



Root growth and biomass partitioning of nine juvenile Sahelian agroforestry tree species under drought and irrigation treatments

Fatou Gning[✉] · Christophe Jourdan[✉] · Diatta Marone · Daouda Ngom · Anders Ræbild[✉]

Received: 6 July 2024 / Accepted: 12 December 2024
© The Author(s) 2025

Abstract

Background and aims Root traits of tree species are of great importance for selection of trees in dry zone agroforestry systems. Climate models predict increased frequency and severity of drought in the Sahel but our understanding on the strategies of root growth of tree species under drought is limited. To increase our knowledge of species differences in rooting patterns we investigated root growth of nine dry-land tree species in West Africa during one year when exposed to drought stress.

Methods Seedlings were planted in 2 m tubes inserted into the soil and subjected to irrigation and

drought (no irrigation during the dry season). After 4, 8 and 12 months, we assessed root growth and root biomass, supplemented with assessments of water potential, leaf phenology, and above-ground growth.

Results Tree species showed significant differences in rooting profile. Drought induced deeper root growth, especially in deciduous species. *Adansonia digitata*, *Sterculia setigera* and *Anacardium occidentale* had shallow roots when irrigated. *Acacia senegal*, *Acacia nilotica* and *Faidherbia albida* had deeper root growth and showed clear differences in leaf water potential between treatments while *A. digitata* and *S. setigera* appeared to be water conserving under drought.

Conclusions Our results link root growth with phenology, physiology and above-ground growth and

Responsible Editor: Bruno Rosado.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s11104-024-07155-y>.

F. Gning (✉) · A. Ræbild
Department of Geosciences and Natural Resource Management, University of Copenhagen, Rolighedsvej 23, 1958 Frederiksberg C, Denmark
e-mail: fag@ign.ku.dk

A. Ræbild
e-mail: are@ign.ku.dk

F. Gning · D. Marone
Centre National de Recherches Forestières/Institut Sénégalais de Recherches Agricoles (CNRF/ISRA), Route Des Pères Maristes, BP 2312, Dakar, Sénégal
e-mail: diatta.marone@isra.sn

C. Jourdan
UMR Eco&Sols, Univ Montpellier, CIRAD, INRAE, IRD, Montpellier SupAgro, Montpellier, France
e-mail: christophe.jourdan@cirad.fr

C. Jourdan
CIRAD, UMR Eco&Sols, 34398 Montpellier, France

C. Jourdan
LMI IESOL, Centre IRD-ISRA de Bel Air, Dakar, Sénégal

D. Ngom
Department of Plant Biology, Cheikh Anta Diop University, BP: 5005, Dakar Fann, Dakar, Senegal
e-mail: daouda11.ngom@ucad.edu.sn

provide an attempt to group dryzone tree species in functional types based on their root growth.

Keywords Drought stress · Phenology · Root traits · Root biomass allocation · Soil depth

Introduction

Water is a crucial requirement for plant growth and a principal determinant of vegetation distributions worldwide as it plays a central role in all physiological processes of the plant (Stephenson 1990). South of the Sahara broad vegetation bands shift from desert in the north to rainforest in the south, and plant species' distributions in this region are thus strongly correlated with availability of water (Magill et al. 2013). Plants require water for growth and except a small amount that may come from aboveground foliage, trunk and branches during raining events (e.g. Jensen et al. 2020), most of this water is taken up through the root system. Root systems thus play a critical role in determining the capacity of trees to use water (Landsberg 2000) and the ecological ranges of species. Coarse roots provide nutrients and water transports, stores carbohydrates and anchors the plant in the soil (Bayala et al. 2008; Bayala and Prieto 2020). Fine roots on the other hand represent the majority of length and surface area of the root system (Rewald et al. 2011) and are thought to be the most important organs for nutrient and water uptake and supply to the rest of the plant (Lu et al. 2022).

Root growth may be influenced by both biotic and environmental factors (Schenk and Jackson 2005). Plants vary in their strategy in response to different environmental conditions, and trees with deep root systems may thus have the opportunity to maintain high transpiration rates in zones with irregular rainfall particularly during the long dry season (Bleby et al. 2010). In these zones, characterized by low rainfall and where water is often not available in the upper layers, many tree species have developed deep root systems to reach the water table (Dupuy and Dreyfus 1992; Canadell et al. 1996; Alvarez-Flores et al. 2018). In a review of global rooting depths, Canadell et al. (1996) found that the average maximal rooting depth may reach more than 13 m depth in desert vegetation. In addition, species in drylands are generally thought to have a higher root/shoot ratio

to balance water availability with water use (Barbour 1973). Thus, especially under semi-arid conditions, water acquisition by roots is affected by the root morphology and root distribution, and it seems likely that trees may experience a strong selection pressure to optimize root development and water absorption capacity (Bayala and Prieto 2020).

Several studies found that the root growth is species-dependent and increases with soil temperature (Steinaker and Wilson 2008; McCormack et al. 2014). However, low soil water content limits the fine root growth, and the number of fine roots were found to increase following years with high precipitation (Comas et al. 2005; Withington et al. 2021). In addition, Radville et al. (2016) reported that the root phenology was controlled by the soil moisture in dry sites and that root production was highest during the rainy season. Extensive research has been performed to study the plant responses to drought stress and most of them show that water deficits reduce both shoot and root biomass (McDonald and Davies 1996; Canales et al. 2019; Álvarez et al. 2012; Faye et al. 2019; Wijewardan et al. 2019). However, while drought usually lead to a reduced root growth, the allometric patterns may change, leading the plant to allocate a larger proportion of the biomass to roots through a changed root: shoot ratio (Comas et al. 2013). Also the rooting depth may be affected, drought leading to a faster root growth at depth (Schenk and Jackson 2002b).

Trees in tropical evergreen forests tend to have shallow roots compared to trees in tropical deciduous forests (Canadell et al. 1996). In a study of temperate species, deciduous angiosperm species were found to have a greater root length per unit root mass (specific root length, SRL) than evergreen conifer species, this being due to their ability to build long and thin roots (Alvarez and Körner 2011). However, in a study of co-occurring temperate species, leaf habit was found to have less effect on the root production, being overshadowed by influences of soil humidity (Withington et al. 2021). This suggests that both environmental and intrinsic factors affect the root growth of the species (Dry et al. 2001). In a dry forest in Costa Rica, Smith-Martin et al. (2020) found that evergreen tree species had deeper roots than co-occurring deciduous species. It was suggested that evergreen species need deeper roots to access water during the dry season.

Unfortunately the rooting patterns of tree species in the Sahel are highly under-investigated. Previous

studies have improved our understanding of root development responses to drought, but most of them were carried out on crop species such as maize and millet (Debieu et al. 2018; Faye et al. 2019; Manju et al. 2019). Only few studies have been done on roots of agroforestry tree species, focusing mostly on root biomass and root distribution in relation with soil humidity (Logbo et al. 2013; Marone et al. 2017; Gning et al. 2023). Such studies have confirmed that the general link between humidity and timing of root growth also applies to trees (Logbo et al. 2011 and 2013; Abenavoli et al. 2016; Yandou et al. 2020).

Root systems of a number of important agroforestry tree species thus remain under-investigated, and little is known about root growth in relation to soil water content and distribution (Ma et al. 2013), which could otherwise help to understand the root spatial distribution in the field. Information on biomass allocation and rooting pattern of juvenile trees under drought stress is essential to understand not only how and in which ecosystems they establish, but also how trees may interact with associated crop species in agroforestry systems. In the current study, we address this knowledge gap by comparing root growth of seedlings of nine tree species with different phenology, exposed to different levels of water availability.

Our hypothesis was that root growth of agroforestry tree species differed between deciduous and evergreen species exposed to different levels of soil water. In particular, we expected evergreen species to develop deeper root systems than deciduous species under drought conditions, given their supposed larger need for water.

Materials and methods

Study site

The study was conducted at the nursery of Centre National de Recherches Forestières (CNRF) of the Institute Sénégalais des Recherches Agricoles (ISRA) in Dakar, Senegal, located at 14°43'32''(N) and 17° 26'12''(W). The experiment was performed from March 2019 to June 2020. The climate is tropical Sahelo-Sudanian characterized by two seasons, the rainy season ranging from approximately June to October and the dry season lasting 7–8 months. During the experiment, the rainfall (from July 2019

to June 2020) was 485 mm and the average monthly minimum and maximum air temperatures ranged from 18.3 and 25.8 °C in February 2019 to 26.2 and 31.1 °C in August 2020, respectively. The soil temperatures in the tubes at 10 cm depth were assessed with a Hobo Tidbit v.2 water temperature logger (Onset Computer Corporation, Bourne MA, US) and monthly averages varied between 24.4 °C (January) and 32.8 °C (July) (Fig. S1).

Seed sources and pretreatment

Seeds of nine species were procured from the CNRF/ISRA lab and at the Inspection Regionale des Eaux et Forêts de Dakar. We included five species that are considered deciduous in the Sahel (*Acacia senegal*, *Acacia nilotica*, *Adansonia digitata*, *Faidherbia albida*, *Sterculia setigera*) and four species that are normally evergreen (*Balanites aegyptiaca*, *Anacardium occidentale*, *Borassus akeassii* and *Vitellaria paradoxa*) (Table S1), selected for their multiple uses in providing food, fodder, wood and contributions to soil conservation in the Sahel (Frederiksen and Lawesson 1992; Tomlinson et al. 2013; Logbo et al. 2013). The species were sampled at different locations across Senegal and are all native to Senegal except *A. occidentale*, which comes from South America. Since the tree species were sampled at only one site per species our data necessarily include a confounding of provenance and species effects.

The desiccation sensitive seed of *V. paradoxa* and *B. akeassii* were sown without pretreatment. Seeds of the other species were soaked in a concentrated sulfuric acid solution (95%) for 15 min to 2 h, or in hot water, depending on species, to break seed dormancy. Then, they were washed with tap water during 10–15 min to remove any trace of acid and sowed in petri dishes for pre-germination in the laboratory to synchronize germination of all seeds before sowing. All seeds were sown in polythene bags in March 2019.

Experimental design and sampling

The investigations were conducted under semi-natural conditions exposed to full sunlight. The trial was established by digging holes of 2 m depth with an automated soil auger. PVC tubes with an inner diameter of 12.5 cm and a length of 2 m were inserted into

the hole to a depth of 1.90 m into the natural soil in order to prevent large temperature fluctuations that would have occurred if the tubes were aboveground. The tubes were filled with a homogeneous mixture applied in local nurseries, composed of 1/3 sand and 2/3 natural soil rich in organic material collected in a plantation of *Casuariana equisetifolia*, with a combined density of 0.43 g cm^{-3} . The lower ends of the tubes were closed with a plastic lid with small holes to allow drainage. Tubes were watered daily until the soil had sunk and the surface had reached a stable level.

One month after, in July 2019, all seedlings were transplanted into the PVC tubes. Care was taken not to damage the roots during the transplantation process. 225 plants were placed in a randomized complete block design with five blocks containing five seedlings of each of the nine species (45 seedlings per block). Within each block, the different plant species and treatments were fully randomized, and the number of plants was scaled to allow for three sampling periods and two treatments (see below). The plants were grown with 25 cm between plants and 50 cm between rows to avoid competition for light among plants. Until October 2019, all plants received natural rainfall supplemented by watering (1 L tap water) when the top soil was dry.

The first sampling took place on October 15, 2019, to characterize root depth of plants before treatments were installed, using one plant per species per block. Then, the two treatments were applied: Irrigation, where plants were watered every day with 1 L tap water, and drought, where plants used only the remaining soil water until the end of the experiment (meaning no irrigation from October 2019 to June 2020, where the first rains fell). The two treatments were each applied to two plants per species per block.

Eight months after transplanting, the second sampling was made (February 25 to March 10), sampling 90 plants (one plant from each combination of species and treatment in each block). The third and final sampling took place one year after planting (from June 29 to July 18) harvesting the remaining 90 plants (again representing one plant from each combination of species and treatment per block).

Root measurements

At the first sampling, tubes were dug out to observe the root architecture and to measure the total root

length of each plant. For each plant, the total root length of the taproot was measured with a ruler.

At the second and third sampling, the tubes were dug out and placed on a table. The tubes were cut vertically and the lengths of the roots were measured. The root columns (including soil) were sectioned into 20 cm lengths from the root collar until no root was found. Each sample was put on a plate with a label and two sieves with different mesh sizes (0.25 and 2 mm) were used to recover fine roots. Roots were then separated manually from the soil and organic particles such as dead roots, distinguished by their color and tendency to break. Each sample was placed on a fine-mesh sieve (0.2 mm) with a “root washing pump” to remove any remaining clods of soil from the roots. Roots obtained from the washing activity were wiped and laid on plastic paper, and the fresh weight determined to a precision of 0.01 g using a KERN EMB scale. Then each sample was put in a cooler and transported to the laboratory, where they were stored in a fridge at 6 °C until the scanning procedure.

Coarse (diameter > 1 cm) and medium roots (1 cm > diameter > 2 mm) were sorted and oven-dried over 48 h at 65 °C and weighed. Fine roots (diameter < 2 mm) were scanned with a scanner (Epson perfection V700 Photo, Japan), and images were analyzed using WinRHIZO software (Regent Instruments Inc. Regular version, 2012 b, Canada) to determine fine root length and average diameter. The fine roots were then oven-dried at 65 °C for 48 h to determine 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. The root: shoot ratio was calculated as root mass divided by shoot mass (stem and leaves).

Before analyses, data for the different soil sections were averaged into larger categories, covering the depths 0–40 cm, 40–80 cm, 80–120 cm, 120–160 and 160–200 cm.

The root growth for each treatment was determined for each combination of block, species and treatment by dividing the change in dry biomass or RLD by the length of the growth period (0–8 months and 8–12 months).

Aboveground measurements

Every month except March, plant height and basal diameter were measured and the number of leaves

counted. Phenology was observed on all parts from the start of the treatments in September (06–09–2019) until the end of the experiment and was assessed every week, based on nine scores (Table S2).

Predawn leaf water potential (LWP) was assessed three times in December and once in February on detached leaves from 3 to 7 h AM before sunrise, using a Pump-up Chamber Instrument (PMS Instrument Company, Albany, USA) on 120 plants. Except for *B. akeassii* all species were assessed, as this species had few leaves and the instrument was not suitable to measure its LWP. At the second and third sampling, the aboveground biomass (leaves and stems) were put in a paper bag, oven-dried for 72 h at 80 °C and weighed separately.

Statistical analysis

To analyze the data, we used linear mixed effects models:

$$Y_i = \alpha(\text{time}_i, \text{species}_j, \text{depth}_k, \text{treatment}_l) + A(\text{tree}_m) + B(\text{block}_n) + \text{error}$$

where α parametrize the fixed effects of Time, Species, Depth, and Treatment, and their interactions, A is a random effect of tree (included for variables measured repeatedly on the same tree such as height and phenology), and B is a random effect of block. Errors were assumed to be independent and following a normal distribution with an expected mean value of zero. Since four-factor interactions were not significant for any of the variables, these were removed from the model (Table 1).

All analyses were performed using the lme4 package in R (2020, version 3.6) and R Studio (version 1.2.5001).

Model assumptions of variance homogeneity and normality of residuals were evaluated by the residuals and quantile plots. For some variables, a cubic-root transformation (aboveground variables) or a logarithm (root traits) was used to achieve variance homogeneity and a valid model. The ggplot package in R was used to visualize the relationship between treatment, depth, species and time.

To evaluate the hypothesis of differences between evergreen and deciduous species in root traits, biomass allocation and leaf water potential, we extracted least square means for each combination of species and treatment from the model above. Then, for each variable in each treatment, we performed a t-test of

differences between evergreen and deciduous species. These analyses were based on the measurements at month 8, as at that time only few plants had reached the bottom of the tubes.

To estimate relations between traits across species, we performed a series of correlation analyses based on the results from samplings at 8 and 12 months. Correlations between traits were calculated for each treatment at each sampling time, using estimated marginal means for each species from the model above. For this analysis, we converted the 9-point leaf phenology scale to a scale expressing whether the tree had living leaves or not (Table S2) and calculating the mean number of trees having living leaves. To visualize correlations among variables we conducted a principal component analysis (PCA) on the same variables at month 8 separately for the two treatments (Fig. 5).

Finally, we performed canonical correlation analyses of root traits in order to study how species grouped in the multivariate space. Canonical correlation analyses remove collinearity among variables (Chatfield and Collins 1980; Sharma 1996). These analyses were performed separately for each combination of treatment (irrigation, drought) and the two times of sampling (month 8, 12). The variables root biomass, root diameter, SRL and RLD were log transformed and included as dependent variables, while the independent variables were species, blocks and depths. Mean values of the species were plotted against the first two canonical variates together with the canonical directions.

Results

Seedlings subjected to drought and irrigation, showed strong differences among tree species for almost all variables (Table 1). Furthermore, the numerous interactions demonstrated that treatments had different impacts on the species across time. We observed 58 dead plants in six species at the end of the experiment (Table 2). The evergreen species *A. occidentale*, *V. paradoxa* and *B. akeassii* exhibited the highest mortality rate, while few trees died in the remaining species. This means that the numbers of replicates for these species were reduced compared to species without mortality.

Table 1 Results of analyses of variance for the nine-tree species for model 1, and tests for differences between deciduous and evergreen species at month 8

Variables	Tests from model 1		P-values from tests of differences between deciduous and evergreen species at month 8	
	Factors	P-value	Irrigated	Drought
Root variables				
Maximum depth ¹	Time*Species*Treatment	0.0051**	0.038*	0.140
Root biomass ²	Time*Species*Treatment	0.0023**	0.096	0.023*
	Species*Depth*Treatment	1.8e-05***		
Specific root length ²	Species*Depth*Treatment	0.013*	0.640	0.595
Root length density ²	Time*Species*Treatment	0.0007 ***	0.049*	0.023*
	Species*Depth*Treatment	0.0017***		
	Species*Depth*Treatment	0.001***		
Average diameter	Time*Species*Depth	1.6e-11 ***	0.724	0.270
	Time*Species*Treatment	1.1e-10 ***		
	Species*Depth*Treatment	0.002 **		
Fine root growth	Period*Species	0.032 *	0.065	0.441
	Period*Depth	0.010 *		
	Period*Treatment	0.015 *		
RLD growth	Period*Species*Depth	0.00023 ***	0.037	0.717
Aboveground variables				
Leaf number ²	Species*Date*Treatment	2.2e-16 ***		
Phenology score	Species*Date	2.2e-16 ***		
	Species*Treatment	2.619e-06 ***		
	Date*Treatment	2.2e-16 ***		
	Species*Treatment	6.7e-06 ***	0.551	0.875
Leaf Water Potential ²	Date*Treatment	0.021 *		
	Species*Date	2.2e-16 ***		
Height	Species*Treatment	0.007 **		
	Date*Treatment	2.8e-08 ***		
	Species*Date	2.2e-16 ***		
Diameter ²	Species*Treatment	0.0089 **		
	Date*Treatment	2.2e-16 ***		
	Species*Date	2.2e-16 ***		
Biomass allocation at month 12				
Leaf biomass ²	Species	1.2e-05 ***	0.448	0.202
	Treatment	3.7e-05 ***		
Stem biomass ²	Species	3.9e-09 ***	0.114	0.926
	Treatment	0.0001 ***		
Root biomass ²	Species	1.1e-08 ***	0.006**	0.055
	Treatment	0.014*		
Root:shoot ratio ²	Species	0.0006***	0.142	0.086
	Treatment	0.0243 *		
Biomass total (Plant mass) ²	Species	1.8e-09 ***	0.052	0.153
	Treatment	7.2e-05 ***		

¹Log transformation. ²Cubic root transformation

Only the highest order significant interactions from model 1 are shown (see statistics). Asterisks indicate the levels of significance. * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

Table 2 Leaf water potential (LWP) and mortality (at the end of the experiment) per species and treatment (LWP)

Variables	Months	Species	Deciduous							Evergreen			
			<i>A. senegal</i>	<i>A. nilotica</i>	<i>F. albida</i>	<i>A. digitata</i>	<i>S. setigera</i>	<i>B. aegyptiaca</i>	<i>A. occidentale</i>	<i>V. paradoxa</i>	<i>B. akeassii</i>		
LWP(MPa)	Irrigation	Dec	-0.7 ± 0.4	-0.9 ± 0.4	-0.4 ± 0.4	-0.3 ± 0.4	-0.3 ± 0.4	-0.8 ± 0.4	-0.6 ± 0.4	-0.4 ± 0.4	n.a		
		Feb	-1.4 ± 0.5	-1.4 ± 0.5	-0.8 ± 0.5	-0.7 ± 0.5	-0.4 ± 0.5	-1.0 ± 0.5	-0.8 ± 0.5	-0.5 ± 0.5	n.a		
Drought	Dec	Dec	-1.6 ± 0.4	-2.1 ± 0.4	-0.7 ± 0.4	-0.4 ± 0.4	-0.4 ± 0.4	-1.1 ± 0.4	-0.6 ± 0.4	-0.8 ± 0.5	n.a		
		Feb	-2.1 ± 0.5	-2.1 ± 0.5	-1.0 ± 0.5	-0.5 ± 0.5	-0.6 ± 0.5	-1.9 ± 0.5	-0.6 ± 0.5	-1.0 ± 0.5	n.a		
Mortality(%)	Irrigation		0	0	0	7	7	7	47	20	7		
		Drought	0	0	0	0	0	0	27	27	17		

Values represent the least square means ± standard errors (S.E.) of LWP of the species per treatment. n.a.: non-available

Rooting depth

In all tree species, some individuals grew to the end of the tube, reaching the maximum possible rooting depth of 2 m after 12 months of growth (Figs. 1 and S2). Interactions between Time, Species and Treatment showed that the species had different root development over time (Table 1). Root growth at depth was favored by the drought treatment, and in this treatment, *A. senegal*, *F. albida* and *B. aegyptiaca* reached the maximum depth of the tube already at 8 months after transplanting (Fig. 1). By the end of the experiment at month 12, all species had individuals with roots reaching 2 m depth in the drought treatment, and the experiment can thus not estimate the true maximum rooting depth. Species like *A. digitata*, *S. setigera* and *A. occidentale* had smaller rooting depths under irrigated conditions compared to the *Acacia* species, which showed deeper root growth (Fig. 1 and S2).

T-tests of differences between deciduous and evergreen species showed significant differences in root depth at month 8 for the irrigated plants (Table 1), but contrary to our expectations deciduous species had the deepest roots (Fig. 2).

Root traits

Root biomass was highest in the upper soil layers. However, fine root growth showed significant interactions between period, species and treatment, and between species, depth and treatment (Table 1, Fig. 3, Fig. S2). From month 0–8, root growth tended to be similar for the irrigated and drought treatments. From month 8–12, as drought stress continued, there were large differences between the two treatments, manifested differently in the species. Drought stressed plants had limited root growth, except in the case of *A. occidentale* where substantial growth was observed below 120 cm. When irrigated, *Acacia* species, *F. albida* and *B. aegyptiaca* displayed large growth in the deeper soil layers, while species such as *A. digitata*, *S. setigera*, *V. paradoxa* and *B. akeassii* had large growth near the surface. Negative growth (net loss of roots) was observed for some species, especially *A. senegal* and *S. setigera* from months 8–12 (Fig. 3, 4). Deep root growth was observed in *B. aegyptiaca* and the leguminous species *A. senegal*, *A. nilotica* and *F. albida* in the irrigated treatment, and

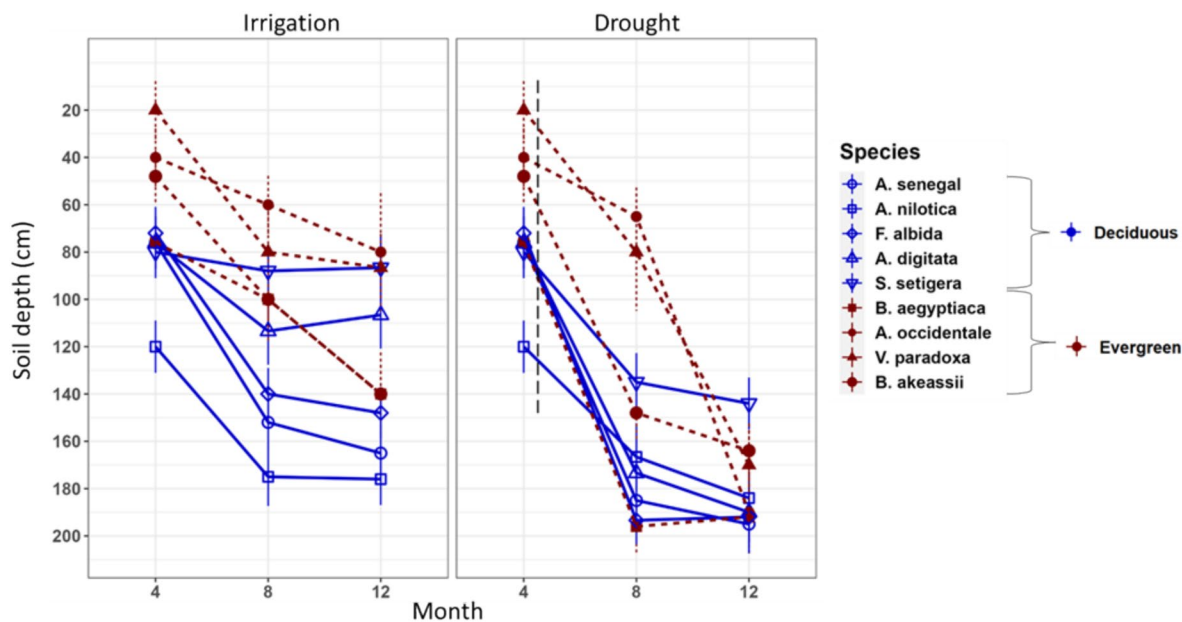


Fig. 1 Average maximum rooting depth of 5 deciduous (blue, solid lines, open symbols) and 4 evergreen (red, dashed lines, closed symbols) tree species across different treatments and harvest times. Drought treatments were initiated immediately

after the harvest at month 4, symbolized by the dashed vertical black line. Note that already at month 8, roots of some species had reached the bottom of the tubes at 2 m, and the full rooting depth can thus not be evaluated

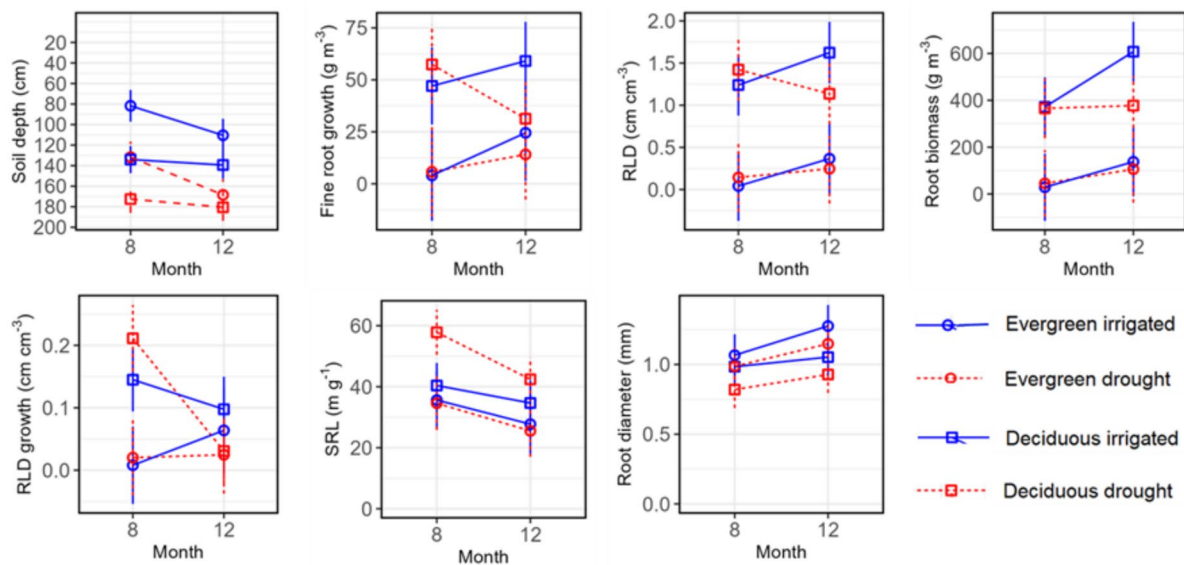


Fig. 2 Test of evergreen (square symbols) and deciduous (circle symbols) across different treatments, drought (red, dashed lines,) and irrigated (blue, solid lines) and harvest times. Error bars denote S.E. ($n=5$)

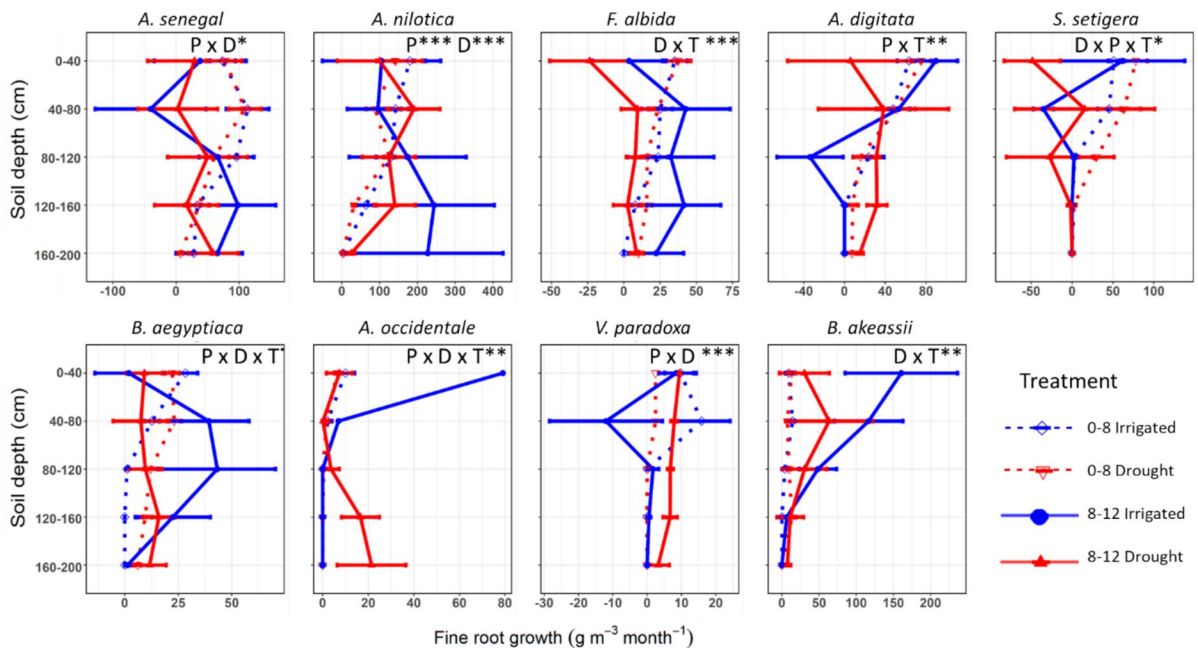


Fig. 3 Vertical distribution of fine root growth of 5 deciduous (top) and 4 evergreen (bottom) tree species harvested after 8 months (0–8 months, dashed lines) and 12 months (8–12 months, solid lines) of cultivation under irrigation (blue) and drought (red) treatments. Inserted text in the upper right

of each graph indicates the significance of the highest order significant interaction from a mixed model analysis within species: D (Depth), P (Period: 0–8 or 8–12) and T (Treatment) correspond to the three factors. Significance levels: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. Error bars indicate \pm S.E. ($n = 5$)

in drought stressed *A. digitata*, *A. occidentale* and *V. paradoxa*.

Root biomass, fine root growth and RLD were correlated among species (Fig. 5, Fig. S7–S10). Hence, the growth of RLD showed a close match with the root biomass growth, and also showed approximately the same patterns across depths. These three variables tended to be higher in deciduous species than in evergreen species (Fig. 2). The formal t-tests confirmed this, as there were significant differences between evergreen and deciduous species for root biomass in the drought treatment, RLD in both treatments, and RLD growth in the irrigated treatment (Table 1).

Among species, SRL showed a negative correlation with root diameter at month 8 (Fig. 5, Fig. S7–8), and was correlated to RLD and RLD growth at month 12 in the irrigated treatment (Fig. S9). As expected, SRL increased with depth for most species. Effects of treatments varied among species, with *A. nilotica* and *S. setigera* having large SRL in the drought treatment, while *F. albida*, *A. digitata* and *B. aegyptiaca* had larger SRL in the irrigated treatment (Fig. S2). However, deciduous and evergreen species did not

vary systematically in SRL as the t-tests showed no significant differences (Table 1, Fig. 2).

Leaf phenology

Frequencies of the nine dominant phenophases varied significantly over time with different patterns among the tree species (Table 1, Fig. 6). In the drought treatment, number of leaves was lower compared to the irrigated treatment for all the tree species except *A. occidentale* and *V. paradoxa*, which seemed to be unaffected by the treatments, and *B. akeassii*, where drought treated plants had a higher final number of leaves. Under irrigation, even the species that we considered to be deciduous kept leaves throughout the experiment, albeit with a large proportion of senescent leaves (Fig. S4). Many trees had fully mature leaves from November to December. After this period, there was a progressive phase of yellowing or loss of leaves, until at the end of the experiment most of the trees showed signs of leaf senescence. This was pronounced in the drought treatment where around

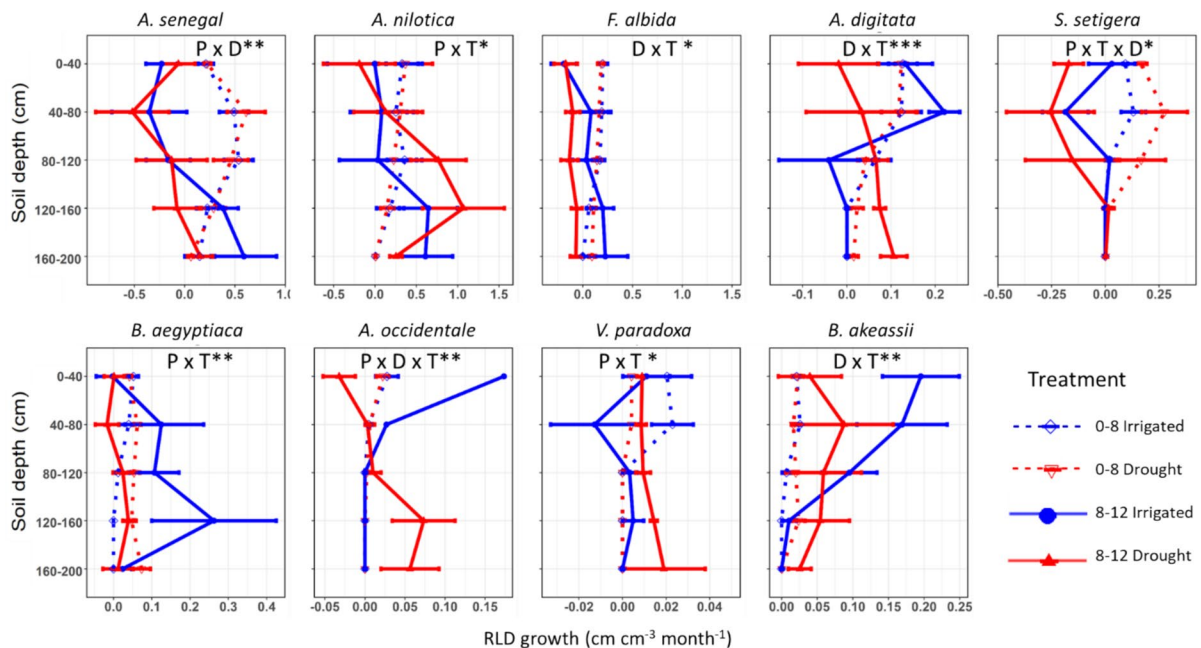


Fig. 4 Vertical distribution of RLD growth of 5 deciduous (top) and 4 evergreen (bottom) tree species harvested after 8 months (0–8 months, dashed lines) and 12 months (8–12 months, solid lines) of cultivation under irrigation (blue) and drought (red) treatments. Inserted text in the upper right

of each graph indicates the significance of the highest order significant interaction from a mixed model analysis within species: D (Depth), P (Period: 0–8 or 8–12) and T (Treatment) correspond to the three factors. Significance levels: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. Error bars indicate \pm S.E. ($n = 5$)

50% of the trees had brown or no leaves at the end of the experiment.

Assessed as presence or absence of living leaves, leaf phenology only showed weak and non-significant correlations with root traits (Fig. S7–S10).

Leaf water potential (LWP)

Treatments had different effects on LWP in the species (Table 1). In the drought treatment, *A. senegal*, *A. nilotica* and *B. aegyptiaca* showed low LWP of ca. -2 MPa, with less extreme values observed for the remaining species. Plants in the irrigation treatment had higher LWP (Table 2), but especially *A. digitata*, *S. setigera* and *A. occidentale* showed limited differences in LWP between treatments (Table 2).

Differences between deciduous and evergreen species were not significant (Table 1). However, in the irrigated treatment, LWP showed a positive correlation with maximum depth, and negative correlations with root biomass, fine root growth, RLD and RLD growth. The negative correlations between LWP and maximum root depth indicates that species with large

and deep root systems also had low water potential. The same trends, but non-significant, were seen in the drought treatment (Figs. S7 and S8).

Growth and biomass allocation

The treatments affected height growth of the species differently as indicated by the significant interactions between species and treatment (Table 1). The height tended to increase with time for irrigated plants of the species *A. senegal*, *A. nilotica*, *A. digitata* and *F. albida* (Fig. S5). However, for the deciduous species in the drought treatment, the height increased until November and then decreased with time due to die-back of shoots (Fig. S5). For the evergreen species, there was little or no growth from October to the end of the experiment in either treatment and only minor differences between treatments. Results for stem base diameter were broadly similar to those of the height. Compared to drought, the irrigation treatments resulted in increased diameters through time. *A. digitata* and *S. setigera* had a fast stem diameter growth in

Fig. 5 Loading plots from principle component analyses of root variables and leaf numbers for the nine tree species at month 8 for the two treatments. Blue color denote irrigated plants, red denote drought

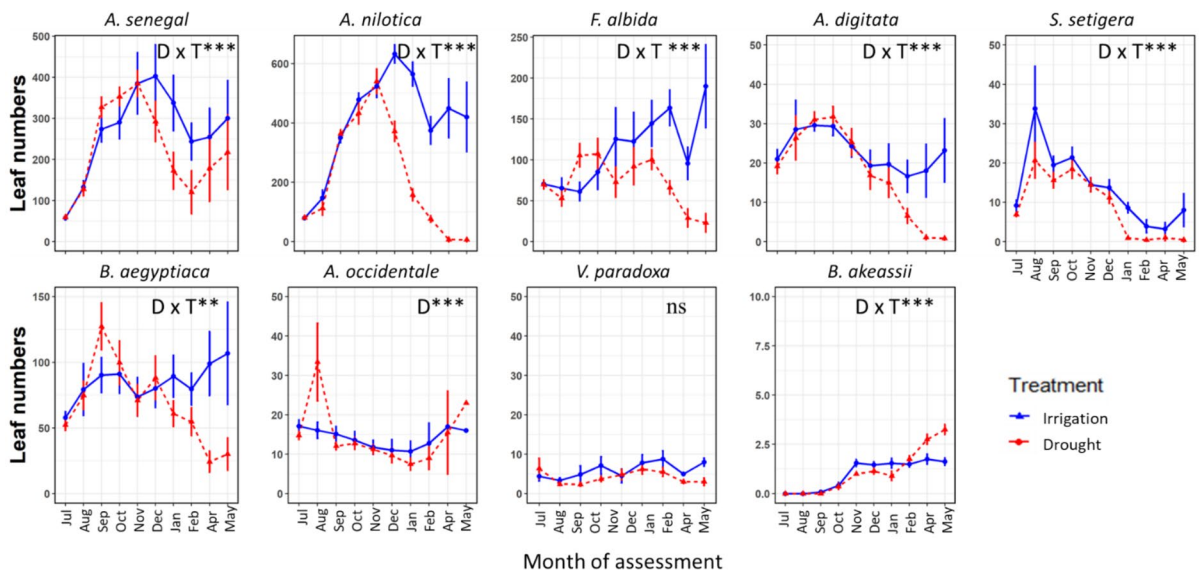
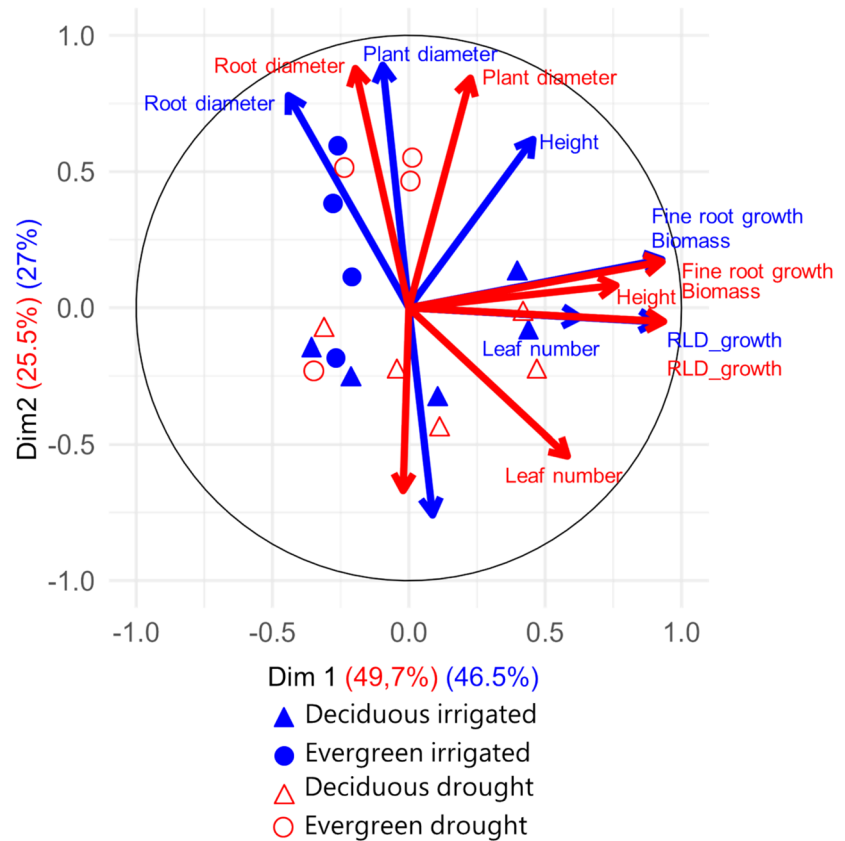


Fig. 6 Mean values of leaf numbers for seedlings of 5 deciduous (upper panels) and 4 evergreen (lower panels) tree species across different treatments and measurement times. Error bars denote S.E. $n=5$. Inserted text in the upper right of each graph indicates the significance of the highest order significant inter-

action from a mixed model analysis within species: D (Date) and T (Treatment) correspond to the two factors. Significance levels: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, ns: non-significant

both treatments whereas *V. paradoxa* tended to grow slowly throughout the experiment (Fig. S6).

Height growth showed a negative correlation with root depth, taller species having deeper roots, but was weakly and positively correlated with root growth and RLD (Figs. S7–S10). Except for a correlation with root diameter at month 12 in the irrigated treatment, plant diameter was not correlated to the other variables.

Seedlings tended to have more leaf, stem and root biomass under the irrigation treatment by comparison to the drought treatment, and the biomass of leaves, stems and roots after 12 months varied significantly with the species and the treatments (Table 1). However, species did not react differently to treatments as indicated by the absence of

interactions between species and treatments. On the other hand, according to the statistical analysis, the root:shoot ratio changed in response to stress, as the treatment effects were significant. Likewise, differences between species were significant, with *S. setigera* having high root:shoot ratios and *A. nilotica*, *A. occidentale* and *B. akeassii* having low ratios (Fig. 7). The total biomass was significantly lower in evergreen than in deciduous species, but only in the irrigation treatment. Especially the N-fixing *A. nilotica* and *A. senegal* were fast growing, while *A. occidentale* and *V. paradoxa* had slow growth. However, the differences between evergreen and deciduous species with respect to root:shoot ratio were non-significant (Table 1).

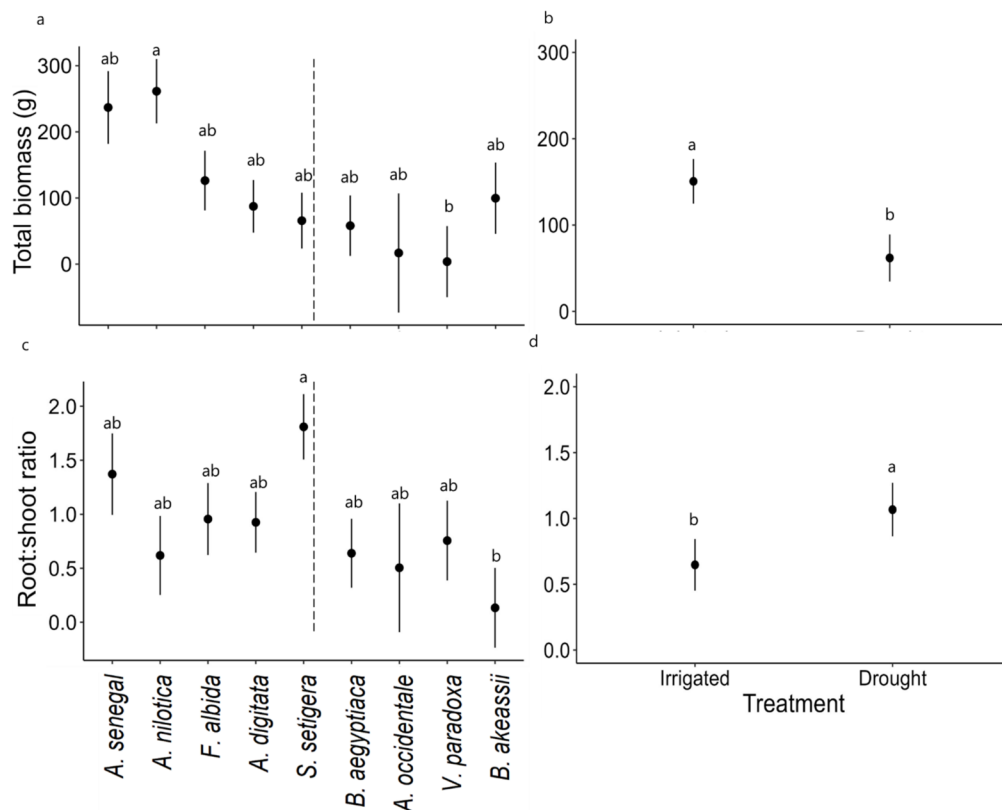


Fig. 7 Total biomass (a, b) and root:shoot ratio (c, d) based on dry weight of seedlings after 12 months of growth. a) and c) Mean values of five deciduous (left) and four evergreen (right) tree species. b) and d) Mean values of treatments. Inter-

actions between species and treatments were non-significant. Deciduous and evergreen are separated by the dashed vertical black line. Error bars denote S.E. ($n=5$)

Canonical variate analysis

Our analysis of canonical variates of root traits, despite being conducted separately for each treatment at the two sampling times (months 8 and 12), showed that the positions of species were rather stable in the two dimensions spanned by the two first canonical variates (Fig. S11). The species were located in clusters with *A. nilotica* and to a lesser extent *A. senegal* being associated with high root biomass, while *F. albida*, *B. aegyptiaca* and to some extent *A. senegal* were associated with high SRL. The remaining species tended to be located in the opposite direction, thus associated with lower root biomass and lower SRL. Although the evergreen species were part of this last group, there was no clear separation between evergreen and deciduous species.

Discussion

Our hypothesis of evergreen species having deeper root systems than deciduous species was rejected, as deciduous species grew faster at depth and tended to have higher root biomass and root length density than evergreen species.

Smith-Martin et al. (2020) showed that evergreen species had deep roots allowing them to access water, suggesting why these species are able to maintain foliage during the dry seasons. This was not the case for the evergreen species included here as the evergreen species tended to have shallow root systems especially when irrigated (Table 1, Fig. 1).

However, the discrimination between deciduous and evergreen species may not be entirely clear. In the deciduous *Tectona grandis*, deep rooting allows trees to extract water and maintain leaves during drought periods in the rainy season, and at the start of the dry season (Clément et al. 2019). Our results showed that water availability affect both leaf longevity and rooting depth. In the irrigation treatment, species normally considered as deciduous such as *A. nilotica* and *A. digitata* kept green leaves throughout the dry season, whereas *B. aegyptiaca* and *A. occidentale* that were supposed to be evergreen did not always carry leaves when subjected to drought stress. It has previously been shown that e.g. *A. digitata* can change to an evergreen habit when water is sufficient (Korbo et al. 2013). Even *F. albida* seedlings in the

non-irrigated treatment lost leaves during the dry season by contrast with what is commonly observed on adult trees that shed their leaves during the rainy season (Roupsard et al. 1999).

Overall, assuming a connection between leaf habit and rooting depth seems to be too simplistic for the species involved in this study. Instead, root growth may depend on other factors that we discuss below.

Root growth dynamics and biomass distribution

Tree species in drylands characterized by low and irregular rainfall regimes frequently develop deep root systems, which seems to be a key root trait for optimizing water uptake (Reader et al. 1993). Precipitation and high soil humidity increases the production of fine roots of savannas species (Kulmatiski et al. 2017; Bazié et al. 2019; Freycon et al. 2015). Fast root growth is not uncommon (Laminou Manzo et al. 2009), but is here shown for a range of dry zone agroforestry tree species especially in the group of deciduous species. Plants under continuous irrigation produced more biomass, but the allocation pattern to organs (root: shoot ratio) was higher under drought treatment (Fig. 6).

We found important differences in responses to water treatments among species (Table 1). Root traits were markedly affected by treatments as rooting depth in most species increased in the drought treatment (Fig. 1). Furthermore, the rooting profile changed in species that were shallow rooted under irrigated conditions but deep rooted when subjected to drought (*A. digitata*, *A. occidentale*, *S. setigera* and *V. paradoxa*). This facultative deep rooting may explain the high rates of dry season transpiration observed in *V. paradoxa* (Bazié et al. 2018). The deep rooting profiles found in the non-irrigated treatments may be triggered by the low availability of water near the soil surface (Hopmans and Bristow 2002), and are likely crucial for their ability to grow in the dry zones (Chiatante et al. 2001; Schenk and Jackson 2002a, 2005). Also, Lobgo et al. (2011) showed that tree species grow deep roots to catch the deep water resources in the soil under water deficit. On the other hand, *Acacia* species seemed relatively insensitive to soil moisture in this character, developing a deep root system irrespective of treatments.

SRL appeared to increase in response to drought in *A. nilotica* and *S. setigera* while decreasing in *B.*

aegyptiaca, but was otherwise only showing few effects of treatments. This may be affected by our methodology, as we applied a uniform diameter cutoff across all species, using a traditional 2 mm threshold for fine roots (e.g. Ostonen et al. 2011; Lynch et al. 2013; Bayala and Prieto 2020). This is advantageous because of a speedy processing of large amounts of roots. However, the diameter threshold at which roots shift from mainly absorptive to transport roles vary between species (McCormack et al. 2015), meaning that a 2 mm threshold as applied in our study cannot be used to compare the root physiology of the species. For this, detailed studies using order-based or functional classifications of roots may be better, and would be especially interesting in agroforestry systems, where these species often share resources with crop species (McCormack et al. 2015). Since absorptive fine roots tend to have a faster turn-over than fine transport roles, this also plays a role for estimates of carbon turnover and may explain why species with large SRL do not necessarily grow faster than species with thicker roots (Weemstra et al. 2020).

Root systems and leaf water potentials

The Pearson's correlations and the canonical correlation analysis indicated a co-variation in root biomass and RLD across species. SRL and root diameter were negatively correlated, and otherwise not strongly linked to other parameters (Fig. S7–S10). As appears from the canonical correlation analysis, the species can thus be characterized on the basis of whether they have high/low root biomass and RLD, and high/low SRL (but note the limitations on the SRL mentioned above).

Species with high root biomass were *A. nilotica* and *A. senegal*, and low root biomass was seen in a group of species including *B. akeassii*, *A. occidentale* and *V. paradoxa*. In the scale of SRL, *F. albida*, *B. aegyptiaca*, and *A. senegal* showed high values (and low root diameters), while species such as *B. akeassii* and *A. digitata* scored low.

An alternative interpretation of the data seems to be in relation to the water conservation status of the species. Especially the *Acacia* species and *B. aegyptiaca* tended to show strong reductions in predawn water potential under drought (Table 2) and developed deep, fibrous roots. Correlations indicated that low LWP was associated with deep rooting, and with

high root biomass and RLD (Fig. S7). This may be related to the concept of isohydry vs. anisohydry (e.g. Klein 2014), and we suggest combined measurements of predawn and midday water potentials of these species to achieve a better understanding of their water economy (Yi et al. 2017).

Tolerance of low water potentials is one adaptation to arid conditions, allowing *Acacia* species to keep their stomata open and to maintain carbon assimilation rates despite low soil water content (O'Grady et al. 2009). *Acacia* and *Faidherbia* species have the capacity to fix nitrogen (Njiti and Galiana 1996; Founoune et al. 2002), and therefore may have better access to N and faster root growth. Querejeta et al. (2022) found that N-fixing species in the Sahel (including *A. senegal*, *A. nilotica* and *F. albida*) had lower water potentials than non-N-fixing species. They hypothesized that this was because of a larger accumulation of N-containing osmolytes giving them larger tolerance to desiccation. Combined with larger rooting depths as observed in our study, these species may be at an advantage under dry conditions.

Adansonia digitata, *S. setigera* and *A. occidentale*, on the other hand, appeared to be water conserving with high water potentials irrespective of treatments. Conservation of water inside the plant such as is observed in *Adansonia* may be another strategy to survive long dry periods (Chapotin et al. 2006). Thus, the smaller rooting depth in *A. digitata* and *S. setigera* may be related to the ability to store water in their tissues, making it less important to attract water from deeper soil layers (Birnbaum 2012). These deciduous species have hypertrophic root systems (tuber-like roots) as seedlings, allowing them to store water and nutrients in their swollen roots, keeping them alive during dry and unfavorable conditions (Ouédraogo and Thiombiano 2012).

Practical implications for afforestation and agroforestry programs

Deep roots play a crucial role for water flux in dry ecosystems, and through the mechanism of hydraulic redistribution, trees may transport water from deep and wet soil horizons and to dryer parts of the soil, for example shallow horizons (Dawson 1993; Bayala and Prieto 2020). Thereby, deep-rooted tree species may provide water for associated shallow-rooted species without access to the water table. Such capability

may provide a key role for savanna tree species in agroforestry systems. This study showed deep root development of all species in the non-irrigated treatment (Fig. 1), suggesting that they could potentially redistribute water from deeper soil layers towards the surface, depending on their fine root traits. Hydraulic redistribution was demonstrated in *V. paradoxa* (Bayala et al. 2008) but whether the species studied here differ in their capability for hydraulic redistribution remains to be seen. For example, it can be speculated that water-conserving species would tend to limit diffusion of water into the soil in comparison with species that have a profuse water use. On the other hand, species with low predawn water potentials may dry out the soil to a larger degree and could limit the growth of associated non-perennials. This has a profound influence on the way we should think of agroforestry practices.

A decrease of crop yields under tree canopies was shown for *A. digitata* (Sanou et al. 2012), *S. setigera* (Bakhoun et al. 2001) and *V. paradoxa* (Bayala et al. 2002), suggesting that water conserving species are not especially beneficial for crop species. However, according to the authors, reductions of crop yields may also be related to the effects of their excessive shade, and competition for nutrients. On the other hand, there is evidence of increased crop yields under *F. albida* and *A. senegal* canopies that form common components of agroforestry system in the Sahel (Fadl 2013; Roupsard et al. 2020). These species tended to show depletion of soil water in our experiment, but on the other hand are also known for their ability to fix atmospheric nitrogen, to provide medium shade and for their deep root systems reaching the water table (Dupuy and Dreyfus 1992). However, for *A. nilotica*, which seems to be water depleting, Pandey et al. (2000) observed a lower crop yield under the tree and an increased yield with distance from the tree. Clearly, relationships between rooting architecture of trees, water use and associations with crop species merit additional studies to understand the performance of different species in the agroforestry systems.

Limits of the methods

Root growth in the study was fast, with some species extending to a depth below 1 m only four months after planting, and 2 m after eight months. The cultivation

of plants in long tubes allowed the monitoring of root morphology, shoot traits and leaf phenology through time, and showed that dug-down PVC tubes may be useful as a technique for high throughput root phenotyping (Shashidhar et al. 2012). In spite of the modification of root geometry, obliging them to grow vertically instead of laterally, this approach might contribute to decipher the response of water stress on the whole root system. Limitations of the approach are actually due to the fast root growth meaning that some plants quickly reached the bottom of the tubes, failing to reveal the maximum of their root growth potential. This may have been influenced by the low density of the mixed organic and sandy soil, giving a porous and well-aerated soil allowing fast root growth. Also, the tubes forced the species to grow vertically, modifying the root architecture of species like *A. digitata*, *S. setigera* and *B. akeassii* that tended to have spiraling and shallow roots. By restricting the root horizontal growth, the volume of soil exploited by the trees has been limited, which could make the responses to drought more severe. Nevertheless, the approach has several advantages over the traditional pot cultivation, because root growth is relatively unrestricted at least in one direction, and temperatures in the tubes more closely resemble the natural soil temperatures (Fig. S1). Still, there is a huge need to expand studies of these important species to larger trees in their natural environments.

Conclusion

Our data provide an overview on the strategy of root growth for nine rarely studied agroforestry tree species under irrigation and water depletion and show the first results on biomass partitioning between juvenile evergreen and deciduous savanna tree species under semi-natural conditions in the Sahel. Overall, our study indicates that drought leads to reduction of root and shoot biomass and deep root growth, which is a mechanism to tolerate water deficits in arid environments. Deciduous species had faster root growth at depth than evergreen species. The LWP measurements suggested water-conserving behavior of *A. digitata*, *A. occidentale*, *S. setigera* and *V. paradoxa* and water spending behavior of *B. aegyptiaca*, *F. albida* and *Acacia* species. Because they tend to develop deep root systems, the latter group may

have an advantage under long periods of drought. The enhancement of deep root growth under drought stress emphasizes that root plasticity is an important characteristic for plant growth and survival in arid ecosystems. However, further investigations combining physiological measurements with root phenotyping and studies on larger trees are needed to confirm our suggestions about the adaptive patterns of these dry zone species.

Acknowledgements We are grateful to Marietou Sankhare for conducting the experiment at ISRA/CNRF when FG was absent. Access to root scanner and WinRHIZO software at LCM laboratory was generously granted by director Dr. Saliou Fall, Alexandre Grondin, Ndiampaly Diouf, Mr. Paul Diouf and colleagues. We thank Dr. Cheikh O. Samb for assistance during the setup of the experiment, and Dr. Bo Markussen for help on statistical analyses. Finally, we thank the editor and the anonymous reviewers for their constructive comments that improved the manuscript considerably. The work was supported by the Islamic Development Bank (IDB), grant no. 600035540 and by the University of Copenhagen.

Authors' contribution All authors contributed to the study conception and design. Material preparation and data collection were performed by Fatou Gning, while data analysis was conducted by Fatou Gning in collaboration with Anders Ræbild and Christophe Jourdan. The first draft of the manuscript was written by Fatou Gning. All authors commented on previous versions of the manuscript, and approved the final manuscript.

Funding Open access funding provided by Copenhagen University.

Data Availability Data raw and semi-processed data supporting the findings of this study will be available from the corresponding author.

Declarations

Financial interests The authors declare they have no financial interests that could influence the conclusions of the paper.

Open Access This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit <http://creativecommons.org/licenses/by/4.0/>.

References

- Abenavoli MR, Leone M, Sunseri F, Bacchi M, Sorgonà A (2016) Root phenotyping for drought tolerance in bean landraces from Calabria (Italy). *J Agron Crops Sci* 202(1):1–12. <https://doi.org/10.1111/jac.12124>
- Álvarez S, Castillo M, Acosta JR, Navarro A, Sánchez-Blanco MJ (2012) Photosynthetic response, biomass distribution and water status changes in *Rhamnus alaternus* plants during drought. *Acta Hort* 937:853–860
- Alvarez FR, Nguyen TN, Peredo PS, Joffre R, Winkel T (2018) Rooting plasticity in wild and cultivated Andean *Chenopodium* species under soil water deficit. *Plant Soil* 425:479–492. <https://doi.org/10.1007/s11104-018-3588-7>
- Alvarez-Uria P, Körner K (2011) Fine root traits in adult trees of evergreen and deciduous taxa from low and high elevation in the Alps. *Alp Botany* 121:107–112. <https://doi.org/10.1007/s00035-011-0092-6>
- Bakhoun C, Samba NAS, Ndour B (2001) *Sterculia setigera* del: effet sur les cultures. *Ann Forest Sci* 58(2001):207–215
- Barbour MG (1973) Desert dogma reexamined: root/shoot productivity and plant spacing. *Am Midl Nat* 89:41–57
- Bayala J, Prieto I (2020) Water acquisition, sharing and redistribution by roots: applications to agroforestry systems. *Plant Soil*. <https://doi.org/10.1007/s11104-019-04173-z>
- Bayala J, Teklehaimanot Z, Ouédraogo SJ (2002) Millet production under crown pruned trees of *Parkia biglobosa* and *Vitellaria paradoxa* in Burkina Faso. *Agrofor Syst* 54:203–214
- Bayala J, Heng LK, van Noordwijk M, Ouedraogo SJ (2008) Hydraulic redistribution study in two native tree species of agroforestry parklands of West African dry savanna. *Acta Oecol* 34(3):370–378
- Bazié HR, Sanou J, Bayala J, Bargués-Tobella A, Zombré G, Ilstedt U (2018) Temporal variations in transpiration of *Vitellaria paradoxa* in West African agroforestry parklands. *Agrofor Syst* 92:1673–1686. <https://doi.org/10.1007/s10457-017-0115-4>
- Bazié P, Ky-Dembele C, Jourdan C, Rouspard O, Zombré G, Bayala J (2019) Synchrony in the phenologies of fine roots and leaves of *Vitellaria paradoxa* in different land uses of Burkina Faso. *Agrofor Syst* 93:449–460. <https://doi.org/10.1007/s10457-017-0135-0>
- Birnbaum P (2012) Biodiversité au Sahel. Les forêts du Mali. Édition Quae CIRAD, IFEMER, INRA, IRSTEA, France. 208 p.
- Bleby TM, Mcelrone AJ, Jackson RB (2010) Water uptake and hydraulic redistribution across large woody root systems to 20 m depth. *Plant Cell Environ* 33(12):2132–2148. <https://doi.org/10.1111/j1365-3040201002212x>
- Canadell J, Jackson RB, Ehleringer JB, Mooney HA, Sala OE, Schulze ED (1996) Maximum rooting depth of vegetation types at the global scale. *Oecologia* 108:583–595. <https://doi.org/10.1007/BF00329030>
- Canales FJ, Nagel KA, Müller C, Rispaill N, Prats E (2019) Deciphering root architectural traits involved to cope with water deficit in oat. *Front Plant Sci* 10:1558. <https://doi.org/10.3389/fpls.2019.01558>
- 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(9):1251–1264. <https://doi.org/10.3732/ajb.93.9.1251>
- Chatfield C, Collins AJ (1980) Introduction to multivariate statistics. Chapman and Hall Ltd, London, p 246
- Chiatante D, Scippa GS, Di Iorio A, Sarnataro M (2001) The stability of trees growing on slope depends upon a particular conformational structure imposed by mechanical stress in their root system. Proceedings of the International Conference: Forest Research: a challenge for an integrated European approach, Thessaloniki, Greece, 477–482
- Clément C, Pierret A, Maeght JL, Hartmann C, Xayyathip K, Soullieuth B, Sounyafong P, Latsachack K, Thammahacksa C, Sengtaheuanghoung O (2019) Linking tree-rooting profiles to leaf phenology: a first attempt on *Tectona grandis* Linn F. *Trees* 33:1491–1504. <https://doi.org/10.1007/s00468-019-01876-9>
- Comas LH, Anderson LJ, Dunst RM, Lakso AN, Eissenstat DM (2005) Canopy and environmental control of root dynamics in a long-term study of concord grape. *New Phytol* 167:829–840. <https://doi.org/10.1111/j.1469-8137.2005.01456.x>
- Comas LH, Becker SR, Cruz VM, Byrne PF, Dierig DA (2013) Root traits contributing to plant productivity under drought. *Front Plant Sci* 4:442
- Dawson TE (1993) Hydraulic lift and water use by plants: implications for water balance, performance and plant-plant interactions. *Oecologia* 95:565–574
- Debieu M, Sine B, Passot S, Grondin A, Akata E, Gangashetty P, et al (2018) Response to early drought stress and identification of QTLs controlling biomass production under drought in pearl millet. *PLoS ONE* 13(10):e0201635. <https://doi.org/10.1371/journal.pone.0201635>
- Dry PR, Loveys BR, McCarthy MG, Stoll M (2001) Strategic irrigation management in Australian Vineyards. *J Int Sci Vigne Vin* 35(129):139
- Dupuy NC, Dreyfus BL (1992) Bradyrhizobium populations occur in deep soil under the leguminous tree *Acacia alba*. *Appl Environ Microbiol* 58(8):2415–2419
- Fadl KEM (2013) Influence of *Acacia senegal* agroforestry system on growth and yield of sorghum, sesame, roselle and gum in north Kordofan State, Sudan. *J For Res* 24:173–177. <https://doi.org/10.1007/s11676-012-0319-4>
- Faye A, Sine B, Chopart JL, Grondin A, Lucas M, Diedhiou AG, Gantet P, Cournac L, Min D, Audebert A, Kane A, Laplaze L (2019) Development of a model estimating root length density from root impacts on a soil profile in pearl millet (*Pennisetum glaucum* (L.) R. Br.). Application to measure root system response to water stress in field conditions. *PLoS One* 14(7):e0214182. <https://doi.org/10.1371/journal.pone.0214182>
- Founoune H, Duponnois R, Bâ AM, Fouad EB (2002) Influence of the dual arbuscular endomycorrhiza / ectomycorrhizal symbiosis on the growth of *Acacia holosericea* (A. Cum Ex G Don) in glasshouse conditions. *Ann For Sci* 59:93–98
- Frederiksen P, Lawesson JE (1992) Vegetation types and patterns in Senegal based on multivariate analysis of field and NOAA-AVHRR satellite data. *J Veg Sci* 3(4):535–544
- Freycon V, Wonkam C, Fayolle A, Laclau J, Lucot E, Jourdan C, Cornu G, Gourlet-Fleury S (2015) Tree roots can penetrate deeply in African semi-deciduous rain forests: evidence from two common soil types. *J Trop Ecol* 31(1):13–23. <https://doi.org/10.1017/S02664674140000595>
- Gning F, Jourdan C, Marone D, Ngom D, Ræbild A (2023) Root distribution of *Adansonia digitata*, *Faidherbia albida* and *Borassus akeassii* along a climate gradient in Senegal. *Agrofor Syst* 97(4):605–615. <https://doi.org/10.1007/s10457-023-00813-7>
- Hopmans JW, Bristow KL (2002) Current capabilities and future needs of root water and nutrient uptake modeling. *Adv Agro* 85:103–183
- Jensen AM, Mintschenko H, Ræbild A (2020) Transpiration reduction and absorption of intercepted water in Leyland cypress (*x Cupressocyparis leylandii*) and European common oak (*Quercus robur*). *Eur J For Res* 139:585–593
- Klein T (2014) The variability of stomatal sensitivity to leaf water potential across tree species indicates a continuum between isohydric and anisohydric behaviours. *Funct Ecol* 28(6):1313–1320. <https://doi.org/10.1111/1365-2435.12289>
- Korbo A, Kjær ED, Sanou H, Ræbild A, Jensen JS, Hansen JK (2013) Breeding for high production of leaves of baobab (*Adansonia digitata* L) in an irrigated hedge system. *Tree Genet Genomes* 9(3):779–793. <https://doi.org/10.1007/s11295-013-0595-y>
- 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(1–2):523–533. <https://doi.org/10.1007/s11104-017-3277-y>
- Laminou Manzo O, Campanell AB, Paul R (2009) Sélection d'espèces ligneuses adaptées à la fixation biologique de dunes au Niger. *Revue Internationale De Géologie, De Géographie Et D'écologie Tropicales* 33:99–106
- Landsberg JJ (2000) Tree water use and its implications in relation to agroforestry systems. ISBN 0 642 57811 7. ISSN 1440–6845. CSIRO Land and water pp 1–31
- Logbo J, Bada F, Gnacadia LS, Ameglio T, Akpo LE (2011) Estimation de la biomasse racinaire en fonction de la teneur en eau du sol chez les espèces sahéliennes : cas d'*Acacia tortilis* (Forsk.) Hayne ssp *Raddiana* (Savi) Brenand et de *Balanites aegyptiaca* (L) Del, en station et en milieu réel. *Int J Biol Chem Sci* 5(1):94–110
- Logbo J, Diouf M, Ngaryo F, Ameglio T, Akpo LE (2013) Effect of water stress on root architecture of seedlings of *Acacia tortilis* (Forsk.), *Balanites aegyptiaca* (L) Del., and *Zizyphus mauritiana*. *Int J Biol Chem Sci* 7(3):1011–1033. <https://doi.org/10.4314/ijbcs.v7i3.10.hal-01189803>
- Lu B, Qian J, Hu J, Wang P, Jin W, Tang S, Zhang C (2022) The role of fine root morphology in nitrogen uptake by riparian plants. *Plant Soil* 472(1):527–542. <https://doi.org/10.1007/s11104-021-05270-8>
- Lynch DJ, Matamala R, Iversen CM, Norby RJ, Gonzalez-Meler MA (2013) Stored carbon partly fuels fine-root respiration but is not used for production of new fine roots. *New Phytol* 199:420–430. <https://doi.org/10.1111/nph.12290>
- Ma LH, Liu XI, Wang YK, Wu PT (2013) Effects of drip irrigation on deep root distribution, rooting depth, and soil water profile of jujube in a semiarid region.

- Plant Soil 373:995–1006. <https://doi.org/10.1007/s11104-013-1880-0>
- Magill CR, Ashley GM, Freeman KH (2013) Water, plants, and early human habitats. *Proc National Acad Sci* 110(4):1175–1180. <https://doi.org/10.1073/pnas.1209405109>
- Manju V, Kaur K, Sharma KA (2019) Identification of promising sources for drought tolerance in cultivated and wild species germplasm of barley based on root architecture. *J Environ Biol* 40:309–315
- Marone D, Poirier V, Coyea M, Olivier A, Munson AD (2017) Carbon storage in agroforestry systems in the semi-arid zone of Niayes, Senegal. *Agrofor Syst* 91:941–954. <https://doi.org/10.1007/s10457-016-9969-0>
- McCormack ML, Adams TS, Smithwick EAH, Eissenstat DM (2014) Variability in root production, phenology, and turnover rate among 12 temperate tree species. *Ecology* 95:2224–2235
- McCormack ML, Dickie IA, Eissenstat DM, Fahey TJ, Fernandez CW, Guo D, ... Zadworny M (2015) Redefining fine roots improves understanding of below-ground contributions to terrestrial biosphere processes. *New Phytol* 207(3):s505–518. <https://doi.org/10.1111/nph.13363>
- McDonald A, Davies W (1996) Keeping in touch: responses of the whole plant to deficits. *Adv Bot Res* 22:229
- Njiti CF, Galiana A (1996) Symbiotic property and rhizobium requirement for effective nodulation of five tropical dry zone acacias. *Kluwer Acad* 33(3):265–271
- O'Grady AP, Cook PG, Eamus D, Duguid A, Wischusen JDH, Fass T, Worledge D (2009) Convergence of tree water use within an arid-zone woodland. *Oecologia* 160:643–655
- Ostonen I, Helmisaari HS, Borken W, Tederloo L, Kukumägi M, Bahram M, Lindroos AJ, Nojdö P, Uri V, Merilä P (2011) Fine root foraging strategies in Norway spruce forests across a European climate gradient. *Glob Change Biol* 17:3620–3632. <https://doi.org/10.1111/j.1365-2486.2011.02501.x>
- Ouédraogo A, Thiombiano A (2012) Regeneration pattern of four threatened tree species in Sudanian savannas of Burkina Faso. *Agroforest Syst* 86:35–48. <https://doi.org/10.1007/s10457-012-9505-9>
- Pandey CB, Singh AK, Sharma DK (2000) Soil properties under *Acacia nilotica* trees in a traditional agroforestry system in central India. *Agrofor Syst* 49:53–61
- Querejeta JI, Prieto I, Armas C, Casanoves F, Diémé JS, Diouf M, Yossi H, Kaya B, Pugnaire FI, Rusch GM (2022) Higher leaf nitrogen content is linked to tighter stomatal regulation of transpiration and more efficient water use across dryland trees. *New Phytol* 235:1351–1364. <https://doi.org/10.1111/nph.18254>
- Radville L, Post E, Eissenstat DM (2016) Root phenology in an Arctic shrub-graminoid community: the effects of long-term warming and herbivore exclusion. *Clim Chang Responses* 3:4. <https://doi.org/10.1186/s40665-016-0017-0>
- Reader RJ, Jalili A, Grime JP, Spencer RE, Matthews N (1993) A comparative study of plasticity in seedling rooting depth in drying soil. *J Ecol* 81(3):543–550. <https://doi.org/10.2307/2261532>
- Rewald B, Ephrath JE, Rachmilevitch S (2011) A root is a root is a root? Water uptake rates of citrus root orders. *Plant Cell Environ* 34:33–42. <https://doi.org/10.1111/j.1365-3040.2010.02223.x>
- 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, Seghier J, Cournac L, Leroux L (2020) How far does the tree affect the crop in agroforestry? New spatial analysis methods in a *Faidherbia* parkland. *Agric Ecosyst Environ* 296:106928
- 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* 85:431–44128. <https://doi.org/10.1007/s10457-011-9405-4>
- Schenk HJ, Jackson RB (2002a) The global biogeography of roots. *Ecol Monogr* 72(3):311–328
- Schenk HJ, Jackson RB (2002) Rooting depths, lateral root spreads and below-ground/above-ground allometries of plants in water-limited ecosystems. *J Ecol* 90:480–494
- Schenk HJ, Jackson RB (2005) Mapping the global distribution of deep roots in relation to climate and soil characteristics. *Geoderma* 126:129–140
- Sharma S (1996) *Applied Multivariate Techniques*. John Wiley & Sons Inc., New York, p 493
- Shashidhar HE, Gowda HS, Raveendra GM, Pavan J, Naveen KG, Suprabha N Upadhyaya P, Sonam R (2012) PVC tubes to characterize roots and shoots to complement field plant productivity studies. *Methodologies for Root Drought Studies in Rice*. Los Baños (Philippines): International Rice Research Institute; p. 15–21
- Smith-Martin CM, Xu X, Medvigy D, Schnitzer SA, Powers JS (2020) Allometric scaling laws linking biomass and rooting depth vary across ontogeny and functional groups in tropical dry forest lianas and trees. *New Phytol* 226:714–726
- Steinaker DF, Wilson SD (2008) Phenology of fine roots and leaves in forest and grassland. *J Ecol* 96:1222–1229. <https://doi.org/10.1111/j.1365-2745.2008.01439.x>
- Stephenson N (1990) Climatic control of vegetation distribution: the role of the water balance. *Am Nat* 135(5):649–670
- Tomlinson KW, Poorter L, Borghetti F, Ward D, de Bie S, van Langevelde F (2013) Leaf adaptations of evergreen and deciduous trees of semi-arid and humid savannas on three continents. *J Ecol* 101(2):430–440. <https://doi.org/10.1111/1365-2745.12056>
- Weemstra M, Kiorapostolou N, van Ruijven J, Mommer L, de Vries J, Sterck F (2020) The role of fine-root mass, specific root length and life span in tree performance: a whole-tree exploration. *Funct Ecol* 34:575–585. <https://doi.org/10.1111/1365-2435.13520>

- Wijewardan C, Alsajri FA, Irby JT, Krutz LJ, Golden BR, Henry WB, Reddy KR (2019) Water deficit effects on soybean root morphology and early-season vigor. *Agronomy* 9:836. <https://doi.org/10.3390/agronomy9120836>
- Withington JM, Goebel M, Buřaj B, Oleksyn J, Reich PB, Eissenstat DM (2021) Remarkable similarity in timing of absorptive fine-root production across 11 diverse temperate tree species in a common garden. *Front Plant Sci* 11:623722. <https://doi.org/10.3389/fpls.2020.623722>
- Yandou IB, Rabiou H, Soumana I, Laouali A, Mahamane A (2020) Effect of Water stress on the seedlings growth of acacia tortilis subsp. raddiana in nursery in Sahelian Zone, Niger. *Eur Sci J, ESJ* 16(21):228. <https://doi.org/10.19044/esj.2020.v16n21p228>
- Yi K, Dragoni D, Phillips RP, Roman DT, Novick KA (2017) Dynamics of stem water uptake among isohydric and anisohydric species experiencing a severe drought. *Tree Physiol* 37(10):1379–1392. <https://doi.org/10.1093/treephys/tpw126>

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.