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Water stress responses of *Saba senegalensis* provenances during the seedling stage

Photo 1.
Flowering and leafy shoots of *Saba senegalensis*.
Photo S. Diawara.

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RÉSUMÉ

Réponses au stress hydrique de plantules de *Saba senegalensis* selon leurs provenances

Saba senegalensis est une liane à usages multiples d'Afrique subsaharienne aujourd'hui menacée par la surexploitation de ses fruits, la dégradation des sols et l'irrégularité des précipitations, compromettant sa régénération. Cette recherche vise à évaluer la survie, la croissance et la répartition de la matière sèche dans les réponses aux régimes hydriques des semis de *S. senegalensis* provenant de neuf zones légèrement, modérément et sévèrement sèches au Burkina Faso. Les paramètres de l'étude sont les provenances, les régimes hydriques et la durée du stress dû à la sécheresse. Au total, 567 plantules (63 par provenance) ont été cultivées selon un plan factoriel. Cinq mois après la germination, trois régimes hydriques ont été appliqués : teneur en eau du sol élevée, moyenne et faible, correspondant respectivement à 100, 75 et 50 % de la capacité de rétention en pots. Les expériences ont duré 6, 9 et 12 mois après le début du stress hydrique. Les taux de survie, les paramètres de croissance, la production de biomasse, les indices de tolérance et de sensibilité au stress ont été calculés et les données analysées à l'aide d'un modèle linéaire mixte. Le stress dû à la sécheresse a réduit la survie des semis et la production de biomasse, tandis que le taux de croissance relatif du diamètre au collet a augmenté. À mesure de la durée du stress dû à la sécheresse, le taux de croissance relatif du diamètre au collet des plantules diminue et le rapport pousses-racines augmente : après six mois de stress, les plantules ont investi davantage dans leurs racines, tandis qu'après neuf et douze mois la tendance inverse est observée. En outre, les plantules de la zone légèrement sèche produisent plus de biomasse lorsqu'elles sont arrosées sous un régime à faible teneur en eau du sol, et sont plus tolérantes à la sécheresse que celles des zones sévèrement et modérément sèches. Cela indiquerait que les plantules originaires de ces zones sont bien adaptées à la croissance dans des conditions de stress hydrique sévère. Pour les programmes de domestication de *S. senegalensis*, les plantules provenant de zones légèrement sèches peuvent être propagées avec succès dans les systèmes agroforestiers où l'eau est un facteur limitant.

Mots-clés : taux de croissance précoce, rapport pousses-racines, production de biomasse, acclimatation, tolérance à la sécheresse, *Saba senegalensis*.

ABSTRACT

Water stress responses of *Saba senegalensis* provenances during the seedling stage

Saba senegalensis is a multi-purpose liana from sub-Saharan Africa that is under threat from over-exploitation of its fruits and from land degradation and erratic rainfall affecting its regeneration. This research aims to assess survival, growth and dry matter distribution in the responses to water regimes of *S. senegalensis* seedlings of nine provenances from slightly, moderately and severely dry zones in Burkina Faso. The study parameters were provenance, water regimes and duration of drought stress. A total of 567 seedlings (63 per provenance) were grown using a factorial design. Five months after germination, three water regimes were applied: high, medium and low soil water content, corresponding respectively to 100, 75 and 50% of soil pot capacity. The experiments lasted for 6, 9 and 12 months after water stress began. Survival rates, growth parameters, biomass production, stress tolerance and stress sensitivity indexes were calculated and the data analyzed using a linear mixed model. Drought stress reduced seedling survival and biomass production, while the relative growth rate in collar diameter increased. Concerning the duration of drought stress, the relative growth rate of seedlings in collar diameter decreased and the shoot to root ratio increased. After six months under stress, the seedlings had invested more in roots, whereas after nine and twelve months the reverse trend was observed. Furthermore, seedlings from the slightly dry zone produced more biomass when watered under a low soil water content regime, and were more drought-tolerant than those from severely and moderately dry zones. This could indicate that the seedlings originating from these zones are well adapted to growth under severe water stress. For *S. senegalensis* domestication programs, seedlings originating from the slightly dry zones can be successfully propagated in agroforestry systems where water is a limiting factor.

Keywords: early growth rate, shoot to root ratio, biomass production, acclimation, drought tolerance, *Saba senegalensis*.

RESUMEN

Respuestas al estrés hídrico de la *Saba senegalensis* durante la fase de plántula según su procedencia

La *Saba senegalensis* es una liana polivalente del África subsahariana amenazada por la sobreexplotación de sus frutos y por la degradación del suelo y la irregularidad de las precipitaciones que afectan a su regeneración. El objetivo de esta investigación es evaluar la supervivencia, el crecimiento y la distribución de la materia seca en respuesta a los regímenes hídricos de las plántulas de *S. senegalensis* de nueve procedencias: zonas ligera, moderada y severamente secas de Burkina Faso. Los parámetros de estudio fueron la procedencia, los regímenes hídricos y la duración del estrés por sequía. Se cultivaron 567 plántulas (63 por procedencia) siguiendo un diseño factorial. Cinco meses después de la germinación, se aplicaron tres regímenes hídricos: alto, medio y bajo contenido de agua en el suelo, correspondientes respectivamente al 100, 75 y 50 % de la capacidad de la tierra de la maceta. Los experimentos duraron 6, 9 y 12 meses tras el inicio del estrés hídrico. Se calcularon las tasas de supervivencia, los parámetros de crecimiento, la producción de biomasa y los índices de tolerancia y sensibilidad al estrés. Los datos se analizaron mediante un modelo lineal mixto. El estrés por sequía redujo la supervivencia de las plántulas y la producción de biomasa, mientras que aumentó la tasa de crecimiento relativo del diámetro del cuello. Respecto a la duración del estrés por sequía, la tasa de crecimiento relativo en el diámetro del cuello de las plántulas disminuyó y la relación brote-raíz aumentó. Tras seis meses bajo estrés, las plántulas habían invertido más en las raíces, mientras que tras nueve y doce meses se observó la tendencia inversa. Además, las plántulas de la zona ligeramente seca produjeron más biomasa cuando se regaron en un régimen de bajo contenido de agua en el suelo, y fueron más tolerantes a la sequía que las de las zonas severa y moderadamente secas. Esto podría indicar que las plántulas procedentes de estas zonas están bien adaptadas al crecimiento en condiciones de estrés hídrico severo. Para los programas de domesticación de *S. senegalensis*, las plántulas procedentes de las zonas ligeramente secas pueden reproducirse con éxito en sistemas agroforestales donde el agua es un factor limitante.

Palabras clave: tasa de crecimiento precoz, relación brote-raíz, producción de biomasa, aclimatación, tolerancia a la sequía, *Saba senegalensis*.

Introduction

Seed germination is the first step in a plant's life cycle (Rajjou *et al.*, 2012) and is followed by the post germinative growth of the seedling (Hao *et al.*, 2017). Successful germination and seedling development are crucial steps in the growth of a new plant (Wolny *et al.*, 2018). Seed germination can be influenced by various intrinsic factors (e.g. dormancy in its various forms, seed quality, maturity, tolerance to desiccation, age) and environmental conditions (e.g. water, oxygen, pH, temperature, light) (Simão and Takaki, 2008). Germination starts when the seed imbibes water. In water deficit conditions, seeds do not imbibe enough water, which ultimately decreases the rate of germination and reduces overall plant number per unit area (Jajarmi, 2009).

After seedling emergence, plants are frequently exposed to environmental stresses. Some environmental factors, such as air temperature, can become stressful in just a few minutes; others, such as soil water content, may take days to weeks, and factors such as soil mineral deficiencies can take months to become stressful (Taiz and Zeiger, 2006). Water stress characterizes arid and semi-arid tropical zones, where it constitutes a major constraint on plant growth, development and productivity (Bayen *et al.*, 2021; Brunetti *et al.*, 2018; Fathi and Barari Tari, 2016). During prolonged stress situations, plant survival and growth are impacted. The effects are highly variable, depending on length and promptness of stress imposition and stage of plant development (Ferreira *et al.*, 2015). In general, water stress induces morphological, physiological and biochemical changes within plants (Ohashi *et al.*, 2000; Zarafshar *et al.*, 2014), what can affect the growth of plant parts differently, and may alter the pattern of dry mass accumulation within the plant (Shao *et al.*, 2008). These changes occur as soon as the quantities of available water are insufficient to support the needs of the plant. Overall, drought negatively affects various growth parameters such as plant height, root length, shoot and root fresh and dry weight, number of leaves, tillers, leaf area, and root area (Kagambèga *et al.*, 2019; Anjum *et al.*, 2011). Under water-stress conditions, the shoot to root ratio decreases to facilitate water absorption and to maintain the osmotic pressure (Lisar *et al.*, 2012), because root length and shoot length usually follow the phenomena of hydrotropism (Anjum *et al.*, 2011).

In arid and semi-arid tropical zones, many woody species have developed avoidance or tolerance strategies in response to water stress.

Shedding of leaves and development of root depth and morphology also play a critical role in water stress tolerance (Bayen *et al.*, 2021). These changes occur as soon as the quantities of available water are insufficient to support the needs of the plant (Bayala *et al.*, 2018; Bouda *et al.*, 2015; Fargeon *et al.*, 2016). For many tree species growing in semi-arid agroforestry systems, the lack of knowledge on their biological and ecological characteristics and their acclimation to abiotic stress is a major issue for their adequate use (Gebrekirstos *et al.*, 2006). Better understanding of their resilience to water-deficit stress is essential to develop adequate strategies for their sustainable management in semi-arid areas.

In most cases, stress is measured in relation to plant survival, crop yield, growth (biomass accumulation), or the primary assimilation processes (CO_2 and mineral uptake), which are related to overall growth (Taiz and Zeiger, 2006). In addition, to measure the impact of water stress on seedlings, ratios and indices such as survival rate, stress susceptibility index (Fischer and Maurer, 1978), stress tolerance index (Fernandez, 1992), relative water content, shoot to root ratio can be calculated.

In the Sudano-Sahelian zone of West Africa, tree growth performance under drought is a well-documented issue. Studies on the response of woody plants from different provenances to drought stress have focused on species such as *Adansonia digitata* (Bouda *et al.*, 2015; De Smedt *et al.*, 2012), *Faidherbia albida* (Koech *et al.*, 2016), *Vitellaria paradoxa* (Bayala *et al.*, 2018), *Senegalia dudgeonii*, *Senegalia gourmaensis, Vachellia nilotica* and *Vachellia tortilis* (Bayen *et al.*, 2021). However, the knowledge on the drought tolerance of *Saba senegalensis* is still limited. Since environmental conditions vary extensively within the natural settlement of the species, it is reasonable to expect genetic differentiation in various traits among *S. senegalensis* populations. Moreover, to the best of our knowledge, no studies on the behavior of *S. senegalensis* under water-stress conditions have been previously conducted.

To promote the domestication of multi-purpose trees, especially fruit trees, and to define a strategy for their conservation in semi-arid conditions context, understanding their response to water-deficit and identifying drought-resistant traits are necessary. These characteristics can make it possible to select populations that are able to grow and

Photo 2.
Ripe fruit of *Saba senegalensis*.
Photo A. Ouedraogo.

give satisfactory yields in areas with water deficit. Therefore, the current study has a general aim of understanding the potential for acclimation of *S. senegalensis* to different climatic conditions. The study specific aims to (i) understand the effects of water stress on seedlings survival and growth of *S. senegalensis* (ii) assess the shoot to root ratio in seedlings and (iii) demonstrate whether tolerance or resistance to water stress is related to the provenance of the species.

The hypotheses are (i) water stress has a differential impact on the survival and growth of *S. senegalensis* depending on their provenances, and (ii) plants derived from dry areas are more drought-tolerant than those from wetter areas.

Material and methods

Study site description

Experiments were conducted at the Research Station of the Institute of Environment and Agricultural Research (Burkina Faso) located in Saria (figure 1) during August 2017 to January 2019. The site is an open, flat terrain at 300 m asl. The climate is characterized by marked seasonality, with the majority of precipitation occurring during a wet season lasting for 6 months from May to October. Climate data (i.e. monthly mean precipitation and temperature) were collected from in-situ weather station during the eighteen months of the experiment. Soils at the study site are mostly Ferric Lixisols with generally low fertility (Ouattara *et al.*, 2006).

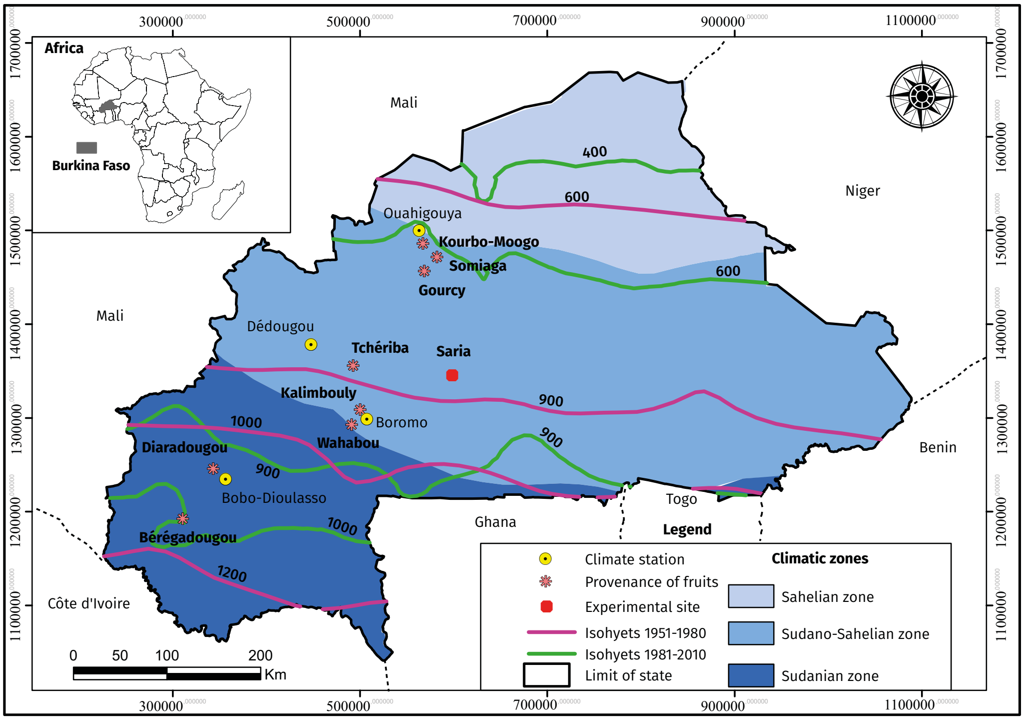
Description of the studied fruit species

The experiment was carried out on *S. senegalensis* (A. DC.) Pichon, a multi-purpose plant with a high ecological and socio-economic value (Lamien *et al.*, 2010; Orwa *et al.*, 2009; Sarr *et al.*, 2018). It is a woody liana species native to sub-Saharan Africa whose distribution area covers countries such as Burkina Faso, Gambia, Guinea, Mali, Niger, Guinea Bissau, Senegal, Côte d'Ivoire, Ghana and Tanzania. It occurs in areas where annual precipitations range from 600 to 1,500 mm (Le Houérou, 1986; Orwa *et al.* 2009). It is commonly found in riverine areas and open woodlands.

Fruits collection and seedlings production

Mature fruits of *S. senegalensis* were collected in August 2017 from nine provenances across a climatic gradient in Burkina Faso: Diaradougou, Mondon and Bérégadougou, located in the Sudanian zone; Tchériba, Kalimbouly, Gourcy, Kourbo-Moogo and Somiaga, located in the Sudano-Sahelian zone; and Wahabou, located between the Sudanian zone and Sudano-Sahelian zones (figure 1).

In the Sudanian zone the rainy season lasts 5 to 6 months with average annual rainfall exceedingly sometimes 1,100 mm. The mean temperature of this area varies between 20 and 25 °C. In the Sudano-Sahelian zone, the annual rainfall varies between 600 and 900 mm and last 4 to 5 months with an average temperature ranging from 20 to 30 °C (Fontes and Guinko, 1995). The climate data used for the fruits collection sites are those of the nearest weather station (table I). After fruits harvesting, damage-free fruits were de-pulped, and the seeds were soaked in cold water for 24 hours, following the conventional treatment recommended by the National Tree Seed Center of Burkina Faso. In August 2017, two seeds were sown directly into cylindrical aluminum pots (10 cm diameter × 50 cm height) containing 6 kg of substrate composed of arable soil from the natural soils at the research station, manure and sand (1:1:1). A total of 567 pots were used for the experiment (63 per provenance and 21 per water stress for each provenance). Due to the recalcitrant nature of seeds, sowing was done in a greenhouse immediately after harvesting. Watering was done once daily with tap water to avoid drying of the medium. Two weeks after



Source : IGB - National meteorology agency and GPS data October 2019 Author : NABALOUM M.

Figure 1.
Location of sites for *Saba senegalensis* fruit collection and site for water-deficit experiments on the climate map of Burkina Faso.

Table I.
Geographical and climate data of the provenance's sites of *Saba senegalensis* fruits from 2007 to 2019.

Provenance	Climate station	Latitude (°)	Longitude (°)	Altitude (m)	Mean annual air temperature (°C)	Annual rainfall (mm)	Humidity (%)	PET (mm /year)	Number of arid months	Annual water deficit (mm)
Somiaga Kourbo-Moogo Gourcy	Ouahigouya	13.56	2.41	336	29.7	799	38.9	2871	10.3	2072
Tchériba	Dédougou	12.46	3.48	300	29.3	862	46.1	2626	9.8	1764
Kalimbouly Wahabou	Boromo	11.75	2.93	271	28.9	926	49.2	2445	9.7	1519
Diaradougou Bérégadougou Mondon	Bobo-Dioulasso	11.16	4.31	460	27.9	1022	53.9	2056	9	1034

Climate data were from meteorology service of Burkina Faso and PET (potential evapotranspiration) is from Hargreaves (1963).

sowing, emergence was completed in all pots, then one seedling per pot was kept and the same amount of water was uniformly supplied to allow early growth before initiating the watering regimes, in January 2018.

Experimental design and treatments

The applied quantities of water were calculated based on soil water content at field capacity, which is the value of soil moisture when gravity drainage becomes close to zero after saturation (Taiz and Zeiger, 2006; Ward and Robinson, 1990). In practice, ten pots with dry substrate (dried in an oven at 60 °C for 72 h) were weighed (W1). The pots were watered and let to drain for 48 h before being weighed again (W2). The difference (W2 - W1) corresponded to the amount of water added to reach 100 % field capacity for a completely dry substrate. Three water regimes were applied for twelve months: irrigation to 50, 75 and 100 % of soil pot capacity, referred as low-water content (LWC, 277 ml per week), medium water content (MWC, 396 ml per week) and high-water content (HWC–control, 554 ml per week), respectively.

Table II.
Drought characterization according to the standardized precipitation evapotranspiration index (SPEI) values (Ye *et al.*, 2019).

Drought categories	SPEI values
Extremely wet	[2.0, +1)
Severely wet	[1.5, 2.0)
Moderately wet	[1.0, 1.5)
Slightly wet	[0.5, 1.0)
Near normal	(-0.5, 0.5)
Slightly dry	(-1.0, -0.5]
Moderately dry	(-1.5, -1.0]
Severely dry	(-2.0, -1.5]
Extremely dry	(-∞, 2.0]

After five months, the drought stress treatment was initiated by applying the three water regimes. The experiment followed a split plot design, with watering regimes and provenances as factor. There were three replications, with provenance as the main plot and water regime as the sub-plot, with seven plants within each sub-plot. Each of the three blocks contained 3 water regimes × 9 provenances × 7 plants, giving a total of 567 plants for the whole experiment.

Data collection

Root collar diameter, height and the fresh and dry weight of root and shoot (comprising stem and leaves) of the five-month old seedlings were recorded before the water regimes and 6, 9 and 12 months, after applying the different water regimes. Equally, seedling survival rate was calculated at the same periods. In addition, the number of leaves was determined by directly counting. In July 2018, after six months of drought stress, one-third of the pots were randomly selected within each subplot (189 pots in total), and the living seedlings (165 seedlings) were uprooted for dry matter and root assessments. Nine months after the drought stress, the second third of the seedlings were harvested and assessed (184 seedlings), and after 12 months of stress, the remaining living seedlings were uprooted (120 seedlings). The variation in the numbers of seedlings uprooted at each date is due to mortality. To obtain the dry weights, each seedling's roots, stems and leaves were placed into envelopes and placed in the oven at 70 °C until constant weight is reached.

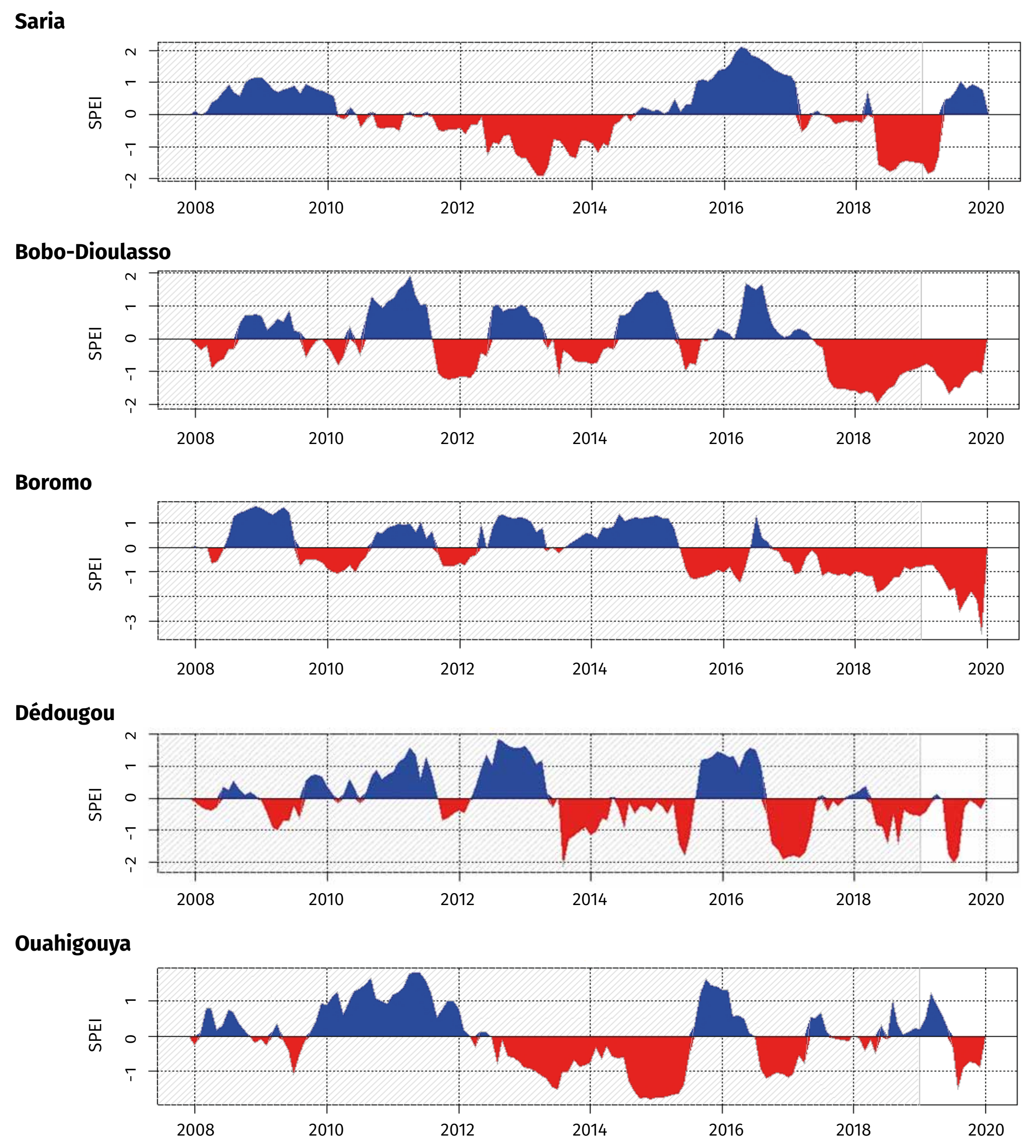


Figure 2.
Evolution of the standardized precipitation evapotranspiration index (SPEI) at the Saria Research Station and climate stations, Burkina Faso.

Based on biomass data, the ratios of fresh /dry weight and shoot to root ratio dry weight were obtained. The shoot to root ratio is often used to estimate relative absorption-transpiration capacities. The relative growth rate of diameter, height and total dry weight were also derived. The accumulated water uses efficiency (WUE) after 6, 9 and 12 months of drought stress were determined, based on the estimated dry matter at month 0, the dry matter harvested after 6 months of drought stress and the total amount of water applied from 0 to 6 months:

$$WUE = (TDW_6 - TDW_0) / TWA$$

where TDW_0 and TDW_6 are the initial and final dry matter, respectively, and TWA is the total water applied. WUE is expressed in mg/ml.

At the end of each drought stress duration, survival rates were calculated. Also, the mean relative growth rate (RGR) was calculated for diameter, height and number of leaves. The RGR is generally used to compare the growth of seedlings that differ in initial size, to account for the growth differences due to size variations and to determine which seedlings are inherently more efficient (Hunt, 1982).

The equation is:

$$RGR = \frac{lnXF - lnXI}{TF - TI}$$

where *lnXF* and *lnXI* are the means of the natural logarithm-transformed plant weights.

To compare the adaptability among provenances, stress tolerance index (STI) and stress sensitivity index (SSI) were analyzed on the growth parameters (i.e. seedling height and root collar diameter). The STI was analyzed using the following formula (Fernandez, 1992):

$$STI = (ypi \times ysi) / YP^2$$

where *ysi* and *ypi* were each provenance's parameters under stress and non-stress conditions, respectively, and *YP* is the parameter means of all provenances under non-stress conditions.

The SSI was analyzed using the following formula (Fischer and Maurer, 1978):

$$SSI\ (\%) = 100 \text{ x } \frac{PMT - PMS}{PMT}$$

where *PMT* and *PMS* were each provenance's parameters (shoot height and root elongation) under stress and non-stress conditions, respectively.

Standardized precipitation evapotranspiration index

To characterize the local climate of the fruits collection and experimentation sites, the standardized precipitation evapotranspiration index (SPEI) was used. This index has the advantage of including the effects of temperature variability on drought assessment (Lorenzo-Lacruz *et al.*, 2010; Vicente-Serrano *et al.*, 2010). The SPEI is a monthly index that was calculated on annual base (from 2007 to 2019 for Saria site and fruits provenances sites). The levels of drought were categorized as shown in table II (Ye *et al.*, 2019). For the current study, subject to data availability, Hargreaves (1975) method was used to calculate Potential Evapotranspiration (PET). The SPEI package for R developed by Vicente-Serrano *et al.* (2010) was used to calculate the SPEI drought index.

Statistical analysis

Before analysis, mean values for all variables in each sub-plot were calculated. The data collected on seedling survival and growth (i.e. diameter, height, number of leaves, RGR in diameter, RGR in height, variation in number of leaves and dry weight for shoots, leaves and roots), WUE, biomass production, STI and SSI for each water regime, provenance and duration of drought stress were fitted in a series of linear mixed effect models by using the "nlme" package (Pinheiro and Bates, 2002) in R. In each model, seedlings provenance, water regime, duration of drought stress and their interaction were treated as fixed factors and block as random factor.

Homogeneity of variances was examined before the analysis using Levene's test. The results were considered significant when $P < 0.05$. The analysis was conducted using Rstudio version 4.1.2 (R Core Team, 2021).

Results

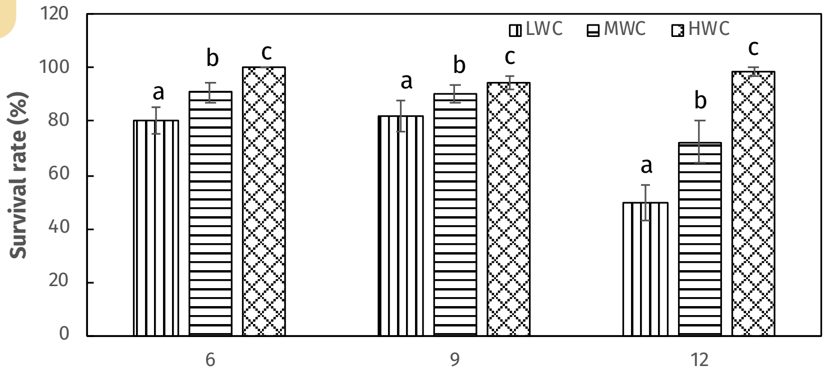
Sites climate conditions

SPEI was calculated for 4 meteorological stations and experimentation sites to analyze the local conditions of drought at various time scales. The local climate of Diaradougou, Mondon and Bérégadougou provenances was characterized by Bobo SPEI; those of Tchériba provenance by Dédougou SPEI. Also, local conditions of drought of Kalimbouly and Wahabou provenances were characterized by Boromo SPEI and those of Gourcy, Kourbo-Moogo and Somiaga by Ouahigouya SPEI. SPEI monthly values varied from −5.4 to 2.6, −5 to 2.9, −4.6 to 3.1, −3.1 to 3.0 and −4.5 to 3.0 for Ouahigouya, Dédougou, Boromo, Bobo and Saria sites, respectively. In general, the climatic conditions of the Bobo station (SPEI = −0.86) were slightly dry ($-1.0 < SPEI \le -0.5$) and those of Boromo (SPEI = −1.27) and Dédougou (SPEI = −1.4) stations were moderately dry ($-1.5 < SPEI \le -1.0$). In the Ouahigouya station (SPEI = −1.7), the climatic conditions were severely dry ($-2.0 < SPEI \le -1.5$). The climatic conditions of experimentation site were moderately dry (figure 2).

Table III.
Description of the fitted linear mixed-effects models on survival rate of *Saba senegalensis* seedlings. The table presents the inclusion of both fixed and random effects for each model. For each model, the *p*-value as well as the Akaike Information criterion (AIC) are presented.

	Dependent variable	**Survival rate**	
	Number of blocks	**3**	
	Number of observations	**453**	
		***p*-value**	**AIC**
Random effect:	Block	< 0.001***	2,244.0
Fixed effects:	Provenance (P)	0.178	2,234.6
	Water regime (W)	< 0.001***	2,212.0
	Duration of drought stress (T)	< 0.001***	2,219.5
	P × W	0.735	2,210.2
	P × T	0.970	2,181.4
	W × T	< 0.001***	**2,168.8**
	P × W × T	0.974	2,152.5

Significant codes: *** 0.001; ** 0.01; * 0.05.



LWC low water content, MWC medium water content, HWC high water content.

Figure 3.
Water regime and duration of drought stress effects on survival rate of *Saba senegalensis* seedlings. For each duration of drought stress, values (mean ± standard error) with different letters are significantly different at the 5% level.

Seedlings survival

At the time 0 of the experiment, the survival rate of the seedlings was 100%. After 12 months of water stress, the mean survival rate of *S. senegalensis* seedlings was decreased to 84.3 ± 26.8%. Also, at the end of the experiment, the survival rate was reduced by 50%, 28% and 2% for the LWC, MWC and HWC regimes, respectively. The seedlings survival of *S. senegalensis* in terms of SPEI was influenced by the block ($P < 0.001$), water regime ($P < 0.001$) and duration of drought stress ($P < 0.001$). Significant interaction was also observed between water regime and duration of drought stress ($P < 0.001$), indicating that for each duration of drought stress, species responses to drought. However, the interaction W × T better explains the seedlings survival, as his model recorded the lowest AIC (table III). In general, the severity of the drought was dependent to the duration of the applied stress. Irrespective of the duration of drought stress application, control (well-watered) seedlings had the highest survival rate, while plants subject to the LWC regime had the lowest survival rate (figure 3).

Seedlings growth and shoot to root ratio

After 12 months' application of water stress, the mean relative growth of *S. senegalensis* seedlings in height, collar diameter and number of leaves was 0.11 ± 0.05 cm/month, 0.09 ± 0.04 mm/month and 0.10 ± 0.07 mm/month, respectively. The block, the water regime and the duration of drought stress had a significant effect on the RGR of height and number of leaves. However, no significant interaction was found between these factors. The model containing the water regime better explains the growth of the seedlings in height and number of leaves, as it recorded the lowest AIC (table IV). Seedlings subject to the low and moderate watering regime showed higher RGR height and RGR in number of leaves (table VA). In general, the RGR of *S. senegalensis* seedlings in height and number of leaves increased with decreasing of amount of watering regime. Also, the block, the provenance and the duration of drought stress had a significant effect on the RGR in collar diameter. In contrast, the duration of drought stress better explains the growth in seedling diameter, as his model recorded the lowest AIC (table IV). Seedlings subject to the low and moderate watering regime showed higher RGR in collar diameter (table VB). In general, the RGR of *S. senegalensis* seedlings in collar diameter decreases with the duration of drought stress.

Regardless of provenance and water regime, at 12 months following the application of water stress, shoot

Table IV.
Description of the fitted linear mixed-effects models on morphological parameters of *Saba senegalensis* seedlings. The table presents the inclusion of both fixed and random effects for each model. For each model, the *p*-value as well as the Akaike Information criterion (AIC) are presented.

	Dependent variable	**RGR height**		**RGR diameter**		**RGR number of leaves**	
		***p*-value**	**AIC**	***p*-value**	**AIC**	***p*-value**	**AIC**
Random effect:	Block	0.001**	-966.5	0.001**	-1,103.1	< 0.001***	-463.0
Fixed effects:	Provenance (P)	0.674	-945.9	0.001***	-1,100.0	0.312	-445.2
	Water regime (W)	< 0.001***	-979.2	0.231	-1,084.4	< 0.001***	-469.3
	Duration of drought stress (T)	< 0.001***	-972.6	< 0.001***	-1,107.2	0.002***	-462.5
	P × W	0.783	-930.0	0.379	-1,056.8	0.640	-428.8
	P × T	0.278	-926.5	0.988	-1,072.0	0.241	-425.2
	W × T	0.097	-964.6	0.367	-1,061.3	0.275	-448.5
	P × W × T	0.697	-842.9	0.777	-951.1	0.812	-350.1

Significant codes: *** 0.001; ** 0.01; * 0.05.
RGR: Relative growth rate.

Table V.
Growth parameters of *Saba senegalensis* seedlings under three water regimes (A) and three durations of drought stress (B).

A. **Water regime**	**RGR of height**	**RGR of collar diameter**	**RGR of number of leaves**
Low water content	0.12 ± 0.04a	0.10 ± 0.05a	0.11 ± 0.07a
Medium water content	0.12 ± 0.04a	0.09 ± 0.03a	0.12 ± 0.07a
High water content	0.09 ± 0.05b	0.09 ± 0.05a	0.08 ± 0.09b

Values are means ± standard error. Means followed by the same letter in the same column are not significantly different at $P < 0.05$ for the same morphological parameter.
RGR: Relative growth rate.

B. **Duration of drought stress**	**RGR of height**	**RGR of collar diameter**	**RGR of number of leaves**
6 months	0.12 ± 0.05a	0.11 ± 0.05a	0.13 ± 0.09a
9 months	0.11 ± 0.05b	0.08 ± 0.04b	0.09 ± 0.07b
12 months	0.09 ± 0.03c	0.08 ± 0.03b	0.07 ± 0.06c

Values are means ± standard error. Means followed by the same letter in the same column are not significantly different at $P < 0.05$ for the same morphological parameter.
RGR: Relative growth rate.

length ranged from 12 cm to 86 cm and root length varied from 5 cm to 70 cm. The shoot to root ratio ranged from 0.21 to 8.4 and the mean ratio was 1.0 ± 0.57. The block, the duration of drought stress and interaction P × W had influenced the shoot to root ratio. However, the duration of drought stress better explains the shoot to root ratio, as his model recorded the lowest AIC (table VI). At six months of drought stress, seedlings had invested more in roots, whereas after nine and twelve months the reverse trend was observed. The observed ratio was similarly higher in plants after nine (1.17 ± 0.06) and twelve months (1.06 ± 0.03) of drought stress as compared with the value recorded for seedlings after six months (0.79 ± 0.02).

Table VI.
Description of the fitted linear mixed-effects models on shoot to root ratio of *Saba senegalensis* seedlings. The table presents the inclusion of both fixed and random effects for each model. For each model, the *p*-value as well as the Akaike Information criterion (AIC) are presented.

	Dependent variable	**Shoot to root ratio**	
		***p*-value**	**AIC**
Random effect:	Block	0.002**	747.4
Fixed effects:	Provenance (P)	0.420	759.9
	Water regime (W)	0.807	760.8
	Duration of drought stress (T)	< 0.001***	718.9
	P × W	0.020*	775.8
	P × T	0.352	742.3
	W × T	0.742	745.3
	P × W × T	0.442	786.9

Significant codes: *** 0.001; ** 0.01; * 0.05.

Water use efficiency and dry matter allocation

Apart from the provenance and water stress, at 12 months of drought stress, the mean WUE of *S. senegalensis* seedlings was 0.90 ± 0.70 mgm/l. The accumulated WUE showed significant differences between blocks, provenances, water regimes and duration of drought stress Also, the results showed that all interactions had effects on WUE ($P < 0.001$), except the interaction P × T ($P = 0.655$). However, the water regime better explains the WUE, as his model recorded the lowest AIC (table VII). Seedlings subject to the moderate and high watering regimes showed smallest WUE and the higher was recorded for seedlings watered under the LWC regime (table VIII).

The biomass production showed significant difference between the block ($P = 0.011$), the water regimes ($P < 0.001$), the times of the stress applied ($P < 0.001$), and the interactions P × W ($P = 0.004$), W × T ($P < 0.007$) and P × W × T ($P = 0.001$). However, there was no significant variation between provenances ($P = 0.056$) and the interaction P × T ($P = 0.056$) for biomass production. Of the models with a significant effect on biomass production, the interaction P × W × T model explained biomass production best, as it recorded the lowest AIC (table VII). After 12 months of water stress, seedlings from the slightly arid zone watered with LWC had produced the highest biomass. The biomass of control seedlings was greater after six, nine and twelve months of water stress in the seedlings from the moderately, severely and slightly dry zones, respectively (figure 4). In addition, above and below-ground biomass showed significant differences between provenances aridity ($P < 0.001$) and duration of drought stress

Table VII.
Description of the fitted linear mixed-effects models on water use efficiency, total biomass production and stress tolerance index of *Saba senegalensis* seedlings. The table presents the inclusion of both fixed and random effects for each model. For each model, the *p*-value as well as the Akaike Information criterion (AIC) are presented.

	Dependent variable	Water use efficiency		Total biomass production		Stress tolerance index	
		***p*-value**	**AIC**	***p*-value**	**AIC**	***p*-value**	**AIC**
Random effect:	Block	0.002**	-4,054.8	0.011*	3,075.6	< 0.001***	378.6
Fixed effects:	Provenance (P)	0.029*	-4,499.2	0.056	3,073.1	< 0.001***	342.1
	Water regime (W)	< 0.001***	-4,521.3	< 0.001***	3,070.5	0.077	-979.2
	Duration of drought stress (T)	< 0.001***	-4,513.9	< 0.001***	3,051.8	0.034*	383.7
	P × W	< 0.001***	-4,450.1	0.004**	3,069.4	0.195	-930.0
	P × T	0.655	-4,413.2	0.056	3,037.6	0.702	352.9
	W × T	< 0.001***	-4,454.4	< 0.001***	3,052.7	0.519	-964.6
	P × W × T	< 0.001***	-4,239.1	0.001**	3,042.7	0.845	-842.9

Significant codes: *** 0.001; ** 0.01; * 0.05.

Table VIII.
Water use efficiency of *Saba senegalensis* seedlings under three water regimes.

Water regime	Water use efficiency*1000
Low water content	1.16 ± 0.07a
Medium water content	0.78 ± 0.05b
High water content	0.80 ± 0.05b

Values are means ± standard error. Means followed by the same letter are not significantly different at $P < 0.05$ for the water use efficiency.

Table IX.
Effects of the provenance aridity on the stress sensitivity index of plants parts.

Provenance	SSI of shoot (%)	SSI of root (%)
Severely dry	35.85 ± 6.06a	52.32 ± 3.17a
Moderately dry	36.98 ± 12.09a	49.27 ± 7.42b
Slightly dry	-40.95 ± 9.78b	0.65 ± 6.25c

Values are means ± standard error. Provenance values followed by the same letter in the same column are not significantly different at $P < 0.05$ for the same plant part. *SSI* Stress sensitivity index

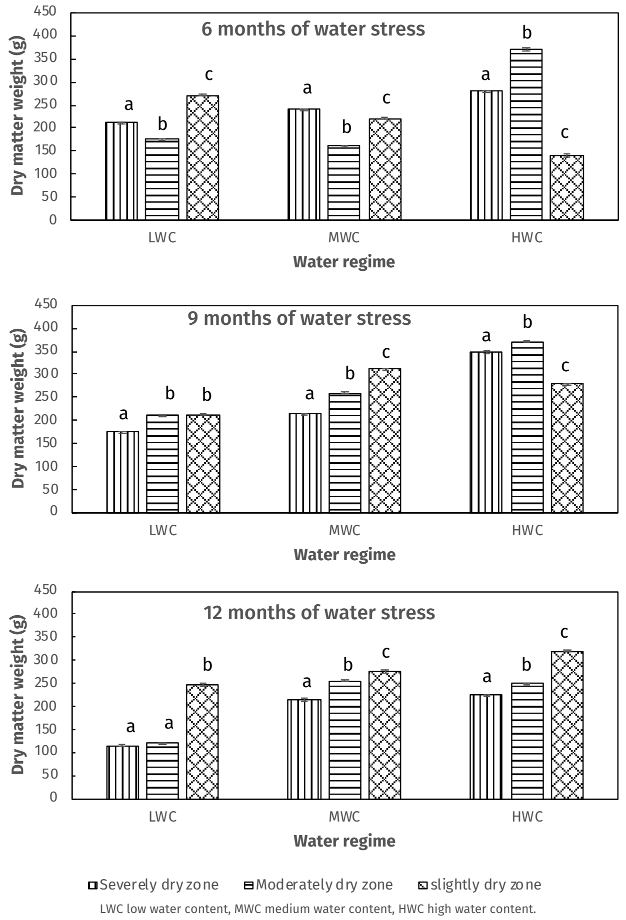
($P = 0.023$) and these differences depended on the provenance aridity. Within the plants from moderately and severely dry zones, root biomass was larger than above-ground biomass, while above-ground biomass was greatest than root biomass in those from slightly dry zone (figure 5 A). Also, regardless of duration of drought stress, root biomass was larger than above-ground biomass (figure 5 B).

Drought stress tolerance and sensitivity

Regardless of provenance, water regime and duration of drought stress, the overall mean value STI of seedlings was 0.96 ± 0.80. There was significant variation between blocks ($P < 0.001$), provenances ($P < 0.001$) and duration of drought stress ($P = 0.034$) for seedlings tolerance to drought stress. However, the provenance better explains this tolerance to drought stress, as his model recorded the lowest AIC (table VIII). Seedlings from slightly dry zone are more drought-tolerant than those from severely dry zone (figure 6). In addition, we showed that plants parts reacted differently to drought stress ($P = 0.004$) and that their sensitivity depended on provenance aridity ($P < 0.001$). In general, seedlings shoot was the least sensitive to drought stress and roots the most sensitive. Plants parts from slightly dry zone were the least sensitive to drought stress and those of moderately and severely dry zone were the most sensitive (table IX).

Discussion

This study examined the potential for acclimation of *S. senegalensis* to different climatic conditions. The results of the experiment revealed that the block showed a higher AIC than the three fixed factors for seedlings survival, RGR



LWC low water content, MWC medium water content, HWC high water content.

Figure 4.
Provenance and water regime effects on total biomass production of *Saba senegalensis* seedlings for three durations of drought stress. For each duration of drought stress, values (mean ± standard error) with different letters are significantly different at the 5% level.

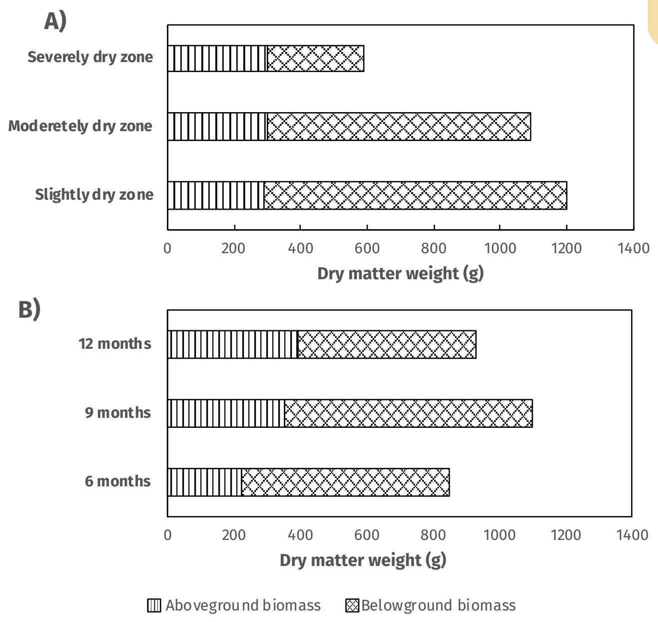


Figure 5.
Provenance (A) and duration of drought stress (B) effects on the aboveground and belowground biomass of *Saba senegalensis* seedlings.

in height, diameter and number of leaves, WUE, biomass production and tolerance to drought stress, which shows thatthe experiment was carried out under homogeneous conditions in the greenhouse. Drought stress reduced seedlings survival, aboveground biomass, while RGR in collar diameter increased. Seedlings from the slightly dry zone provenances produced more biomass when watered with LWC regime, and were more drought-tolerant than those from severely and moderately dry zone provenances.

Survival rate is one of the most important variables that shows the tolerance of species to stress (Bouda *et al.*, 2015). In response to drought, not only the seedlings survival is reduced, but growth parameters, such as the RGR in height and number of leaves, are also affected. Seedlings height and number of leaves increased with decreasing of amount of watering regime. Concerning the duration of drought stress, the RGR of *S. senegalensis* seedlings in collar diameter decreases and shoot to root ratio increases. Our first hypothesis, stating that water stress has a differential impact on the survival and growth of *S. senegalensis* depending on their provenances, is rejected. The decrease in these parameters has also been observed in many other species from the semi-arid region of Africa, such as *A. digitata* (Bouda *et al.*, 2015), *F. albida* (Koech *et al.*, 2016) and *V. paradoxa* (Bayala *et al.*, 2018). The literature does not have results of comparative studies of *S. senegalensis* seedling survival. A possible reason for the decrease in survival during 12 months of drought stress could be the limitation on the seedlings' potential root growth imposed by the small size of the pots. Thus, in terms of survival, the best genotype can be found from all provenances, because no significant difference was observed between seedlings provenances.

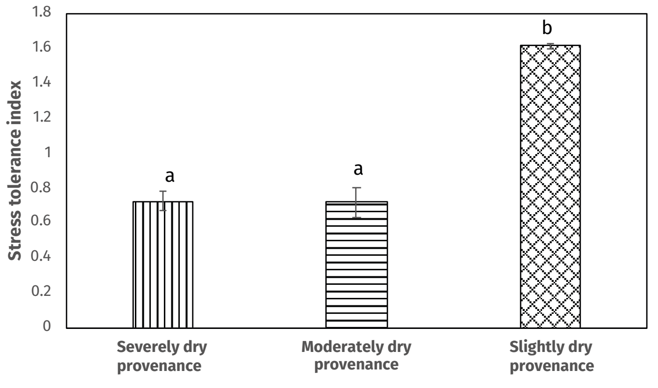


Figure 6.
Provenance effects on the tolerance to drought stress of *Saba senegalensis* seedlings.

Photo 3.
Measurement of the height of *Saba senegalensis* seedling.
Photo S. Diawara.

Photo 4.
Measurement of the root collar diameter of *Saba senegalensis* seedling.
Photo S. Diawara.

Results from this study indicated that the nine provenances of *S. senegalensis* seedlings use several morphological mechanisms to withstand drought. After the initiation of drought stress, all growth parameters and biomass production were affected through an increased intensity of drought stress (i.e. lower watering regime and longer duration of drought stress). This would mean acclimation to the longer duration of stress could directly decrease the growth as a consequence. This is confirmed by the RGR of collar diameter and roots length which decreases with the duration of drought stress. It is possible that this shift reflects an ontogenetic change and a corresponding change in strategy: after six months of drought stress, seedlings tend to invest more in roots, whereas after nine months the strategy changes to invest more in shoots to facilitate carbon capture. These finding merits further studies and underlines that long-term drought stress experiments are needed to understand the performance of *S. senegalensis* in the field.

We found that *S. senegalensis* seedlings subject to the moderate and high watering regimes showed smallest WUE and the higher was recorded for seedlings watered under the LWC regime. Many previous studies have found that WUE was improved under water limitation (Liu *et al.*, 2005; Binghua *et al.*, 2012). In theory, plants with high WUE would have a relatively fast dry matter accumulation compared to plants with low WUE (Hall *et al.*, 1994). According to these authors, under stress, plants with higher WUE are relatively more drought-resistant than plants with lower WUE.

Drought stress reduced biomass production of seedlings. The decrease in biomass production of the stressed seedlings can be explained by the reduction of seedling growth due to the severity of drought stress. To manage water availability limitations, plants have developed mechanisms to help withstanding water stress. These mechanisms include changes in leaf anatomy and ultrastructure, reductions in leaf size, thickening of leaf cell walls, increases in the number of large vessels, and reductions of stomata (Lisar *et al.*, 2012). The reduction of the seedlings' growth under water stress could be due to a consequence of loss of the cellular turgescence (Chartzoulakis *et al.*, 1993), because the processes implied in the growth (i.e. division, differentiation and cellular widening) are dependent upon turgor pressure and therefore highly sensitive to the water deficit. In addition, the amount of biomass of seedlings from the slightly dry zone was greater than those of seedlings from severely and moderately dry zones. This is because *S. senegalensis* is widely distributed across a broad geographical area and there are generally variations in both morphological and physiological attributes associated with the different provenances (Bayala *et al.*, 2018; Bouda *et al.*, 2015; Weber *et al.*, 2019).

As a result, the difference in provenances is associated with a variation in their acclimation ability in a particular area. Large variations between provenances may be mainly due to the genotypes, as all the experiments were conducted under same environmental conditions and they received similar treatments. Furthermore, decreases in biomass were reported by many studies as a response of seedlings to drought (Ludewig *et al.*, 2018; Stanik *et al.*, 2021). Thus, in terms of biomass production, the best genotype was found from slightly dry zone and sensitive genotypes were observed in seedlings from moderately and severely dry zones.

Saba senegalensis seedlings derived from slightly dry zone were more drought-tolerant than those from moderately and severely dry zones as we hypothesized. Thus, seedlings from slightly dry zone have superior tolerance under stress, because they have higher WUE under stress. In addition, plants parts from this zone were the less sensitive to drought stress and those of moderately and severely dry zone were the most sensitive. The difference in adaptive response of *S. senegalensis* seedlings to water stress among provenances indicate that establishment of the species under severe environments can be improved by selection of matching provenances in terms of their drought tolerance. This will favor selection of these provenances from slightly dry zone for planting in sites with high drought stress.

Conclusions

This study allows some conclusions about the ranking of *S. senegalensis* provenances in terms of seedling response to different watering regimes to aid in the selection of drought-tolerant provenances. The duration and severity of drought stress reduced seedling survival and RGR in collar diameter. The provenance variation, mainly in biomass production (above and below-ground) and tolerance stress index, indicates marked differences which can be used to aid the selection of the most suitable provenances for different locations. The best provenances, based on their tolerance to drought stress and high biomass production, that could be recommended for integration into semi-arid ecosystems of Burkina Faso, are those of the slightly dry zones (Bérégadougou, Mondon and Diaradougou). However, we recommend future research on the genetic diversity of *S. senegalensis* and its planting *in situ* under drought stress conditions to confirm these findings.

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Photo 5.
Uprooting of living seedling after six months of drought stress.
Photo S. Diawara.

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Data
The data used in this article is available on the private numerical drive with the following Internet link: https://doi.org/10.5281/zenodo.7867991
Inform the authors, and refer to this article when you use this data.

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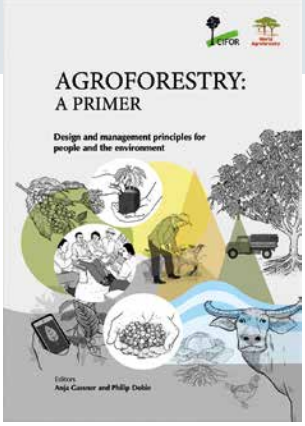

GASSNER A., DOBIE P., 2022. **AGROFORESTRY: A PRIMER – DESIGN AND MANAGEMENT PRINCIPLES FOR PEOPLE AND THE ENVIRONMENT.** INDONESIA-KENYA, ICRAF-CIFOR, 181 P.

Conventional agriculture is very productive. But high productivity comes at a cost: soil that is depleted or eroded, watercourses that are polluted or drying up, and a food system that produces 20–40% of greenhouse gas emissions. Many people now agree that we urgently need to transform the food system, including agriculture. Agroforestry, as a nature-based approach to production and land use, will play an important role in this transformation. Agroforestry is not new; farmers have practised it for thousands of years, and scientists have recognized it since the 1970s as a productive and ecologically sustainable form of agriculture and land use. But now agroforestry is suddenly at centre stage; it is promoted as a land-use strategy to support climate change mitigation and climate change adaptation, biodiversity conservation, sustainable agriculture and other goals. Many organizations recommend or use it as a tool for restoring ecosystems – not only agricultural ones, but also forest landscapes. Although not a cure-all, agroforestry has great potential to contribute to all the goals mentioned above. However, agroforestry is not just a matter of adding trees to farms. To realize its potential, practitioners need to understand its principles. Agroforestry: A primer is a guide to agroforestry principles and concepts – and how to use them effectively.

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INSTITUT NATIONAL DE L'INFORMATION GÉOGRAPHIQUE ET FORESTIÈRE, 2022. **INVENTAIRE FORESTIER NATIONAL – MÉMENTO 2022.** FRANCE, IGN, 35 P.

Créé en 1958 pour connaître la forêt de manière experte et neutre, l'inventaire forestier est le seul outil qui décrit l'ensemble des écosystèmes forestiers et la ressource en bois des forêts publiques et privées sur le territoire métropolitain. L'inventaire forestier national est basé sur une méthode dite « en continu », adoptée en 2005 pour rendre mieux compte des évolutions plus rapides qui traversent nos forêts suite aux tempêtes de décembre 1999 et à la sécheresse/canicule de 2003. Les résultats annuels sont basés sur les données collectées sur le terrain pendant les cinq années précédentes. Les principales données et résultats de l'inventaire sont publiés chaque année au sein de ce mémento. Il dresse un état des lieux de la forêt métropolitaine, en mettant en avant une partie des données collectées comme la surface, le volume de bois, les essences, la production, les prélèvements et la mortalité. Ces informations, basées sur les cinq campagnes de terrain menées de 2017 à 2021, sont produites à partir de mesures collectées sur près de 70 000 placettes d'observation (dont 13 000 placettes annuelles en 2021). Plus de cent agents, techniciens de terrain, photo-interprètes, experts de divers domaines, collectent et traitent les données, permettant de produire les résultats forestiers et sur les écosystèmes, et font évoluer les protocoles pour répondre aux évolutions du contexte environnemental. Ils s'appuient sur un ensemble de partenaires dont l'Office national des forêts (ONF), le Centre national de la propriété forestière (CNPF), l'Institut national de recherche pour l'agriculture, l'alimentation et l'environnement (INRAE), les services des mairies.

Adapté du résumé de l'éditeur.

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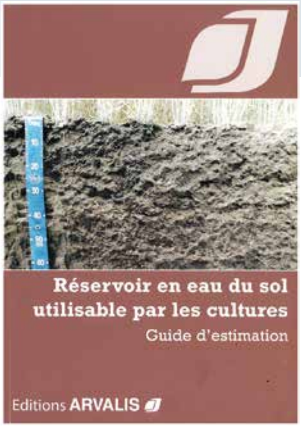

SCHEURER O., SEGER M., LAGACHERIE P., BEAUDOIN N., DESCHAMPS T., SAUTER J., FORT J.-L., COUSIN I., 2022. **RÉSERVOIR EN EAU DU SOL UTILISABLE PAR LES CULTURES – GUIDE D'ESTIMATION.** FRANCE, ÉDITIONS ARVALIS, 104 P.

Ce guide rassemble les résultats les plus récents issus de programmes de recherche qui ont réuni des communautés diverses (des spécialistes de l'hydrodynamique aux conseillers agronomes de terrain), comme par exemple ceux ayant trait au réservoir en eau des fractions grossières du sol (les cailloux) dont l'enjeu est considérable au regard de la surface agricole concernée. Il arrive à point nommé, alors que les impacts du changement climatique sont clairement perceptibles, et que la gestion de l'approvisionnement en eau des cultures devient un enjeu de premier plan dans de nombreuses régions de France. Il illustre aussi qu'une meilleure connaissance de la diversité des sols et de la variabilité de leurs propriétés, mais aussi de la diversité des cultures et de leurs systèmes racinaires, sont des clefs pour la gestion et l'adaptation des agroécosystèmes aux conditions climatiques actuelles et futures. Les nombreuses références opérationnelles rassemblées facilitent le dialogue et la mutualisation des indispensables observations et mesures nécessaires aux démarches agronomiques rénovées mais toujours ancrées sur de solides fondements scientifiques.

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