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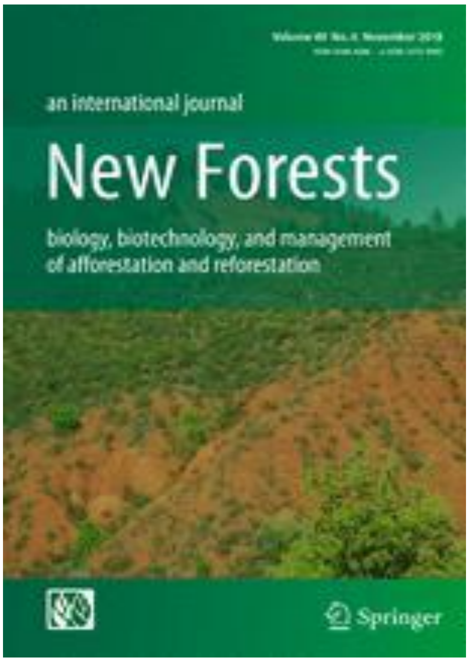

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Genetic and geographic variation in growth of *Balanites aegyptiaca* in Niger: comparing results from provenance/progeny tests in the nursery and field

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Abstract

Some tree improvement programs in Africa use nursery tests to investigate genetic and geographic variation in growth, but do they lead to the same conclusions as field tests? We investigated this question using provenance/progeny tests (12 provenances, 108 families) of *Balanites aegyptiaca* from semi-arid Niger. The nursery test included treatments for time (12–16 months) and watering regime (reduced and normal). Family variation was significant for shoot diameter (Sdia), height (Sht), dry weight (Swt) and root dry weight (Rwt) in the nursery, and for tree height at 1 and 2 years (Fht-1, Fht-2) but not at 13.5 years (Fht-13.5) in the field. Provenance variation was significant only for root/shoot weight ratio (RSwt) in the nursery. Family mean Fht-1 and Fht-2 were positively correlated with all nursery growth variables except RSwt. Provenance mean Fht-2 was positively correlated with Sht, while provenance mean Fht-13.5 was negatively correlated with Swt and positively correlated with RSwt. Family mean survival at 13.5 years was positively correlated with Swt, Sdia, Fht-1 and Fht-2. Family mean Rwt, RSwt and Fht-2 increased from the more humid western to the drier eastern locations. Most correlations with nursery growth variables were stronger at 16 than at 12 months and in the normal compared with the reduced watering regime. Results suggest that Swt and Sdia may be useful for predicting family survival in the field, and Rwt and RSwt may be useful for investigating geographic variation in growth in the field. We recommend conducting both nursery and long-term field tests.

Keywords Nursery root and shoot growth · Field height and survival · Correlations between nursery and field · Geographic clines

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Introduction

Understanding genetic and geographic variation in tree growth is essential in order to recommend appropriate seed sources for reforestation, and this is particularly important for reforestation in a changing climate (Dawson et al. 2011; Jacobs et al. 2015). Long-term field tests have been traditionally used to investigate genetic and geographic variation in tree growth (Morgenstern 1996), but they are costly to establish and maintain. As an alternative, some tree improvement programs in Africa use short-term nursery tests (Sniezko and Stewart 1989; Dangasuk et al. 1997; Ibrahim et al. 1997; Ngulubu et al. 1997; Loha et al. 2006, 2008; Akinnagbe and Oni 2007; Zida et al. 2008; Elfeel et al. 2009; Diallo et al. 2010; Cuni-Sanchez et al. 2011; Korbo et al. 2012; Bouda et al. 2013, 2015; Ky-Dembele et al. 2014; Weber et al. 2015; Bayala et al. 2017; Bezzalla et al. 2017). Studies are needed, however, to determine whether nursery and field tests lead to the same general conclusions. To the best of our knowledge, there has been only one such study for a native tree species in Africa (Weber et al. 2015). In this paper, we investigate genetic and geographic variation in growth and correlations between growth in nursery and field tests of *Balanites aegyptiaca* (L.) Delile. (Zygophyllaceae family) from the Sahelian ecozone of Niger.

The West African Sahel is a semi-arid ecozone between the more humid Sudanian ecozone to the south and the Sahara desert to the north, so there are steep rainfall gradients with latitude and also with longitude (Buontempo 2010: drier in north and east). The climate is becoming increasingly hotter and drier with greater variability in rainfall (Buontempo 2010). In such an environment, we hypothesize that genetic variation in tree growth is related to latitude and longitude, and seed sources from drier locations are more appropriate than those from more humid locations for reforestation in the increasingly hotter and drier climate (Weber et al. 2008).

Seedling characteristics in the nursery such as shoot height, shoot weight, root collar diameter, root weight, root growth potential and root/shoot weight ratio can affect early growth in the field (Rawat and Singh 2000; Villar-Salvador et al. 2004; Zida et al. 2008; Trubat et al. 2011). For native tree species in the West African Sahel, seedling height and root/shoot weight ratio in the nursery may be useful for predicting growth in the field, but tree height after several years in the field may be negatively correlated with seedling height and positively correlated with root/shoot weight ratio (Weber et al. 2015). This is because many taxa adapted to semi-arid environments invest much of their carbohydrate reserve into root growth, so they grow relatively slowly above ground until the roots reach the water table. Trees with deeper roots may have a comparative advantage in semi-arid environments, and in time may be taller than trees with shallower root systems. This could result in a positive correlation between root/shoot weight ratio in the nursery and tree height after several years in the field. Since seedling height and root/shoot weight ratio are negatively correlated, seedling height in the nursery may be negatively correlated with tree height after several years in the field. Assuming that root and shoot growth are heritable and contribute to fitness in natural populations, we hypothesize that height and traits positively correlated with height of seedlings grown in a nursery without water stress are greater for seed sources from more humid locations, while root/shoot weight ratio in the nursery and height after several years in the field are greater for seed sources from drier locations (Weber et al. 2015).

For purposes of selection, tree improvement programs need test environments that uncover genetic and geographic variation in growth (Campbell and Sorensen 1978). An environment where plants grow more rapidly may uncover relatively greater genetic variation in growth than an environment where they grow more slowly (Sotelo Montes et al. 2006; Weber et al. 2011). In addition, genetic variation in growth may increase with time (Weber et al. 2009). Watering regime and time affect root and shoot growth in the nursery (e.g., Zida et al. 2008), so they may also affect the expression of genetic and geographic variation in growth in the nursery.

Balanites aegyptiaca is native to semi-arid regions in Africa and the Arabian Peninsula. It is shade-intolerant, grows very slowly above ground as a single-stemmed tree or multi-stemmed shrub, produces a deep taproot, sprouts after coppicing, spreads asexually from sucker shoots, starts producing fruits after 5–7 years, and can live for more than 100 years (Hall and Walker 1991). It is insect pollinated and primarily out-crossing (Ndoye et al. 2004). Seeds are dispersed by humans and animals (e.g., large hornbill birds, monkeys, cattle, goats, camels, giraffes, elephants) over potentially long distances (A.B. Bationo, personal observations). The species provides many products for rural and urban communities in the West African Sahel, including food, fodder, medicines and wood (Faye et al. 2011). Unfortunately, desertification has reduced its abundance in the West African Sahel (Gonzalez 2001), and high seedling and sapling mortality is limiting its regeneration in parkland agroforests in Niger (Idrissa et al. 2018).

Provenance/progeny tests of *B. aegyptiaca* from Niger were established in the nursery and field at one relatively dry site in Niger. Results from the field test at 13.5 years indicated that there was a weak relationship between longitude and provenance mean height (Weber and Sotelo Montes 2010: increase in mean height from the more humid western to the drier eastern part of the sample region). Results from the nursery test and other results from the field test have not been previously reported.

The objectives of this research are to determine (1) if there is genetic variation in growth variables (shoot diameter, shoot height, shoot dry weight, root dry weight, root/shoot weight ratio) of seedlings in the nursery and tree height at 1, 2 and 13.5 years in the field; (2) if survival at 13.5 years is associated with families and provenances; (2) if growth variables in the nursery are correlated with tree height at 1, 2 and 13.5 years; (3) if tree height at 1 and 2 years are correlated with tree height at 13.5 years; (4) if growth variables in the nursery and tree height at 1, 2 and 13.5 years are correlated with survival at 13.5 years; (5) if growth variables in the nursery, tree height at 1,2 and 13.5 years and survival at 13.5 years are correlated with latitude and longitude; and (6) if genetic variation in seedling growth in the nursery and correlations of seedling growth with tree height, survival, latitude and longitude differ due to time and/or watering regime in the nursery. Correlations are based on family and provenance means.

Materials and methods

Sample region, populations sampled and seed processing

The sample region in southwestern Niger extends approximately 250 km from south to north and 325 km from west to east (Fig. 1). The rainy season typically lasts approximately 3 months (mid-June to mid-September), followed by a long, hot dry season. There are few meteorological stations in the region, so accurate data for rainfall and temperature are not available. Based on the WorldClim database (www.worldclim.org), mean annual rainfall is approximately 550 mm in the southern part of the sample region, and decreases to approximately 350 mm in the northwestern part and 300 mm in

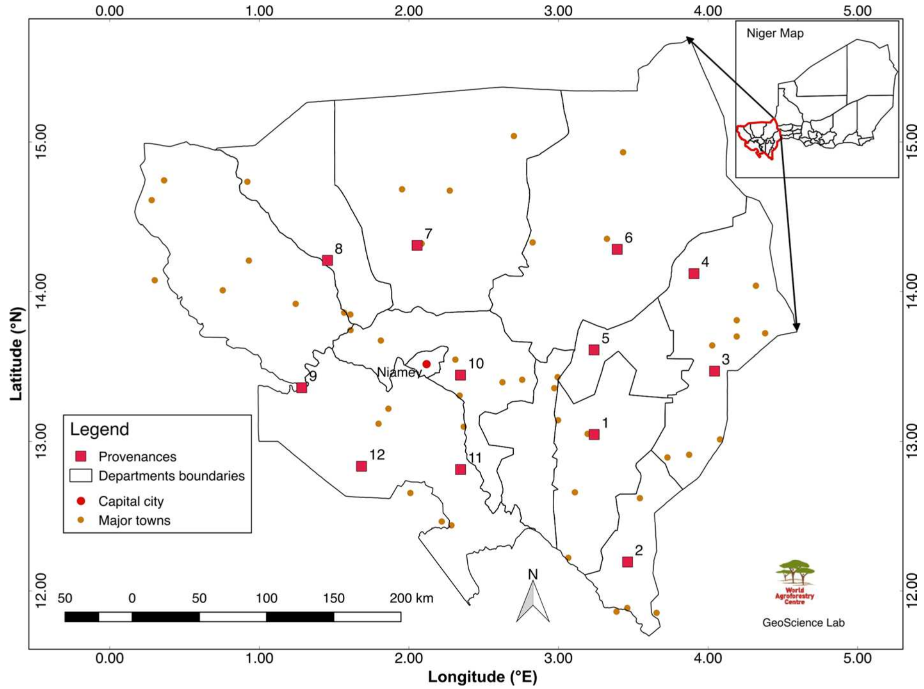

Fig. 1 Geographic location of 12 *Balanites aegyptiaca* provenances (identified by numbers 1–12) sampled in southwestern Niger for provenance/progeny tests in the nursery and field; provenance names and geographical coordinates are given in Table 1; provenance/progeny tests were established at the ICRISAT Sahelian Centre, located 40 km southeast of Niamey; the location of the sample region in Niger is shown in the upper right corner of the figure; *B. aegyptiaca* is naturally distributed throughout southern Niger

the northeastern part of the sample region. Mean annual temperature is approximately 29 °C (Sivakumar et al. 1993). Soils are sandy and infertile, and classified as arenosols (FAO 2007).

Fruits of *B. aegyptiaca* were collected in October 1993 from 138 mother trees located in 12 populations (referred to below as provenances) in the sample region (Fig. 1). Trees were selected if they appeared to have sufficient seeds for both field and nursery tests, and had no obvious external disease symptoms. To reduce the chance of sampling siblings, at least 100 m was maintained between any two selected trees. Latitude, longitude and elevation were recorded for each mother tree using a GPS receiver. Only 108 mother trees provided sufficient viable seeds for the nursery and field tests. The number of mother trees per provenance varied from 4 to 13 (Table 1).

The fruit of *B. aegyptiaca* is a drupe with a fleshy pulp surrounding a single seed. Seeds were processed separately from each mother tree, and seeds from the same mother tree are referred to below as a family. The pulp was removed, seeds were surface-sterilized with bleach, air-dried for 1 month and then stored in cloth bags at room temperature. In preparation for sowing, the hard seed coats were cracked using a rubber mallet in order to extract the kernels, and kernels were soaked in water for 24 h. Three kernels per family were sown in heavy-duty polyethylene nursery bags (2 L volume) filled with soil substrate (2:1 mixture of sand and topsoil). To help prevent roots from escaping the

Table 1 Geographic location of 12 *Balanites aegyptiaca* provenances and number of mother trees sampled in Niger for the provenance/progeny tests in the nursery and field

Number	Name	Latitude (°N)[a]	Longitude (°E)[a]	Elevation (m)[a]	Mother trees
1	Dosso	13°3′	3°14′	251	13
2	Yelou	12°12′	3°28′	244	5
3	Dogondoutchi	13°28′	4°3′	311	6
4	Soukou	14°7′	3°54′	286	6
5	Loga	13°37′	3°14′	169	11
6	Filingue	14°17′	3°24′	234	12
7	Oualam	14°18′	2°3′	208	4
8	Tillaberi	14°12′	1°27′	220	12
9	Bossebangou	13°22′	1°17′	259	12
10	Hamdallaye	13°27′	2°21′	182	5
11	Tamou	12°49′	2°21′	227	11
12	Makalondi	12°50′	1°41′	230	11

[a]Mean latitude, longitude and elevation calculated from the location of the mother trees in each provenance

bags, we used two nursery bags. Shoot emergence was monitored for 3 weeks, at which time the most vigorous of the three seedlings was selected and the other seedlings were culled.

Experimental design and management of the nursery and field tests

The nursery and field tests were conducted at the Sahelian Centre of the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT: 13°14′N, 2°17′E, 230 m elevation), located 40 km southeast of Niamey, the capital city of Niger (Fig. 1). Mean annual rainfall and temperature at the test site were 539 mm and 29 °C (I. Maïkano, personal communication). Mean annual rainfall at the test site varied from 372 to 794 mm during the 13.5 years of the field test.

The nursery test included two treatments: time (approximately 12–16 months) and watering regime (normal and reduced watering). The test started in March 1994 for the 16-months plot and in July 1994 for the 12-months plot, and ended in June 1995. The experimental design was a modified split–split–split plot. The two levels of time were randomly assigned to two main plots, and the two levels of watering regime were randomly assigned to two subplots in each main plot. In each subplot, three replications were randomly allocated to three sub-subplots, so replications were nested in both main plots and subplots. In each replication, the 108 families were randomly assigned to 108 sub–sub–sub plots containing one seedling. The total number of seedlings measured in the test was 1296 (12 replications × 108 families). Each replication was surrounded by one border row of seedlings, but these were not measured.

During the dry season, seedlings in the normal watering regime were watered early in the morning and late in the afternoon so that the soil substrate was always moist (but never saturated), while seedlings in the reduced watering regime were only watered late in the afternoon. We did not quantify the volume of water that seedlings received. During the rainy season, seedlings were not watered on days with heavy rain. Millet-stem mats were placed above and on the sides of each replication to provide partial shade and protection from heavy rain and hot, dry winds. Plastic tarps were placed under the nursery bags to control weeds. A millet-stem windbreak surrounded each main plot. Nursery bags were weeded and soil substrate was added if necessary. Dead seedlings (2% overall) were replaced but not included in the analyses.

For the field test, seedlings were grown for approximately 6 months in the nursery (January to July 1994). These seedlings were not part of the nursery test. Seedlings were grown in a randomized complete block design with eight blocks (replications). In each replication, families were randomly assigned to 108 single-seedling plots, and the replication was surrounded by a border row of seedlings. Seedlings were managed using the same procedures described above for the nursery test, except that all seedlings received the normal watering regime.

The field test site had been previously used to test crop varieties. The site is level, and the soil is classified as arenosol. The vegetation was removed by hand and burned on site in April–May 1994, and the ashes were tilled by hand into the soil. In July 1994, the eight replications (containing 864 seedlings) and their border rows were transplanted from the nursery to the field. Mean height of the transplanted seedlings was approximately 30 cm. Plant spacing in the field test was 3 m within and between rows. Dead seedlings were replanted in August and early September 1994, but these seedlings and seedlings in the border rows were not included in the analyses. Replications were weeded during the first year, but not thereafter. No fertilizers or insecticides were applied at any time.

Growth variables measured in the nursery and field tests

At the end of the nursery test, we measured shoot diameter at the root collar (mm), shoot height (cm), and dry weights (mg) of shoots and roots. Due to natural leaf abscission during the dry season, most seedlings had no leaves and the other seedlings had very few leaves when they were harvested, so we determined shoot dry weight without leaves. This underestimated shoot weight of seedlings that had leaves, but the weight of a few leaves would have been minor compared with the weight of the stem and branches. Each seedling was removed from its bag, and carefully washed to remove soil and remaining leaves without losing root or shoot tissue (fine-root hairs were of course lost during processing). After washing, each seedling was placed in a paper bag and air-dried under a canopy for 1 week. Each seedling was then cut at the root collar, and the root and shoot were placed in separate paper bags. Roots and shoots were oven-dried (100 °C) until there was no further change in weight (approximately 48 h), and then the oven-dry weights were recorded. The ratio of root dry weight to shoot dry weight, referred to hereafter as root/shoot ratio, was calculated for each seedling. Thirteen samples of roots and shoots were damaged during processing and were not included in the analysis.

Tree height and survival were recorded in the field test in June 1995, June 1996 and December 2007, i.e., at approximately 1, 2 and 13.5 years after planting the field test. Height was measured to the nearest cm with a telescopic measuring pole. Each tree was coded as either alive or dead, and the proportion of living trees was calculated for each family and provenance.

Mortality was very high (75%) in the field test at 13.5 years so spacing and potential inter-tree competition differed among trees. We adjusted tree height for the number of living trees (0–8) immediately surrounding each tree (Weber and Sotelo Montes 2010). Tree height at 1 and 2 years in the field test were not adjusted because mortality was low (8%) so most trees were immediately surrounded by a similar number of trees (7 or 8). The field test was not monitored between 2 and 13.5 years, so we do not know why mortality was so high at 13.5 years. We think the high mortality was the result of a few years of low rainfall (mean annual rainfall as low as 372 mm) coupled with seasonally high temperatures and desiccating winds during the last few months of the dry season, but we have no data to support this statement.

Data analysis

The SAS® statistical package (SAS Institute Inc. 2004) was used for all analyses, and the significance level was $\alpha \leq 0.05$ for all tests. Data transformations for growth variables were not considered necessary because the data and residuals from the analysis of variance exhibited normal distributions (determined from statistics provided by the univariate procedure). Proportion data for survival at 13.5 years were not transformed because the proportions exhibited normal distributions for both families and provenances.

For the nursery test, analysis of variance (mixed procedure, restricted maximum likelihood method) was used to determine if growth variables varied significantly due to provenances and families, and if there were significant interactions with time and watering regime. The model included the following sources of variation: time, watering regime [water], interaction time × water, replication nested in time and water [rep(time-water)], provenance [prov], family nested in prov [fam(prov)], time and water interactions with prov and fam(prov) [time × prov, water × prov, time × water × prov, time × fam(prov), water × fam(prov), time × water × fam(prov)], and residual variation. Time, water and their interaction were treated as fixed effects, and the other sources of variation were treated as random effects. Significant differences were tested using the F-ratio for fixed effects and the Z test for random effects. Least-squares means for time and water were compared using the Tukey honestly significant difference (HSD) test.

Ideally time and watering treatments would have been randomly allocated within replications but that was not possible for practical nursery management reasons. As a result, we had to use the replication error variation [rep(time-water)] to test the effects of time and water treatments. We were primarily interested in variation in growth variables due to families and provenances, rather than the effects of time and watering regime. Our design and the ideal design would essentially produce the same results regarding variation due to families and provenances.

To determine if variation due to provenances and families differed due to time or watering regime, we did the analysis of variance of growth variables separately for each time (across watering regimes) and each watering regime (across time). The model for analysis by time included the following sources of variation: water, rep(water), prov, fam(prov), water × prov, water × fam(prov), and residual variation. The model for analysis by watering regime included the following sources of variation: time, rep(time), prov, fam(prov), time × prov, time × fam(prov), and residual variation. We also analyzed variation separately in each of the four treatment combinations (i.e., reduced watering at 12 months, reduced watering at 16 months, normal watering at 12 months, normal watering at 16 months), but there were only three seedlings per family in each treatment combination so we did not feel that the sample size was sufficient.

For the field test, analysis of variance was used to determine if tree height at 1, 2 and 13.5 years differed significantly due to provenances and families. The model included four random effects: rep, prov, fam(prov), and residual variation.

In the analyses of variance, we were mainly interested in the variation due to families and provenances. For each growth variable, we calculated the total variance for random effects in the model (i.e., sum of variance components) and the percent of the total variance (referred to below as percent variance) due to provenances and families nested within provenances. We used the percent variance to assess whether genetic variation in seedling growth differed due to time and/or watering regime in the nursery.

The Chi Square test of independence (freq procedure) was used to determine if there was a significant association between survival at 13.5 years in the field test and both provenances and families. The analyses were based on the number of living and dead trees in each family and provenance.

Pearson correlation coefficients (corr procedure) were used to assess linear relationships among variables. Correlations were computed using family and provenance means. However, correlations were not computed with family mean height at 13.5 years because the sample size was too small for most families (average of two living trees per family). The following correlations were computed: growth variables in the nursery with tree height at 1, 2 and 13.5 years; tree height at 1 and 2 years with tree height at 13.5 years; growth variables in the nursery and tree height at 1, 2 and 13.5 years with survival at 13.5 years; growth variables in the nursery, tree height at 1, 2 and 13.5 years and survival at 13.5 years with latitude and longitude. Survival at 13.5 years was estimated using the proportion of living trees. We expected that some correlations with growth variables in the nursery would differ due to time and/or watering regime, so we computed these correlations using data from all seedlings in the nursery (across time and watering regimes), and separately for each time (across watering regimes) and watering regime (across times). In addition, correlations were computed among growth variables of all seedlings in the nursery and separately for seedlings in each time/watering regime combination. Latitude and longitude of families were based on the recorded values at the location of the mother trees. Mean latitude and longitude of provenances were calculated from the values of all mother trees in the provenance.

We did not investigate relationships directly with mean annual rainfall because we did not think that the available data were very accurate. Mean annual rainfall decreases from south to north and from west to east in the sample region (e.g., WorldClim database), so we assume that geographic variation related to latitude and longitude primarily reflects the rainfall gradient (Weber et al. 2008).

This study has five major limitations. Provenances were sampled from a relatively small area in southwestern Niger with a relatively small range in mean annual rainfall. Provenance means were based on a small number of mother trees, and the number of mother trees differed among provenances (Table 1). Family means in the nursery and field tests were based on a small number of seedlings/trees (maximum = 12 across time and watering regimes in the nursery, and eight in the field). The field test was conducted at only one site.

Results

Variation in growth in the nursery

Time in the nursery had significant effects on shoot diameter and shoot and root weights, but not on shoot height and root/shoot ratio, and watering regime had significant effects on all growth variables except root/shoot ratio (Table 2). The time by watering regime

Table 2 Analysis of variance of growth variables of *Balanites aegyptiaca* seedlings in a provenance/progeny nursery test in Niger

Source of variation[b]	DF[b]	Growth variables[a]				
		Significance of F or Z test[b]				
		Sdia	Sht	Swt	Rwt	RSwt
Main plots						
Time[c]	1	**	ns	***	***	ns
Subplots						
Water[c]	1	***	***	***	***	ns
Time × Water[c]	1	ns	*	ns	ns	ns
Sub-Subplots						
Rep(Time-Water)[c]	8	*	*	*	ns	*
Sub–Sub–Subplots						
Prov	11	ns	ns	ns	ns	*
Fam(Prov)	96	***	***	***	***	**
Time × Prov	11	ns	ns	ns	ns	ns
Water × Prov	11	ns	ns	ns	ns	ns
Time × Water × Prov	11	ns	ns	ns	ns	ns
Time × Fam(Prov)	96	ns	ns	ns	ns	ns
Water × Fam(Prov)	96	ns	ns	ns	ns	ns
Time × Water × Fam(Prov)	96	ns	ns	ns	ns	ns
Residual	814 or 827	–	–	–	–	–
Total	1253 or 1266					

[a]Growth variables: Sdia = shoot diameter at the root collar (mm), Sht = shoot height (cm), Swt = shoot dry weight (g), Rwt = root dry weight (g), RSwt = ratio of root/shoot dry weights

[b]Sources of variation: time = duration of the test (12–16 months), water = watering regime (reduced and normal), Time × Water = interaction of time by water, Rep(Time-Water) = replication nested in time and water, Prov = provenance, Fam(Prov) = family nested in provenance, interactions of time and water by Prov and Fam(Prov) = Time × Prov, Water × Prov, Time × Water × Prov, Time × Fam(Prov), Water × Fam(Prov), Time × Water × Fam(Prov); time, water and their interaction are fixed effects, and all other sources of variation are random effects; fixed effects tested using F-ratios, random effects tested using Z tests; significance of F-ratios and Z tests ***$P < 0.001$, **$P < 0.01$, *$P < 0.05$, ns $P > 0.05$; DF = degrees of freedom; residual DF and total DF vary due to missing values; residual DF and total DF, respectively = 814 and 1253 for Swt, Rwt and RSwt, 827 and 1266 for Sdia and Sht

[c]Rep(Time-Water) used as error variance for testing Time, Water, and Time × Water

interaction was significant for shoot height (larger difference in shoot height between watering regimes at 12 than at 16 months).

All growth variables differed significantly due to families nested in provenances (referred to below simply as families), but root/shoot ratio was the only growth variable that differed significantly due to provenances (Table 2). Interactions of time and watering regime with provenances and families were not significant for any growth variable. Percent variance was greater for families than for provenances (not tabled). Percent variance due to families was largest for root and shoot weights (11.5% and 10.1%, respectively), intermediate for shoot height and diameter (8.1% and 6.7%, respectively) and smallest for root/shoot ratio (3.8%). Percent variance due to provenances was 3.1% for root/shoot ratio, 0.8% for root weight and 0.0% for shoot diameter, height and weight.

Percent variance of growth variables due to families and provenances did not differ in any consistent manner between the normal and reduced watering regimes or between 12 and 16 months (supplementary Table S1). For example, percent variance due to families was greater for shoot diameter, shoot weight and root/shoot ratio in the normal watering regime, but greater for shoot height and root weight in the reduced watering regime. Analyses in each of the four treatment combinations also showed no consistent difference in percent variance of families and provenances between watering regimes and time (not tabled).

Mean values for most growth variables were significantly greater at 16 than at 12 months and in the normal compared with the reduced watering regime (Table 3). Differences were not significant for shoot height and root/shoot ratio between 12 and 16 months, and for root/shoot ratio between watering regimes. In contrast to means, coefficients of variation for growth variables were greater at 12 than at 16 months (except for root/shoot ratio) and in the reduced compared with the normal watering regime (Table 3).

Table 3 Mean, standard deviation and coefficient of variation of growth variables of *Balanites aegyptiaca* seedlings in a provenance/progeny nursery test in Niger

Growth variables[a]	12 months	16 months	Reduced watering	Normal watering
Mean[b]				
Sdia	5.8a	6.8b	5.4a	7.1b
Sht	47.1a	49.4a	40.4a	56.1b
Swt	7.9a	13.3b	7.5a	13.8b
Rwt	18.2a	34.4b	20.7a	31.9b
RSwt	2.6a	2.8a	3.0a	2.4a
Standard deviation				
Sdia	1.9	2.0	1.7	1.9
Sht	16.3	14.3	13.6	12.9
Swt	4.7	5.7	4.3	5.5
Rwt	9.7	14.1	12.5	14.2
RSwt	1.2	1.4	1.5	0.9
Coefficient of variation (%)[c]				
Sdia	32.1	30.0	31.7	27.1
Sht	34.5	29.0	33.4	23.1
Swt	58.5	42.5	57.0	40.1
Rwt	52.4	41.0	60.0	44.3
RSwt	45.0	48.1	50.0	37.6

[a]Growth variables: Sdia = shoot diameter at the root collar (mm), Sht = shoot height (cm), Swt = shoot dry weight (g), Rwt = root dry weight (g), RSwt = ratio of root/shoot dry weights

[b]Tabled means are least squares means: means for time (12–16 months) are calculated across watering regimes (reduced and normal), and means for watering regimes are calculated across time; means for time and watering regime are compared with the Tukey HSD test—means with the same letter are not significantly different ($P > 0.05$) and those with different letters are significantly different ($P < 0.05$); sample size for each mean = 618 or 626 at 12 months, 636 or 641 at 18 months, 617 or 630 in reduced watering regime, 637 or 638 in normal watering regime (smaller value for Swt, Rwt and RSwt; larger value for Sdia and Sht)

[c]Coefficient of variation (CV) = standard deviation/mean; tabled means, standard deviations and CVs are rounded up, so CVs calculated from tabled means and standard deviations differ slightly from the tabled CVs

Variation in tree height and survival in the field

Tree height varied significantly due to families at 1 and 2 years in the field (not tabled: $P<0.001$, sample size = 791), but variation due to provenances was not significant ($P>0.05$). In contrast, tree height at 13.5 years did not vary significantly due to either families or provenances (not tabled: $P>0.05$, sample size = 225). Percent variance in height due to families was 12.2% at 1 year but it decreased to 7.9% at 2 years and 5.2% at 13.5 years. Percent variance due to provenances was essentially zero at 1 and 2 years and only 2.6% at 13.5 years. The mean and standard deviation of tree height, respectively, were 46.4 cm and 16.0 cm at 1 year, 69.7 cm and 30.6 cm at 2 years, and 2.22 m and 0.76 m at 13.5 years. Mean height at 13.5 years ranged from 0.99 to 3.89 m for families, and from 1.84 to 2.55 m for provenances.

At 13.5 years, there was a significant but weak association between survival and families (Chi Square test of independence not tabled: $P<0.05$, sample size = 108) indicating that survival differed among some of the families. There was no significant association between survival and provenances ($P>0.05$, sample size = 12). The proportion of living trees ranged from 0.0 to 0.75 for families, and from 0.19 to 0.39 for provenances.

Correlations among growth variables in the nursery

Shoot diameter, height and weight were positively correlated with root weight and negatively correlated with root/shoot ratio (Table 4). The strongest correlation was between shoot and root weights. Correlations of root and shoot weights with root/shoot ratio were low. Correlations of shoot diameter and height with root/shoot ratio were even lower because they were not significant in some treatment combinations (not tabled).

Correlations between growth variables in the nursery and the field

Using family means across time and watering regimes in the nursery, all growth variables except root/shoot ratio were positively correlated with family mean height at 1 and 2 years in the field (Table 5, part A). Correlations were generally stronger for family means at 16 months than at 12 months in the nursery, and in the normal compared with the reduced watering regime. Correlations with family means at 13.5 years in the field were not computed due to the low sample size for families at that age.

Table 4 Pearson correlation coefficients among growth variables of *Balanites aegyptiaca* seedlings in a provenance/progeny nursery test in Niger; correlations based on all seedlings in the test

Growth variables[a,b]	Sdia	Sht	Swt	Rwt	RSwt
Sdia	–				
Sht	0.469***	–			
Swt	0.641***	0.600***	–		
Rwt	0.529***	0.469***	0.732***	–	
RSwt	−0.107***	−0.118***	−0.307***	0.283***	–

[a]Growth variables: Sdia = shoot diameter at the root collar, Sht = shoot height, Swt = shoot dry weight, Rwt = root dry weight, RSwt = ratio of root/shoot dry weights

[b]Significance of Pearson r: ***$P<0.001$; sample size = 1253–1267

Table 5 Pearson correlation coefficients between growth variables of *Balanites aegyptiaca* in a provenance/progeny nursery test and a field test at 1, 2 and 13.5 years in Niger; correlations are calculated using family means (part A) and provenance means (part B); means in the nursery are calculated across times and watering regimes and separately for each time and watering regime; only significant correlations are shown

Field growth variables[b]	Nursery growth variables[a]				
	Sdia	Sht	Swt	Rwt	RSwt
A. Correlations between family means[c]					
Across times and watering regimes					
Fht-1	0.374***	0.410***	0.388***	0.293**	ns
Fht-2	0.366***	0.321***	0.270**	0.320***	ns
12 months (across watering regimes)					
Fht-1	0.333***	0.289**	0.303**	0.202*	ns
Fht-2	0.311**	0.224*	0.216*	0.259**	ns
16 months (across watering regimes)					
Fht-1	0.324***	0.392***	0.394***	0.304**	ns
Fht-2	0.338***	0.312***	0.307**	0.335***	ns
Reduced watering regime (across times)					
Fht-1	0.242*	0.310**	0.216*	ns	ns
Fht-2	0.236*	0.287**	ns	0.245*	ns
Normal watering regime (across times)					
Fht-1	0.369***	0.399***	0.420***	0.293**	ns
Fht-2	0.360***	0.261**	0.271**	0.281**	ns
B. Correlations between provenance means[c]					
16 months (across watering regimes)					
Fht-2	ns	0.607*	ns	ns	ns
Reduced watering regime (across times)					
Fht-2	ns	0.669*	ns	ns	ns
Normal watering regime (across times)					
Fht-13.5	ns	ns	−0.588*	ns	0.639*

[a]Nursery growth variables: Sdia = shoot diameter at the root collar, Sht = shoot height, Swt = shoot dry weight, Rwt = root dry weight, RSwt = ratio of root/shoot dry weights

[b]Field growth variables: Fht-1, Fht-2 and Fht-13.5 = tree height at 1, 2 and 13.5 years, respectively

[c]Significance of Pearson r: ***P < 0.001, **P < 0.01, *P < 0.05, ns P > 0.05; sample size for family mean correlations = 108 with Ht-1 and Ht-2, 93 with Ht-13.5; sample size = 12 for provenance mean correlations

Most correlations between provenance means in the nursery and the field at 1, 2 and 13.5 years were not significant (Table 5, part B). Provenance mean height at 2 years in the field was positively correlated with nursery height at 16 months and in the reduced watering regime. Provenance mean height at 13.5 years in the field was negatively correlated with nursery shoot weight and positively correlated with root/shoot ratio in the normal watering regime.

Mean height of provenances at 2 years in the field was positively correlated with mean height at 13.5 years ($r = 0.579$, $P < 0.5$, sample size = 12). The correlation was not significant at 1 year.

Correlations of growth variables in the nursery and field with survival at 13.5 years

Most correlations of growth variables in the nursery and tree height in the field with survival at 13.5 years were not significant, and the significant correlations were very weak (not tabled). Based on family means, survival at 13.5 years was positively correlated with shoot weight and diameter in the nursery. The correlations were significant for shoot weight across time and watering regimes, at 16 months and in the normal watering regime, and for shoot diameter in the normal watering regime ($r = 0.220$, 0.189, 0.239 and 0.197, respectively; $P < 0.5$, sample size = 108). Family means for tree height at 1 and 2 years were also positively correlated with survival at 13.5 years ($r = 0.262$ and 0.293, respectively; $P < 0.01$, sample size = 108). In contrast to family means, correlations of provenance mean height at 1, 2 and 13.5 years with survival at 13.5 years were not significant ($P > 0.05$).

Correlations of growth variables in the nursery and field and survival at 13.5 years with latitude and longitude

Mean root weight and root/shoot ratio of families in the nursery were significantly correlated with longitude, but the correlations were very weak (not tabled). Mean root weight of families increased from west to east at 16 months, and mean root/shoot ratio of families increased from west to east at 16 months and in the normal watering regime ($r = 0.246$–0.251, $P < 0.01$, sample size = 108). All other correlations of family and provenance means in the nursery with latitude and longitude were not significant ($P > 0.05$).

Family mean height at 2 years (but not at 1 year) in the field also showed a weak relationship with longitude, increasing from west to east ($r = 0.191$, $P < 0.05$, sample size = 108). Correlations of provenance mean height at 1 and 2 years and family and provenance mean survival at 13.5 years with latitude and longitude were not significant ($P > 0.05$).

Discussion

Effects of time and watering regime on growth in the nursery

Although means for all growth variables of *B. aegyptiaca* increased from 12 to 16 months, the difference was not significant for shoot height and root/shoot ratio. This suggests that seedlings were investing more in diameter than in height growth during that period, a response that is commonly observed in plants that are not competing for light (van Gelder et al. 2006). Although not quantified, it is unlikely that seedlings were competing for light in this test because branches of adjacent seedlings were not intertwined.

As expected, mean root/shoot ratio was greater in the reduced watering regime, while means for the other growth variables were greater in the normal watering regime. However, the difference in root/shoot ratio between watering regimes was not significant. Other studies have shown that root/shoot ratio increases with water stress, but the effect of watering regime on root/shoot ratio may or may not be significant, depending on the species, provenance, watering treatment and test duration (Zida et al. 2008; Bouda et al. 2013, 2015; Bezzella et al. 2017).

Genetic variation in growth in the nursery and field

The nursery test and the field test at 1 and 2 years gave similar results regarding genetic variation in height due to families and provenances of *B. aegyptiaca*: variation in height was significant due to families but not due to provenances. The similarity in results probably reflects the fact that there was little difference in age between seedlings in the nursery and young trees in the field. The other growth variables in the nursery also differed significantly due to families, but families accounted for little of the variation. This suggests that family selection based on growth in the nursery may not be very effective because heritability of most growth variables is likely to be low (Weber et al. 2015).

Root/shoot ratio of *B. aegyptiaca* was the only growth variable in the nursery test that varied significantly due to provenances. However, provenances accounted for very little of the variation, so there is little opportunity for selection of *B. aeyptiaca* provenances from the limited sample region in this test, based on root/shoot ratio in the nursery. In contrast to this study, provenances and families of two other native tree species in the West African Sahel [*Khaya senegalensis* A. Juss and *Prosopis africana* (Guill., Perrott. and Rich.) Taub.] accounted for more variation in root/shoot ratio than in seedling height and other growth variables in the nursery (Weber et al. 2015; Ky-Dembele et al. 2014).

There was no consistent difference in genetic variation due to time or watering regime in the nursery. Nevertheless, results indicate that in future nursery tests of *B. aegyptiaca*, a normal watering regime may be more appropriate to uncover genetic variation in shoot diameter, shoot weight and root/shoot ratio, while a reduced watering regime may be more appropriate to uncover genetic variation in shoot height and root weight.

Tree height of *B. aegyptiaca* at 13.5 years in the field did not vary significantly due to families, in contrast to the nursery test and field test at 1 and 2 years. Results at 13.5 years were probably due to the high mortality and consequently low sample sizes for families. It could also reflect crown dieback during years of low rainfall, but we did not monitor this. In contrast to this study, conclusions about genetic variation in growth variables of *P. africana* from Burkina Faso and Niger were similar based on a nursery test and a long-term field test at the same site used in this study (Weber et al. 2015). This illustrates that nursery and field tests may or may not lead to similar conclusions, and underscores the importance of conducting both nursery and long-term field tests.

Correlations of growth variables between the nursery and field

One would expect that growth of seedlings in the nursery would be positively correlated with growth at 1 and 2 years in the field. Correlations among family means of *B. aegyptiaca* were consistent with this expectation: all nursery growth variables except root/shoot ratio were positively correlated with tree height at 1 and 2 years in the field. Due to the small sample sizes for families at 13.5 years, we did not examine the correlations with family mean height at that age. In *P. africana*, there were weak negative correlations between family means for shoot height and weight in the nursery and tree height at 13 years in the field (Weber et al. 2015). Further studies with larger sample sizes are needed to determine if family means for shoot growth variables of *B. aegyptiaca* in the nursery are also negatively correlated with tree height after several years in a field.

Correlations between family mean height (and growth variables positively correlated with height) of *B. aegyptiaca* in the nursery and height at 1 and 2 years in the field were generally stronger in the normal compared with the reduced watering regime and at 16 compared with 12 months in the nursery. These results suggest that nursery tests with normal watering and longer duration may be better for identifying superior families of *B. aegyptiaca* in the nursery.

Consistent with our hypothesis, mean tree height of provenances at 13.5 years in the field was negatively correlated with shoot weight and positively correlated with root/shoot ratio in the nursery. Similar results were observed in *P. africana* (Weber et al. 2015). The correlations with provenance height at 13.5 years were significant for shoot weight and root/shoot ratio in the normal but not in the reduced watering regime, suggesting that nursery tests of *B. aegyptiaca* with normal watering may be better for identifying superior seed sources. Among the top three provenances based on height at 13.5 years in the field, two were among the top three based on root/shoot ratio in the normal watering regime in the nursery, while the tallest provenance at 13.5 years had the lowest shoot weight in the normal watering regime in the nursery.

Correlations of growth variables in the nursery and field with survival at 13.5 years

Family means for shoot weight and diameter in the nursery and tree height at 1 and 2 years in the field were positively correlated with survival at 13.5 years in the field. Although the correlations were very weak, these results suggest that shoot weight and diameter in the nursery may be useful for predicting family survival of this species in the field. In contrast to this study, survival of *P. africana* provenances at 13 years in the field was negatively correlated with shoot height and weight and positively correlated with root/shoot ratio, while correlations with family means were not significant (Weber et al. 2015). This illustrates that correlations between seedling growth variables in the nursery and survival after several years in the field differ among species, once again underscoring the importance of conducting both nursery and long-term field tests.

The correlation between mean tree height and survival of provenances at 13.5 years was not significant in this study. Similar results were reported for provenances of *P. africana* at 11 years, but there was a weak positive correlation between height and survival of families at that age (Weber et al. 2008). Unfortunately we could not assess the correlation between mean tree height and survival of *B. aegyptiaca* families at 13.5 years due to the small sample size for height of families at that age.

Correlations of growth variables in the nursery and field and survival at 13.5 years with latitude and longitude

We hypothesized that seedling height (and traits positively correlated with height) of *B. aegyptiaca* in the nursery would increase from drier to more humid locations (i.e., from north to south and/or from east to west), while root/shoot ratio in the nursery and tree height in the field would increase from more humid to drier locations (Weber and Sotelo Montes 2010; Weber et al. 2015). Results were partially consistent with these hypotheses: root weight and root/shoot ratio of families in the nursery and tree height of families at 2 years in the field increased from west to east.

The longitudinal clines in root weight and root/shoot ratio of *B. aegyptiaca* in the nursery were only observed in certain treatments: the cline in root weight was significant at 16 months but not at 12 months, and the cline in root/shoot ratio was significant in the normal but not in the reduced watering regime. These results suggest that nursery tests with longer duration and normal watering may be more appropriate than tests with shorter duration and reduced watering for detecting clinal variation in growth variables of *B. aegyptiaca*.

The longitudinal cline in root/shoot ratio in this study suggest that *B. aegyptiaca* trees in natural populations may have greater root/shoot ratios in drier than in more humid locations. Studies of variation in seed weight are consistent with this hypothesis. A study of *B. aegyptiaca* trees in natural populations in southeastern Niger showed that mean seed weight increased from the more humid southern to the drier northern locations, which could facilitate faster and deeper root growth of seedlings in the drier locations (Abasse et al. 2011). Mean seed weight of trees in this study showed a similar trend, increasing from the more humid western to the drier eastern locations, and mean seed weight was positively correlated with most seedling growth variables in the nursery, especially with root weight and root/shoot ratio [Weber and Sotelo Montes, unpublished data: mean seed weight based on 100 seeds per family; Pearson $r = 0.213$ with longitude ($P < 0.05$), 0.408 with root weight and 0.412 with root/shoot ratio ($P < 0.001$), 0.291 with shoot diameter ($P < 0.01$), 0.191 with shoot height ($P < 0.05$), and not significant with shoot weight ($P > 0.05$); sample size = 108].

Survival of families and provenances of *B. aegyptiaca* at 13.5 years in the field did not vary significantly with latitude or longitude. In contrast to this study, survival of provenances of *P. africana* from Burkina Faso and Niger increased from the more humid western to the drier eastern locations at 11 years in the field (Weber et al. 2008). Both of these field studies were conducted at the same time and test site in Niger. Whether these contrasting results reflect biological differences between the species or the larger sample region for the *P. africana* test requires further research.

Several other studies of African tree species have investigated whether variation in provenance growth in the nursery is related to geographic coordinates and/or climatic variables at the provenance location (e.g., Ngulubu et al. 1997; Loha et al. 2006; Elfeel et al. 2009; Bouda et al. 2013, 2015; Ky-Dembele et al. 2014; Weber et al. 2015; Bayala et al. 2017) but only this study and the study of *P. africana* (Weber et al. 2015) found significant relationships. This may reflect limitations of the methodologies used in some of the nursery studies (e.g., short-duration tests, small sample regions), the biology of the species (e.g., high phenotypic plasticity and/or long-distance gene flow leading to limited variation among populations), inaccurate climatic data, and/or weak relationships between geographic coordinates and climatic variables.

We must emphasize that this study was conducted in a small sample region with a limited range in mean annual rainfall. This species has an extensive natural distribution in Africa and the Arabian Peninsula, and is found at sites with mean annual rainfall between 250 and 1250 mm (Orwa et al. 2009). Further research is needed to investigate variation in growth and survival among provenances and families sampled over a wider geographic and climatic range.

Conclusions and recommendations

The nursery test and field test at 13.5 years led to the same conclusion about variation in height of *B. aegyptiaca* due to provenances. Given the low survival in the field test at 13.5 years, we cannot draw any conclusion about variation in height among families at that age and, therefore, we cannot state whether the nursery and field tests led to the same conclusion.

Correlations between root/shoot ratio in the nursery and tree height at 13.5 years, and geographic clines in root/shoot in the nursery and tree height at 2 years in the field were consistent with our hypotheses. Root/shoot ratio in a nursery test may be useful, therefore, for predicting geographical variation in growth of *B. aegyptiaca* in a field test, but results depend on the nursery test environment.

Shoot weight and diameter in the nursery were positively correlated with survival of families at 13.5 years in the field. These growth variables may be useful, therefore, for predicting survival of *B. aegyptiaca* families in the field, but results depend on the nursery test environment.

A nursery test with longer duration (at least 16 months) and normal watering regime may be better than a test with shorter duration and reduced watering regime for detecting genetic and geographic variation in growth of this species.

Without field tests, it is difficult to know if nursery tests provide reliable information about genetic and geographic variation in growth in the field. If tree improvement projects in Africa plan to continue to use nursery tests to recommend seed sources for reforestation in a changing climate, it would be prudent to establish field tests (preferably at several locations along a rainfall gradient) together with nursery tests using different methodologies (e.g., differing in duration and watering regimes), and compare the results of the field and nursery tests to determine if they lead to the same general conclusions.

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