing that species behavior depended on sites (Table 3). As expected, root biomass tended to be higher at 1 and 2 m from the stem than at 4 m. Only in *A. digitata* did we record roots at 5 and 7 m (see methods). For all species, the total root biomass appeared to be higher at the wet site at Djifanghor in the south than at the two other sites. Root biomass of *A. digitata* tended to be highest in the topsoil (0-30 cm) at Djifanghor, whereas it was more evenly distributed through the profiles at Fandene and Ndiambe Fall, respectively. For *F. albida*, there was a high concentration of roots at Djifanghor at 30–60 cm depth and 1 m from the stem, which was not observed in other distances and sites. *B. akeassii* had more root biomass than the two other species at 1 m from the trunk, but this was less pronounced at 2 and 4 m from the trunk (Fig. 2).

Root length density (RLD)

Results for RLD were broadly similar to those of root biomass, the analysis generally indicating the presence of several interactions between the factors (Table 3). Values of RLD in shallow layers at Djifanghor were high compared to the other sites, and with RLD tending to be higher in the shallow layer for *A.*
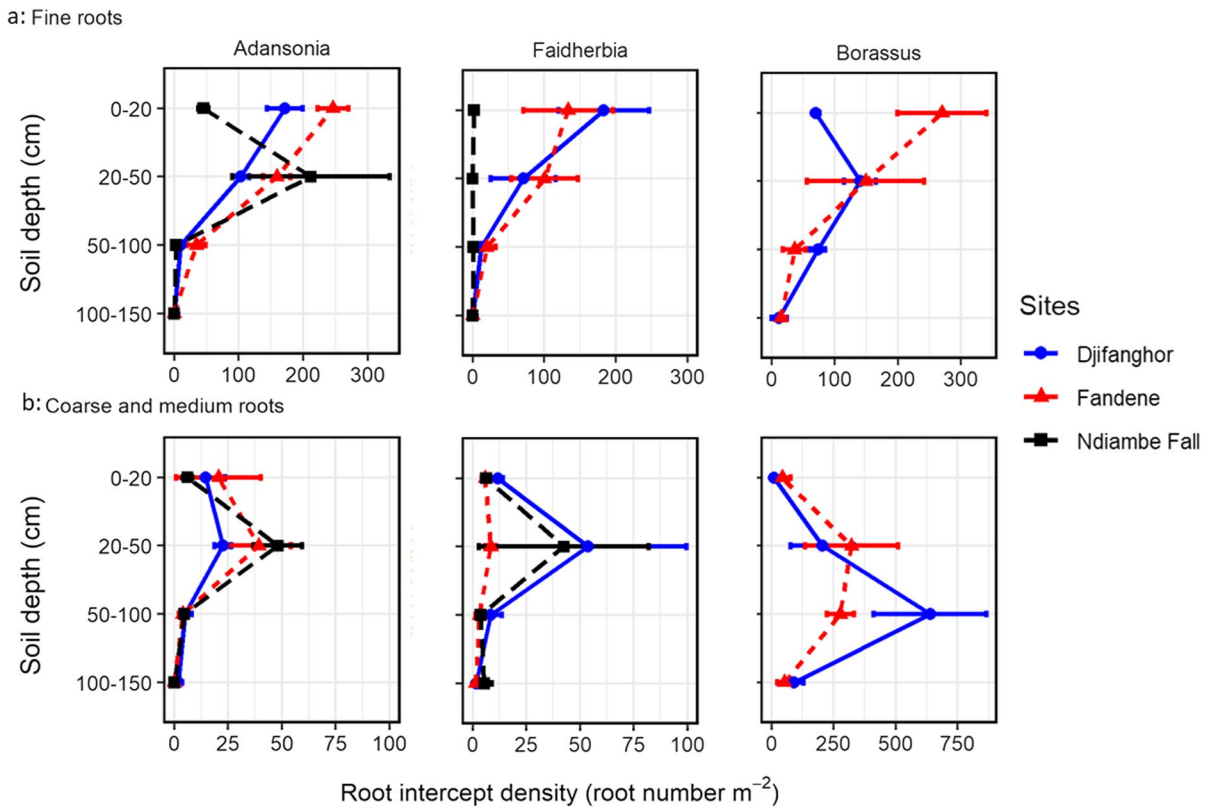
Fig. 1 Variations in Root Intercept Density (RID) by sites (north—Ndiambe Fall, center—Fandene and south—Djifanghor) for *A. digitata (left column)*, *F. albida* (center) and *B. akeassii* (right column) for each soil depth within each root type. a: Fine roots. b: Coarse and medium roots. Values represent estimated marginal means ± s.d. (n = 3). Note that x-axis scales vary between species for coarse and medium roots

digitata in comparison to the other two species. In *F. albida*, the RLD was relatively stable across the three sites except for high values (around 0.85 cm cm^{-3}) observed at 60–90 cm at 1 m distance from the stem in Djifanghor (Fig. S3).

Specific root length (SRL)

Also SRL was affected significantly by tree species, sites, soil depths, distances to trees and their interactions (Table 3). The highest values were observed at Ndiambe Fall, where values for *F. albida* reached 500 m g^{-1}. Values were lower for the two other species, *B akeassii* having values < 30 m g^{-1}. For *A. digitata,* the SRL was high at 2 and 3 m from the trunk in Ndiambe Fall. For *B. akeassii,* SRL was higher in Fandene compared to Djifanghor except at 4 m from

the trunk where the SRL at Fandene was close to zero (Fig. S4).

Discussion

Differences between sites

Despite comparing trees of similar sizes at the three sites, root densities at different soil depths and distances to trees varied considerably. The results presented here show several interactions between tree species and sites, indicating that it is difficult to generalize across the three sites. As sampling was undertaken at the end of the rainy season, where the soil is wet and nutrients are most abundant in the top soil (Schroth and Sinclair 2003), we expected fine root densities to be at their maximum. The trends of the vertical distribution observed in the trench profile
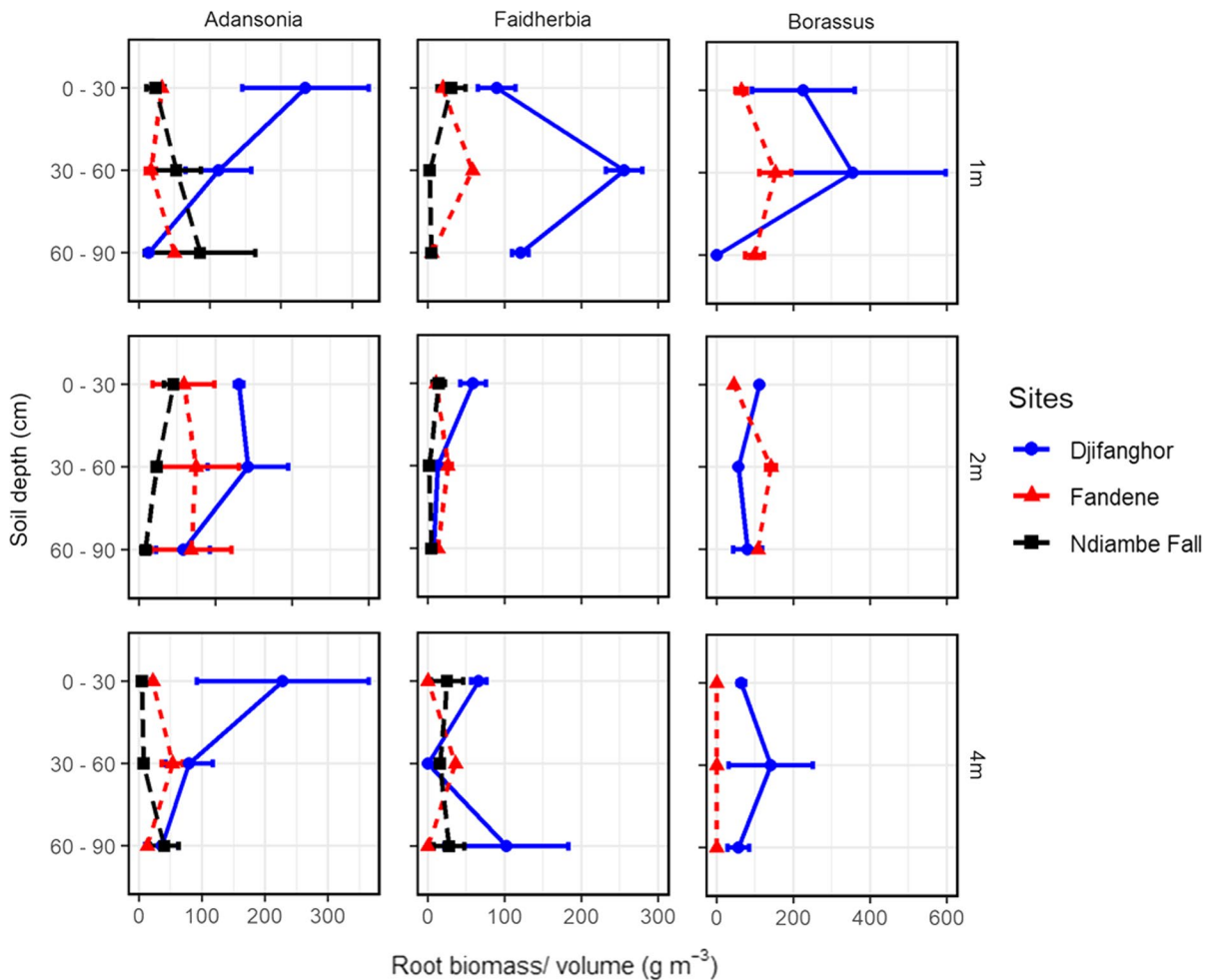
Fig. 2 Vertical distribution of root biomass by sites (north—Ndiambe Fall, center—Fandene and south—Djifanghor) for *A. digitata (left column)*, *F. albida* (center) and *B. akeassii* (right column) for each soil depth within each distance to tree (1 m: top, 2 m: middle, 4 m: bottom). Values represent estimated marginal means ± s.d. (n = 3). Note that x-axis scales vary between species

were similar to those of the fine roots in the soil cores, adding confidence to our results.

The higher RID in the southern site confirms our hypothesis that trees have larger and shallower root biomass under humid conditions than in semi-arid sites. This may be due to the easier access to water resources because of the higher rainfall, leading to the development of many roots near the topsoil. Conversely, lower root biomass at the northern site may be a response to low rainfall, as the dynamics of fine roots, especially those near the soil surface, are most sensitive to changes in soil moisture (Wilczynski and Pickett 1993). In savanna ecosystems, Kulmatiski

et al. (2017) observed similar results with abundant fine root production under a high precipitation regime, but on clay soils, Schenk and Jackson (2005) found that tree species tended to develop deep rooting in areas characterized by low rainfall, which match our observations particularly for *A. digitata*. Jansen et al. (2020) obtained similar results in baobab seedlings showing that the investment in taproots on humid soil was higher than in dry areas.

Sites varied also in terms of soil characteristics, and different rooting distributions across sites cannot be ascribed solely to humidity. Indeed, in the north, the lower root biomass may be due to the poor

soil fertility of the sandy soil (Marone 2015). Low amounts of root biomass in sandy soils may be related to their lack of organic matter and their particle structure with few aggregates (Pallo et al. 2008).

We observed a high SRL in the northern site. This may also be explained by the lower soil nutrient content in the sandy soils in the Sahel as several authors have observed a higher SRL in sites where soil resources are limited (Ostonen et al. 2007; Marone 2015).

Differences between tree species

Our comparative analysis shows different trends in the rooting distribution across the three species and confirms our hypothesis of their different performance across sites. While *A. digitata* root densities were higher in the topsoil, *F. albida* and *B. akeassii* reached maximum levels in the subsoil to an average depth of 60 cm. The root biomass of *B. akeassii* was higher than the other two species, maybe due to the fibrous root system architecture, specific to monocotyledonous plants, exhibiting large amounts of primary coarse roots around the palm tree (Jourdan and Rey 1997). Moreover, these adventitious roots have a high branching rate, leading to abundant fine roots (Jourdan 1995).

A. digitata is deciduous and a succulent tree species with capacity to store resources and water in its tissues (Birnbaum et al. 2012) allowing great resistance to drought stress. However, the water in the stem appears to be retained throughout the dry season to be mobilized for use when the new leaves are flushing (Chapotin et al. 2006). Still, the ability to keep high amounts of water in the stem tissue may make it less critical for this species to access deeper water sources, which would explain the tendency for shallow rooting.

F. albida is also a deciduous tree species but with a reverse phenology, as it loses its leaves at the beginning of the rainy season and remains defoliated until the onset of the dry season (Roupsard et al. 1999). According to Dupuy and Dreyfus (1992), *F. albida* can reach the water table at depths reaching more than 30 m in the Sahelian regions. This rooting depth may allow the tree to compensate water loss through transpiration. The lateral branching is rather poor in shallow soil layers and increases with soil depth (Wood 1989), which would confirm our results.

Root distribution and agroforestry

Soil moisture is an important issue for agroforestry functioning and production, and consequently root traits may influence competition for water especially under low rainfall conditions found in the northern site (Wilczynski and Pickett 1993). Moreover, by the process called hydraulic redistribution, water can be redistributed by tree roots through the entire rooting profile; from deeper and wetter soil layers to shallower and drier horizons (Bayala and Prieto 2020). In addition lower air temperature, soil evaporation, and higher rain interception may benefit crops under tree canopies (Jonsson 1995).

The deep rooting of *F. albida* and *B. akeassii* suggest a potential facilitation role in AFS. Previous studies in dryland have demonstrated the crucial role of *F. albida* and *Elaeis guineensis* in improving microclimate conditions and crop yields (Camara et al. 2017; Roupsard et al. 2020). *F. albida* trees planted in intercropping systems developed fewer roots throughout the soil profile compared to *Acacia* species that reduced the crop yields by more than 50% (Cazet 1989). With its reverse phenology, *F. albida* grows at different times compared to the associated crops, which may allow the crops to benefit from almost full sun conditions and to increase their photosynthetic performance.

B. akeassii is associated with various crops in traditional agroforestry systems in Africa (Salako et al. 2018), and producers perceive better growth and development of crops cultivated near palm trees suggesting limited competitive effect of trees on the associated crops (Yameogo et al. 2016). However, crop productivity under *B. akeassii* needs to be further investigated to confirm the facilitation of tree roots on the associated crops.

On the other hand, the shallow rooting patterns suggest a potential root competition between *A. digitata* and associated crops for belowground resources. A rare study made in a parkland system in West Africa found a negative effect on millet yields under baobab (Sanou et al. 2012). Although one study found that *A. digitata* had a wide spreading root system that may extend laterally up to 50 m from the trunk (Rahul et al. 2015). Our study suggests a relatively modest expansion of roots from the stem. A suggestion may be to consider a minimum distance (that is, 4 m) between the crops and the tree trunk to avoid

competition. Alternatively, other species including *B. akeassii* and *F. albida* may be chosen to reduce competition.

Conclusion

This study provides a first glimpse on root distribution of three sub-Sahelian agroforestry tree species across a rainfall gradient. Our results show that tree species tend to produce fewer but deeper roots under dry soil conditions and demonstrate that *B. akeassii* and *F. albida* tended to produce more roots between 30 and 60 cm depth while *A. digitata* roots were concentrated in the surface layers. These findings suggest that climate and soil conditions have a large impact on root distribution of the three-tree species. As deep roots may facilitate the growth of associated crops under dry conditions, AFS practices must consider this in selection of species. Detailed studies of root traits and yields of associated crop species across climatic conditions are still needed to fully evaluate this.

References

Aanderud ZT, Richards JH (2009) Hydraulic redistribution may stimulate decomposition. Biogeochemistry 95:323–333. https://doi.org/10.1007/s10533-009-9339-3

Anderson LS, Sinclair F (1993) Ecological interactions in agroforestry systems. Agroforestry Abstracts 6:57–91

Bayala J, Prieto I (2020) Water acquisition, sharing and redistribution by roots: applications to agroforestry systems. Plant Soil 453:17–28. https://doi.org/10.1007/s11104-019-04173-z

Bayala J, Sanou J, Teklehaimanot Z, Ouedraogo SJ, Kalinganire A, Coe R, Noordwijk MV (2015) Advances in knowledge of processes in soil–tree–crop interactions in parkland systems in the West African Sahel: a review. Agric Ecosyst Environ 205:25–35

Bazié HR, Bayala J, Zombre´ G, Sanou J, Ilstedt, (2012) Separating competition-related factors limiting crop performance in an agroforestry parkland system in Burkina Faso. Agrofor Syst 84:377–388. https://doi.org/10.1007/s10457-012-9483-y

Birnbaum P (2012) Biodiversité au Sahel. Les forêts du Mali. Édn Quae CIRAD, IFEMER, INRA, IRSTEA, France. p 208

Camara B, Sagna B, Ngom D, Niokane M, Gomis ZD (2017) Importance socioéconomique de *Elaeis guineensis* Jacq. (Palmier á huile) en basse-Casamance (Senegal). Europ Sci J Ed 13: 214–230. https://doi.org/10.19044/esj.2017.v13n12p214

Cazet M (1989) Les plantations linéaires denses sur les sols sableux dégradés de la zone Centrale-Nord du Sénégal. Comportement et effets sur les cultures adjacentes de quelques espèces locales et introduites. Revue Bois Et Forêts Des Tropiques 222:27–37

Chapotin SM, Razanameharizaka JH, Holbrook NM (2006) A biomechanical perspective on the role of large stem volume and high water content in baobab trees (*Adansonia spp*.; Bombacaceae). Am J Bot 93:1251–1264

De Kroon H (2007) How do roots interact? Science 318:1562–1563

Dupuy NC, Dreyfus BL (1992) Bradyrhizobium populations occur in deep soil under the leguminous tree *Acacia albida*. Appl Environ Microbiol 58:2415–2419

Groot JJR, Traoré M, Koné D (1998) Description du système racinaire de trois espèces fourragères en zone soudano-sahélienne: *Andropogon gayanus, Vigna unguiculata* et *Stylosanthes hamata*. Biotechnol Agron Soc Environ 2:106–119

Harris I, Osborn TJ, Jones P, Lister D (2020) Version 4 of the CRU TS monthly high-resolution gridded multivariate climate dataset. Sci Data 7:109. https://doi.org/10.1038/s41597-020-0453-3

Hu XS, Brierley G, Zhu HL, Li GR, Fu JT, Mao XQ, Yu QQ, Qao N (2013) An exploratory analysis of vegetation strategies to reduce shallow landslide activity on loess hillslopes, northeast Qinghai–tibet Plateau, China. J Mt Sci 10:668–686. https://doi.org/10.1007/s11629-013-2584-x

IUSS Working Group WRB, (2015) World reference base for soil resources 2014, Update 2015. In: International soil classification system for naming soils and creating legends for soil maps. World Soil Resources Reports No. 106, Rome: FAO.

Jackson RB, Canadell J, Ehleringer JR, Mooney HA, Sala OE, Schulze ED (1996) A global analysis of root distributions for terrestrial biomes. Oecologia 108:389–411

Jansen L, Darr D, Hansohm N, Gebauer J, Meinhold K, Munthali CRY, Wichern F (2020) Variation in baobab Adansonia digitata L. root tuber development and leaf number among different growth conditions for five provenances in Malawi. J

Agricult Rural Develop Trop Subtrop 121:161–172. https://doi.org/10.17170/kobra-202007291508

Joly H (1992) The genetics of Acacia albida (syn. Faidherbia albida). In: Vandenbelt RJ (ed) Faidherbia albida in the West African Semi-Arid Tropics. ICRISAT, Patancheru India, pp 53–62

Jonathan PL (2019) Root phenotypes for improved nutrient capture: an under exploited opportunity for global agriculture. New Phytolog 223:548–564

Jonsson K (1995) Agroforestry in dry savannah areas in Africa: interactions between trees, soils and crops. PhD dissertation. Swedish University of Agricultural Sciences, Umea, Sweden

Jourdan C, Rey H (1997) Architecture and development of the oil-palm (*Elaeis guineensis* Jacq.) root system. Plant Soil 189:33–48

Jourdan C (1995) Modélisation de l'architecture et du développement du systéme racinaire du palmier á huile. Ph.D Dissertation University of Montpellier II. p 243

Ju C, Buresh RJ, Wang Z, Zhang H, Liu L, Yang J, Zhang J (2015) Root and shoot traits for rice varieties with higher grain yield and higher nitrogen use efficiency at lower nitrogen rates application. Field Crop Res 175:47–55

Kulmatiski A, Sprous SRC, Beard KH (2017) Soil type more than precipitation determines fine-root abundance in savannas of Kruger national park, South Africa. Plant Soil 417:523–533. https://doi.org/10.1007/s11104-017-3277-y

Marone D (2015) Étude du potentiel de stock de carbone d'espèces agroforestières et de leurs traits fonctionnels en lien avec les systèmes d'utilisation des terres au Sénégal. Dissertation, Université de Laval: Canada. p 166

Mulatya JM, Wilson J, Ong CK, Deans JD, Sprent JJ (2002) Root architecture of provenances, seedlings and cuttings of *Melia volkensii*: implications for crop yield in dryland agroforestry. Agrofores Syst 56:65–72

Mulia R, Dupraz C (2006) Unusual fine root distributions of two deciduous tree species in southern France: What consequences for modelling tree root dynamics? Plant Soil 281:71–85

Ostonen I, Püttsepp Ü, Biel C, Alberton O, Bakker MR, Lõhmus K, Majdi H, Metcalfe D, Olsthoorn AFM, Pronk A, Vanguelova E, Weih M, Brunner I (2007) Specific root length as an indicator of environmental change. Plant Biosystems 141:426–442

Pallo FJP, Sawadogo N, Sawadogo L, Sedogo MP, Assa A (2008) Statut de la matière organique des sols dans la zone sud-soudanienne au Burkina Faso Biotechnologie. Agron Société Et Environ 12:291–301

R Core Team (2020) A language and environment for statistical computing R Foundation for statistical computing, (Vienna, Austria URL)

Rahul J, Jain MK, Singh SP, Kamal R, Anuradha K, Naz A, Gupta AK, Mrityunjay SK (2015) *Adansonia digitata* L. (baobab): a review of traditional information and taxonomic description Asian. Pac J Trop Biomed 5:79–84

Roupsard O, Ferhi A, Granier A, Pallo F, Depommier D, Mallet B, Joly H, Dreyer E (1999) Reverse phenology and dry-season water uptake by Faidherbia albida (Del) A Chev in an agroforestry parkland of Sudanese west Africa. Funct Ecol 13:460–472

Roupsard O, Audebert A, Ndour AP, Dauphin CC, Agbohessou Y, Sanou J, Koala J, Faye E, Sambakhe D, Jourdan C, le

Maire GL, Tall L, Sanogo D, Seghieri J, Cournac L, Leroux L (2020) How far does the tree affect the crop in agroforestry? New spatial analysis methods in a *Faidherbia* parkland. Agr Ecosyst Environ 296:106928

Salako KV, Moreira F, Gbedomon RC et al (2018) Traditional knowledge and cultural importance of *Borassus aethiopum* Mart in Benin: interacting effects of socio-demographic attributes and multi-scale abundance. J Ethnobiol Ethnomed 14:36

Sanou J, Bayala J, Teklehaimanot Z, Bazie P (2012) Effect of shading by baobab (*Adansonia digitata*) and néré (*Parkia biglobosa*) on yields of millet (*Pennisetum glaucum*) and taro (*Colocasia esculenta*) in parkland systems in Burkina Faso. West Africa Agroforest Syst 85:431–441

Schenk HJ, Jackson RB (2005) Mapping the global distribution of deep roots in relation to climate and soil characteristics. Geoderma 126:129–140

Schroth G, Zech W (1995) Root length dynamics in agroforestry with *Gliricidia sepium* as compared to sole cropping in the semi-deciduous rainforest zone of West Africa. Plant Soil 170:297–306

Schroth G, Oliver R, Balle P, Gnahoua GM, Kanchanakanti N, Leduc B, Mallet B, Peltier R, Zech W (1995) Alley cropping with Gliricidia sepium on a high base status soil following forest clearing: effects on soil conditions, plant nutrition and crop yields. Agroforestry Syst 32:261–276. https://doi.org/10.1007/BF00711714

Schroth G, Sinclair FL (2003) Trees, crops and soil fertility concepts and researches methods Wallingford, UK, CABI

Sokalska DI, Haman DZ, Szewczuk A, Sobota J, Deren D (2009) Spatial root distribution of mature apple trees under drip irrigation system. Agric Water Manag 96:917–924. https://doi.org/10.1016/j.agwat.2008.12.003

Van Noordwijk M, Purnomoshidi P (1995) Root architecture in relation to tree-soil-crop inter-actions and shoot pruning in agroforestry. Agrofor Syst 30:161–173

Walkley A, Black CA (1934) An examination of the degtjareff method for determining soil organic matter and a proposal modification of the chromic acid titration method. Soil Sci 37:29–38

Wilczynski CJ, Pickett STA (1993) Fine root biomass within experimental canopy gaps: evidence for a below-ground gap. J Veg Sci 4:571–574

Wood PJ (1989) *Faidherbia albida* (Del) a chev (synonym: *Acacia albida* Del): a monograph. CTFT, Nogent-sur-Marne, France

Yameogo J, Samandoulgou Y, Belem M (2016) Le rônier *Borassus akeassii* BOG dans les parcs agroforestiers à Kokologho, Sakoinse et Ramongo dans la province du Boulkiemde, centre-ouest du Burkina Faso. J Appl Biosci 100:9557–9566