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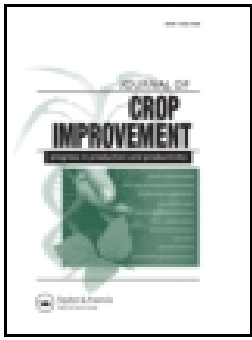
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Phenotypic characterization of maize landraces from Sahel and Coastal West Africa reveals marked diversity and potential for genetic improvement

Charles Nelimor^{a,b}, Baffour Badu-Apraku^b, Simon P. A. Nguetta^a,
Antonia Y. Tetteh^c, and Ana Luísa Garcia-Oliveira^b

^aDepartment of Bioscience, Université Felix Houphouët Boigny, Abidjan, 34 Côte d'Ivoire; ^bMaize Improvement Unit, International Institute of Tropical Agriculture, Ibadan, Nigeria; ^cDepartment of Biochemistry and Biotechnology, Kwame Nkrumah University of Science and Technology, Kumasi, Ghana

ABSTRACT

Landraces of maize (*Zea mays* L.) are invaluable sources of genetic variability for improving agronomic traits, and they hold great promise in developing new maize varieties with enhanced resilience to stresses. Even though phenotypic characterization is an inexpensive approach for elucidating variation hidden in genetic resources, information on the genetic diversity patterns in large collections of landraces remains limited and this constitutes a major impediment for their optimal utilization in modern maize breeding programs. We investigated the extent of phenotypic diversity among 196 maize landraces, representing gene pools from Burkina Faso, Ghana and Togo, and 14 improved populations/varieties from the Maize Improvement Program of International Institute of Tropical Agriculture (IITA-MIP). The germplasm was assessed for 26 agronomic traits. Highly significant differences ($P < 0.001$) were observed among the accessions for all measured traits. Cluster analysis separated the maize germplasm into five major groups, differentiated largely by phenology and overall phenotypic appeal, enabling identification of outstanding genotypes for further screening for stress tolerance. Wide genetic diversity was observed between Burkinabe and improved gene pools, suggesting that the original Sahelian gene pool might not have contributed much to modern cultivars. This gene pool offers opportunities for pre-breeding by providing novel alleles for enriching elite maize germplasm. Shannon-Weaver diversity index (H') revealed high genetic variability among the landraces ($H' = 0.73$) and a narrow genetic base in the improved populations and varieties ($H' = 0.46$). These results provide new insights into the potential of tropical maize landraces for genetic improvement of maize.

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Introduction

Maize is endowed with remarkable phenotypic diversity because of its allogamous system of reproduction and the repeated selection practiced by farmers to meet

CONTACT Baffour Badu-Apraku  b.badu-apraku@cgiar.org

 Supplemental data for this article can be accessed [here](#).

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their basic needs, leading to adaptation to local conditions (McCann 2005). After its introduction into Africa around 1500 A.D, maize has adapted well to different local growing conditions (Matsuoka 2005). Presently, maize occupies the largest area of all staple crops in sub-Saharan Africa (SSA), with more than 208 million people depending on it for food and economic well-being (Abate et al. 2017). Maize consumption in SSA ranges from 52 to 450 g/person/day (Ranum, Peña-Rosas, and Garcia-Casal 2014; FAOSTAT 2016), which makes it the most important staple in the region. However, maize continues to perform poorly in the region, with average yield estimated at 2.1 tons ha⁻¹ (FAOSTAT 2017).

The low productivity of maize in SSA can be attributed to a number of constraints, including frequent drought and heat stresses, poor soil fertility and incidence of parasitic weeds, particularly, *Striga hermonthica* (Cairns et al. 2012; Badu-Apraku and Fakorade 2017; Das et al. 2019). While demand for maize, between now and 2050, is expected to increase three-fold (Ekpa et al. 2018), yields are predicted to be negatively affected by climate change (Cairns et al. 2012). With the current effects of climate change, rainfall in SSA will either occur late or stop earlier than usual, whereas temperatures in large areas have already exceeded the threshold for maize growth (Cairns et al. 2012).

Breeding for stress tolerance has been proposed as an efficient strategy to adapt crops to climate change (Atlin, Cairns, and Biswanath 2017). To achieve this goal, plant breeders must have consistent access to new genetic variation (Liu et al. 2019). The value of landraces in accelerating genetic gains for grain yield by providing resilience against prevalent stresses is well-recognized (Hellin, Bellon, and Hearne 2014). Maize research results from previous studies have indicated that landraces are invaluable for improving abiotic stress resilience in modern breeding programs (Meseka et al. 2013; Pineda-Hidalgo et al. 2013). For example, tropical maize landraces, such as “Tuxpeño Sequia” and “Cateto”, have greatly contributed to drought tolerance and aluminum tolerance in modern hybrids (Liu et al. 2003; Wen et al. 2012). However, despite their potential, only a very small proportion of the large collection of maize landraces existing in germplasm banks as reservoirs of useful alleles has been used in maize improvement programs (Prasanna 2012).

The gene bank at IITA, Ibadan, Nigeria, conserves approximately 1,600 maize landraces. The under-utilized but useful variation within this collection, when introgressed into elite genetic backgrounds, could provide diverse benefits, including increased stress resilience and yield potential, and improved nutritional quality.

Phenotypic description is the foremost step in germplasm identification and classification (Govindaraj, Vetriventhan, and Srinivasan 2015). Phenotypic descriptors are easy to record, inexpensive and are reliable for estimating heritability (Govindaraj, Vetriventhan, and Srinivasan 2015; Mengistu, Afeworki, and Mario 2015). For these reasons, they are highly preferred in developing countries, where labor is readily available at reduced cost. Phenotypic

assessment has proven efficient for diversity analysis in cereal crops, including maize (Salazar et al. 2016; Sattler et al. 2018; Yadav et al. 2018; Tiwari et al. 2019).

The primary objective of this study was to examine the pattern of genetic diversity in 196 maize landraces, originating from Burkina Faso, Ghana and Togo, sourced from gene banks in IITA and Ghana. Another important objective of this study was to compare the genetic diversity of each landrace gene pool with that of 14 improved populations and varieties from the IITA-MIP.

Materials and methods

Genetic material

In this study, 196 landraces originating from Burkina Faso (59), Ghana (46), and Togo (91) and 14 improved open-pollinated populations and varieties (OPVs), developed by IITA in collaboration with national partners, were evaluated (online Supplementary Table S1). The landraces from Burkina Faso and Togo were randomly sampled from the IITA gene bank, whereas the landraces from Ghana, and the improved populations and OPVs were provided by the Plant Genetic Resources Institute (PGRI) of Ghana, and the IITA-MIP, respectively.

The seeds of all the accessions were multiplied (*via* pair/plant-to-plant crossing) during the off-season in 2017. Flowering records were kept during seed multiplication to classify the accessions into four maturity groups, namely, extra-early (≤ 85 days to physiological maturity), early (90–95 days), intermediate (100–110 days) and late (> 110 days).

Trial establishment and management

The trials were carried out at the IITA experimental station, Ikenne, ($6^{\circ}53' N$, $3^{\circ} 42' E$, 60 m altitude, 1200 mm annual rainfall) in Nigeria, during the main growing seasons of 2017 and 2018. In both years, accessions were evaluated using a 15×14 lattice design with two replications. To minimize competition between plants of different maturity groups of the blocks, restricted randomization of the entries of each maturity group was adopted to ensure that entries in each group were randomized before randomly assigning them to the blocks of the respective replications. A plot consisted of a single, 3-m long row. Rows were spaced 0.75 m apart and distance between hills was 0.40 m. Three seeds were planted per hill and seedlings were thinned to two per hill two weeks after planting (WAP), resulting in a final plant density of 66,666 plants/ha. Two WAP, 60 kg ha⁻¹ each of nitrogen (N), phosphorus (P) and potassium (K) fertilizer was applied. Four weeks later, the trials were top-dressed with 30 kg N ha⁻¹ of urea. Trials were kept weed free through manual weeding.

Data collection

Data collection was done on a plot basis for 26 agro-morphological traits following the CIMMYT-IBPGR (1991) maize descriptor list (Table 1).

Data analysis

The experiment was carried out in one location for two years. A combined analysis of variance (ANOVA) was performed to determine whether or not significant differences existed among the accessions for various measured traits. The ANOVA was conducted with PROC GLM in SAS 9.4 using a RANDOM statement with the TEST option (SAS Institute Inc 2017). In the combined ANOVA, environments, replications within environments, and blocks within replication-by-environment were regarded as random effects, whereas genotypes were considered fixed effects. Variances were estimated by REML (restricted maximum likelihood) method using the MIXED procedure in SAS.

The repeatability (R) of the traits was computed on an accession-mean basis using the following formula suggested by Falconer and Mackay (1996):

$$R = \frac{\sigma_g^2}{\sigma_g^2 + \frac{\sigma_{ge}^2}{e} + \frac{\sigma_e}{r}}$$

where σ_g^2 is the genotypic variance, σ_{ge}^2 is the genotype \times environment interaction variance, σ_e is the residual variance; e is the number of environments, and r is the number of replicates per environment.

Cluster analysis (CA), which displayed a constellation plot, including a phylogenetic heatmap, and pairwise Mahalanobis genetic distances (D^2) between clusters and gene pools, were conducted using JMP Pro 14.1.0 (SAS Institute Inc 2017). NTSYS.pc 2.2 software (Rohlf 2009) was used for principal component analysis (PCA). For PCA, only principal components that explained at least 5% of the total variation and had Eigen value ≥ 1 were used to determine the discriminatory traits. Biplot analysis was performed to further elucidate the relationships between genetic groups.

The sequential stepwise multiple-regression procedure, described by Mohammadi, Prasanna, and Singh (2003), was adopted to categorize predictor variables into first, second, third and fourth order paths based on their respective contributions to variation in grain yield, with minimal multicollinearity. Only traits with repeatability estimates of $\geq 75\%$ were used for the stepwise multiple-regression analysis in JMP Pro 14.1.0.

Shannon-Weaver diversity index (H') was calculated to estimate the diversity within each germplasm group, as well as the overall phenotypic diversity (Shannon 1948). H' was calculated using the following equation:

Table 1. List of the 26 agro-morphological descriptors of maize used in the study.

| No. | Descriptor | Abbreviation | Measurement procedure/description |
|-----|--|--------------|---|
| 1 | Anthesis date (days) | AD | Number of days from planting to when 50% of the plants in the plot had shed pollen. |
| 2 | Silking date (days) | SD | Number of days from planting to when 50% of the plants in the plot had emerged silks of least 1cm long |
| 3 | Anthesis-silking interval (days) | ASI | Calculated as SD-AD (days) |
| 4 | Number of leaves per plant | NL | Average number of leaves of 10 representative plants per plot at flowering |
| 5 | Number of leaves above the uppermost ear | NLAE | Average number of leaves above the uppermost ear of 10 representative plants per plot at flowering |
| 6 | Tassel length (cm) | TL | Measured from the point of origin to the tip of the central spike at blister stage on 10 representative plants per plot |
| 7 | Number of primary tassel branches | NPTB | Record the average number of primary tassel branches on 10 representative plants per plot at blister stage |
| 8 | Ear leaf length (cm) | ELL | Length of leaf which subtends the uppermost ear at flowering |
| 9 | Ear leaf width (cm) | ELW | Width of leaf which subtends the uppermost ear at flowering |
| 10 | Plant height (cm) | PLHT | Measured as the distance from the base of the plant to the height of the first tassel branch at milk stage |
| 11 | Ear height (cm) | EHT | Measured as distance from the base of the plant to the node bearing the upper ear at milk stage |
| 12 | Ear position | EPLA | Calculated as EHT divided by PLHT |
| 13 | Plant aspect | PASP | Rated on plot basis after milk stage using a scale of 1 to 9, where 1 = excellent overall phenotypic appeal and 9 = poor overall phenotypic appeal. |
| 14 | Stay green characteristics | SG | Recorded on plot basis at physiological maturity using a scale of 1 to 9, where 1 = almost all leaves green and 9 = virtually all leaves dead. |
| 15 | Husk cover | HC | Scored on plot basis after milk stage using a scale of 1 to 9, where 1 = husks tightly arranged and extended beyond the ear tip and 9 = ear tips exposed |
| 16 | Response to <i>Helminthosporium turcicum</i> | Turc. | Scored for each plot at milk stage based on severity of the disease symptom, using a 1 to 9 scale, where 1 = no symptom and 9 = very susceptible |
| 17 | Ear aspect | EASP | Rated for each plot based on freedom from disease and insect damage, ear size, and uniformity, using a scale of 1 to 9, where 1 = clean, uniform, large, and well-filled ears and 9 = rotten, variable, small, and partially filled ears. |
| 18 | Number of ears per plant | EPP | Calculated as total number of ears divided by number of plants harvested per plot |
| 19 | Number of kernels per row | NKR | Average number of kernels of 10 rows from five representative uppermost ears in a plot after harvest |
| 20 | Ear length (cm) | EL | Length of ears located on the highest point on plant on plot basis after harvest |
| 21 | Grain yield (Mg/ha) | GY | Computed for each plot based on 80% shelling percentage, and adjusted to 15% moisture content. |
| 22 | Ear diameter (cm) | ED | Recorded at central part of the uppermost ear of five representative plants per plot after harvest. |
| 23 | Number of rows per ear | NRE | Count number of kernel rows in central part of five representative uppermost ears in a plot after harvest |
| 24 | Kernel length (mm) | KL | Average length of 10 kernels from the middle of five uppermost ears in a plot, measured with a calliper after harvest |

(Continued)

Table 1. (Continued).

| No. | Descriptor | Abbreviation | Measurement procedure/description |
|-----|----------------------|--------------|---|
| 25 | Kernel width (mm) | KW | Average width of 10 kernels from the middle of five uppermost ears in a plot, measured with a calliper after harvest |
| 26 | Kernel diameter (mm) | KD | Average diameter of 10 kernels from the middle of five uppermost ears in a plot, measured with a calliper after harvest |

$$H' = \frac{[\sum (n/N) \times \{\log_2(n/N) \times (-1)\}]}{\log_2 k}$$

where H' represent the standardized Shannon-Weaver diversity index, k is the number of phenotypic classes for a trait, n is the number of observations in the phenotypic class of that trait and N is the total number of observations for that trait. Subsequently, was classified as high ($H' \geq 0.60$), considerable ($0.40 \leq H' \leq 0.60$), or low ($0.10 \leq H' \leq 0.40$), as described by Mengistu, Afeworki, and Mario (2015).

Results

Phenotypic variability among accessions

There were highly significant differences ($p < 0.001$) among genotypes for all measured traits (Table 2). The number of days to anthesis and silking averaged 55 and 58, respectively (Supplementary Table S1). The difference in flowering dates between the earliest and latest accession was approximately 33 days for anthesis (AD) and 37 days for silking (SD). Anthesis-silking interval (ASI) ranged from 1 to 6 days, with an average of 3 days. Plant height ranged from 103 to 261 cm (mean = 190 cm), whereas ear height ranged from 30 to 193 cm (mean = 100 cm). Coefficients of variation (CV) were high for ASI (32.30%), husk cover (HC) (27.21%), and grain yield (GY) (21.06%), but low for AD (2.56%) and SD (2.59%). Grain yield ranged from 0.85 Mg/ha for TZm-1321 to 6.92 Mg/ha for TZEE-W HDT C3 STR C5, with a mean of 2.78 Mg/ha. TZm-1284, a landrace from Togo, yielded 6.12 Mg/ha, which was comparable to the yield of the best-improved population, TZEE-W HDT C3 STR C5 (6.92 Mg/ha). Thirteen other landraces yielded between 4.0 Mg/ha and 5.8 Mg/ha. High-yielding accessions were generally intermediate to late maturing, whereas low-yielding accessions were remarkably extra-early (online Supplementary Table S1).

Genotypic variances for a majority of the traits were larger than variances attributable to genotype-by-environment interaction and residual variance. Consequently, repeatability values were high (i.e., ≥ 0.60), ranging between 0.57 for HC and 0.99 for ear height (EHT), with an average of 0.86 across measured traits (Table 2).

Table 2. Mean squares from combined analysis of variance of 26 agro-morphological traits† of 210 maize accessions evaluated during the main growing seasons in 2017 and 2018 at Ikenne, Nigeria.

| Source | df | AD (day) | SD (day) | ASI (day) | PLHT (cm) | EHT (cm) | EPLA | HC (Scale:1-9) | NL | NLAE |
|-------------------|-----|-----------|------------|------------|--------------|-------------------|------------------|----------------|------------------|------------|
| Years | 1 | 735.47*** | 1694.34*** | 197.20*** | 20,552.41*** | 5175.27*** | 0 | 22.34*** | 450.28*** | 202.08*** |
| Rep (Year) | 2 | 11.75** | 14.15*** | 0.68 | 722.75** | 984.84*** | 0.01* | 0.09 | 0.15 | 1.24* |
| Blocks (Year×Rep) | 56 | 4.21*** | 4.37** | 0.84 | 262.81*** | 112.95* | 0* | 0.85* | 1.24** | 0.32 |
| Genotypes | 209 | 43.54*** | 50.66*** | 3.03*** | 1625.40*** | 1288.37*** | 0.01*** | 1.80*** | 7.00*** | 1.63*** |
| Genotypes × Years | 209 | 4.55*** | 5.53*** | 1.38*** | 0.91 | 0.25 | 0 | 0.82** | 0.02 | 0.01 |
| Residual | 362 | 2.02 | 2.27 | 0.8 | 130.15 | 76.05 | 0 | 0.58 | 0.7 | 0.35 |
| Repeatability | | 0.91 | 0.91 | 0.6 | 0.96 | 0.99 | 0.98 | 0.57 | 0.95 | 0.91 |
| Source | df | ELL (cm) | ELW (cm) | NPTB | TL (cm) | Turc. (Scale:1-9) | PASP (Scale:1-9) | EPP | EASP (Scale:1-9) | ED (cm) |
| Years | 1 | 157.38** | 38.71*** | 1461.64*** | 562.91*** | 167.41*** | 0.2 | 0.26*** | 10.74*** | 1854.17*** |
| Rep (Year) | 2 | 112.08*** | 9.60*** | 8.50* | 33.94* | 6.79*** | 2.05* | 0 | 0.78 | 8.46 |
| Blocks (Year×Rep) | 56 | 24.97*** | 0.60*** | 2.26 | 9.83 | 1.10*** | 0.64* | 0.01 | 0.44 | 2.66 |
| Genotypes | 209 | 352.95*** | 4.51*** | 25.17*** | 62.38 | 3.018*** | 2.86*** | 0.06*** | 3.28*** | 78.13*** |
| Genotypes × Years | 209 | 4.21 | 1.44*** | 5.15*** | 18.45*** | 1.08*** | 0.60** | 0.02 | 0.52** | 0.08 |
| Residual | 362 | 10.84 | 0.23 | 2.38 | 8.71 | 0.55 | 0.44 | 0.01 | 0.36 | 4.11 |
| Repeatability | | 0.98 | 0.76 | 0.83 | 0.73 | 0.66 | 0.79 | 0.8 | 0.83 | 0.98 |
| Source | df | EL (cm) | KD (mm) | KL (mm) | KW (mm) | NKR | NRE | SG (Scale:1-9) | GY (Mg/ha) | |
| Years | 1 | 190.29*** | 1.92** | 8.24*** | 2.06* | 204.04*** | 0 | 116.63*** | 4.81 | |
| Rep(Year) | 2 | 1.83 | 0.69* | 0.63 | 0.01 | 4.04 | 0.55 | 1.89* | 1327.87* | |
| Blocks (Year×Rep) | 56 | 1.85** | 0.19 | 0.52* | 0.52 | 3.95 | 0.96 | 0.61* | 382.52 | |
| Genotypes | 209 | 13.84*** | 0.78*** | 3.55*** | 2.06*** | 67.80*** | 9.91*** | 2.94*** | 4433.41*** | |
| Genotypes × Years | 209 | 0.1 | 0 | 0 | 0 | 0.02 | 0.02 | 0.62*** | 297.84 | |
| Residual | 362 | 1.13 | 0.21 | 0.34 | 0.38 | 3.94 | 0.75 | 0.41 | 341.65 | |
| Repeatability | | 0.95 | 0.86 | 0.96 | 0.89 | 0.96 | 0.95 | 0.78 | 0.93 | |

*, **, *** Significant at 0.05, 0.01 and 0.001 probability levels, respectively.

†AD = days to anthesis; SD = days to silking; ASI = anthesis silking interval; PLHT = Plant height; EHT = Ear height; EPLA = Ear position, HC = Husk cover, NL = number of leaves per plant; NLAE = Number of leaves above the uppermost ear; ELL = Ear leaf length; ELW = Ear leaf width; NPTB = number of primary tassel branches; TL = Tassel length; Turc. = reaction to Turcicum; PASP = Plant aspect; EPP = Ears per plant; EASP = Ear aspect; ED = Ear diameter; EL = Ear length; KD = Kernel diameter; KL = Kernel length; KW = Kernel width; NKR = Number of kernels per row; NRE = Number of rows per ear; SG = Stay green characteristics; GY = Grain yield.

Germplasm structure and phylogenetic relationships

The genetic relatedness was estimated via cluster analysis based on Mahalanobis distance using the Ward's algorithm, which displayed a constellation plot. The constellation plot grouped the 210 maize germplasm accessions into five main clusters, each further divided into sub-clusters (Figure 1). The number of accessions belonging to a specific cluster varied from 27 (12.8% in cluster IV) to 65 (31% in cluster II) (online Supplementary Table S2). Clusters I and V were represented primarily by early and extra-early-maturing landraces from Burkina Faso; some improved populations, notably, TZEE-Y HDT C3 STR C5, 2014 TZEE-Y HDT STR, 2017 TZEE-Y HDT STR, 2011 TZE-W DT STR- Synthetic and DT STR-W syn 2-Y, were also included. Clusters II and III consisted mainly of a mixture of improved populations and varieties, together with landraces from Ghana and Togo, that were generally intermediate to late maturing, with good phenotypic appeal and high grain yield. Cluster IV contained predominantly late-maturing accessions from Ghana (online Supplementary Table S2).

To better understand the genetic relatedness among the different groups, neighbor-joining (NJ) analysis based on Mahalanobis genetic distance was

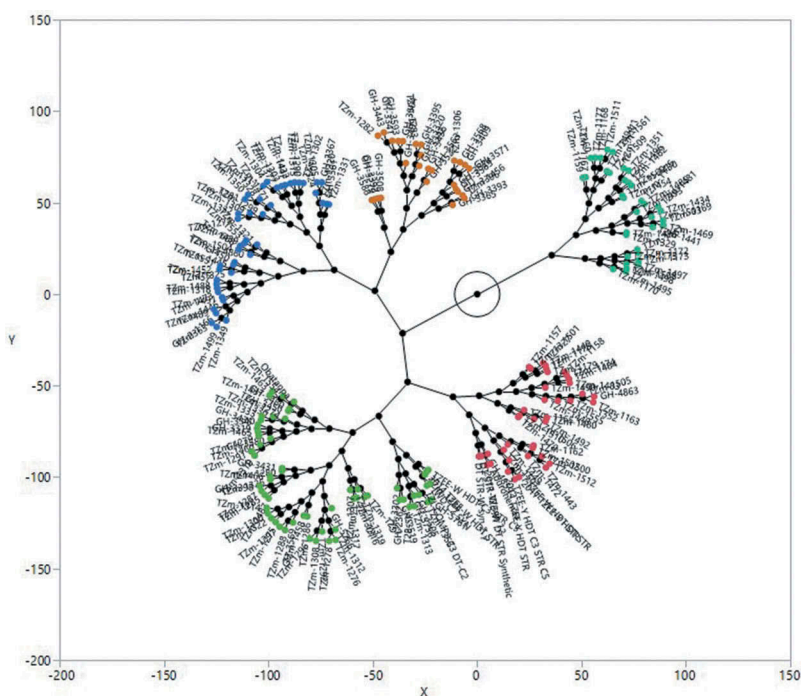


Figure 1. Cluster analysis depicting constellation plot of maize collections. Clusters I, II, III, IV and V represent collections as red (mainly Burkinabe landraces), green (mixture of Togolese, Ghanaian and improved varieties), blue (mainly Togolese landraces), orange (mainly Ghanaian landraces) and indigo points (mainly Burkinabe landraces).

performed. The NJ-analysis separated the four different maize gene pools into three groups (Figure 2). The first and third groups were represented by improved populations/varieties and Burkinabe landraces, respectively, whereas the second group contained admixture of landraces from Ghana and Togo. Intra-population genetic distances were lower than inter-population distances (Table 3). The largest inter-population distance was observed between Burkinabe germplasm and improved populations/varieties (78.10), whereas the smallest distance was between Togolese and Ghanaian germplasm (22.22).

Principal component, biplot and path-coefficient analyses

The PCA based on 26 agro-morphological traits showed that the first three principal components (PCs) accounted for 76.48% of the total variance in the germplasm (online Supplementary Table S3). The first PC accounted for 47.87% of the variance, and all the traits were discriminatory, except ASI, ear length (EL), kernel diameter (KD), and number of kernels per row (NKR). The second PC explained 19.86% of the total variance, in which AD, SD, ASI, stay green characteristics (SG), NKR, GY, ear aspect (EASP), ears per plant (EPP), plant aspect (PASP and EHT were the principal contributory traits. In the third PC, which explained 8.75% of the total variation, KD, number of primary tassel branches (NPTB), EL, NKR and HC were the major contributors. The biplot, constructed on the basis of the first two PCs, also largely classified Burkinabe and modern cultivars into two independent groups, and an admixture group of Ghanaian and Togolese populations (Figure 3).

The stepwise regression analysis identified EASP, kernel length (KL), SG, and ear leaf width (ELW) as first-order traits, accounting for about 90% of the grain-yield variation (online Supplementary Fig. S1). EASP had the largest direct effect (-0.61), whereas ELW had the least direct effect (-0.09). Second-order traits

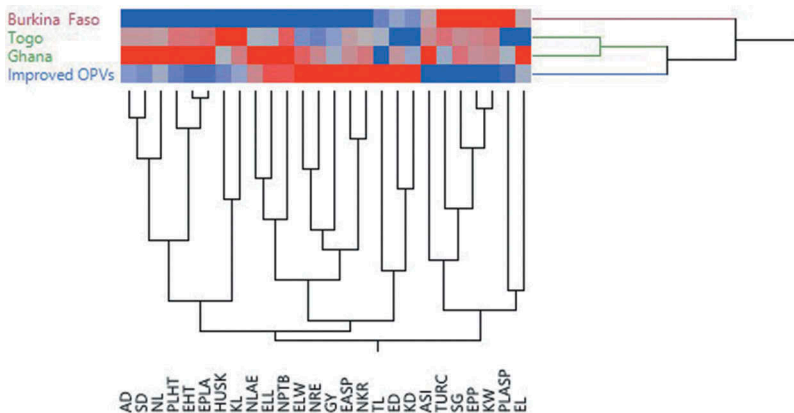
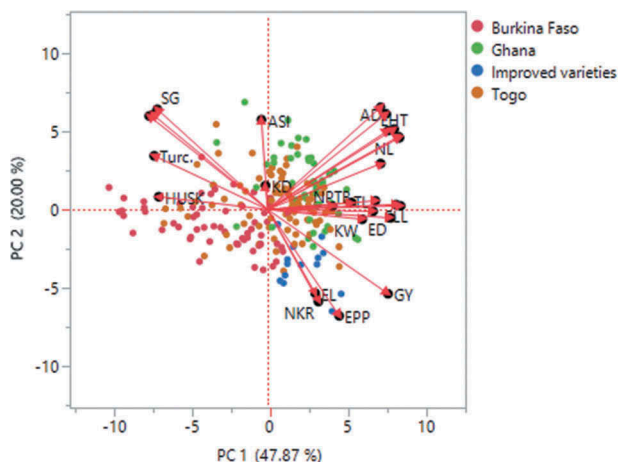


Figure 2. Agro-morphological traits heatmap showing the clustering of four gene pool of maize germplasm.

Table 3. Intra (bold) and inter-population genetic distances (D^2) of four maize gene pools based on 26 agro-morphological traits.

| Gene pool | Burkina Faso | Togo | Ghana | Improved populations/varieties |
|--------------------------------|--------------|--------------|--------------|--------------------------------|
| Burkina Faso | 25.56 | | | |
| Togo | 45.46 | 25.71 | | |
| Ghana | 69.41 | 22.22 | 25.44 | |
| Improved populations/varieties | 78.10 | 48.36 | 48.45 | 24.00 |

**Figure 3.** Accession by trait biplot of the 210 maize germplasm showing aggregation of the four gene pools and associated traits.

included PASP, EL, EPP, AD, NPTB, ear diameter (ED), plant height (PLHT), kernel width (KW), KD, number of leaves per plant (NL), ear position (EPLA), ear leaf length (ELL) and number of leaves above the uppermost ear (NLAE). Apart from EPLA, ELL and NLAE, all second-order traits contributed indirectly to grain yield through EASP, KL, SG, and ELW. PASP and EPP contributed indirectly to grain yield through EASP, KL, and SG. SD, NKR, number of rows per ear (NRE) and EHT were categorized as third-order traits, each contributing indirectly to grain yield through eight or more second-order traits.

Pattern of phenotypic variation

The estimated H' pooled across the entire germplasm for individual traits varied from 0.21 for KW to 0.98 for EPLA, with a mean of 0.72 (Table 4). Similarly, H' , pooled across landraces as a group, ranged from 0.23 for KW to 0.97 for EPLA, with a mean of 0.73. For individual gene pools, H' was completely monomorphic ($H' = 0.00$) for ASI, HC, SG, KW and turcicum rating in modern cultivars. The most polymorphic trait in modern cultivars was AD ($H' = 0.77$). KW was monomorphic in Ghanaian landraces but showed considerable diversity ($H' = 0.40$) in Burkinabe landraces. For all

Table 4. Descriptor states and Shannon-Weaver index (H') estimates of 26 agronomic traits across the 210 maize accessions.

| Trait† | Descriptors | Entire collection | Burkina Faso | Ghana | Togo | Improved varieties | Pooled Landraces |
|-----------------------------|---|-------------------|--------------|-------------|-------------|--------------------|------------------|
| AD | Extra-early, early, intermediate and late | 0.97 | 0.54 | 0.41 | 0.92 | 0.77 | 0.96 |
| SD | Extra-early, early, intermediate and late | 0.94 | 0.80 | 0.32 | 0.80 | 0.65 | 0.92 |
| ASI | Short, medium and long | 0.56 | 0.36 | 0.74 | 0.57 | 0.00 | 0.58 |
| PLHT | Short, intermediate and tall | 0.84 | 0.87 | 0.16 | 0.60 | 0.47 | 0.83 |
| EHT | Short, intermediate and tall | 0.81 | 0.41 | 0.38 | 0.70 | 0.37 | 0.80 |
| EPLA | Low, medium and high | 0.98 | 0.57 | 0.50 | 0.83 | 0.59 | 0.97 |
| PASP | Good, intermediate and poor | 0.65 | 0.57 | 0.67 | 0.40 | 0.55 | 0.56 |
| NL | High, intermediate and low | 0.82 | 0.33 | 0.69 | 0.68 | 0.62 | 0.84 |
| NLAE | High, intermediate and low | 0.62 | 0.63 | 0.38 | 0.61 | 0.23 | 0.64 |
| ELL | Short, intermediate and long | 0.76 | 0.83 | 0.56 | 0.64 | 0.62 | 0.77 |
| ELW | Narrow, intermediate and wide | 0.70 | 0.52 | 0.72 | 0.67 | 0.63 | 0.68 |
| HC | Good, intermediate and poor | 0.51 | 0.69 | 0.42 | 0.36 | 0.00 | 0.53 |
| NPTB | High, intermediate and low | 0.89 | 0.60 | 0.89 | 0.86 | 0.63 | 0.90 |
| TURC. | Good, intermediate and poor | 0.71 | 0.66 | 0.54 | 0.74 | 0.00 | 0.72 |
| SG | Good, intermediate and poor | 0.67 | 0.59 | 0.71 | 0.74 | 0.00 | 0.67 |
| TL | Short, medium and long | 0.78 | 0.88 | 0.60 | 0.69 | 0.62 | 0.79 |
| EPP | High, intermediate and low | 0.70 | 0.77 | 0.43 | 0.68 | 0.55 | 0.68 |
| EASP | Good, intermediate and poor | 0.70 | 0.63 | 0.71 | 0.59 | 0.55 | 0.74 |
| ED | Large, medium and small | 0.88 | 0.87 | 0.83 | 0.71 | 0.37 | 0.89 |
| EL | Short, medium and long | 0.60 | 0.60 | 0.78 | 0.37 | 0.62 | 0.59 |
| NKR | High, intermediate and low | 0.75 | 0.81 | 0.83 | 0.62 | 0.76 | 0.74 |
| NRE | High, intermediate and low | 0.55 | 0.63 | 0.66 | 0.32 | 0.37 | 0.56 |
| KD | Large, medium and small | 0.74 | 0.63 | 0.63 | 0.59 | 0.62 | 0.61 |
| KL | Short, medium and long | 0.63 | 0.69 | 0.63 | 0.88 | 0.55 | 0.95 |
| KW | Large, medium and small | 0.21 | 0.40 | 0.00 | 0.10 | 0.00 | 0.23 |
| GY | High, intermediate and low | 0.83 | 0.44 | 0.88 | 0.83 | 0.76 | 0.77 |
| Number of accessions | | 210 | 58 | 48 | 90 | 14 | 196 |
| Mean H' | | 0.72 | 0.63 | 0.58 | 0.63 | 0.46 | 0.73 |

†AD = days to anthesis; SD = days to silking; ASI = anthesis silking interval; PLHT = Plant height, EHT = Ear height, EPLA = Ear position, HC = Husk cover; NL = number of leaves per plant; NLAE = Number of leaves above the uppermost ear; ELL = Ear leaf length; ELW = Ear leaf width, NPTB = number of primary tassel branches; TL = Tassel length, Turc. = reaction to Turcicum; PASP = Plant aspect; EPP = Ears per plant; EASP = Ear aspect; ED = Ear diameter; EL = Ear length; KD = Kernel diameter; KL = Kernel length; KW = Kernel width; NKR = Number of kernels per row; NRE = Number of rows per ear; SG = Stay green characteristics; GY = Grain yield.

other traits, high diversity indices ($H' \geq 0.60$) were obtained for each gene pool, with the highest ($H' = 0.92$) value being for AD in Togolese landraces. Mean H' was 0.63 for Burkinabe and Togolese landraces, and 0.58 for the Ghanaian germplasm.

Discussion

The highly significant differences observed among the accessions for all measured traits indicated that the germplasm evaluated in the present study were genetically diverse, which is in agreement with the findings of previous studies

(Asare et al. 2016; Twumasi et al. 2017; Salami et al. 2017), which reported the existence of substantial variability in different gene pools of maize landraces from Africa. The high variability observed, particularly for flowering traits (SD, AD and ASI) and GY, suggested that the germplasm was adapted to a wide range of environmental conditions, and could provide valuable alleles for maize improvement (Aci et al. 2018). The high repeatability estimates ($\geq 60\%$) observed for the studied traits indicated minimal environmental influence; the observed variation was largely attributable to the genetic background of the germplasm. However, repeatability can be overestimated in single-location trial(s) because genetic variance and genotype \times trial interaction variance are confounded (Cairns et al. 2013; You et al. 2016).

The late-maturing landraces, such as TZm-1284, GH-3302, GH-5756, TZm-1313 and TZm-1312, which displayed outstanding features, such as reduced ASI, good phenotypic appeal and high grain yield, could be used as potential sources of gene diversity for developing inbred lines with high grain yield *per se*. These results corroborated the findings of Aci et al. (2018), who reported that maize landraces characterized by short ASI were the most productive. Interestingly, in the present study, low-yielding landraces, such as TZm-1170, TZm-1173, TZm-1486, TZm-1508, TZm-1454, TZm-1498 and TZm-1495, were remarkably extra-early and thus, might possess novel genes that could be exploited to improve earliness in tropical maize (online Supplementary Table S1). Moreover, the landraces that combined high GY (≥ 4 Mg/ha) with very good HC rating (2), e.g., TZm-1307, GH-3505, TZm-1312, TZm-1278, TZm-1286, TZm-1284 and TZm-1472, might contain desirable alleles for enhancing grain yield in areas where insects, birds and pre-harvest rain are likely to pose threats. Furthermore, landraces with good ear placement/position ($0.48 \geq \text{EPLA} \leq 0.51$), such as TZm-1309, TZm-1319, TZm-1284, TZm-1303, and TZm-1372, can be incorporated into breeding programs to improve stalk quality (reduced root and stalk lodging). In addition, landraces, such as TZm-1276, TZm-1312, TZm-1284, TZm-1278, GH-3450, GH-3519, and GH-3480, which combined desirable phenotypic appeal (PASP = 2 or 3) with high resistance to *H. turcicum*, can be invaluable sources of genes/alleles to cope with yield losses in rain-forest zones, where diseases are prevalent during the growing season (online Supplementary Table S1).

The identification of phenology, overall phenotypic appeal and yield by PCA as the principal contributors to variation in grain yield, suggested farmers' preference for these traits. This finding largely corroborated farmers' perception and criteria for selection of cultivars and are consistent with previous results (Beyene, Botha, and Myburg 2006; Twumasi et al. 2017; Aci et al. 2018). Traits, such as EASP, KL, SG, and ELW, which collectively accounted for 90% of the variation in grain yield, could be used as an indirect selection criterion for improving grain yield. This observation agreed

partially with the results of Badu-Apraku et al. (2017), who identified EASP as a direct contributor to grain yield under optimal growing conditions.

The clustering pattern shown as a constellation plot supported the presence of marked phenotypic diversity within the studied collection of accessions (Figure 1). The clustering revealed that landrace groupings were largely based on maturity and origin. A plausible explanation for this observed clustering could be the continual selection for particular traits by farmers to meet their need for varieties adapted to local conditions. The prevalence of earliness in the Burkinabe landraces is indicative of farmers consciously selecting for this trait as insurance against yield loss attributable to inadequate rainfalls toward the end of the growing season. In contrast, landraces from Ghana and Togo were predominantly late and tall, with a large number of leaves, typical of genotypes adapted to areas with adequate rainfall. Perhaps, systematic hybridization between the two gene pools (Sahel and coastal landraces) could offer opportunities to minimize the yield penalty associated with earliness. It can be inferred that Cluster I (characterized by extra-earliness, short stature and low grain yield) was the most distinguishable, whereas Cluster II (characterized by late maturity, tallness, and high grain yield) was the least distinct. Together, these results indicated that crosses involving genotypes of the different clusters might lead to transgressive recombinant progenies.

Neighbor-joining cluster analysis separated the landraces from the improved cultivars, suggesting that the two classes of germplasm were genetically distinct. The separation of the Burkinabe landraces (Sahelian landraces) from the Ghanaian and Togolese landraces (Coastal landraces) could be explained by the differences in agro-ecologies. The high differentiation (large D^2 genetic distance) between Burkinabe landraces and modern varieties suggested that the original Sahelian gene pool might have contributed less toward the development of improved populations/varieties and thus might harbor beneficial alleles that are absent in modern cultivars. The low genetic distance between Togolese and Ghanaian landraces, which was consistent with the high admixture rate, revealed by the constellation plot (Figure 1), phylogenetic heatmap tree (Figure 2) and PCA biplot (Figure 3), implied that there was high probability that germplasm exchange occurred among farmers in areas with similar climatic conditions. Furthermore, the high genetic similarity observed between the improved populations/varieties and the Togolese/Ghanaian landraces could be attributed to either of the following reasons: 1) landraces from Togo and Ghana might have been included in the pedigrees of the improved varieties; and 2) the improved varieties were recollected as landraces, because farmers usually regarded improved varieties cultivated for longer periods, in a given area, as landraces. The low intra-population distances compared with the inter-population distances indicated that variation was higher among gene pools than within gene pools. Contrary to this finding, high within-population diversity compared with between-population diversity has been reported in high-altitude maize germplasm (Najar et al. 2018).

Estimates of Shannon-Weaver diversity indices revealed a wide range of variation for traits, which is consistent with the ANOVA, cluster analysis and PCA. The high overall H' (0.72) reinforced the existence of remarkable phenotypic diversity characterizing the studied germplasm. These results are comparable to earlier reports in maize (Twumasi et al. 2017) and barley landraces (Yadav et al. 2018). However, the low H' value (0.46) observed for the improved populations/varieties suggested a narrowing of the genetic base and about 37% reduction in phenotypic diversity when compared with the H' of the landrace group (Table 3). The reduced phenotypic variation could be attributed to the primary focus having been on improvement of specific traits, such as disease resistance, delayed leaf senescence, short anthesis-silking interval, and to a lesser extent, reduced plant and ear heights (Menkir and Akintunde 2001).

Conclusions

In the present study, we characterized the genetic diversity of maize landraces collected from different agro-ecologies in West Africa, and compared them with improved populations and varieties. The landraces exhibited higher genetic variation than the improved populations and varieties. In particular, the Burkinabe gene pool was highly distinct and could be tapped for further genetic enhancement of maize in West and Central Africa (WCA). Landraces, which possessed adaptation traits, such as short stature and early flowering, were identified as potential sources of gene diversity for developing varieties with tolerance to abiotic stresses. It may be worthwhile to systematically screen these landraces for tolerance to drought, heat and combined drought and heat stress. Altogether, the results of this study underscore the importance of landraces for future genetic enhancement in maize in WCA. Additional population genetic diversity studies using high-throughput molecular markers should help enhance our understanding of the population structure of this valuable germplasm.

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Disclosure statement

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