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Correlations and clines in tree growth and wood density of *Balanites aegyptiaca* (L.) Delile provenances in Niger

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Abstract *Balanites aegyptiaca* (L.) Delile provides wood and other essential products for farming and pastoralist communities in the West African Sahel. In this region, mean annual rainfall decreases in general from south to north and from west to east, so one might expect clinal variation in fitness-related traits in relation to the rainfall gradients. This paper presents results from a provenance/progeny test of 11 provenances sampled in Niger and established at one relatively dry site in Niger. The objectives were to evaluate phenotypic correlations (Pearson *r*) between tree growth (height, stem diameter) and basic density of the wood, and clines in growth and density at 13 years. Tree growth and wood density were positively correlated, and the correlations differed among provenances. Mean tree height and stem diameter of provenances increased, in general, from the more humid to the drier parts of the sample region. Results suggest that selection of faster-growing trees could lead to an increase in wood volume and density in the subsequent generation, especially in certain provenances; that provenances from drier areas are better adapted to drought; and that tree improvement and conservation programs should collect seeds from populations in the drier areas for planting and conservation.

Keywords Sahel · Tree improvement · Conservation · Drought

Introduction

The correlation between tree growth and wood density is fundamental for timber-tree improvement programs (Zobel and Jett 1995). Wood density is a key trait because it is often correlated with other wood-quality traits (Panshin and de Zeeuw 1980). If the correlation is weak, then selecting faster-growing trees would have little effect on density, or other wood-quality traits correlated with density, in the subsequent generation. The correlation between tree growth and wood density is generally weak for diffuse-porous hardwoods, but it varies in sign and magnitude among species (Zobel and Jett 1995), and it

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may also vary in magnitude among provenances within a species (e.g., Weber and Sotelo Montes 2008).

Tree improvement programs must also understand patterns of intra-specific variation in order to effectively manage and conserve the species' genetic resources. In regions with pronounced rainfall gradients, tree populations may exhibit continuous (i.e., clinal) variation in growth and other adaptive traits as a result of natural selection (Langlet 1971). In general, mean annual rainfall decreases from south to north and from west to east in the West African Sahel, so one would expect clinal variation in adaptively important traits of native tree species distributed throughout this region (Weber et al. 2008).

Balanites aegyptiaca (L.) Delile is native to the West African Sahel and other semi-arid regions in sub-Saharan Africa (Hall and Walker 1991; Hall 1992). It sprouts vigorously after coppicing, spreads asexually from sucker shoots, starts producing fruits after 5–7 years, and can live for more than 100 years. It is insect pollinated and primarily outcrossing (Ndoye et al. 2004). Its seeds are dispersed by animals (e.g., hornbills, monkeys, cattle, goats, camels, elephants) and humans over potentially long distances (A. Bationo, personal communication), which would tend to reduce genetic differences among populations (Hamrick et al. 1992). *B. aegyptiaca* is common in the traditional parkland agroforests in the West African Sahel. The wood is diffuse porous (Hemsley and Poole 2004), moderately dense (Nygard and Elving 2000), durable and easy to work, and is used for poles, furniture, tool handles, utensils, carvings and energy (Hall and Walker 1991). In addition, the species provides food, medicines and fodder. Unfortunately, desertification has reduced its abundance in the West African Sahel (Gonzalez 2001).

A provenance/progeny test of *B. aegyptiaca* was established to investigate variation within and among populations in Niger. Results from the test at 13 years indicated that there was no significant variation in tree growth, wood density or survival due to provenances or families within provenances; and provenance survival did not vary clinally with rainfall gradients in the sample region (Weber and Sotelo Montes, unpublished data). Data from the provenance/progeny test are presented in this paper. The objectives are to (a) evaluate correlations between tree growth and wood density within provenances, and (b) determine if provenance means for growth and density vary clinally with latitude and/or longitude and, by hypothesis, with rainfall gradients in the sample region. We hypothesized that mean growth and density would increase from the more humid to the drier parts of the sample region, when tested at a relatively dry site (Sotelo Montes and Weber 2009). Results are compared with some other tropical hardwoods, and some practical implications and recommendations are discussed.

Materials and methods

Populations sampled, experimental design and management of the provenance/progeny test

Seeds were collected in October 1993 from 138 mother trees located in 12 populations (provenances) in the Sahelian ecozone of central Niger. Results are presented for 11 of the provenances (Table 1): one provenance had only six living trees and was excluded from the analysis. Trees were selected if they had sufficient seeds and 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.

Table 1 Geographic location of 11 *Balanites aegyptiaca* populations in Niger sampled for the provenance/progeny test

Code	Population	Latitude (°N)	Longitude (°E)	Elevation (m)
1	Dosso	13°3′	3°14′	251
2	Yelou	12°12′	3°28′	244
3	Dogondoutchi	13°28′	4°3′	311
4	Soukou	14°7′	3°54′	286
5	Loga	13°37′	3°14′	169
6	Filingue	14°17′	3°24′	234
8	Tillaberi	14°12′	1°27′	220
9	Bossebango	13°22′	1°17′	259
10	Hamdillaye	13°27′	2°21′	182
11	Tamou	12°49′	2°21′	227
12	Makalondi	12°50′	1°41′	230

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

The sample region extends ~325 km from south to north, and ~625 km from west to east. Mean annual rainfall decreases with latitude and longitude in the sample region: from south to north it decreases from ~550 to 350 mm in the western part of the sample region, and from ~450 to 350 mm in the eastern part [data obtained from WorldClim database (www.worldclim.org), described by Hijmans et al. (2005)]. Mean annual temperature is ~29°C (Sivakumar et al. 1993). Soils are sandy and infertile (arenosols: FAO 2007).

Nursery production and the provenance/progeny test were conducted at the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT) Sahelian Centre, located 40 km southeast of Niamey, Niger (13°14′N, 2°17′E, 230 m elevation). Mean annual rainfall and temperature are 539 mm and 29°C, respectively (I. Maïkano, personal communication) at the test site, and the soils are arenosols. Annual rainfall is variable: for example, it ranged from 372 to 794 mm between 1994 and 2005. Seedlings were grown for 6 months in the nursery in the same experimental design used in the field. Only 108 families produced sufficient plants for the test. The test was established in July 1994, using a randomized complete block design with eight blocks (replications). In each replication, families were randomly assigned to 108 single-tree plots. Spacing was 3 m within and between rows. A row of border trees was planted around each replication. Dead trees were replanted in August–September 1994 and the replications were weeded during the first year, but not thereafter. No fertilizers or insecticides were applied at any time.

Traits measured in the provenance/progeny test

Tree growth and basic density of the wood were evaluated in 2007, 13 years after trial establishment. Tree height was measured to the nearest cm using a telescopic measuring pole. Stem diameter over bark (DiaOB) was measured to the nearest 0.1 cm at 30 cm above soil level using diameter tape. Trees were coppiced at 20 cm above soil level. A section of the stem was cut between 20 and 40 cm above soil level, and one disk (2 cm thick, without knots or damage) was obtained from the stem section as close as possible to 30 cm above soil level. In most cases, the disks were obtained at or slightly above 30 cm, but in some cases they were obtained slightly below 30 cm. The bark was removed from the disks, and stem diameter under bark (DiaUB) was measured to the nearest 0.1 cm using diameter tape. The disks were then soaked in distilled water for 48 h, and basic density (BD, oven-dry mass to green volume, kg/m^3) was determined using the water-displacement method (ASTM 1997).

The SAS® statistical package version 9.1 (SAS Institute Inc. 2004) was used for all statistical analyses. The significance level for all tests was $\alpha \leq 0.05$. Replants and resprouts were not included in the analyses. Departure from the normal distribution and homogeneity of variance were tested for the residuals using statistics provided by the UNIVARIATE procedure. Data transformations were not necessary to satisfy the assumptions of analysis of covariance (described below).

The effect of inter-tree competition on tree growth and wood density was tested in a preliminary analysis of covariance. The number of living trees (0–8) immediately surrounding each tree was included as the covariate in the model (MIXED procedure, restricted maximum likelihood method; sources of variation = replication, provenance, family nested in provenance, replication by provenance interaction, and residual). The covariate was significant for height, DiaOB and DiaUB: data were adjusted for these traits using the covariate parameter estimate, and the adjusted data were used in all analyses.

Pearson correlation coefficients (r) were calculated among the growth and wood traits, using data from all trees and separately for trees in each provenance (CORR procedure). The sample sizes were <20 for five of the provenances, so the correlations were not very accurately estimated for these provenances.

Clinal variation in mean tree growth and wood density of provenances was investigated using multiple linear regression (REG procedure). Since mean annual rainfall decreases with latitude and longitude in the sample region, the preliminary model included independent variables involving only latitude and longitude of the provenances (linear and quadratic latitude and longitude, and the linear latitude by longitude interaction). The preliminary model was reduced by eliminating variables that were not significant. Provenance means were based on small sample size (Table 2), so they were not very accurately estimated. Accurate rainfall data were not available for the location of most provenances, so regressions could not be carried out directly with rainfall.

Results

Although there was very high mortality in this test ($\sim$75% at 13 years), there was still considerable variation among trees. Judging from the coefficients of variation (CVs calculated from Table 2), there was relatively more variation in tree growth than in wood density. The CV ranged from 34 to 44% for growth traits (lowest for height, highest for stem diameter under bark), but was only 7% for wood density.

Pearson correlation coefficients indicated that larger trees tended to have higher wood density (Table 3). Correlations among all trees were strongest with stem diameter. The magnitude of the correlations differed among provenances: for example, the correlation between density and stem diameter under bark varied by 0.565 units.

As expected, correlations among growth traits were positive and highly significant ($P < 0.001$, not tabled). The strongest correlation was of course between the two measures of stem diameter (0.98), followed by those between tree height and the two measures of stem diameter ($\sim$0.85).

Multiple linear regressions indicated that provenance means for tree height and stem diameter varied clinally in the sample region (Table 4). Stem diameter increased from south to north, i.e., from the more humid to the drier parts of the sample region. Latitude, however,

Table 2 Growth and wood density of *Balanites aegyptiaca* trees at 13 years in a provenance/progeny test in Niger

	Height (m)		DiaOB (cm)		DiaUB (cm)		BD (kg/m^3)		Fam.	*N*
	Mean	SD	Mean	SD	Mean	SD	Mean	SD		
All	2.22	0.76	6.6	2.7	4.8	2.1	627.2	41.6	90	219
Prov.										
1	2.55	0.89	7.0	3.2	5.1	2.4	631.5	31.8	11	20
2	2.12	0.92	5.7	2.6	4.1	1.9	626.4	34.6	5	14
3	2.07	0.79	6.5	2.9	4.8	2.3	624.4	49.9	5	16
4	2.44	0.71	7.3	3.2	5.4	2.7	623.3	36.5	6	12
5	2.45	0.70	6.8	3.2	5.0	2.5	627.1	39.5	9	17
6	2.26	0.73	6.9	3.1	5.0	2.3	623.9	45.6	9	23
8	2.16	0.64	6.7	2.1	5.0	1.8	641.7	39.6	12	35
9	1.84	0.52	5.6	2.5	4.0	1.8	605.9	48.1	10	27
10	2.34	1.14	7.1	3.4	5.4	2.6	635.0	39.4	4	12
11	2.37	0.79	7.0	2.6	5.3	2.1	644.8	44.6	10	21
12	2.12	0.65	6.0	1.9	4.4	1.5	613.2	28.2	9	22

Means, standard deviations (SD), numbers of families (Fam.) and trees (*N*) are given for all tress (All), and separately for each of the 11 provenances (Prov.)

Variables: Height = tree height; DiaOB and DiaUB = stem diameter over and under bark, respectively at 30 cm above soil level; BD = basic density of wood; Height, DbhOB and DbhUB were adjusted for the number of living trees surrounding the tree

Table 3 Pearson correlation coefficients (*r*) between basic density of the wood and growth traits of *Balanites aegyptiaca* at 13 years in a provenance/progeny test in Niger

	Height	DiaOB	DiaUB	*N*
All	0.608****	0.632****	0.626****	219
Prov.				
1	0.691***	0.761****	0.735***	20
2	0.751**	0.778**	0.768**	14
3	0.620*	0.772***	0.784***	16
4	0.270^{ns}	0.283^{ns}	0.219^{ns}	12
5	0.603*	0.561*	0.592*	17
6	0.757****	0.692***	0.646***	23
8	0.763****	0.664****	0.685****	35
9	0.570**	0.659***	0.653***	27
10	0.748**	0.765**	0.739**	12
11	0.619**	0.619**	0.631**	21
12	0.269^{ns}	0.327^{ns}	0.298^{ns}	22

Correlations are given for all trees (All), and separately for each of the 11 provenances (Prov.)

Variables: Height = tree height; DiaOB and DiaUB = stem diameter over and under bark, respectively at 30 cm above soil level

Significance of Pearson *r*: **** $P \leq 0.0001$, *** $0.0001 < P < 0.001$, ** $0.001 < P \leq 0.01$, * $0.01 < P \leq 0.05$, $^{ns}P > 0.05$

Table 4 Multiple linear regression equations predicting mean tree height and stem diameter of *Balanites aegyptiaca* provenances at 13 years from provenance latitude and longitude in Niger

Trait	Regression equation	SE	R^2
Height	$0.8652 + 1.0718(Lon) - 0.1855(Lon^2)$	Lon = 0.3599	0.588
		Lon^2 = 0.0677	
DiaOB	$-4.9823 + 0.6090(Lat) + 2.7256(Lon) - 0.4818(Lon^2)$	Lat = 0.2015	0.679
		Lon = 0.9983	
		Lon^2 = 0.1884	
DiaUB	$-5.110 + 0.5198(Lat) + 2.4507(Lon) - 0.4400(Lon^2)$	Lat = 0.1865	0.641
		Lon = 0.9238	
		Lon^2 = 0.1744	

Dependent variables: Height = tree height (m); DiaOB and DiaUB = stem diameter (cm) over and under bark, respectively at 30 cm above soil level

Independent variables: *Lat* latitude, *Lon* longitude, Lon^2 quadratic longitude (°decimal)

Significance of regression coefficients $0.01 < P \leq 0.05$; SE = standard error; R^2 = coefficient of determination of model; $N = 11$

did not have a significant effect on tree height. Although mean annual rainfall decreases with longitude, there was no consistent increase in stem diameter and tree height with longitude: they were lowest in the west, increased to a maximum at ~3°E and then decreased to an intermediate value. The regression equation was not significant for wood density.

Discussion

To our knowledge, this is the first published report of clinal variation and correlations between tree growth and wood density in *B. aegyptiaca*. This study may have important practical implications for managing the genetic resources of this species in Niger, and perhaps in other parts of the West African Sahel, but the results and conclusions cannot of course be extrapolated beyond the sample region in Niger. Furthermore, results are based on small sample sizes in a single test at one relatively dry site in Niger. The major results and practical implications are discussed below, followed by some recommendations for future research.

Mean tree growth and wood density

Mean tree height, stem diameter and wood density of *B. aegyptiaca* at 13 years in this test were lower than values observed among trees of similar age in natural stands in Burkina Faso (Nygård and Elving 2000). The difference in tree height and stem diameter is probably due to the lower mean annual rainfall at the test site in Niger, compared with the stands in Burkina Faso (539 mm versus 620–788 mm). For example, tree-ring width of *B. aegyptiaca* was positively correlated with mean annual precipitation in stands in Ethiopia (Gebrekirstos et al. 2008). In addition, the difference in tree height and stem diameter may reflect differences in above- and below-ground biomass allocation between the test site in Niger and the stands in Burkina Faso: all other things being equal, one would expect a larger allocation of total biomass to below-ground growth in drier regions (e.g., Larcher 1975). The difference in wood density between the test site in Niger and the stands in Burkina Faso is related to tree growth and its correlation with wood density (discussed below).

The coefficients of variation indicate that there was relatively more variation in tree growth traits than in wood density in this test. This is consistent with studies of other tropical hardwoods (e.g., Sotelo Montes et al. 2006; Weber and Sotelo Montes 2008; Sotelo Montes and Weber 2009), and illustrates that the test environment generally has a relatively greater effect on tree growth than on wood density (Zobel and Jett 1995) and other wood properties (e.g., Sotelo Montes et al. 2007a, b).

Correlations between tree growth and wood density

Correlations demonstrate that larger trees of *B. aegypiaca* tended to produce denser wood near the base of the tree. Similar results were reported for *Prosopis africana* (Guill., Perrott. and Rich.) Taub. from Burkina Faso and Niger (Sotelo Montes and Weber 2009) and for *Calycophyllum spruceanum* (Benth.) Hook. f. ex K. Shum. from Peru (Sotelo Montes et al. 2006). Wood density had a stronger correlation with stem diameter than with tree height in this test: this probably reflects the die-back that often occurs in the upper stem during the dry season, especially during years with very low rainfall. In this test, there were 2 years when annual rainfall was less than 400 mm (I. Maïkano, personal communication).

The positive correlation between tree growth and wood density could be explained in terms of the mechanical design of trees in response to bending stress produced by wind. Mosbrugger (1990) notes that the base of the tree has the highest bending stress and this can be reduced by increasing the strength of supporting tissue at the base of the tree. Strength at the base of the tree can be increased by producing denser wood, which has a greater Young's modulus of elasticity, as shown experimentally by Niklas (1997). In general, larger trees require greater strength at the base of the stem compared with smaller trees in order to reduce the bending stress. This may be particularly important for species that do not produce buttress roots, and grow in relatively open stands that are potentially exposed to higher wind velocities (like *B. aegyptiaca* and many other Sahelian species). In more humid regions with higher stand densities, root systems and tree crowns may become interwoven to varying degrees over time, and allow the stands to "collectively" reduce the bending stress produced by wind. In the Sahel and other semi-arid regions, this "collective" response to bending stress would be less apparent because stand densities are lower. Species that do not produce buttress roots might require a relatively greater investment in increasing wood density at the base of the tree in semi-arid regions than in more humid regions. However, this is a hypothesis that requires testing.

Results suggest that selecting faster-growing *B. aegyptiaca* trees could increase wood volume and density in the subsequent generation. However, estimates of genetic correlations between tree growth and wood traits (density, strength, stiffness and shrinkage) and the heritability of these traits are needed in order to assess the effect of this selection. For example, genetic correlations between growth and density and the heritability of these traits were higher for *C. spruceanum* (Sotelo Montes et al. 2006) than for *P. africana* (Sotelo Montes and Weber 2009), indicating that a selection strategy to increase wood volume and density could be more effective for *C. spruceanum*. Moreover, genetic correlations indicate that selecting faster-growing trees of *C. spruceanum* would also have a positive effect on wood strength and stiffness, but it would slightly increase volumetric shrinkage in the wood (Sotelo Montes et al. 2007a, b). One might expect similar relationships between tree growth and wood strength, stiffness and shrinkage in *B. aegyptiaca*.

Correlations between tree growth and wood density of *B. aegyptiaca* varied considerably among provenances in this test. Variability in the magnitude of growth-density correlations have also been observed among provenances of *P. africana* from Burkina Faso and Niger (Sotelo Montes and Weber 2009), and *C. spruceanum* (Sotelo Montes and Weber, unpublished data) and *Guazuma crinita* Mart from Peru (Weber and Sotelo Montes 2008). If future research demonstrates that genetic correlations are positive and vary among provenances of *B. aegyptiaca*, then greater gains in wood volume and density could be realized by first selecting provenances that have greater tree growth, wood density and survival, and a stronger genetic correlation between growth and density; and then selecting the fastest growing trees within these provenances.

Clinal variation in tree growth

We hypothesized that mean tree growth and wood density of *B. aegyptiaca* provenances would increase from the more humid to the drier parts of the sample region, when tested at a relatively dry site. However, the clines were not entirely consistent with this hypothesis. Stem diameter did increase from south to north, i.e., from the more humid to the drier parts of the sample region. However, tree height, which was strongly correlated with stem diameter, did not increase with latitude. Rainfall decreases slightly from west to east in the sample region, and tree height and stem diameter increased in general from west to east. However the maximum values for tree height and stem diameter were not observed in the easternmost provenances. Moreover, wood density did not vary significantly with latitude or longitude even though it was highly correlated with tree growth traits (especially stem diameter). In contrast, *P. africana* provenances from Burkina Faso and Niger exhibited consistent clines when tested at the same site in Niger: mean growth and density increased from south to north; and mean growth, but not mean density, increased from west to east (Sotelo Montes and Weber 2009).

Although the clines were not entirely consistent with the hypothesis, in general they support the theoretical expectation that natural populations from drier areas would be better adapted to drought, compared with populations from the more humid areas. The clines in above-ground growth may reflect underlying variation in root growth that is maintained by natural selection pressures along the rainfall gradients in the region. *B. aegyptiaca*, like many other species in semi-arid regions, produces a deep root system. Trees that produce deeper roots could access soil moisture at greater depths, allowing them to grow for a longer period of time during the dry season before entering a state of cambial dormancy: as a result, they could produce greater above-ground biomass. Moreover, they could have a selective advantage during years of extreme drought. This is a reasonable hypothesis, but there are no data on root growth of *B. aegyptiaca* in the sample region to support the hypothesis; and, in addition to root growth, there are several physiological mechanisms and anatomical characteristics that could potentially contribute to drought tolerance of this species (Hemsley and Poole 2004; Gebrekirstos et al. 2006). Moreover, there is no direct evidence to confirm that the clines in above-ground growth are maintained by natural selection on root growth (or other physiological mechanisms and anatomical characteristics). Variation within and among natural populations of tree species reflects the combined historical effects of natural selection, gene flow, genetic drift, mutation (Hu and Li 2002), forest fragmentation, inbreeding, stand density, and harvesting/browsing pressures exerted by humans and animals that directly or indirectly affect reproductive output (Murawski et al. 1994; Hardner et al. 1996; Nason and Hamrick 1997; Cascante et al. 2002).

B. aegyptiaca is an ideal species for reforestation in drought-prone areas because it has a deep root system (Andersen and Krzywinski 2007), uses water conservatively, is very drought tolerant (Gebrekirstos et al. 2006, 2008) and provides many useful products. Assuming that the clines in tree growth of *B. aegyptiaca* provenances reflect adaptive variation, and considering the fact that some computer models predict a drier climate in the Sahel during the twenty-first century (Held et al. 2005), it would be prudent for tree improvement and conservation programs to conserve and collect *B. aegyptiaca* germplasm from the drier parts of Niger for future plantings in Niger. Specifically, we recommend that transfers of germplasm should only be made from the drier to the more humid parts of the region. This strategy could increase the drought tolerance/adaptation of parkland tree populations in subsequent generations as a result of gene flow from the introduced germplasm. As part of a participatory tree domestication program, 45 rural communities in Burkina Faso, Mali, Niger and Senegal are implementing this strategy in order to increase the drought tolerance/adaptation of *B. aegyptiaca* and several other native tree species in anticipation of hotter/drier conditions in the future (ICRAF 2009).

Recommendations for future research

Variation in tree growth, wood properties, survival, and drought tolerance mechanisms of *B. aegyptiaca* should be investigated in multi-location provenance/progeny tests. These tests should include larger sample sizes for estimating provenance and family means, provenance and family by environment interactions, trait heritability, and genetic and age-age correlations in different provenances and planting environments. Estimates of trait heritability and genetic correlations within different provenances and planting environments are important because these parameters may vary among populations and test environments (e.g., Sotelo Montes et al. 2006). The tests should include a systematic sample of provenances/families from the West African Sahel, and be established on farms at several sites that cover the range of environmental conditions where *B. aegyptiaca* could grow. They should be designed to quantify clinal variation related to rainfall gradients, determine patterns of ecotypic variation related to soil types (e.g., Dangasuk et al. 1997; Raddad and Luukkanen 2006), and allow comparison of the local provenance with provenances from other parts in the region. Patterns of variation observed in these tests should then be used to refine the general guidelines for germplasm transfer (mentioned above) and develop dynamic strategies with farming and pastoralist communities to manage and conserve the genetic resources of this species (Dawson et al. 2009). In addition, the provenance/progeny tests could be transformed into seed orchards and managed as community-based enterprises for the production and distribution of selected germplasm for specific environmental conditions.

As part of the participatory tree domestication programme mentioned above, rural communities started multi-location trials of *B. aegyptiaca* and several other native tree species on farms in Burkina Faso, Mali, Niger and Senegal in order to evaluate the performance of local provenances/families compared with provenances/families from drier zones (ICRAF 2009). These trials will be expanded to include more species and locations in order to develop more refined recommendations regarding germplasm transfers and strategies for genetic resource management by the rural communities.

Conclusions

The West African Sahel is a transitional ecozone between the relatively humid savannah woodlands and the Sahara Desert, so one would expect clinal variation in fitness traits in native tree species distributed throughout this region. Studies of genetic variation in *B. aegyptiaca* and other native tree species in the Sahel are needed in order to develop appropriate conservation and improvement strategies, especially for those species that are under intensive extraction pressure and whose habitats are disappearing due to climate change.

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