



Survival and growth of *Acacia senegal* (L.) Wild. (*Senegalia senegal* (L.) Britton) provenances depend on the rainfall at the site of origin

Oulimata Diatta^{1,2} · Mame Sokhna Sarr² · Jon Kehlet Hansen¹ · Adja Madjiguene Diallo² · Lene Rostgaard Nielsen¹ · Anders Ræbild¹ · Erik Dahl Kjær¹

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Abstract

• **Key message** Variation among provenances of *Acacia senegal* (*Senegalia senegal* (L.) Britton) in their survival and growth in height and diameter at two sites in Senegal could be partly explained by the climate at their site of origin and also revealed genotype-by-environment interactions. Breeding programs and forest restoration projects should carefully select germplasm for optimal performance of this socioeconomically important tree species.

• **Context** Several studies have shown important differences in adaptive properties among provenances (origins) of African savanna tree species, but there is a lack of studies on how these differences are expressed in different environments and age and to what extent they reflect local adaptation.

• **Aims** This study investigates the survival and growth of trees from 15 African *Acacia senegal* (*Senegalia senegal* (L.) Britton) provenances tested in two environments and relates the differences among provenances to the climate at their site of origin and tree age.

• **Methods** The study is based on 14 years growth in a common garden trial at two sites (Bambey and Dahra, Senegal) that differ in water availability, followed up by later assessment after 23 years at one of the sites.

• **Results** The variation among provenances in survival, height, and diameter was significant, and differences could be partly explained by the climate at their site of origin. In general, provenances from dry sites survived better at both sites. However, we observed genotype-by-environmental interactions where provenances from dry sites on average performed relatively poorer in height and diameter at the wettest site (Bambey) compared to the drier site (Dahra), while the opposite was the case for provenances from wetter sites.

• **Conclusion** The results support that divergent selection creates and maintains local adaptation of *Acacia senegal* provenances in relation to growth (height and diameter) and survival in areas with different water availability. This has important implications for choice of appropriate planting material for tree planting and for conservation of genetic variation among natural populations, but also for prediction of the effects of climate change.

Keywords Adaptation · Africa · Climate · Genotype-by-environment interaction · *Senegalia senegal*

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✉ Oulimata Diatta
diatta_oulimata@yahoo.com

✉ Erik Dahl Kjær
edk@ign.ku.dk

Mame Sokhna Sarr
sokhize@hotmail.com

Jon Kehlet Hansen
jkh@ign.ku.dk

Adja Madjiguene Diallo
madjidiallo@yahoo.fr

Lene Rostgaard Nielsen
Iron@ign.ku.dk

Anders Ræbild
are@ign.ku.dk

¹ Department of Geosciences and Natural Resource Management, University of Copenhagen, Rolighedsvej 23, 1958 Frederiksberg C, Denmark

² Institut Sénégalais de Recherches Agricoles/Centre National de Recherches Forestières (ISRA/CNRF), Route des Pères Maristes, BP 2312 Dakar, Sénégal

1 Introduction

Africa is reported to be a continent where half of the forest species are threatened (FAO 2014), and the Sudano-Sahelian region is one of the most vulnerable zones characterized by severe changes due to climate variability and human activities (Mertz et al. 2011; Bégué et al. 2011). For centuries, the Sudano-Sahelian region has experienced high rainfall variability (Tschakert 2007; Mertz et al. 2009), and adaptive strategies to respond to harsh natural conditions are important. For plants, drought stress is a factor that strongly limits survival and productivity (Khan et al. 2010), particularly in Senegal where drought is believed to have reduced forest species richness and tree density markedly during the last half of the twentieth century (Gonzalez 2001). Still, recent findings and climate projections suggest a trend of increasing vegetation greenness in arid and semi-arid Sahel (Olsson et al. 2005; Kaptué et al. 2015; Pausata et al. 2020) with 30% of woody tree cover in the sub-humid zone (Brandt et al. 2018). Although the recent observed greening trends in the Sahel region may reflect both changes in rainfall and land management, it pinpoints the uncertain and variable nature of growth conditions in the region. Large-scale planting program such as the Great Green Wall (GGW) aims to contribute to the reforestation efforts and reduction of land degradation in Sahelian regions reinforcing the greening tendency through planting of multipurpose tree species (O'Connor and Ford 2014). In Senegal, the implementation of the GGW has focused on planting of 26 ligneous plant species including the well-known gum Arabic tree, *A. senegal*, but so far only 119,000 ha, i.e., 15% of the targeted degraded lands (817,500 ha), have been restored (PAGGW 2020).

Improved insight in variation among provenances of Sahelian tree species is important in order to support conservation of valuable gene pools with special adaptive features, but also to guide selection and development of suitable seed sources (provenances) for future afforestation and reforestation of wooded landscapes. Natural variation among trees in adaptive traits is important to ensure that a species can cover heterogeneous environments and is essential for a species' ability to respond to new environmental conditions through selection of superior phenotypes.

Phenotypic variation is the combined effect of genetic and environmental heterogeneity and their interaction ($G \times E$ interaction). When studied under controlled environmental conditions, the variation among phenotypes can reveal underlying genetic variation (Dangasuk et al. 1997; Westoby et al. 2002; Stöcklin et al. 2009). By comparing the phenotypic performance of different populations

within and among different environments (test sites), it is further possible to quantify and qualify the genotype-by-environment interactions ($G \times E$) and thereby infer on past and ongoing adaptation of species to their physical environment (Westoby et al. 2002; Raddad 2007; Stöcklin et al. 2009).

By the use of hundreds of provenance trials (also known as common garden trials), it has been possible to compare phenotypic performance of different origins at multiple sites in temperate and boreal forests during the past century, and results have revealed eco-geographic patterns of genetic variation for many species (e.g., Langlet 1971; Morgenstern 1996; Risk et al. 2021). Provenance trials have also been widely applied to test to what extent tree species will be able to adapt to the ongoing climate changes (e.g., Matyas 1994; Rweyongeza 2011; Lobo et al. 2018) and to improve early selection (Chen et al. 2004; Dong et al. 2019). Most of the studied tree species have large geographic distribution areas that encompass substantial ecological variation, and the provenance trials have therefore in general not identified a single outstanding provenance—rather provenance tests have revealed that different provenances are suitable in different planting zones due to $G \times E$ interactions (e.g., Matheson and Raymond 1986; Wu and Matheson 2005). Understanding these patterns of adaptive genetic variation is essential for the development of site specific provenance recommendations, delimitation of breeding zones, and seed transfer guidelines for afforestation and reforestation, as well as to guide conservation programs (e.g., Burdon 1977; Matheson and Raymond 1986; Rehfeldt et al. 1999; Ying and Yanchuk 2006; Malaval et al. 2010).

Unfortunately, much less is known about the geographic and ecological patterns of variation in Sudano-Sahelian tree species, although the need for wise deployment and conservation of the species is immense. Several studies of tree species from the region have shown provenance variation in growth and survival, i.e., *Faidherbia albida* (Delile) A.Chev. (Billand and De Framond 1993), *Prosopis africana* (Guill. & Perr.) Taub. (Weber et al. 2008; Sotelo Montes and Weber 2009), *Balanites aegyptiaca* (L.) Delile (Weber and Sotelo Montes 2010), *Acacia senegal* (Larwanou et al. 2010; Ræbild et al. 2003a, b, c), *Parkia biglobosa* (Jacq.) Benth. (Ouedraogo et al. 2012), and *Vachellia nilotica* (L.) Willd. ex Delile (Larwanou et al. 2014). Observed phenotypic variation can often be associated with clinal patterns of environmental variation. Weber et al. (2008) and Sotelo Montes and Weber (2009) found clinal variation in growth and survival in *P. africana* in Niger. These studies suggested that, under dry conditions, provenances from drier areas performed better in growth and survival compared to provenances from the wetter parts of Niger and Burkina Faso. The same trends were found in 13 years old provenances of *B. aegyptiaca* (Weber and Sotelo Montes 2010)

in Niger and in *P. biglobosa* in Burkina Faso (Ouedraogo et al. 2012). Billand and De Framond (1993) linked provenance variation of *F. albida* grown in Burkina Faso with the latitude and promoted selected Sahelian provenances from Burkina Faso, Niger, and Mali for reforestation programs. In *A. senegal*, Ræbild et al. (2003a, b, c) found large variation in growth and survival among provenances growing in different trials in Burkina Faso with Sahelian provenances (Burkina Faso, Mali, and Niger) being superior to Sudanian provenances and highlighted the weak performance of a provenance from India. In Sudan et al. (2006) found genetic variation in growth, carbon isotope composition, and gum production between *A. senegal* provenances from clayey and sandy soil areas of the gum belt in Sudan and Raddad (2007) reinforced the differences by demonstrating genetic variation in seed morphology and seedlings traits between both type of provenances. Larwanou et al. (2010) assessed a mature *A. senegal* provenance trial in Niger, consisting of 11 provenances from Niger, Mali, and Sudan, and found a better performance of provenances from Mali and Niger in survival, height growth, and basal area that correlated with the rainfall and geographical distances of the origins. In general, these clinal patterns suggest local adaptation and have implications for breeding and planting programs.

Few, if any, studies have compared how different environments influence the variation in performance among Sudano-Sahelian tree populations. Based on results from other regions, $G \times E$ interactions can be expected also for Sudano-Sahelian trees and may indeed be pronounced in the region due to the harsh growing conditions where poor adaptation instantly can generate high mortality and thereby trigger strong selection. In addition, substantial differences in climate, soil type, and mineralogy are present within the natural distribution area of many Sudano-Sahelian tree species across Africa. Here, we study the situation for *Acacia senegal*.

Acacia senegal (L.) Willd. (Fabaceae, sub-family Mimosoideae) (syn. *Senegalia senegal* (L.) Britton) has a wide distribution across Africa (Sahelian belt and southern Africa) (Fagg and Allison 2004) and is also found in India and Pakistan. It is confined to arid zones and usually occurs in areas with low soil fertility and rainfall varying between 200 and 800 mm (Fagg and Allison 2004). The species includes four varieties, namely, vars. *senegal*, *kerensis*, *rostrata*, and *leiorhachis*, where the variety *senegal* (the only variety present in Senegal) is the main gum Arabic producing tree species in Sudano-Sahelian regions (Fagg and Allison 2004, Raddad and Luukkanen 2006, Diallo et al. 2015). *Acacia senegal* is an important source of income for rural populations that collect the gum Arabic. The species provides fodder particularly during dry periods, is used as fuel wood, restores soil fertility by its ability to fix nitrogen (Raddad et al. 2005), and is thus an essential component

of dryland agroforestry systems (Fagg and Allison 2004, Raddad and Luukkanen 2006). Multipurpose tree species such as *A. senegal* are highly recommended in reforestation and agroforestry programs in the Sahel due to their socio-economic importance and their ability to tolerate periods of water deficit.

The present study aimed to investigate the performance and genotype-by-environment ($G \times E$) interaction in survival and growth of African *A. senegal* provenances based on the analysis of two provenance trials in Senegal. We hypothesized that performance of provenances reflected adaptation to the climate at their site of origin and that these differences in adaptation lead to $G \times E$ interactions when grown at sites with different levels of water stress. We analyzed whether provenance choice may be affected by the age at assessment and discussed the implications of our results in relation to future *A. senegal* breeding programs and management of genetic resources.

2 Materials and methods

2.1 Provenances and sites

The study includes two common garden trials established in August 1994 in Dahra (15° 20'N, 15° 28' W, elevation 45 m) and Bambeby (14° 71'N, 16° 47' W, elevation 20 m), Senegal. The trial site at Dahra is characterized by very dry growing conditions with an annual rainfall of 388 mm and an annual mean temperature of 28.1 °C (estimates of WorldClim 2 2017). The soil is sandy, and the natural vegetation consists mainly of grass and sparse trees such as *Acacia tortilis* subsp. *raddiana* (Forssk.) Hayne (syn. *Vachellia tortilis* ssp. *raddiana* (Savi) Kyal. and Boatwr.), *A. senegal*, and *Balanites aegyptiaca* (Göttsche et al. 2016). The trial site at Bambeby is more humid with an annual rainfall of 482 mm and a mean annual temperature of 27 °C (estimates of WorldClim 2 2017). The soil at Bambeby is composed of leached tropical ferruginous sandy clays (Gray et al. 2013). The trials were protected against browsing by cattle and wild animals. Gum production was evaluated on the trees in 2001 and between 2007 and 2009 (Gray et al. 2013) by wounding the bark on selected branches. As all trees were harvested, we assume that the effect would have been similar on all trees.

The provenance trials were established from seeds collected from 15 provenances across the distribution area of *A. senegal* in Africa (Fig. 1; Table 1). Both trials are randomized complete block designs with four blocks. Each block is divided into 15 plots, representing the 15 provenances originally with 25 trees each and a spacing of 5 × 5 m, i.e., 1500 trees at the time of establishment. The mean annual temperatures and the annual rainfall at the sites of origin of provenances were derived from the WorldClim2 database

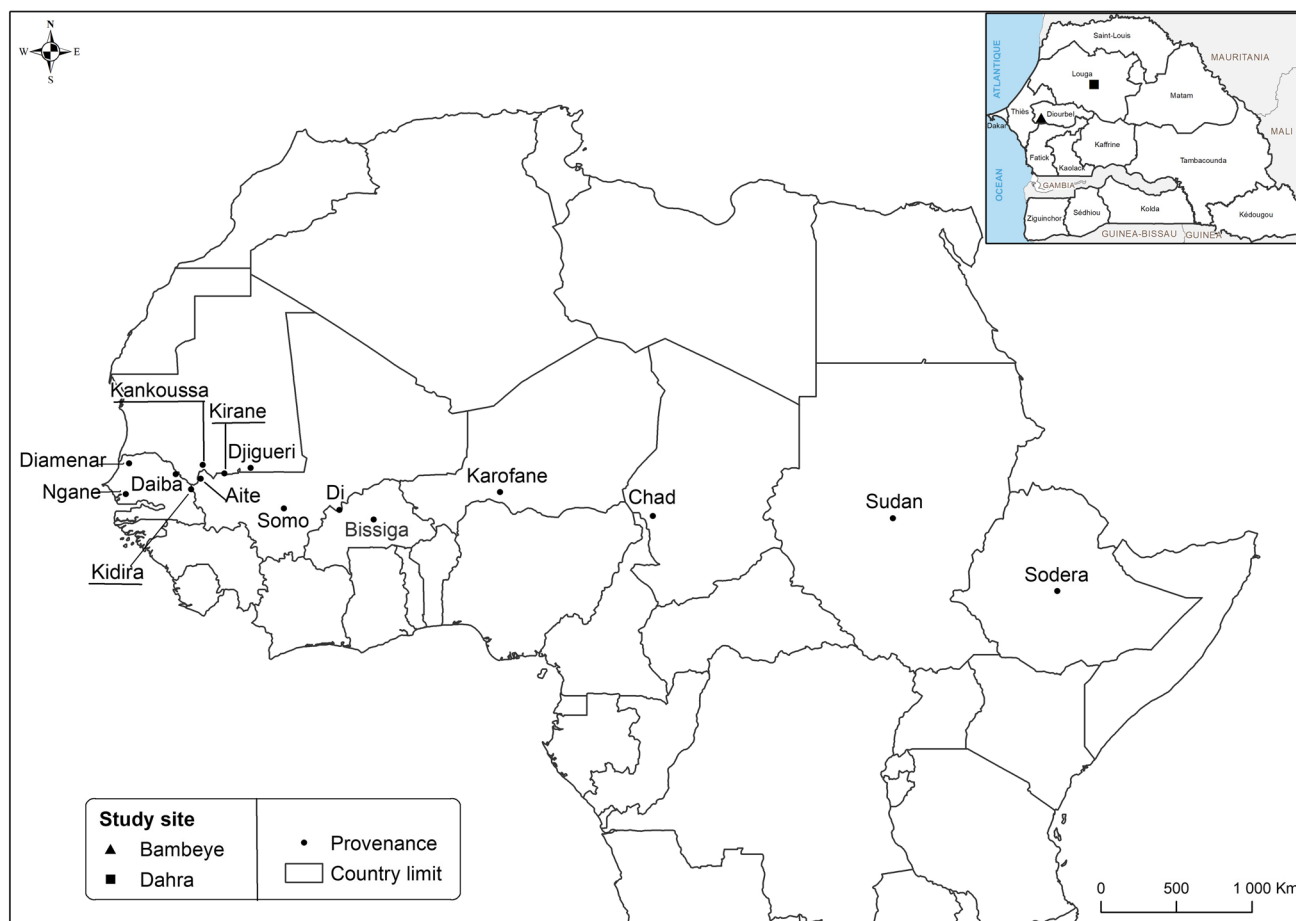


Fig. 1 Distribution the 15 African provenances of *A. senegal* located in the common gardens at Dahra and Bambeje, Senegal. Insert in the upper right shows the location of the two trial sites in Senegal

(Fick and Hijmans 2017). In addition, three aridity indices were used to describe the aridity conditions at the sites of origin, i.e., (i) De Martonne aridity index (A_M) which is the ratio between the mean annual rainfall (P) and temperature (T) plus 10 °C (De Martonne 1926); (ii) Thornthwaite aridity index (A_{TH}) calculated as the yearly sum of monthly ratios between rainfall (P) and evapotranspiration (P/E) (Thornthwaite 1931); and (iii) the monthly water availability indices (WAI) that were estimated as the differences between estimates of rainfall and potential evapotranspiration. These estimates were obtained from the Climatic Research Unit (CRU) East Anglia University version 4.01 database (Harris et al. 2014) for the period 1961–1990. We expect that climate differences among provenance sites for this period reflect the long-term differences in growing conditions that can have led to divergent natural selection in adaptive traits among provenances.

Yearly cumulated WAI (WAI0) was calculated as the sum of monthly WAI for the months where WAI was above zero (0) and provides an estimate of the water surplus available over the rainy season. Based on the yearly estimates, the

average was calculated for the period 1961–1990. Provenances with high WAI0 thus come from wet sites, and provenances with low WAI0 come from dry sites.

2.2 Data collection and analysis

The growth was assessed in 2008, i.e., 14 years after establishment in both common garden trials. The height of the trees was measured using a telescopic measuring pole, and the stem diameter was measured at 30 cm (basal diameter) above ground level using a caliper. For the estimation of survival, a record of (0) was given for a dead tree, and (1) for a living tree. For the Dahra trial, the same measurements were also made in 2017, i.e., at age 23, but similar data could not be obtained from Bambeje.

The analysis of variance was based on average values per plot to assure independence between residuals. The percent of living trees in each plot was calculated and used for the analysis on survival. The R statistical package software (R Core Team 2020) was used for all analysis, and figures were

Table 1 Origins and environmental characteristics of *A. senegal* provenances used in the study. Provenances are arranged according to WAI0

Provenance	Country	Latitude	Longitude	Altitude (masl)	Mean annual temperature (°C) ^a	Rainfall (mm) ^a	PET (mm) ^b	Martonne index (A_M) ^b	Thornwaite index (A_{TH}) ^b	WAI0 (mm) ^b
Diamenar	Senegal	16°00' N	15°54' W	20	27.13	288	1950	8	2	28
Djiguéri	Mauritania	15°44' N	08°40' W	226	28.92	309	2195	8	2	45
Karofane	Niger	14°18' N	06°11' E	280	28.38	366	2412	10	2	51
Sudan	Sudan	12°44' N	29°35' E	620	26.84	408	1775	11	3	56
Kirane	Mali	15°23' N	10°15' W	140	29.32	380	2018	10	3	59
Kankoussa	Mauritania	15°56' N	11°27' W	80	29.71	294	1917	7	3	60
Chad	Chad	12°49' N	15°18' E	280	28.97	349	2098	9	3	64
Daitba	Senegal	15°22' N	13°08' W	28	29.56	437	1813	11	3	65
Aite	Mali	15°05' N	11°39' W	80	29.65	449	1855	11	3	75
Di	Burkina Faso	13°10' N	03°25' W	260	28.02	637	1832	17	5	121
Bissiga	Burkina Faso	12°26' N	00°32' W	280	28.28	696	1915	18	5	128
Kidira	Senegal	14°28' N	12°13' W	39	28.93	611	1724	16	5	184
Somo	Mali	13°17' N	04°54' W	40	27.45	627	1767	17	6	187
Ngane	Senegal	14°08' N	16°12' W	2	27.92	570	1871	15	5	194
Sodera	Ethiopia	08°24' N	39°23' E	1500	21.36	762	1302	24	10	292
Sites										
Dahra	Senegal	15° 20' N	15° 28' W	45m	28.1	388	1805	10	3	75
Bambey	Senegal	14° 71' N	16° 47' W	20m	27	482	1864	13	4	122

^aClimate data derived from WorldClim, ^bEstimates based on climate data from the CRU East Anglia University version 4.01 database (Harris et al. 2014). De Martonne Aridity index ($A_M = P / (T + 10)$), Thornthwaite aridity index ($A_{TH} = \text{yearly sum of monthly ratios (P/E)}$), cumulated water availability index (WAI0) for the months with WAI > 0, mean for the years 1961–1990

produced using the packages *ggplot2* (Wickham 2016) and *ggpubr* (Kassambara 2020).

Analyses were based on three steps:

- 1) Quantifying and testing differences among the *A. senegal* provenances when grown at each of the two test sites. This step was used to calculate the average performance of the provenances at each of the two sites Bambey (age 14) and Dahra (ages 14 and 23). To study the effect of assessment age, we tested the relative performance between years and calculated the correlation between age 14 and age 23 for the Dahra trial where data from both years were available.
- 2) Comparing the performance of the provenances at each of the two sites with the climate at their site of origin based on linear regression. The step allowed us to study the extent to which the differences among the provenances in their survival and growth (height and diameter) can be explained by matches between the climatic conditions at the test site, and at the origin of the provenances, and to what extent such patterns differed between the two test sites.
- 3) Testing if the relative performance of provenances depends on the site and age. To obtain scale free measures of the populations \times site interaction, we estimated correlations between provenance least square means for each site (similarly to the approach suggested by Burdon (1977)). To investigate the potential underlying causes of the interactions, we estimated how much provenance height and diameter (as proxies for growth) and survival were improved at the wetter Bambey site compared to the drier Dahra site and used linear regression models to test if these differences depended on climate at the sites of origin.

For the tests of variation among provenances, years, and $G \times E$ interaction in survival, height, and diameter (Steps 1 and 3), we applied the three general linear models (1), (2), and (3) (for analysis per site and across years and sites, respectively) using the function *lmer* (linear mixed-effect models) in the package *lme4* (linear mixed-effect models using “Eigen” and S4) (Bates et al. 2015) for R (version 3.4.2):

$$Y_{ij} = \mu + B_i + P_j + \varepsilon_{ij} \quad (1)$$

where Y_{ij} is the plot average of the trait in block i , B_i is the random effect of block i , P_j is the fixed effect of provenance j , and ε_{ij} is the residual error assumed to be independent and following a normal distribution.

$$Y_{ijk} = \mu + B_{i(k)} + P_j + Z_k + PZ_{jk} + \varepsilon_{ijk} \quad (2)$$

where Y_{ijk} is the plot average of the trait in the block i at the site k , $B_{i(k)}$ is the random effect of the block i

within site k , P_j is the fixed effect of provenance j , Z_k is the fixed effect of the site k , PZ_{jk} is the random interaction of the provenance j and site k , and ε_{ijk} is the residual error assumed to be independent and following a normal distribution. Residuals were plotted against fitted values and by sites to control for presence of heteroscedasticity, and residual histograms were plotted to check the assumption of normal distribution. Least square means were estimated for the provenances.

Model (3) similar to model (2), but with years replacing sites, was used to test for effects of years and effects of provenance by year interactions at Dahra.

Regression analyses were applied to study relationships between provenance performance on the one side and climate at the origin of the provenance and latitude, longitude, and altitude of the provenance origin on the other side (Step 2). The function *corr.test* in the package *psych* (Revelle 2019) was used to test for significance of correlations. Regression analyses and plots were made using the *ggscatter* function in the package *ggpubr* (Kassambara 2020) as implemented in R (R Core Team 2020).

For Step 3, we first calculated the relative performance of each provenance $Z_{j(k)}$ at each site ($Z_{j(k)} = (X_{j(k)} - \mu_k) / \mu_k$) where $X_{j(k)}$ is the least square mean estimate for provenance j at site k and μ_k is the average of least square mean estimates at site k . $Z_{j(k)}$ values above 0 thus reflected above average performance of a specific provenance at the site, while negative values reflected the opposite. We then calculated the difference between the two sites in the value $G_j = Z_j(\text{Bambey}) - Z_j(\text{Dahra})$. $G_j > 0$ thus reflects that provenance j perform relatively better at Bambey, while $G_j < 0$ reflects that provenance j perform relatively better at Dahra. We tested the regression of G_j on annual rainfall and water availability index (WAI0) at the provenance origins using the *ggscatter* function. Pearson's correlations between sites were estimated based on least square means of provenances for each site.

3 Results

3.1 Survival, height, and diameter

Most provenances had the highest survival and largest height and diameter at the wet site Bambey, compared to the dry site Dahra (Table 2). At age 14, the overall mean survival rate in Bambey was 58%. The overall mean height and diameter were 4.8 m and 11.6 cm, respectively, compared to only an overall mean survival rate of 25% at Dahra and overall mean height and diameter of 4 m and 8.6 cm, respectively

Table 2 Least square means for survival rate, height, and diameter of *Acacia senegal* provenances in Bambey and Dahra (model 1). Provenances are arranged according to WAI.

Provenance	Survival (%)			Height(m)			Diameter (cm)		
	Bambey	Dahra	Dahra	Bambey	Dahra	Dahra	Bambey	Dahra	Dahra
	Age 14	Age 14	Age 23	Age 14	Age 14	Age 23	Age 14	Age 14	Age 23
Diamenar	56	36	29	4.6	3.8	4.0	10.2	7.9	13.2
Djigueri	72	27	26	4.6	4.5	4.2	10.3	9.2	15.6
Karofane	69	24	22	4.3	3.7	3.9	11.0	8.4	13.2
Sudan	72	44	20	4.8	4.5	4.4	11.4	9.6	13.9
Kirane	66	25	18	4.8	4.2	4.3	11.1	9.0	14.1
Kankoussa	49	33	29	4.2	3.4	4.0	9.9	6.6	13.0
Chad	85	28	16	5.3	4.8	4.6	14.5	10.4	18.6
Daïba	60	26	18	4.4	4.4	4.4	9.4	10.2	14.9
Aïte	47	25	20	5.7	4.5	4.7	13.4	8.8	15.1
Di	30	13	3	3.9	3.8	4.1	9.9	8.6	15.6
Bissiga	62	11	9	5.2	4.3	5.0	13.3	10.0	18.9
Kidira	59	23	15	5.5	3.8	4.2	12.4	7.4	11.6
Somo	41	14	8	4.5	2.8	3.7	11.4	5.9	12.8
Ngane	62	21	17	5.8	4.5	4.7	15.2	9.8	16.8
Sodera	38	18	12	4.0	3.3	3.3	10.3	7.4	9.1
<i>p</i> Value	0.0031**	0.0055**	0.02136*	< 0.0001***	0.1376	< 0.0001***	< 0.0001***	0.0451*	0.0003***
Mean	57.9	24.5	17.5	4.8	4.0	4.2	11.6	8.6	14.4
SE	10.8	5.2	4.7	0.2	0.5	0.2	0.5	1.0	1.2

SE standard error of provenance least square means, Significance levels: * $P < 0.01$, ** $P < 0.001$, *** $P < 0.0001$

(Table 2). At age 23, the overall mean survival at Dahra was decreased to 18%, while the overall mean diameter was increased to 14.4 cm (Table 2).

In Bambey, the survival rate, height, and diameter varied significantly among provenances (Table 2). The provenance Chad had the highest survival rate (85%), while the provenance Di (Burkina Faso) had the lowest value (30%). With respect to growth, the local Senegalese Ngane provenance was superior in both height and diameter, but there were also slow growing Senegalese provenances, e.g., Daiba that had the smallest diameter of all provenances at this site (Table 2).

In Dahra, differences among provenances were significant except for height at age 14. Here, the span in survival at age 14 varied from 44% (Sudan) to 11% (Bissiga from Burkina Faso). For diameter, the provenance Chad had the largest diameter (10.4 cm), but based on few trees because of low survival, Somo from Mali had the smallest (5.9 cm) diameter and also low survival (Table 2). At age 23, the span in survival was from 3 to 29% with Bissiga and Somo below 10% (Table 2). The interactions between provenance and year in Dahra were not significant for neither survival, height, or diameter (Table 3), and the age-age correlations between age 14 and 23 correspondingly were high for both diameter ($r_{(14;23)} = 0.75$)

and survival ($r_{(14;23)} = 0.78$) (Fig. 2a, b). The correlations between survival and diameter were non-significant for both age 14 ($r_{(14)} = -0.17$) and age 23 ($r_{(23)} = -0.14$).

Table 3 Analysis of variance for *A. senegal* at Dahra in 2008 (age 14) and 2017 (age 23) (model 2)

Source	df	SS	MS	F	P
Survival rate					
Provenance	14	0.5702	0.0407	4.11	< 0.0001***
Year	1	0.1359	0.1359	13.72	0.0004**
Provenance × year	14	0.0857	0.0061	0.62	0.8431
Height					
Provenance	14	23.2206	1.6586	3.47	0.0002***
Year	1	0.1605	0.1605	0.34	0.58300
Provenance × year	14	2.8037	0.2003	0.42	0.96440
Diameter					
Provenance	14	336.62	24.044	5.56	< 0.0001***
Year	1	250.22	250.221	57.86	< 0.0001***
Provenance × year	14	76.75	5.482	1.27	0.2464

Significance levels: * $P < 0.01$, ** $P < 0.001$, *** $P < 0.0001$

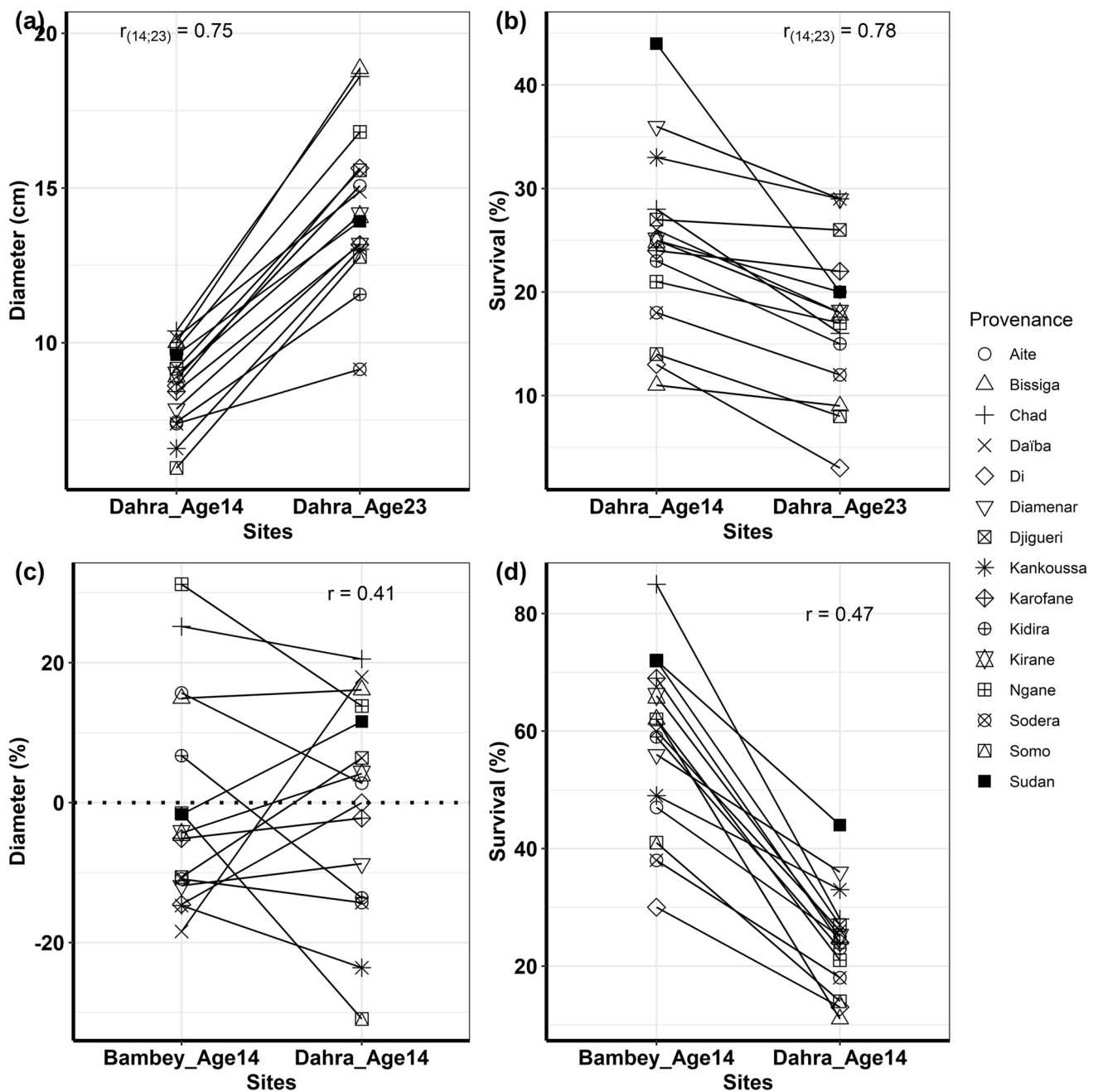


Fig. 2 Performance of *A. senegal* provenances between years (Dahra 2008 and Dahra 2017) and across sites (Dahra and Bambey 2008). (a), (b), and (d) are least square means values of the provenances, and

(c) is Z, % deviation from the mean at the trial site. Note: G \times E interaction for survival was not significant ($p = 0.08$), r: Pearson's correlation coefficient

3.2 Relationship between survival and climate at the site of origin

The regression analyses identified significant relationships between provenance survival at the two sites and annual rainfall at the site of origin (Fig. 3). Generally, provenances from drier areas survived better at both sites, but the relationship was strongest at the driest test site (Dahra). No significant

relationship was found between diameter or height and any of the climate variables. This was the case at both sites (not shown).

3.3 Genotype \times environment interaction

The interaction between provenances and sites (G \times E) was highly significant for diameter, but only close to significance for survival and not significant for height (Table 4). Correspondingly,

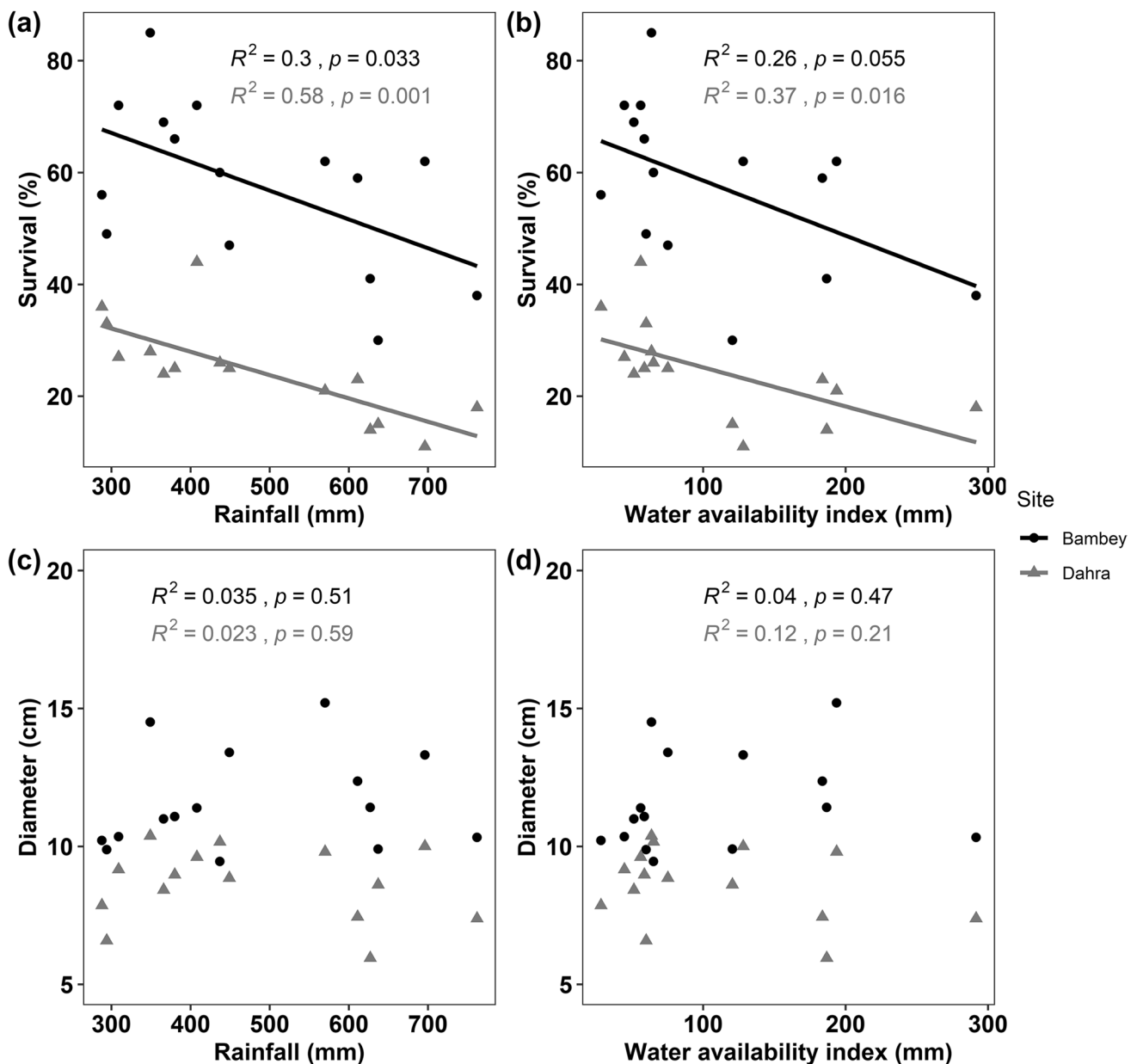


Fig. 3 Pair-wise plots of survival rate and diameter against annual rainfall (a, c) and the cumulated water availability index for the months with precipitation > potential evapotranspiration (WAI0) at Dahra and Bambej (b, d). R^2 and p values from regression analyses are inserted

the Pearson's correlation between provenance least square means for diameter at the two sites was only moderate ($r = 0.41$) with changes in rank between the two sites (Fig. 2c).

As illustrated in Fig. 2c, the Senegalese provenance Kidira had a faster diameter growth (7% above the average) at Bambej, but a poorer growth at Dahra (-14%). Provenances Sudan (Sudan), Kirane (Mali), Djiguéri (Mauritania), and Daiba (Senegal) performed better than the average at Dahra (12%, 4%, 6%, and 18% respectively)

and poorer in Bambej (-2%, -4%, -10%, and -18% respectively). The four provenances Ngane (Senegal), Chad, Aite (Mali), and Bissiga (Burkina Faso) had above average performance at both sites, while Somo (Mali), Karofane (Niger), Diamenar (Senegal), Di (Burkina Faso), Sodera (Ethiopia), and Kankoussa (Mauritania) performed poorly at both sites.

$G \times E$ for survival was close to significance ($p = 0.08$; Table 4), and we observed some change in rank among

Table 4 Analysis of variance for *A. senegal* at Dahra and Bambey (model 3)

Source	Df	SS	MS	F	P
Survival rate					
Provenance	14	1.12	0.08	3.93	< 0.0001***
Sites	1	0.46	0.46	22.53	0.0031**
Provenance × site	14; 1	0.47	0.03	1.66	0.0802
Height					
Provenance	14	29.64	2.12	4.91	< 0.0001***
Sites	1	2.36	2.36	5.46	0.0579
Provenance × site	14; 1	7.50	0.54	1.24	0.263
Diameter					
Provenance	14	195.56	13.97	6.53	< 0.0001***
Sites	1	97.30	97.30	45.51	0.0005***
Provenance × site	14; 1	77.97	5.57	2.60	0.0036**

Significance levels: * $P < 0.01$, ** $P < 0.001$, *** $P < 0.0001$

provenances when plotting provenances' performance at the two sites (Fig. 2d). The Pearson's correlation between provenance least square means for survival at the two sites was also only moderate ($r = 0.47$).

3.4 Relationship between difference in provenance performance at the two sites and climate at their origin

The difference in relative performance in height and diameter of the provenances at the two sites (G_j) was significantly related to water availability index at the provenance sites of origin. Provenances from areas with higher water availability thus ranked relatively better in terms of height and diameter at the wetter site Bambey, compared to drier site Dahra (Fig. 4). Relationships with other climate variables, i.e., mean annual rainfall, temperature, and the A_M and A_{TH} aridity indices, were not significant (Appendix Table 5). For survival, none of the regressions of G_j on annual rainfall, mean annual temperature, and aridity indices were significant.

4 Discussion

4.1 Variation among provenances and sites

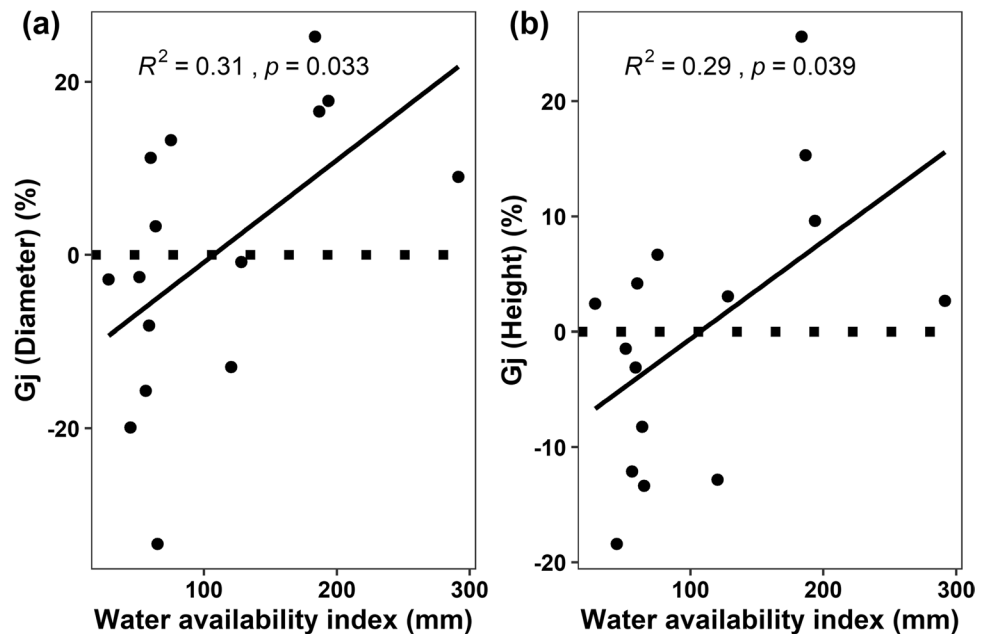
The present study is based on results for only two trials in one country, and the extrapolation of the results should be done with caution. However, the study demonstrated that survival and growth (height and diameter) of

A. senegal trees depended on their genetic origin and that the observed variation among the provenances in survival could be partly explained by the climatic conditions at their sites of origin. Trees that originated from dry sites in general survived better than trees from wetter sites at both test sites. However, with respect to height and diameter, the provenances from wetter sites generally ranked better at the wet test site (Bambey), while provenances from drier sites in general ranked better at the dry site (Dahra). These results support that the observed variation among provenances in their survival and growth reflects adaptation to local climatic conditions. Such development of ecotypes reflects a general trend to differentiation in physiological and morphological traits as response to divergent natural selection (Eriksson et al. 2020).

The significant variation among provenances confirmed the genetic differences in growth traits among natural populations of *A. senegal* when tested in common garden trials in Africa (Ræbild et al. 2003a, b, c; Raddad and Luukkanen 2006; Raddad 2007; Larwanou et al. 2010). Genetic differentiation in growth among provenances tends to be a common feature of Sahelian tree species (Weber and Sotelo Montes 2010; Chládová et al. 2019; Lompo et al. 2020). Genetic variation among origins of *A. senegal* has also been documented based on molecular markers (Assoumane et al. 2012, Ode et al. 2015, Diallo et al. 2015). DNA-based studies have revealed that many natural populations of *A. senegal* consist of a mixture of diploid and polyploid trees, where the ploidy level can influence the fitness of the trees (Diallo et al. 2016). We have in a parallel study found that the provenances analyzed in the present study differ in frequency of polyploids and documented morphological differences that may reflect adaptation to different environments (Diatta et al. 2021).

From an applied perspective, the variation among provenances allows identification and use of productive provenances (in terms of growth) in restoration and tree improvement programs of *A. senegal*. However, the present study documents presence of $G \times E$ interaction, and selection of superior provenances for planting programs must therefore be based on testing at multiple sites in order to be able to reveal the best genetic origin for a specific site. This is a common situation in many species (Wu and Matheson 2005; Correia et al. 2009; Rweyongeza 2011; Belaber et al. 2020), but here shown for the first time in *A. senegal*. Our study is based on only two sites and can therefore only be seen as a pilot study when it comes to mapping $G \times E$. A finer scaled set of test sites will be required to guide number and location of test sites for breeding of *Acacia senegal*. However, an alternative to classical breeding programs with multiple

Fig. 4 The relative advantage of growth at the wetter site Bambeby compared to the dry site Dahra (G_j) of the provenances related to the cumulated water availability index for the months with precipitation > potential evapotranspiration (WAI0) at their sites of origin of the provenances. Values above 0 denote relative superiority at the wet site Bambeby, and values below 0 denote relative superiority at the dry site Dahra



test sites can be to accommodate the presence of $G \times E$ by applying domestication based on a decentralized, multiple breeding concept (see Namkoong et al. 1980; Dhakal et al. 2005).

Previous studies have suggested presence of local adaptation in *A. senegal*. When investigating genetic variation among African provenances, Larwanou et al. (2010) found that performance varied clinally with rainfall, while Ræbild et al. (2003a,b,c) demonstrated that local West African Sahelian provenances performed better than Sudanian provenances in trials in Burkina Faso. Raddad (2007) highlighted the formation of ecotypes differentiated by morphological and growth parameters in young plants. The $G \times E$ interactions presented here based on a reasonably high number of provenances confirm local adaptation to rainfall with respect to growth parameters. Still, the present study is only based on two sites. Future investigations based on establishment of a larger number of trials across Sahel based on an internationally coordinated effort will be highly valuable.

Clinal variations in survival have previously been observed in provenances of *Prunus africana* in Niger (Weber et al. 2008; Sotelo Montes and Weber 2009; Weber and Sotelo Montes 2010). It was demonstrated that growth and survival of *P. africana* increase from more humid to drier parts of the sample region. This is in line with our observed clines in survival that likely reflect a local adaptation of *A. senegal* to drought. The eco-physiological background of the observed clines remains unknown, but may be due to differences in rooting depth

and the ability of roots to withstand drought stress and the maintenance of physiological functions (Poorter et al. 2012; Olmo et al. 2014; Brunner et al. 2015). *Acacia senegal* like many Sahelian species is a drought tolerant species with an ability to use water and nutrients efficiently and a relatively large allocation of biomass to roots (Raddad and Luukkanen 2006; Raddad 2007; Gray et al. 2013; Merine et al. 2014). A general feature of tree species adapted to dry environments is that they develop higher root-to-shoot ratios and deeper root systems compared to species from mesic environments (Markesteijn and Poorter 2009; Hartmann 2011; Brunner et al. 2015). Differences in rooting depth and the ability of plants to access soil moisture at depth are likely to influence plant survival (Padilla and Pugnaire 2007; Poorter et al. 2012; Olmo et al. 2014). The initial growth in *A. senegal* is predominantly underground with seedlings developing a long tap-root (Fagg and Allison 2004), and in a provenance trial in Sudan, seedlings of *A. senegal* provenances from sandy soils had longer root lengths compared to provenances from clayey soils (Raddad 2007). Generally, as a response to drought, plants tend to decrease shoot biomass and increase root biomass, allowing them to reduce water loss by transpiration and increase the efficiency of soil exploration and water acquisition, leading to a higher probability of survival (Lloret et al. 1999; Poorter et al. 2012). Based on the findings of the present study, it will therefore be interesting to test if *A. senegal* provenances from the dry sites develop deeper rooting systems compared to provenances from wetter sites.

4.2 Ecology and implications of the G × E interaction

While data indicate that *A. senegal* provenances from the drier parts of the distribution area in Africa are superior with respect to survival, provenances from the wetter parts show superior performance with respect to above-ground growth under favorable (less dry) conditions. This suggests that while survival is the most critical for fitness under dry conditions, it may come with a negative fitness trade-off against fast growth (which may increase competitiveness for other resources, and options for earlier and more abundant seed production) under more humid conditions.

The relative advantages of different *A. senegal* provenances to grow under either wet or dry conditions may reflect different water-use strategies (Raddad and Luukkanen 2006; Gray et al. 2013; Li and Wang 2003) as also discussed above. The WAI0 is higher at Bambey (122 mm) compared to Dahra (75 mm). In addition, the sandy-clay soils at Bambey are likely to have higher water holding capacity compared to the sandy soils at Dahra and therefore less prone to desiccation in the growing season. Studies of stable isotopes suggested variation among *A. senegal* provenances in their water use efficiency (Raddad and Luukkanen 2006; Gray et al. 2013; Sarr et al. 2021; Diatta et al. 2021). For example, *A. senegal* provenances from clay soils displayed a less conservative water use efficiency (WUE) resulting in fast growth and high gum productivity compared with provenances from sandy soils that displayed more conservative water use (Raddad and Luukkanen 2006). Similar results on variation on WUE were found in *A. tortilis* ssp. *raddiana* at three semi-arid sites in Kenya (Newton et al. 1996), in dominant woody species on a moisture gradient in an African savanna in Bostwana (Midgley et al. 2004), and in dominant species along a continental-scale climate gradient in Australia (Rumman et al. 2018). However, Gray et al. 2013 found that seedlings and mature *A. senegal* trees may exhibit different WUE strategies suggesting plasticity in WUE that optimizes carbon assimilation and water use at young age, while plants are shallow-rooted, but relax water control at an advanced age when roots are deeper and able to access groundwater. Indeed, the root system of adult *A. senegal* trees represents 40% of the total biomass compared to the aboveground biomass, i.e., stem and branches (Poupon 1977 in Fagg and Allison 2004). Whether our provenances from wetter sites exhibited a prodigal water use strategy that led to a faster diameter and height growth but lower chances of survival will have to be tested in follow up experiments.

4.3 Choice of provenances for planting activities

Regarding selection of future germplasm for breeding, the provenances Sudan, Kirane, Djigueri, and Daiba that had the largest diameter at Dahra and originate from areas with WAI0s close to the WAI0 of the trial site. According to Gray et al. (2013), the Sudanese provenance has high gum production. As Bambey is located outside the zone of gum production in Senegal (Gray et al. 2013), we suggest to prioritize the best provenances at Dahra when planning selection for gum production, because we consider this site the better representative of sites suitable for plantings of *A. senegal* for gum Arabic production. However, the observed G × E calls for caution against providing general recommendation based on the trial when planting the species under environmental conditions that differs from the trial site in Dahra. As discussed above, working in multiple breeding zones based on selection of genotypes from origins having similar environmental conditions to the site of planting is therefore advisable.

The comparison of survival and growth after 14 and 23 years at Dahra showed that the main patterns in general did not change much during the 9 years. An interesting exception is the provenance from Sudan that had highest survival and good growth at the Senegal trial after 14 years, but has lost its superiority when assessed at age 23. The general provenance-by-age interaction was not significant, but the changed rank of the Sudan provenance draws attention to the fact that especially exotic provenances should be tested for longer periods before it can be concluded that they are superior to native origins.

5 Conclusion

The present study supports that African provenances of *A. senegal* are genetically differentiated in important adaptive traits as a result of local adaption to different ecological conditions within the species' natural distribution in Africa. The results point towards the need for development of seed transfer guidelines and policies to avoid planting trees with poor adaptation in planting programs. This implies that breeding programs should carefully identify breeding and deployment zones. The results also highlight the importance of conserving genetic resources of the economically very valuable species based on a network of multiple populations in order to sample variation among populations. This is crucial in the face of ongoing climatic change where today's arid sites may become important seed sources for tomorrow's plantings programs in desertified areas.

Appendix

Table 5 Pairwise correlations between relative advantage of growth (height and diameter) and survival at the wetter site Bambey compared to the dry site Dahra (G_j) of populations means and climate variables at their sites of origin.

	G_j (height)	G_j (Diameter)	G_j (Survival)	Latitude	Longitude	Altitude	Rainfall	Mean_temp	A_M	A_{TH}	WAI0
G_j (Height)	-	0.89***	0.08	-0.05	-0.25	-0.11	0.40	-0.07	0.36	0.40	0.54*
G_j (Diameter)		-	0.08	-0.18	-0.07	0.02	0.35	-0.14	0.33	0.41	0.55*
G_j (Survival)			-	-0.20	-0.07	0.01	0.41	0.13	0.32	0.20	0.27
Latitude				-	-0.84**	-0.9***	-0.72**	0.84***	-0.81***	-0.84***	-0.73**
Longitude					-	0.88***	0.27	-0.72**	0.4	0.48	0.31
Altitude						-	0.48	-0.89***	0.64*	0.72**	0.56*
Rainfall							-	-0.53*	0.98***	0.9***	0.88***
Mean_temp								-	-0.69**	-0.76***	-0.67**
A_M									-	0.96***	0.920***
A_{TH}										-	0.96***
WAI0											-

Mean_temp: annual mean temperature, A_M : De Martonne aridity index ($P/(T + 10)$), A_{TH} : Thornthwaite aridity index (yearly sum of monthly ratios (P/E)), WAI0: cumulated water availability index for the months with WAI > 0, mean for the years 1961–1990, Bold values represent significant correlations. Significance levels: * $P < 0.01$, ** $P < 0.001$, *** $P < 0.0001$.

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Data availability Data is publicly available through the University of Copenhagen - Electronic Research Data Archive (ERDA). <https://erda.ku.dk/archives/845762612be1bf53dd482052126ce220/published-archi-ve.html>.

Declarations

Ethics approval Not applicable.

Consent to participate Not applicable.

Consent for publication All authors gave their informed consent to this publication and its content.

Conflict of interest The authors declare no competing interests.

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