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BREEDING AND GENETICS

Evaluation of The Heritability of Key Architectural Traits and Yield Components In The Beninese Cotton Breeding Program

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ABSTRACT

Classical plant breeding relies upon the high heritability of traits under selection. The objective of this study was to evaluate the heritability of important agronomic and morphological plant descriptors which are routinely recorded in the Beninese cotton (*Gossypium* spp.) breeding program. These descriptors collected through plant mapping are: plant height (HT), height of the first fruiting branch (HPBF), height of the top fruiting branch (HDBFC), position of first fruiting branch (NPBF), length of the longest vegetative branch (LBV), length of the longest fruiting branch (LBF), number of vegetative branches (NBV), number of bolls on the longest vegetative branch (NCV), and number of bolls on the longest fruiting branch (NCF). Data were collected from micro-trials conducted from 2013 to 2016, using a total of 74 accessions. Broad-sense heritability was estimated using variance components from a linear mixed model. Results reveal that height-related traits (HT, HPBF, HDBFC) were highly heritable (H^2>0.60) and positively correlated to the seed cotton yield. NBV and NPBF also were highly heritable. These traits are considered useful descriptors. Other architectural traits (LBV and LBF) are less heritable, they were less consistently evaluated, and their utility in a classical plant breeding program is suspect. NCV and NCF are characterized by high coefficients of variation (CV) and inconsistent estimates for heritability. Other descriptors may be more useful as yield components, since seed cotton yield was not a reliable descriptor.

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Cotton is the major textile fiber crop and an important oilseed crop in the world. The genus *Gossypium* (L) contains 50 species, 45 of these are diploid and belong to eight genome groups named A-G, and K (Wendel and Cronn, 2003, Fang et al, 2014). Five other species are allotetraploid of the AD genome group, including *G. barbadense* (L) and *G. hirsutum* (L). The latter, also referred to as 'upland cotton', is the most widely grown. Therefore, most of the genetic improvement has been achieved with this species. Further improvement is sought, and requires better knowledge and utilization of available genetic resources. Therefore, it is important to characterize cotton germplasm to provide relevant information for breeding programs.

For cultivated crops, 'descriptors' are widely used to describe the diversity of a germplasm collection and to classify this variability (Ahoton Leonard, personal communication). They also are used to assist breeders to identify material of interest for genetic improvement efforts (Percy et al, 2014). Despite the interest in biochemical and molecular characterization, phenotyping remains a cost-effective system that provides useful information. Cotton descriptors were historically developed and released by the International Board of for Plant Genetic Resources (IBPGR) currently known as Bioversity International (IBPGR, 1985). Over time, these descriptors have been expanded (see http://distribution.grin-global.org/gringlobal/search.aspx or www.cotton-gen.org) and there is still a call to further include more morphological, agronomic and molecular traits (Wallace et al, 2009). For instance, Texas A&M Agri-Life Research, Lubbock, Texas, adopted a set of agronomic trait characteristics for phenotypic evaluation. These traits include plant architecture (plant height and growth habit), physiological (photoperiod), fruit organ retention, morphological and production-related traits ('productiveness' and seed-index). A basic quality of descriptors proposed by Percy et al (2014) is that they are standard and must be universal. For breeding purposes, one may add that descriptors should be reliable, i.e. they account for genotype by environmental

interactions. Disentangling genotypic, environmental effects, as well as their interactions is not an easy task. For instance, Liu et al (2013) found that lint yield gains of 10 Australian cultivars developed by CSIRO could be attributed to genetics (48%), management (28%) and their interaction (24%). But these results were obtained under irrigation and high input conditions using an indirect (historical) approach. In the United States, authors (Meredith, 2000; Bayles et al, 2005) do not agree whether a genetic improvement was achieved, especially in dry-land farming. For improved resistance to insect pests and diseases, a genetic improvement is more obvious, but further research is needed to ascertain the heritability of agronomic traits.

Initially developed as a monitoring tool for management decisions, cotton plant mapping has been used for genetic characterization in developing countries (Lançon et al, 2000a; Lançon et al, 200b; Sekloka, 2006). Genetic cotton mapping in Benin is described by Lançon (1994). The method includes recording many characteristics: plant height (HT), height of the top fruiting branch (HDBFC), number of vegetative branches (NBV), number of fruiting branches (NBF), height of the first fruiting branch (HPBF), first fruiting branch position (NPBF), length of the longest fruiting branch (LBF), length of the longest vegetative branch (LBV), number of nodes above the white flower (NAWF), etc. Some traits are thought to express plant vigor (HPBF, LBF, LBV), growth potential (HT), or growth to development balance (HPBF/NPBF). Yield components are measured as total number of bolls, boll weight (PMC), number of bolls on the most developed vegetative branch (NCV), number of bolls on the most developed fruiting branch (NCF), etc. Cotton plants can be partially mapped at many times during the plant's development; however, the final plant mapping is the most definitive. Plant mapping in West African cotton research centers has not been standardized, therefore there are questions about quality of data analysis and interpretation.

Several countries in francophone Sub-Saharan Africa (SSA) rely on cotton exports as a major basis of income for their national economies (Minot and Daniels, 2002). In these countries, breeding programs have been developed to increase yield while improving fiber qualities such as reflectance, fineness, length, tenacity, micronaire, etc. (Konan et al, 2015; Hougni et al, 2016). The breeding program in Benin started in 1995 and is based on a variant of the pedigree selection breeding scheme. Mass selection and other related breeding methods (such as pedigree selection) are most successful when traits are highly heritable, and the magnitude of genetic gain depends both on selection intensity and heritability (Kang et al, 2007). The objective of this study was to evaluate descriptors used in phenotypic characterization of cotton from breeding programs in Benin based on final plant mapping, with the ultimate goal of assessing their usefulness.

Advances in genetics of cotton agro-morphological traits. Many have reported relationships between genetic traits and morphological differentiations with other self-pollinated species like rice (*Oryza* spp.) (Bashir et al, 2013; do Nascimento et al, 2011). In cotton, broad sense heritability values have been estimated by different authors under various conditions and experimental designs. At the beginning of the cotton breeding program in Benin, Lançon (1994) found heritability values to be low for LBF, NBV, and NBF, (less than 0.10), relatively low (0.10-0.25) for HDBFC, and NPBF, relatively high (0.25-0.50) for HT, HPBF, LBV and yield. Traits with high heritability (over 0.50) were not found. Using eight local varieties in Pakistan, Khan et al (2010), found that seed cotton yield, number of seed per boll, and seed-index were highly heritable (0.98, 0.67, and 0.77 respectively). Ashan et al. (2015) found high values of heritability (above 0.99) for all the traits under study, including plant height, number of bolls per plant, boll size, seed cotton production per plant, and seed-index. For Australian cultivars, Tang et al. (1996) and Clement et al. (2015) also found high values of heritability: 0.63-0.81 for yield, 0.62-0.99 for fiber elongation, 0.57-0.90 for micronaire, 0.74-0.94 for fiber length. Gore et al. (2014) used Recombinant Inbred Lines (RIL) of *G. barbadense* and *G. hirsutum* for phenotype evaluation and found heritability values ranging from 0.46 to 0.96 for plant height, 0.55-0.93 for boll size, 0.48-0.85 for lint yield, 0.80-0.96 for lint index, 0.62-0.94 for micronaire, 0.43-0.89 for fiber elongation, 0.48-0.91 for fiber strength, 0.37-0.88 for fiber elongation.

Overall fiber quality traits received more attention than agronomic traits. There are clear indications that heritability of some characters may vary from one germplasm line to another. Other sources of variations likely include the diversity and genetic structure of the accessions, the experimental design, experimental conditions, and the estimation method. Because quantitative inheritance of yield and fiber quality traits is complex, with negative associations

among traits (Fang et al, 2015), new breeding methods have received greater attention, with the recent development of genomics. Many studies aimed at Quantitative Trait Loci (QTL) identification for architectural traits and yield-related traits (Gore et al., 2014, Nie et al., 2015, Song and Zhang, 2009, Yu et al., 2014). Nevertheless, many contradictions arise which makes it difficult to rely on QTL for analysis of trait inheritance. Further research is needed to ascertain polymorphism in *G. hirsutum*. Moreover, the sense of allelic expression (positive or negative) of traits displayed for selected genotypes must be identified in order to foster genetic progress through targeted parent selection.

MATERIAL AND METHODS

The breeding method in Benin. Since 1995, Benin has launched a cotton breeding program which is based on pedigree selection as described by Lançon (1994) and Kang et al. (2007). The overall goal of this program is to improve yield performances of local genotypes well adapted to Benin. Therefore, the female parent is selected among local accessions while the male parent originates from other places including Argentina (e.g. 'Guanzucho 2'; Sekloka et al., 2016), Australia (e.g. 'Sicala 34'; Liu et al., 2013), the United States (e.g. 'MARS 88-214'; Sekloka et al., 2016), etc. Most of these accessions originate from CIRAD's collection.

The breeding scheme is a variant of the 'progeny row system' described by Munro (1987). It starts in Year 1 with hybridization run at the Bohicon experimental station (including approximately 20 crosses per year). The F_1 plants are raised in the dry season (November-April) with full irrigation. Plants are self-pollinated from F_2 to F_6, while further generations are advanced with open-pollination. The F_2 is the single plant stage ending up with approximately 300 individuals. The plant-derived seed are sown in rows of 9 m (F_3). Progeny Rows (PR), F_3 to F_5, selected lines, are advanced in the following generation, using seed of the best plants (10-20) on the superior rows. At F_2, F_4 and F_5, visual selection is practiced to cull undesirable lines before plant mapping and fiber trait evaluation. At F_3, an early evaluation (EP) occurs in a statistical design with three replications. F_4 and F_5 are run with two replications. At F_6, 24 lines are tested in several micro-trials (ME) which involve a randomized complete block design with five replications and larger experimental units (rows of 20m). The main aim of the micro-trials is to evaluate yield with more robust statistical tools. At this step, plant mapping is used as part of the line description. Evaluation criteria for each stage of breeding are described in Table 1. Three promising lines are selected from ME and are submitted to multi-location tests run on-station and on farm over 2-3 years. When they prove to be superior to common check cultivars, the new cultivars are released. In 2016, a change occurred in the breeding program to account for the genotype*environment interaction. The decision was made to designate cultivars according to agro-climatic adaptability to production areas. Three cultivars were released for four zones: 'ANG 956' (Hougni et al., 2014) in the extreme north (Atacora and Alibori Provinces), 'OKP 768' (Hougni et al., 2014) in the north (Borgou and Donga Provinces) and center (Collines Province), and 'KET 782' (Hougni et al., 2014) in the south (Zou, Mono, Couffo, Plateaux Provinces). These cultivars replaced 'H279-1' (Hougni et al., 2014) which was a popular cultivar throughout Benin from 2003 to 2015.

Crop management includes sowing at field density (41600 plants/ha). Fertilizers (200kg/ha of $N_{14}P_{23}K_{14}S_5B_1$ and 50kg/ha of urea) are provided 15 and 40 days after sowing (DAS) respectively. Starting from 40 DAS, insecticides are sprayed weekly until the first open boll. Seed cotton is hand-picked for yield determination. Fiber quality is determined after ginning and further lab analyses (ginning percentage, lint yield, seed-index).

Table 1: Selection steps and criteria in the Beninese cotton breeding program

Steps and acronyms	Generation	Evaluation criteria
Initial selection	**F2**	**Seed cotton yield, lint percent, seed-index, leaf hairiness, sensitivity to bacterial blight**
Early evaluation (EP)	**F3**	**Seed cotton yield, agro-morphological traits, earliness**
Side-lines (PR)	**F4**	**Seed cotton yield, agro-morphological traits, earliness, fiber quality traits**
Main population (PP)	**F5**	**Seed cotton yield, agro-morphological traits, fiber quality traits**
Micro-Trial (ME)	**F7**	**Seed cotton yield, agro-morphological traits**
Multi-local test (EVCL)	**-**	**Seed cotton yield and farmers' preference**

Five to ten plants from each plot, are randomly selected, and plant mapping related measurements are taken. The following data are collected during the final plant mapping:

- Plant height (HT): length from the cotyledonous node to the apex.
- Height of the first fruiting branch (HPBF): length from the cotyledonous node to the lower fruiting branch (first sympodial branch that appears after monopodial branches).
- Height of the top fruiting branch (HDBFC): the length from the cotyledonous node to the upper fruiting branch bearing a boll position.
- First fruiting branch position (NPBF): the number of nodes beginning with the cotyledonous node counted as zero.
- Number of vegetative branches (NBV): the count of all monopodial branches.
- Length of fruiting branch (LBF): the length of the longest sympodial branch.
- Length of the vegetative branch (LBV): the length of the longest monopodial branch.
- Number of bolls on the vegetative branch (NCV) which length has been measured.
- Number of bolls on the fruiting branch (NCF) which length has been measured.

Trial design. Broad-sense heritability of selected traits under consideration has been estimated following Bashir et al. (2013, p37), Ashan et al. (2015, p148) and Clement et al. (2015, p146-147). Data are retrieved from a large dataset of early generation lines evaluated in ME from 2013 to 2016. Forty-one, nine and twenty-five lines were tested respectively in 2013, 2015, and 2016.

Each year (2013, 2015 and 2016), accessions evaluated in ME are grown in a randomized complete block design, experimental units are single row 20m long, with 5 replications. Blocks comprised of nine accessions include the control variety ('H279-1' in 2013 and 2014 or 'OKP768' in 2016). Six border rows are provided for each experiment. Ten plants are randomly selected per plot for phenotypic characterization. Of these ten plants, five are subsampled from which a total of 20 bolls per plot are hand-picked to determine seed-index, and fiber characteristics: average length of all fiber (ML), Upper Half Mean Length (UHML), fiber uniformity (UI), micronaire (IM), fiber maturity (PM), reflectance (Rd), yellowness (b+).

[1] $H^2 = \sigma_g^2 / \sigma_p^2$

[2] $\sigma_p^2 = \sigma_g^2 + \frac{\sigma_\varepsilon^2}{r}$

Broad-sense heritability (H^2) is estimated as shown in Equation [1] in which σ_g^2 and σ_p^2 respectively represent the genotypic and phenotypic variances (Acquaah, 2012). The estimation of the phenotypic variance has been detailed in Equation [2] with σ_ε^2 and r representing the residual variance and the number of replications respectively (Comstock and Robinson, 1952 cited by Sekloka, 2006, p46; Falconer, 1989 cited by Ashan et al., 2015). This corresponds to the equation 2.1.13.B as suggested by Holland et al. (2003) considering a single environment (e=1) while neglecting the genotype*environment interaction. H^2 is calculated using the variance components of the analysis of variance (ANOVA). The ANOVA is run following the Restricted Maximum Likelihood (REML) procedure under a linear mixed model fitted with year as fixed effect and genotypes as random effects. Consistency of heritability is searched among values of heritability per trait, by comparing their overall values and from one year to another. Correlations between traits were further analyzed.

The quality and usefulness of descriptors are assessed after screening data for outliers, by comparing observed residuals to theoretical residuals. This has been achieved using the qqPlot procedure in R software (Fox and Weisberg, 2011). Data are further checked for consistent CV, based on literature. The descriptors are found reliable and useful when data CV are low (less than 20%) or fairly acceptable (from 20 to 30%), and H^2 high enough (above 50%).

RESULTS AND DISCUSSION

Table 2 and Fig 1 show mean values and variability of the different descriptors collected in the final step of on-station selection (ME). Coefficients of variation (CV) over 30% are considered out of the acceptable range, depicting either an unreliable data collection or a higher influence of unperceived factors on the trait's expression. This only occurs for the number of bolls on the longest vegetative branch (NCV) and that on the longest fruiting branch (NCF). Whether due with physiological stress or parasitism, shedding may have dramatically increased the variability of the number of bolls. For the other variables, coefficients of variation ranged from 11.18% (NPBF) to 29.10% (NBV). Traits with consistently low coefficients of variation are total plant height (HT),

height of the first fruiting branch (HPBF), height of the top fruiting branch (HDBFC), and position of the first fruiting branch (NPBF). Traits with higher CV include seed cotton yield (Yield), number of vegetative branches (NBV), length of the longest vegetative branch (LBV), and length of the longest fruiting branch (LBF).

Table 3 presents the results of ANOVA based on a linear-model for each descriptor. It shows that significant differences ($P<0.05$) arise among genotypes for all measured traits, with few variations of the level of signification from one year to another. Only the number of bolls (either on the vegetative branch or on the fruiting branch) did not significantly differ from one genotype to another in the 2013 trial. Yield data for 2013 are not available. In general, it is arguable that significant differences occur among cultivars for each descriptor. The significance of differences suggests that all the descriptors discriminate among cultivars. Results from Bartlett's test reveals that variances for each trait are not homogeneous (data not shown); having a high number of accessions and pooling three years of data have probably contributed to this heterosedasticity. Moreover, Table 3 does not provide any evidence about the genetic nature of such differences, nor is the influence of environment on breeding line performances offset.

Table 2: Descriptive statistics of the population under study

Statistics		HT (cm)	HPBF (cm)	HDBFC (cm)	LBV (cm)	LBF (cm)	NBV	NCF	NCV	NPBF	Yield (kg/ha)
Range	All years	63 - 190	12 - 42.5	46 - 172.5	16.5 - 132	15.5 - 86.5	0.7 - 4.8	0 - 21.7	0.1 - 21.4	3.4 - 8.5	434.38 - 3778.13
	2013	92.5 - 180	15.5 - 42	73 - 172	33 - 132	32.5 - 75.5	0.9 - 4.3	4 - 19.8	0.6 - 6.1	4.2 - 8.5	928.13 - 2740.63
	2015	80.5 - 146.5	12 - 29.5	68.5 - 127	19 - 91.5	28.5 - 80	0.7 - 4	7.8 - 21.7	0.1 - 21.4	3.4 - 6.8	NA
	2016	63 - 190	15.5 - 42.5	46 - 172.5	16.5 - 123	15.5 - 86.5	1.2 - 4.8	0 - 11.7	4.1 - 16.1	4.5 - 7.8	434.38 - 3778.13
Mean (± sd)	All years	129.04 ±19.58	24.35 ±4.93	111.41 ±20.26	69.52 ±17.69	50.99 ±10.83	2.25 ±0.6	9.73 ±4.88	5.22 ±4.39	5.7 ±0.78	2038.76 ±562.56
	2013	130.68 ±15.75	23.93 ±4.85	108.65 ±17.1	66.95 ±13.69	49.77 ±7.75	2.22 ±0.49	10.2 ±3.55	2.3 ±0.99	5.83 ±0.75	1791.45 ±346.36
	2015	113.95 ±13.25	23.16 ±2.59	100.57 ±14.41	61.62 ±16.01	49.92 ±11.06	1.89 ±0.55	14.62 ±3.15	3.94 ±3.4	5.13 ±0.73	NA
	2016	140.83 ±21.23	26.2 ±6.16	126.44 ±21.31	81.4 ±19.17	54.05 ±14.03	2.63 ±0.61	4.41 ±2.1	11.27 ±2.13	6 ±0.61	2450.93 ±611.13
CV	All years	15.17	20.25	18.19	25.45	21.24	26.67	50.15	84.10	13.68	27.59
	2013	12.05	20.27	15.74	20.45	15.57	22.07	34.80	43.04	12.86	19.33
	2015	11.63	11.18	14.33	25.98	22.16	29.10	21.55	86.29	14.23	NA
	2016	15.07	23.51	16.85	23.55	25.96	23.19	47.62	18.90	10.17	24.93

NA: not available; sd= standard deviation

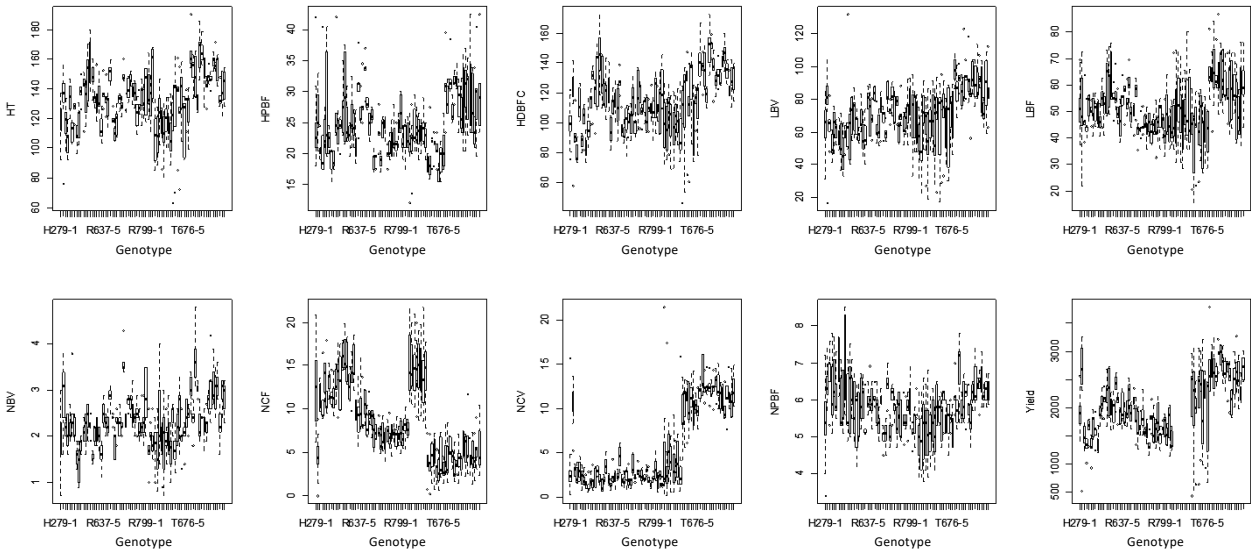

Figure 1: Box-plots of ten agronomic and morphological traits showing high variation

Genetic and environmental variances as well as the heritability of the different traits are displayed in Table 4. Values of trait's heritability ranged from 0 (NCF in 2013) to 0.85 (overall HT). Variations of heritability occur due to year, especially for the number of bolls on fruiting branches ($0 \leq H^2_{NCF} \leq 0.93$), the number of bolls on vegetative branches ($0 \leq H^2_{NCV} \leq 0.76$), the position of the first fruiting branch ($0.24 \leq H^2_{NPBF} \leq 0.87$), the length of the longest fruiting branch ($0.22 \leq H^2_{LBF} \leq 0.76$), the height of the first fruiting branch ($0.40 \leq H^2_{HPBF} \leq 0.83$), and yield ($0.36 \leq H^2_{Yield} \leq 0.76$). High variations of the heritability values for the same trait may be considered as an inconsistency in its estimation, since it may be argued that traits are transmitted in the same manner within a given population.

In general, heritability values recorded in 2015 were far lower than that calculated for 2013 and 2016. A higher environmental influence (E) in that year probably contributed to lower the contribution of the genotype (G) in the phenotypic expression of plants (P=G+E). Another possibility is that genotypes used in that year are closer to each other so that σ^2_g is far lower than that of 2013 and 2016. So far, heritability values for plant height ($H^2_{HT} \approx 0.83$), height of the first fruiting branch ($H^2_{HPBF} \approx 0.68$), height of the top fruiting branch ($H^2_{HDBFC} \approx 0.78$), and number of vegetative branches ($H^2_{NBV} \approx 0.84$) are considered to be consistent. Heritability values for the position of the first fruiting branch ($H^2_{NPBF} \approx 0.73$) and length of the longest vegetative branch ($H^2_{LBV} \approx 0.51$) are considered to be fairly reliable for they are slightly variable.

It clearly appears that plant height (HT) and height of the top fruiting branch (HDBFC) are highly heritable, with low CVs which can be an indicator of high-precision data. They are thus the most reliable descriptors for the cotton varieties in selection in Benin. Ashan et al. (2015) and Gore et al. (2014) reported high heritability values for cotton plant height using germplasm of different geographical origins. As differences among varieties are highly significant ($P<0.001$, Table 3), it is arguable that plant height and height of the top fruiting branch are useful descriptors that can effectively discriminate genotypes under selection in Benin. However, the correlation matrix reveals that HT and HDBFC are redundant variables ($\chi^2=0.93$, $P<0.001$). Furthermore, these two variables proved to have similar correlation coefficients (Pearson's χ^2) with the other variables, confirming the redundancy hypothesis (Table 5). Thus, collecting both variables seems to be an inefficient use of resources. If a choice must be made, HDBFC might be preferred to HT, since its coefficients of correlation generally are higher.

Table 3: P-values and significance of differences of ANOVA for architectural and agronomic traits recorded on ME trials run from 2013 to 2016

Source of variation	HT	HPBF	HDBFC	LBV	LBF	NBV	NCF	NCV	NPBF	Yield
All genotypes	< 2.2e-16***	< 2.2e-16***	< 2.2e-16***	< 2.2e-16***	< 2.2e-16***	< 2.2e-16***	< 2.2e-16***	2.171e-08***	< 2.2e-16***	< 2.2e-16***
Genotypes in 2013	< 2.2e-16***	1.231e-10***	< 2.2e-16***	1.345e-07***	4.967e-16***	< 2.2e-16***	< 2.2e-16***	2.862e-10***	< 2.2e-16***	< 2.2e-16***
Genotypes in 2015	2.936e-06***	8.098e-05***	2.872e-04***	2.386e-04**	0.02038*	1.825e-05***	0.4784252 ns	0.479069 ns	0.002267***	NA
Genotypes in 2016	< 2.2e-16***	< 2.2e-16***	< 2.2e-16***	3.831e-11***	< 2.2e-16***	< 2.2e-16***	0.01831*	8.855e-06***	4.736e-08***	5.156e-11***

NA: not available, ns=non significant,* $P<0.05$, ** $P<0.01$, *** $P<0.001$

Table 4: Variances (±sd) and broad-sense heritability of agro-morphological traits evaluated in micro-trials from 2013 to 2016

Variance components		HT	HPBF	HDBFC	LBV	LBF	NBV	NCF	NCV	NPBF	Yield
Genotypic variance	All years	180.40 ±13.43	12.38 ±3.52	137.50 ±11.73	71.44 ±8.45	44.90 ±6.70	0.18 ±0.43	15.25 ±3.91	2.86 ±1.69	0.30 ±0.55	42,049 ±205.10
	2013	98.52 ±9.93	4.59 ±2.14	79.48 ±8.92	25.82 ±5.08	6.27 ±2.50	0.11 ±0.33	0.15 ±0.39	0.38 ±0.62	0.11 ±0.33	22,136 ±148.80
	2015	24.59 ±4.96	0.74 ±0.86	18.60 ±4.31	33.31 ±5.77	4.36 ±2.09	0.05 ±0.21	≈0.00	≈0.00	0.01 ±0.11	NA
	2016	77.21 ±8.79	2.19 ±1.48	63.90 ±7.99	11.84 ±3.44	2.20 ±1.48	0.13 ±0.36	0.02 ±0.14	0.10 ±0.31	0.06 ±0.24	10,690 ±103.40
Error variance	All years	156.70 ±12.52	12.74 ±3.57	182.00 ±13.49	193.52 ±13.91	71.81 ±8.47	0.17 ±0.41	5.60 ±2.37	4.79 ±2.19	0.22 ±0.47	11,7840 ±343.30
	2013	87.25 ±9.34	14.22 ±3.771	117.67 ±10.85	115.33 ±10.74	29.25 ±5.41	0.10 ±0.32	3.53 ±1.88	0.59 ±0.77	0.18 ±0.42	34,480 ±185.70
	2015	123.49 ±11.11	5.49 ±2.3426	135.70 ±11.65	193.81 ±13.92	53.77 ±7.33	0.27 ±0.52	6.02 ±2.45	7.79 ±2.79	0.20 ±0.44	NA
	2016	94.79 ±9.74	7.68 ±2.771	96.40 ±9.82	105.12 ±10.25	37.86 ±6.15	0.12 ±0.34	2.30 ±1.52	1.95 ±1.40	0.22 ±0.47	94,979 ±308.20
H^2	All years	0.85	0.83	0.79	0.65	0.76	0.84	0.93	0.75	0.87	0.64
	2013	0.85	0.62	0.77	0.53	0.52	0.84	0.18	0.76	0.76	0.76
	2015	0.50	0.40	0.41	0.46	0.29	0.46	0.00	0.00	0.24	NA
	2016	0.80	0.59	0.77	0.36	0.22	0.85	0.04	0.20	0.57	0.36

NA: not available; sd= standard deviation

Table 5: Pearson's coefficients of correlation between agro-morphological traits

Traits	HT	HDBFC	HPBF	LBV	LBF	NBV	NCF	NCV	NPBF
HDBFC	*0.93***								
HPBF	0.52***	0.53***							
LBV	0.76***	0.74***	0.52***						
LBF	0.62***	0.67***	0.57***	0.66***					
NBV	0.55***	0.49***	0.48***	0.67***	0.33***				
NCF	0.06 ns	0.22***	0.20***	0.10*	0.42***	-0.17***			
NCV	0.30***	0.36***	0.36***	0.54***	0.36***	0.48***	0.30***		
NPBF	0.34***	0.26***	0.33***	0.27***	0.03 ns	0.44***	-0.02 ns	0.21***	
Yield	0.62***	0.72***	0.39***	0.62***	0.61***	0.33***	0.45***	0.52***	0.11*

Pairs of cells colored in blue show similarity in χ^2 for HT and HDBFC as correlated to the other traits. ns=non significant,* *P*<0.05, ** *P*<0.01, * *P*<0.001**

Height of the first fruiting branch (HPBF) and number of vegetative branches (NBV) are characterized by high heritability and relatively high CVs (15-30%). Under the assumption of reliable data collection, these traits can also be considered as plant descriptors. It would mean that the population under study displays a greater variation of these traits as compared to HT and HDBFC. The position of the first fruiting branch (NPBF) is also highly heritable, with a relatively low CV, which makes it an interesting trait for consideration in a cotton breeding program.

NCF and NCV have coefficients of variation (CV) over 30%. Moreover, heritability of these descriptors is not consistent; therefore, they are of low interest in a conventional cotton breeding program. These variables are likely more under control of environmental and/or management factors which interact with genotypes. The lengths of vegetative and fruiting branches (LBV and LBF) have high CVs (15-30%) with heritability values of approximately 0.50, but can be inconsistent. These two impairments cast doubts on data quality and usability. Consequently, assessment of these traits in this study is problematic. Although they contribute together with HT to help the breeder visualize the plant's form, these two architectural descriptors fail to capture a similar descriptive phenotype as height-related traits (HT, HPBF, HDBFC). If additional data led to lower CV and more consistent H^2 gathered through panel data and further experimentation regarding these two descriptors, they may be useful descriptors.

Seed cotton yield can be an important variable used in cotton breeding programs. However, in this dataset, yield has a moderately high CV with an inconsistent heritability estimate. This inconsistency makes it difficult to assess the usefulness and quality of yield data collected in the Beninese cotton breeding program. However, it can be observed from Table 5 that seed cotton yield is positively and significantly correlated to four architectural traits: plant height, height of the top fruiting branch, length of the longest vegetative branch, and length of the longest fruiting branch (χ^2>0.60, P<0.001). As a consequence it might be useful to choose one of these architectural traits as a yield proxy. Interseasonal vagaries could have impaired the expression of this genetic potential. Instead of evaluating the heritability of seed cotton yield, it might be more useful to focus on the heritability of yield components. The number of bolls and number of fruiting sites together with average boll weight and boll retention might also be valuable predictors of yield.

Highly heritable traits are mainly architectural (HT, HPBF, HDBFC, NBV, NPBF). At first hand, it is admitted that an increase of HT, HPBF and HDBFC are preferred, as these are positively and significantly correlated to seed cotton yield. One may like to reduce NBV and NPBF to partition assimilates to fruiting structures, which appear later in the growing season and located higher than vegetative branches. However, there is no clear empirical evidence of this relation between NBV, NPBF and seed cotton yield or yield components.

CONCLUSION

Final plant mapping helps breeders to collect important data used for the agro-morphological characterization of cotton genotypes. However, some traits (NCV and NCF) are found to be highly variable suggesting a high degree of experimental

error while collecting data or in the experimental design. Other traits (LBV, LBF, and Yield) show inconsistent heritability values from one experiment to another. Redundancy was found for plant height (HT) and height of the top fruiting branch (HDBFC) as these trait values tend to track together. Variables with high heritability are HDBFC, HPBF, and NBV, which are useful in the characterization of genotypes. Seed cotton yield needs to be recorded, even though the heritability of yield can be inconsistent across years, but because of significant and positive correlations between yield and architectural traits, these have been suggested as proxies of potential yield. It is predicted that selecting cotton varieties with better architectural characteristics also leads to yield improvement.

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