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Association between morphological traits and yield components in the durra sorghums of Ethiopia

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The Ethio-Sudan region is recognized as the center of origin and diversity for cultivated sorghum. All major races of the crop are widely grown in Ethiopia with durras being dominant. The objective of the present study was to determine the extent of morphological variability among the Ethiopian durras and examine the pattern of relationships among these traits and their association with yield and yield components. Two hundred accessions collected from major sorghum-growing regions of the country were evaluated during the 2007 season at two locations representing hot and dry low land and mild mid-altitude environments. A randomized complete block design with three replications was used. Data were collected on phenology, plant height, a range of leaf traits and yield components. Significant variation was observed among all traits measured. Phenological traits and plant height were significantly correlated with each other and with all leaf traits. There was positive correlation among leaf traits, and between leaf traits and yield components except thousand kernel weight (TKW) and panicle length (PL). Grain fill duration was negatively correlated with all traits except days to maturity, TKW, and leaf length. Yield components except PL and TKW were positively correlated with each other. Selection that focuses on key yield components, larger leaf area, and on enhancing the grain filling rate by reducing excessive grain fill duration may contribute to yield improvement.

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The northeast quadrant of Africa is considered the center of origin and domestication for cultivated sorghum (DOGGETT 1965; DILLON et al. 2007). This can be recognized from abundant feral relatives in the region occurring in sympatry with cultivated forms (AYANA et al. 2000a; TESSO et al. 2008). Ethiopia, one of Vavilov's centers of origin for several crop species, hosts wide genetic variability for sorghum; all races of sorghum occur in the country's major sorghum-growing areas (STEMLER et al. 1977; DOGGETT 1988). Sorghum is grown by almost all of the more than 80 ethnic nationalities of the country stretching from the hot, dry lowlands with a typical semiarid climate to the cool highlands with temperate weather. This assortment of environments along with the ethnic, social, and cultural diversity of the population have contributed to the development of diverse and distinct pool of sorghum germplasm, many of which are represented in international gene banks and the USDA/GRIN database (GEBREKIDAN 1973; <www.ars-grin.gov/npgs/searchgrin.html>).

Besides the diverse growing conditions and complex ethno-cultural settings, the different cropping systems practiced throughout Ethiopia (DAVIS and WOOLLEY 1993; O'LEARY and SMITH 1999; TAMADO and ESHETU 2000;

SANTALLA et al. 2001) and the diverse uses of the crop (OSAFU et al. 1993, REED et al. 1986) may have also contributed to the evolution, cultivation, and maintenance of unique types of sorghum. For example as a result of years of cultivation under multiple cropping systems (GEORGIS et al. 1990), farmers in eastern Ethiopia have identified unique variants of the crop suited for intercropping with both legume and non-legume species. Likewise, continued use of the crop as a major ingredient for local brew in the north and as a chief source of energy and protein throughout the country has led to selection and maintenance of sorghum types with high fermentation efficiency and others with improved grain and nutritional quality (SINGH and AXTELL 1973; GEBREKIDAN and KEBEDE 1979). Moreover, the need for sorghum biomass as source of fuel, animal feed, and construction material has resulted not only in sustained cultivation of the tall, crook-necked durra but also in selective adaptation and production of sweet and high biomass types used as dual-purpose crops. The value of these traits is well recognized in modern plant breeding, which seeks to improve sorghum for use as a major food, feed, and bioenergy crop.

The wealth of genetic variability in the Ethiopian sorghum germplasm sources has always attracted the attention of

regional and international sorghum breeding programs. Several accessions possessing traits of economic importance have been identified among Ethiopian sorghums. These include sources of post-flowering drought tolerance (HAUSSMANN et al. 2002; KEBEDE et al. 2001, XU et al. 2000; TAO et al. 2000), high grain quality and high yield potential (PRASADA RAO and MENGESHA 1981), and sources of high lysine and high protein digestibility (SINGH and AXTELL 1973). Over the past 30 yr, the Ethiopian Inst. of Biodiversity Conservation (IBC) has collected and maintained more than 5000 sorghum accessions. However, although Ethiopia's diverse sorghum-growing environments are presumed to harbor wide genetic variability, many of these areas are inaccessible for germplasm collection. Thus, the accessions in the gene bank represent only a fraction of the existing *in situ* variability. Regardless, these are valuable resources and have already rendered service to the international sorghum research community in many ways.

Attempts have been made to document the extent of genetic variability among these accessions (TESHOME et al. 1997, 1999; AYANA et al. 2000b; TUNSTALL et al. 2001; AYANA and BEKELE 2004; MAMO et al. 2007). But the efforts were fragmented in that they focused either on accessions originated only from specific localities or on a narrow set of samples too small to fully reflect the breadth of genetic variability that exists in the gene bank. Nonetheless, these efforts generated useful information that is relevant to both plant breeding and germplasm collection and conservation efforts. Results of these previous studies revealed the existence of wide variability for a range of morphological characteristics and yield components. However, little effort was made to investigate the association between those observable phenotypic traits and how the traits interact with each other and the environment to affect grain and biomass yields. This study was conducted on representative sorghum germplasm samples from the Ethiopian gene bank and was aimed to understand the extent of variability between the accessions and determine the pattern of relationship between phenological and morphological traits, and yield components. Based on the results, priority traits for consideration in breeding programs will be identified.

MATERIAL AND METHODS

Genetic materials and description of study sites

Two hundred sorghum accessions randomly drawn from the gene bank collections were used in this study. The sampling procedure was customized to allow equal representation of accessions from all sorghum-growing regions in the three major altitudinal categories of less than 1600 m, between 1601 and 1900 m and 1901 m and

above representing the lowland, mid altitude and highland sorghum growing environments, respectively. This procedure also helped capture the ethno-cultural diversity which is thought to have played a role in shaping the present genetic structure, but many of the accessions may be grown across altitudinal categories just described as these are seldom used by farmers to delineate adaptation zones. The profile of the accessions with respect to collection regions and adaptation zones is presented in Table 1.

The accessions were evaluated at two research stations, Melkassa and Arsi Negelle under the Ethiopian Inst. of Agricultural Research. The Melkassa station is located in the Rift Valley region at 8°30'N and 39°21'E at 1500 m elevation. The area receives mean annual rainfall of 763 mm and has mean maximum and minimum temperatures of 24.8 and 14.0°C, respectively. The area is categorized as dry semiarid and has a well-drained sandy loam soil with an average pH of 8. The Arsi Negelle station is located at 7°35'N and 38°65'E at elevation of 1990 m. The area receives mean annual rainfall of 806.8 mm and has mean annual maximum and minimum temperatures of 23.3 and 13.8°C, respectively. Compared with Melkassa, Arsi Negelle has milder weather and heavier soil with a neutral pH. The two locations represent the typical hot dry lowland and mild mid-altitude environments where sorghum is widely grown.

Experimental design and field procedure

The study was conducted during the 2007 main season using a randomized complete block design with three replications. To reduce variability among experimental units each replication was folded in to four blocks each

Table 1. *Collection regions and adaptation zones of sorghum germplasm accessions evaluated at Melkassa and Arsi Negelle, Ethiopia, during the 2007 season.*

Region	Altitudinal zone (number of accessions)
Gamo Gofa (south)	highland (0), mid-altitude (3); lowland (7)
Hararghe (eastern)	highland (4); mid-altitude (11); lowland (6)
Illubabor (southwest)	highland (0); mid-altitude (0); lowland (12)
Shewa (central)	highland (4); mid-altitude (2); lowland (0)
Tigray (north)	highland (37), mid-altitude (23); lowland (16)
Wollega (west)	highland (0); mid-altitude (7); lowland (7)
Wollo (north-central)	highland (24), mid-altitude (14); lowland (23)
Total	200

containing 50 entries such that the entire experiment fitted in 75×69 m area. Seeds were manually drilled into 5-m-long paired rows spaced 0.75 m apart. At about 20 d after emergence, the plants were thinned to 0.2-m spacing. The plots were fertilized with $46 \text{ kg ha}^{-1} \text{ P}_2\text{O}_5$ and $18 \text{ kg ha}^{-1} \text{ N}$ applied in the form of di-ammonium phosphate at the time of planting and additional $23 \text{ kg ha}^{-1} \text{ N}$ was applied in the form of urea at 40 d after planting. Weeds were removed as they appeared. At Melkassa, supplemental water was provided twice with furrow irrigation, once before flowering and again during grain fill. At both locations, 10 plants in each plot were tagged with colored tapes during flowering for use for future data collection. At milk stage, all tagged plants at Melkassa were covered with pollination bags to prevent bird damage; the bags were removed as soon as the grain was hardened to evade bird attack.

Data collection

Data were collected on days to flowering (DF), days to maturity (DM), plant height (PH), and grain fill duration (GFD) and leaf characteristics including leaf length (LL), leaf number (LN) and leaf width (LW). At maturity, grain yield and major yield components including panicle width (PWD), panicle length (PL), panicle weight (PW), panicle yield (PY) and thousand kernel weight (TKW) were recorded at both locations. The procedure outlined in the IBGR/ICRISAT sorghum descriptor was used to measure each trait (IBGR and ICRISAT 1993). Days to flowering was measured on a plot basis as the number of days from planting to when approximately 50% of the plants in a plot reached half bloom stage. Days to maturity was recorded as the number of days from planting to when seeds on 50% of the plants in a plot exhibited black layer on the lower third of the panicle. Grain fill duration was measured as the number of days between DF and DM. Leaf width was recorded as the width of the largest section of the leaf and LL was measured as the length between the collar and the tip of the leaf. Both LW and LL were measured on the top third leaf at dough stage. LN was the total number of leaves on the plant. Leaf area (LA) per plant was calculated on the basis of the length and width of the third top leaf multiplied by the total number of leaves and a coefficient of 0.71 (KRISHNAMURTHY et al. 1974).

At maturity, all tagged plants were cut at ground level and used to measure the remaining parameters. Plant height was determined as the length of the plant between the base and the tip of the panicle. Then the panicles were carefully detached from the stalk and used for measuring yield components. Panicle width was measured as the average width of the panicle at its widest section and PL as the length between the base and tip of a panicle. Panicle weight was measured as the weight of the un-threshed

head, and PY was measured as the weight of the seed threshed from individual panicles. Thousand seed weight was recorded as the weight of one thousand kernels from bulk seeds from all heads in each plot. The average of measurements taken from 10 plants in each plot was used in the analysis. Grain yield was recorded as the total weight of the grain harvested from each plot. Data on grain yield, PY, TKW and PW was adjusted to 12.5% moisture for statistical analysis. Because of severe bird damage, grain yield data from Melkassa were not included in the analysis.

Statistical analysis

Data were subjected to analysis using SAS ver. 9.1 (SAS 2004). The PROC GLM procedure was used to estimate variance for all traits. All factors (accession, block, and environment) were treated as random variables. The Pearson correlation coefficient was calculated for every pair of traits using the PROC CORR procedure. To better explain the relationship between grain yield and other traits, Mean trait values of a subset of accessions representing the top yielders (10 accessions) and the lowest yielders (10 accessions) were related to that of individual accessions and the overall mean. A graph depicting the deviation of mean values of all traits for both top- and low-yielding accessions from the overall mean was computed to represent the effect of each trait on grain yield.

RESULTS

Phenology and leaf characteristics

The analysis of variance for the combined data and individual locations is presented in Table 2. The accession effect was highly significant for all phenological traits, PH, GFD and leaf characteristics both in the combined data and individual location analyses. Environment and accession \times environment interaction effects were also highly significant for all traits except LL and LA (Table 2). The across-location accession means for DF, DM and GFD were 93.5, 172.3 and 79.1 d, respectively, and the ranges were 59 to 145 d for DF, 134 to 211 d for DM, and 22 to 124 d for GFD (Table 3). Leaf characteristics were also highly variable among accessions; LW ranged from 4.5 to 16.3 cm, LL from 49.4 to 102.9 cm, LN ranged 5.4 to 17.2, and LA from 1531 to 12 036 cm^2 (Table 3). However, values for each of these traits were markedly different under the two environments, and there was a significant accession \times environment interaction for most of them. Generally, DF, DM and GFD were significantly longer at Arsi Negelle than at Melkassa (100.1 vs 86.7, 193.3 vs 150.4, and 93.2 vs 64.3 d, respectively). But the accessions were remarkably taller at Melkassa than at Arsi

Table 2. Combined mean and range of vegetative growth parameters and yield components of sorghum accessions evaluated at Melkassa and Arsi Negelle, Ethiopia.

Variable	Mean	SD	Range	
			Minimum	Maximum
Days to flowering (d)	93.49	15.13	59	145
Days to maturity (d)	172.28	23.42	134	211
Grain filling duration (d)	79.07	18.00	22	124
Plant height (cm)	293.73	75.16	121	515
Leaf width (cm)	8.53	1.20	4.52	16.30
Leaf length (cm)	76.83	7.59	49.40	102.88
Leaf number	12.04	2.14	5.40	17.20
Leaf area (cm ²)	5655	1531	1055	12036
Panicle width (cm)	8.22	1.56	4.2	21.60
Panicle length (cm)	25.08	7.96	8.2	98.00
Panicle weight (g)	95.16	39.62	10.04	310.52
Yield/panicle (g)	70.99	30.92	2.3	224.45
Thousand kernel weight (g)	29.5	7.31	10.8	54.0
Grain yield (Mg ha ⁻¹)	3.54	1.74	0.16	10.24

Negelle (330.1 vs 258.7 cm, respectively). Mean LW, LN and LA were also noticeably higher at Melkassa, whereas LL was slightly higher at Arsi Negelle.

There was significant correlation among the traits both in the combined data and individual locations (Table 4, 5). Days to flowering was significantly correlated with DM, PH and leaf traits but not correlated with GFD (Table 4). The same trend was noted at individual locations, except the correlation between GFD and PH showed opposing trends at the two locations (Table 5). Days to maturity correlated significantly and positively with PH, GFD and LL and negatively with all other traits except LA, for which the correlation was not significant (Table 4). The situation at individual locations was slightly different in that all correlations were positive at both locations, except LW and LL at Melkassa were not significantly correlated with DM (Table 5). Grain fill duration was negatively and significantly correlated with all leaf traits in the combined analysis and for individual location, except correlation with LL was positive but not significant at Melkassa. Plant height had a strong positive association with all leaf traits except LW at Arsi Negelle and LL at Melkassa, and the correlation between PH and LW in the combined analysis was not significant (Tables 4 and 5). All leaf traits were significantly and positively correlated with each other at both locations except between LW and LN and between LW and LL at Melkassa.

Yield and yield components

Similar to the phenology and leaf traits, accession effect was highly significant for all yield components in the

combined analysis as well as for individual locations (Table 2). Grain yield was significantly ($P \leq 0.01$) different among accessions and ranged from 0.16 to 10.24 Mg ha⁻¹ with a mean of 3535 kg ha⁻¹. Mean yield components ranged from 4.2 to 21.6 cm for PWD, 10.0 to 310.5 g for PW, 2.3 to 224.5 g for PY, and 10.8 to 54.0 g for TKW. Environment and accession \times environment interaction effects were significant for all yield components except TKW (Table 2). Scores for PL, PW, and PY were markedly higher at Melkassa than at Arsi Negelle (mean values of 26.9 vs 23.3 cm, 110.6 vs 80.5 g, and 80.6 vs 61.9 g, respectively), whereas TKW was higher at Arsi Negelle.

There was a remarkable association among yield components, though there were differences between test environments. Thousand-kernel weight was positively and significantly correlated with PWD, PW and PY at Melkassa and with PW and PY at Arsi Negelle and in the combined analysis (Table 4, 5). The correlation between TKW and PWD in the combined analysis was not significant (Table 4). However, the correlation between TKW and PL at Melkassa and between TKW and PL and TKW and PWD at Arsi Negelle were significant but negative (Table 5). Panicle weight and PY were highly correlated with each other ($r = 0.91$ in the combined analysis) and also had a similar pattern of association with other yield components at both locations. Panicle weight was also significantly and positively correlated with PW and PY and negatively with PL at both locations. The correlation between PWD and PL was significant and negative at Melkassa and positive at Arsi Negelle, but it was not significant when the data were combined. Grain yield was positively and significantly correlated with all yield components except TKW.

Correlation between vegetative growth characteristics and yield components

Most yield components had a marked relationship with phenological traits, PH, GFD and leaf traits at both locations. Panicle width was positively and significantly correlated with all phenological and leaf traits in the combined data and individual location analyses. The only exceptions were DM and GFD at Melkassa, which were not significant, and GFD at Arsi Negelle, for which the correlation was significant but negative. At Melkassa, PL was significantly and negatively correlated with GFD and all leaf traits except LL. At Arsi Negelle, PL was significantly correlated with only LW, LN and LA (Table 5). All of phenological and leaf traits were negatively correlated with PL in the combined analysis except PH and LL, which had positive correlation, and LN and LA for which the relationship was not significant (Table 4). Panicle weight and PY were significantly and positively correlated with all phenological and leaf traits except

Table 3. Analysis of variance for vegetative growth parameters and yield components of sorghum germplasm collections tested at Melkassa and Arsi Negelle, Ethiopia.

Source	df	Days to flowering	Days to maturity	GFD [†]	Plant height	Leaf width	Leaf length	Leaf Number	Leaf area	Panicle width	Panicle length	Panicle weight	Panicle yield	TKW [‡]	Grain yield
Melkassa															
Replication	2	2.54	6.52	2.78	448.76	3.87*	55.8	6.69**	3837696**	1.32	35.71	563.19	764.53	0.53	—
Accession	199	510.99**	282.97**	208.3*	13413.87**	2.33**	71.05**	9.97**	4027378**	3.08**	186.50**	3014.98**	1753.47**	1.25**	—
Error	396	9.62	10.1	19.24	497.45	0.88	21.21	0.55	809645	0.87	24.77	782.35	524.25	0.09	—
Mean	—	86.74	150.39	64.27	330.06	8.71	75.01	12.83	5970	7.69	26.94	110.63	80.58	2.86	—
Arsi Negelle															
Replication	2	4.19	89.48	52.76	315.38	1.39	61.93	4.89	1063620	0.14	85.53*	586.05	925.17	0.11	2399115
Accession	199	515.97**	149.18**	329.33**	9770.73**	3.27**	153.43**	10.38**	6632265**	5.82**	109.28**	2537.16**	1620.07**	1.4**	6.09**
Error	396	22.27	30.87	49.08	821.92	0.55	27.75	0.87	488593	1.4	5.44	411.71	329.99	0.135	1.33
Mean	—	100.14	193.32	93.21	258.73	8.36	78.61	11.26	5346	8.71	23.32	80.52	61.9	3.03	3.53
Combined															
Environment (E)	1	51569.40**	517704.15**	245642.26**	1482041.60**	35.21**	4078.99**	698.36**	104601686**	292.04**	3378.94**	257330.31**	94122.29**	9.17**	—
Replication/E	4	221.87**	348.01**	77.78	4882.07	2.63*	158.86	24.78	7236949	6.73*	60.62*	1074.62	994.85	0.32	—
Accession (A)	199	948.55**	285.46**	408.31**	21348.44**	4.2*	441.53**	118.72**	9026712**	225.14**	268.97**	4320.01**	2502.67**	2.37**	—
A × E	196	59.87**	145.26**	118.67**	1651.04**	1.34**	80.54	1.49*	1490502	2.91*	24.14*	1183.19**	835.61**	0.24	—
Error	771	16.02	20.75	34.61	664.1	0.71	24.52	0.71	647254	1.14	14.72	589.73	423.41	0.12	—
Mean	—	93.49	172.28	79.01	293.73	8.53	76.83	12.04	5655	8.22	25.08	95.16	70.98	2.94	—

*, **significantly different at $P \leq 0.05$ and $P \leq 0.01$, respectively; [†]GFD = grain fill duration; [‡]TKW = thousand-kernel weight

Table 4. Combined correlation coefficients among vegetative growth parameters and yield components of sorghum accessions evaluated at Melkassa and Arsi Negelle, Ethiopia.

	Days to flowering	Days to maturity	Plant height	GFD [†]	Leaf width	Leaf length	Leaf Number	Leaf area	Panicle width	Panicle length	Panicle weight	panicle yield
Days to maturity	0.64**	–	–	–	–	–	–	–	–	–	–	–
Plant height	0.19**	0.30**	–	–	–	–	–	–	–	–	–	–
GFD	0.00	0.77**	–0.54**	–	–	–	–	–	–	–	–	–
Leaf width	0.11**	–0.13**	0.00	–0.26**	–	–	–	–	–	–	–	–
Leaf length	0.38**	0.27**	0.07*	–0.14**	0.26**	–	–	–	–	–	–	–
Leaf number	0.45**	–0.19**	0.59**	–0.55**	0.15**	0.13**	–	–	–	–	–	–
Leaf area	0.48**	–0.03	0.38**	–0.43**	0.66**	0.54**	0.72**	–	–	–	–	–
Panicle width	0.33**	0.33**	0.07*	0.16**	0.15**	0.27**	0.06*	0.21**	–	–	–	–
panicle length	–0.08**	–0.21**	0.14**	–0.20**	–0.09**	0.06*	–0.03	–0.05	–0.03	–	–	–
Panicle weight	0.08*	–0.27**	0.39**	–0.42**	0.35**	0.14**	0.54**	0.53**	0.26**	–0.16**	–	–
Panicle yield	0.09**	–0.22**	0.35**	–0.36**	0.33**	0.14**	0.47**	0.49**	0.30**	–0.17**	0.91**	–
TKW [‡]	–0.15**	0.09*	–0.22**	0.23**	0.06	0.08**	0	0.06*	–0.03	–0.42**	0.31**	0.30**

*, **significantly different at $P \leq 0.05$ and $P \leq 0.01$, respectively; [†]GFD = grain fill duration; [‡]TKW = thousand-kernel weight.

correlations with DM and GFD were negative (Table 4). At individual locations, both PW and PY were significantly and positively correlated with all phenological and leaf traits except GFD for which the correlations were negative but not significant at Melkassa and negative and significant at Arsi Negelle (Table 5). Thousand kernel weight was negatively correlated with DF and PH and positively correlated with DM and GFD at both locations (Table 4, 5). The correlations between TKW and LW at Melkassa, and between TKW and LN and TKW and LA at Arsi Negelle were also positive and significant. Grain yield at Arsi Negelle was significantly and positively correlated with DF, PH and all leaf traits and negatively correlated with GFD (Table 5).

We further investigated the association of phenology and leaf traits with yield and yield components by forming two separate pools of accessions representing top-yielding and low-yielding groups (based on plot yield at Arsi Negelle) and comparing their across-location trait values with each other and with the overall mean. Mean values for DF, DM, LW and LA for the top-yielding accessions were remarkably higher than those for the overall accession mean. Only LN was lower but not significantly different from the overall mean (Table 6). For the low-yielding accessions, mean value for traits were remarkably lower than the overall mean except DM that were remarkably higher. Similar to phenology and leaf traits, there was a marked difference in mean values of yield components between the top- and low-yielding accessions. All yield components for the top-yielding accessions except PL and TKW were markedly higher than those for the low-yielding accessions and the overall mean. The TKW for the top-yielding accession was 22% lower than that for the overall mean and low-yielding accessions. Similarly, PL in the top-yielding group was

remarkably longer than that in the low-yielding group but shorter than that for the overall mean. Yield components for the low-yielding accessions were low compared to the overall mean except TKW, which was also lower but not significantly different from the overall mean (Table 6). However, some members of the low-yielding group had scores similar to those of the top accession for some traits. Accession no. 167 had mean PH, DF, DM, GFD and all leaf traits that were higher than or similar to those of the top-yielding group but had a significantly low score for all yield components except TKW.

DISCUSSION

Following the report by SNOWDEN (1936) which described variations among cultivated races of sorghum, a number of studies confirmed the presence of tremendous variability among cultivated sorghum for a range of phenotypic and physiological traits as well as molecular markers (HARLAN and DE WET 1972; DJÈ et al. 2000; GHEBRU et al. 2002; MENZ et al. 2004; ALI et al. 2008; XIN et al. 2009). Most of the morphological traits have shown to be related to each other in certain ways (EZEAKU and MOHAMED 2006), but because of differences in panicle morphology between races, the nature of the relationship in different races may be different. The current study is focused on elucidating these relationships in the durra sorghums of Ethiopia.

We noted marked relationships between the various traits measured. Days to flowering, DM, and PH were significantly correlated with each other under both environments. The positive correlation between DF and DM was anticipated, and these traits' positive association with PH is not surprising for tropical germplasm such as those used in the present study. A correlation of this type

Table 5. Individual location correlation coefficients among vegetative growth characteristics and yield components of diverse sorghum accessions evaluated at Melkassa (above diagonal) and Arsi Negelle (below diagonal), Ethiopia.

	Days to flowering	Days to maturity	Plant height	GFD†	Leaf width	Leaf length	Leaf number	Leaf area	Panicle width	Panicle length	Panicle weight	Panicle yield	TKW‡
Days to flowering	–	0.70**	0.55**	-0.61**	0.02	0.06	0.77**	0.54**	0.08	0.08	0.16**	0.12**	-0.37
Days to maturity	0.50**	–	0.46**	0.15*	-0.05	-0.02	0.58**	0.32**	0.06	-0.01	0.17**	0.12**	-0.19**
Plant height	0.50**	0.29**	–	-0.25**	-0.19**	-0.06	0.56**	0.23**	0.17**	0.05	0.20**	0.17**	-0.24**
GFD	0.79**	0.13**	-0.37**	–	-0.10*	0.08	-0.42**	-0.38**	-0.01	-0.11**	-0.04	-0.03	0.27**
Leaf width	0.36**	0.11**	0.05	-0.34**	–	0.32**	-0.02	0.68**	0.27**	-0.13**	0.22**	0.22**	0.11*
Leaf length	0.50**	0.28**	0.43**	-0.37**	0.29**	–	-0.06	0.49**	0.14**	0.21**	0.13**	0.12**	0.05
Leaf number	0.70**	0.40**	0.46**	-0.51**	0.22**	0.44**	–	0.62**	0.16**	-0.11**	0.40**	0.34**	0.05
Leaf area	0.72**	0.38**	0.43**	-0.55**	0.64**	0.69**	0.78**	–	0.30**	-0.05	0.43**	0.38**	0.04
Panicle width	0.29**	0.08*	0.36**	-0.28**	0.18**	0.24**	0.24**	0.29**	–	-0.20**	0.55**	0.57**	0.17**
Panicle length	-0.01	0.03	0.04	0.03	-0.15	0.05	-0.16**	-0.17**	0.29	–	-0.33**	-0.31**	-0.39**
Panicle weight	0.47**	0.26**	0.33**	-0.35**	0.43**	0.37**	0.54**	0.60**	0.37	-0.20**	–	0.91**	0.44**
Panicle yield	0.43**	0.22**	0.33**	-0.33**	0.38**	0.33**	0.49**	0.55**	0.37	-0.17**	0.88**	–	0.45**
TKW	-0.12**	0.14**	-0.14**	0.24**	0.04	0.05	0.15**	0.12**	-0.24	-0.46**	0.31**	0.26**	–
Grain yield	0.19**	-0.04	0.28**	-0.24**	0.23**	0.21**	0.20**	0.26**	0.31**	0.11	0.42**	0.43**	-0.04

*, ** significantly different at $P \leq 0.05$ and $P \leq 0.01$, respectively; †GFD = grain fill duration; ‡TKW = thousand-kernel weight.

may have resulted from the reported linkage between one of the height loci (*Dw2*) and the major photoperiod sensitivity locus, *Mal* (QUINBY and KAPER 1967; LIN et al. 1995). No attempt was made to determine specific alleles at *Dw* and *Ma* loci in the present study, but we assumed that most of the tall and late-maturing accessions might carry wild-type alleles at these loci. However, the associations of DF, DM, and PH with the different leaf characteristics were slightly different between the two environments. At Melkassa, neither LW nor LL had a meaningful relationship with DF or DM, and there was no association between LL and PH and a negative association between LW and PH. All leaf traits were positively and significantly correlated with DF, DM, and PH, except that there was no correlation between LW and PH at Arsi Negelle (Table 4, 5). This difference appears to be due to differential sensitivity of the traits to the different environments. Plant height and all leaf traits except LL were larger at Melkassa, and DF and DM were longer at Arsi Negelle (Table 2). Melkassa has warmer temperatures throughout the growing season, and the enhanced growth at this location appears to be related to this factor. Earlier studies showed that both thermal period and photoperiod have significant effects on LA development in sorghum (MUCHOW and CARBERRY 1990).

Leaf traits generally appeared to have a positive relationship with DF, DM, and PH, though there was some difference between locations. Tall and long-maturing accessions tend to produce more leaves that are also larger than those of semi-dwarf short-cycle accessions. It is not clear whether this is the result of the maturity genes or their interaction with *Dw* loci that is known to influence leaf number (QUINBY and KAPER 1967; PAO and MORGAN 1986). Similar results have been reported in other species. In corn, LN was reported to be significantly correlated with days to silking and maturity (ALLEN et al. 1973).

Grain fill duration was significantly and positively correlated with DM at both locations; the relationship between GFD and DF was also significant at both locations but negative at Melkassa and positive at Arsi Negelle. This variation also might be related to the differential reaction of accessions to the different environments that may have affected the rate of grain fill. Moisture stress during the grain filling stage at Melkassa must have accelerated maturity (shortened GFD) of accessions that were otherwise long maturing, resulting in a negative relationship between DF and GFD. Arsi Negelle generally has mild weather and higher rainfall well distributed in the season. It also has heavier soil that stores moisture better than the soil at Melkassa. This, along with a lower evapotranspiration demand, contributed to better moisture availability during grain filling. It is evident from the data in Table 3 that the difference in DF between the two locations was not proportional to the difference in DM and GFD, that

Table 6. Comparison of vegetative growth characteristics and yield components of subsets of top-yielding and low-yielding sorghum accessions.

Accessions	Grain yield kg ha ⁻¹	Days to flowering d	Days to maturity d	Plant height cm	GFD [†] d	Leaf width cm	Leaf length cm	Leaf number No.	Leaf area cm ²	Panicle width cm	Panicle length cm	Panicle weight g	Panicle yield g	TKW [‡] g
Top yielding accessions														
Accession no. 43	7373.1	105	186	292	80	9.5	74.25	12.7	7135	9.03	25.5	92.9	78.5	22.1
Accession no. 196	7266.2	109	189	255	80	9.5	76.84	12.8	6506	9.40	28.3	126.0	117.0	22.9
Accession no. 17	7123.1	117	195	340	78	8.6	82.76	12.9	6266	8.83	21.7	123.5	106.0	23.9
Accession no. 81	7045.7	105	189	244	84	10.3	73.99	10.0	6294	9.33	29.4	93.4	65.9	18.7
Accession no. 62	6948.3	122	199	303	78	10.6	86.56	12.6	8870	12.87	30.0	131.4	103.3	22.1
Accession no. 34	6941.4	103	178	302	76	10.1	82.28	10.6	6294	9.20	23.9	138.9	102.4	27.2
Accession no. 31	6889.4	101	180	316	79	9.9	76.21	11.2	6267	8.00	16.7	94.9	88.9	26.7
Accession no. 35	6674.8	106	187	279	81	9.9	84.16	11.4	6657	9.03	22.1	84.4	67.7	24.7
Accession no. 91	6628.2	107	192	332	85	9.3	81.43	11.0	6484	9.00	24.1	107.9	81.7	25.9
Accession no. 39	6407.1	104	188	326	84	9.6	75.84	12.1	7156	9.60	19.7	129.2	99.6	25.3
Mean	6929.7	108	188.3	299	80.5	9.7	79.43	11.7	6793	9.45	24.1	112.2	91.1	24.0
Low yielding accessions														
Accession no. 163	1443.6	88	191	197	103	6.6	53.5	6.9	2733	5.9	19.9	28.6	21	34.5
Accession no. 160	1354.1	77	189	174	111	5.7	56.4	6.3	2477	7.93	25.6	31.3	22.7	27.5
Accession no. 128	1182.9	78	183	158	104	8.3	62.1	7.6	3271	7.93	16.7	42.3	27.63	28.9
Accession no. 127	933.1	81	195	202	104	7.4	66.3	7.3	3273	6.6	16.7	28.2	14.6	28.9
Accession no. 167	879.2	125	206	312	81	9.3	81.0	15.2	8172	8.13	14.1	61.6	35.5	30.7
Accession no. 129	779.9	73	192	130	119	7.7	63.8	8.2	3867	5.27	20.6	18.6	6.99	31.8
Accession no. 165	750.9	104	194	200	90	8.4	75.1	12.9	5794	5.53	8.6	53.0	30.93	29.1
Accession no. 130	666.6	78	187	184	109	7.3	67.0	7.1	3475	5.33	19.7	15.0	7.3	30.7
Accession no. 166	490.7	94	193	200	99	7.8	79.1	9.5	4697	5.53	8.6	26.9	17.13	25.9
Accession no. 126	177.0	85	185	158	100	7.3	32.2	7.1	2282	7.56	17.5	40.8	29.1	28.9
Mean	865.8	87	192	192	102	7.6	63.7	8.8	4004	6.57	16.5	30.6	21.29	29.7

[†]GFD = grain fill duration; [‡]TKW = thousand-kernel weight.

both were clearly accelerated at Melkassa. Grain fill duration accounted for 48% of the entire growth duration at Arsi Negelle but only 42% at Melkassa, and this difference appears to be due to accelerated GFD at the later location. Moreover, GFD was significantly and negatively correlated with PH and all leaf traits except LL at Melkassa (Table 5). Genotypes with larger LA and LA components appeared to have a higher net photosynthesis rate during the grain filling stage and thus required a shorter time to fill the grain than genotypes with less LA. The negative relationship between PH and GFD can be explained in the same way; taller plants had more number of leaves ($r = 0.59$) and thus a greater LA ($r = 0.38$), which may have accelerated the grain filling process.

Relationships between phenological traits, PH, GFD and yield components were significant and largely positive with few exceptions. But PL was negatively correlated with all of the traits except PH and also negatively correlated with all other yield components. To explain this, we pooled 10 accessions with the longest panicles and compared their trait means with the overall mean. Mean panicle length among this pool was 44% longer than the overall mean. This pool also had 6% longer GFD, but 8, 34, 29, 13, 22, 13 and 19% lower PWD, PW, PY, TKW, LA, LW and GY, respectively. But DF, DM, LL and PH of this pool were not significantly different from the overall mean. Accessions with long panicles appear unique in that they have a significantly higher than average score for one trait and lower than average scores for most other traits. Those accessions are perhaps introgressions with other races, most likely the bicolor or wild relatives. In another study, we reported the prevalence of wild and weedy sorghums in major sorghum-growing regions of Ethiopia occurring either within pollen-reach distance or in the same field with cultivated sorghum (TESSO et al. 2008) that spontaneous crossing between cultivated sorghums and wild relatives is possible.

Grain yield was significantly and positively correlated with all traits except DM, GFD and TKW. It is always assumed that a longer GFD will lead to larger seed size. However, seed size has been reported often as having no positive effect on yield in most crops including corn (GRAVEN and CARTER 1990; NAFZIGER 1992), sorghum (MARANVILLE and CLEGG 1977) and wheat (TALBERT et al. 2001). However, EZEAKU and MOHAMMED (2005) and ABA and OBILANA (1994) reported positive association between grain yield and TKW but those results are based on relatively small set of genotypes and among materials of common pedigree background that such correlation is possible. But when large number of unrelated accessions like in the present study is used such correlation may not necessarily occur. The association of grain yield with these and other traits was better revealed when mean trait values of top- and low-yielding groups were compared

with each other and with the overall mean. Mean grain yield of the top-yielding accessions was eight times as large as the low-yielding accessions (6929.7 vs 865.8 kg ha⁻¹) and twice as large as the overall mean (Table 3, 6). Mean DF, PH, LW, LL, NL, LA, PW, PL, PW and PY of the top-yielding accessions were significantly higher than those of the low-yielding accessions, but GFD and TKW were higher for the low-yielding group. Neither group varied with respect to DM. Scores for most of the traits in the top-yielding accessions were not markedly different from the overall mean except DF, LW, PD, PW and PY (Fig. 1a–c). Values for some traits, including LN, PL and TKW, were remarkably lower than the overall mean. Most traits for the low yielding accessions had lower scores than traits for the overall mean except DM and GFD. As reported by earlier investigators, this result indicates that extended grain filling period and seed size do not necessarily contribute to grain yield.

Results of this study confirm that breeding for yield improvement is a complex endeavor; several traits are directly or indirectly associated with yield. The greatest challenge is on systematically interpreting the complex association among the traits and exploiting them to enhance the genetic potential of the crop. Comparison of the top- and low-yielding accessions showed that the difference in yield was not proportional to the difference in any of the other traits (Fig. 1d), proving that yield is a cumulative or multiplicative result of a multitude of traits, including those not considered in this study. The approach to enhancing sorghum yield should thus be comprehensive and take into account the direct and indirect contribution of each individual trait. But there is obviously a limit to the number of traits that can be improved at the same time in any breeding scheme. Even with the use of molecular markers to aid selection, not many traits can be effectively handled at one time because many of these traits are polygenic and several genes or genomic regions may account for their expression. Thus, the breeder must make a choice between the many apparently relevant traits and focus on those that are most important. In the present study, we investigated the complex interactions among several traits and then identified three key areas that we suggest breeders to focus on in order to enhance sorghum yield for this and similar environments: 1) directly targeting the high yield potential traits (yield components), 2) focusing on traits that enhance LA development, and 3) reducing the period and increasing the rate of grain fill.

The first focus area is on identification and use of key characteristics among a suite of traits commonly targeted by most sorghum breeding programs. It capitalizes on few major yield components that are closely associated with grain yield. But all yield components considered in this study are positively correlated with each other and with grain yield. Based on our results, we identify PW as

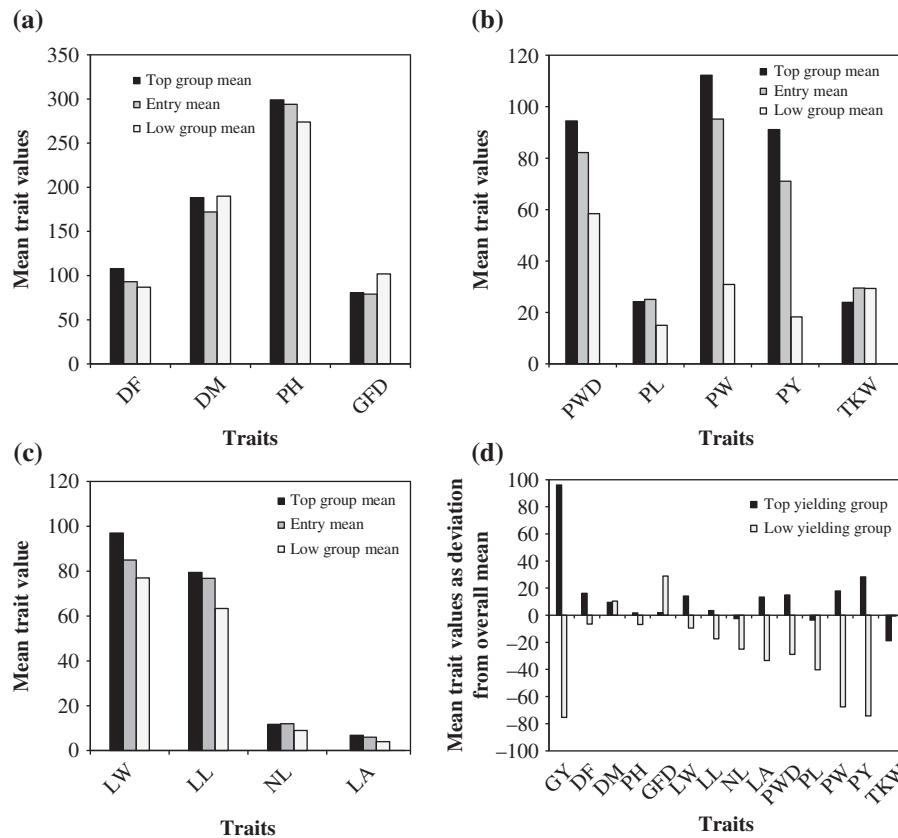


Fig. 1a-d. Differences in vegetative growth characteristics and yield components between a subset of experimental accessions representing high- and low-yielding groups.

representative trait for the entire yield components included in this study. We believe that improving this trait along with other compatible plant characteristics should result in improved yield. However, there are other traits that may have positive correlation with grain yield that are not considered in the present study such as number of kernels per panicle and number of panicles per unit area. Those can be considered along with panicle weight in selection of genotypes with improved yield potential.

The other group of traits that needs to be improved along with the yield component is the LA. Improving the LA involves manipulation of leaf characteristics and other traits related to LA development. Our results indicate that several traits contribute to LA development including LL, LW, LN, PH and DF. Delayed flowering contributed to LA either by allowing more time for additional leaves to initiate and develop or through permitting optimal growth and expansion of the leaves; similarly, taller plants contributed to LA by having more leaves. All these traits have been shown to have positive relationship with grain yield. Therefore, for sub-Saharan countries such as Ethiopia, breeding for dwarf extra early cultivars may not be the best approach. Although such cultivars have shown excellent promise in Africa, the yield potential could be further

enhanced if maturity and height were considered. In the temperate environments, sorghum has to fit in a 120- to 130-d growing window, but in tropical Africa, sorghum can be grown over an extended period of time, which provides an opportunity to exploit growth resources for maximum yield. In addition to allowing more LA development and thereby contribute to improved yield, this approach would also contribute to improved stover yield to help meet other needs, serve as animal feed and as source of fuel.

The third approach is based on increasing the rate and reducing the duration of grain fill. An extended grain filling period has always been perceived as indicator of potential for yield improvement. Theoretically, it makes sense to assume that a longer grain filling period allows more time for photosynthesis and storing more carbohydrate in the grain, but this has rarely been translated to increased yield in several crops (HAWKINS and COOPER 1979). The accessions included in this study had a mean maturity period of 172 d, and the grain filling period accounted for nearly half of this entire growing period. Also, some accessions in the current study had a grain filling period of only 38 d, and their seed weight was lower but not significantly different from the entire accession

mean. On the other hand, the low-yielding accessions had an average grain filling period of 102 d, compared with only 82 d for the high-yielding accessions. It appears that long grain fill types have low grain fill rate that they needed much longer period of time to fill an average size grain. But the long grain fill accessions are widely grown in the country where this study was conducted even though there is no yield benefit associated with long grain filling period. The use of accessions with extended grain fill duration is rather a disadvantage in that it increases the likelihood of exposure to damage by both man-made and natural calamities. We believe that substantially reducing the GFD and enhancing the grain filling rate while maintaining average DF will lead to increased yield if the traits are bred into backgrounds that have enhanced yield components (e.g. PW and number of panicles per unit area) and large LA. But this endeavor should first examine the positive values of the long grain fill types that farmers recognize as worthy to maintain them in production.

Conclusions

There is significant variability for various phenological traits and yield components among durra sorghums. Days to flowering, PH, and LA and LA components are significantly correlated with grain yield and yield components. This shows that in a tropical environment where freezing temperatures do not restrict crop growth, extended vegetative growth may positively contribute to grain yield perhaps through bigger sink size (yield components) and improved LA development. However, extended grain filling period of 45 d or longer seem to have no or little benefit to enhancing sorghum yield. Our results suggests that variety development approach that focuses on exploiting long vegetative growth period (taller plant and extended flowering) and major yield components (e.g. head size and number of heads per unit area) by reducing prolonged grain filling period may contribute to enhanced yield in durra sorghums under a tropical environment.

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