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Correlations, Path Coefficient Analysis and Heritability for Quantitative Traits in Finger Millet Landraces

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Knowledge of association between traits and heritability is important in breeding for purposes of effective trait selection. Such information on finger millet in east Africa is very limited. This study was intended to determine the association and heritability for 19 quantitative traits of 340 finger millet landraces from Kenya, Tanzania and Uganda and 80 global minicore accessions from ICRISAT Genebank in India. There were inherent strong genetic relationships among most traits as evidenced by the higher genotypic than phenotypic correlations. Grain yield had high, positive correlations with finger width (r_g =0.876), grains per spikelet (r_g =0.623), threshing percent (r_g =0.677), peduncle length (r_g =0.517) and panicle exertion (r_g =0.571). These traits could be considered for grain yield selection. Path coefficient analysis revealed that productive tillers per plant (0.473), 1000 grain mass (0.136), grains per spikelet (0.131) and threshing percent (0.118) had positive, direct effects on grain yield. Due consideration should be placed on these traits when selecting for grain yield improvement in finger millet. There were also strong, positive indirect effects contributed to grain yield by finger width, peduncle length, panicle exertion and leaf sheath width. It will be necessary to simultaneously select for these traits together with those with strong positive, direct effects on grain yield in order to improve grain yield in finger millet. High broad-sense heritability estimates were recorded for fingers per panicle, flag leaf blade length, 1000 grain mass, productive tillers per plant, finger length, peduncle length and panicle exertion indicating the potential for their improvement through selection.

Key words: correlations, finger millet, heritability, path analysis

INTRODUCTION

Although many trait relationships are useful in selection, the associations between yield and other component traits would be of key consideration for all crop breeders. Observed and true associations between traits may be quantified in terms of simple phenotypic and genotypic correlation coefficients (Sonnad 2005). However, yield is a complex trait and is influenced directly as well as indirectly by its various components (Wolie and Dessalegn 2011). Correlation coefficients alone do not elucidate the complexity of the biological associations between traits or how a change in a trait affects an associated trait (Dabholker 1992; Dewey and Lu 1959). To address this deficiency, path coefficient, a standardized regression coefficient developed by Wright (1921), disaggregates

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the correlation coefficient into the direct and indirect effects of various traits on a dependent trait (El-Din et al. 2012). Direct effects are where a trait directly affects another without being influenced by other traits whereas indirect effects occur when the relationship between two traits is mediated by one or more traits (Tyagi and Lal 2007). Knowledge of the associations between yield and its component traits and among the component traits themselves would allow for more effective selection for yield. In finger millet, grain yield has been reported to be highly directly associated with: panicle mass and straw yield per plant (Sonnad et al. 2008); productive tillers and 1000 grain mass (Bezawelataw et al. 2006); biomass yield, finger length and number of fingers per panicle (Ganapathy et al. 2011; Wolie and Dessalegn 2011); and basal tillers, flag leaf blade length, and panicle length and width (Bharathi 2011). Studies which have generated such information on finger millet in east Africa are limited.

As much as progress in a crop improvement programme will depend on the amount of genetic variability in the target trait in the base population (Ganapathy et al. 2011), variability alone does not indicate the extent of improvement achievable through selection (Priyadharshini et al. 2011). Estimates of broad-sense heritability (H^2) are important genetic statistics that provide an indication of the potential progress that will be made through selection in a breeding programme. Traits with high percent heritability are less affected by the environment in their expression and quantitative traits usually have low heritabilities due to their sensitivity to the environment. However, broad sense heritability alone cannot be an accurate indicator of response to selection (Johnson et al. 1955). Genetic gain which is the product of the selection differential (k), the phenotypic standard deviation and the heritability estimate (broad or narrow) estimates the expected gain from a cycle of selection (Johnson et al. 1955). For effective selection, Falconer (1981) proposes using a combination of genetic parameters, genetic and phenotypic coefficients of variation, heritability and genetic advance to indicate response to selection.

This study was conducted to determine the associations between grain yield and related quantitative traits, the degree and direction of association and heritability in finger millet for the effective formulation of a breeding strategy/selection scheme to generate higher yielding finger millet lines.

MATERIALS AND METHODS

The genotypes assessed in this study were 340 finger millet landraces collected across agro-ecologies in Kenya (154), Tanzania (81) and Uganda (105), 80 global minicore accessions sourced from ICRISAT Genebank in India and five checks. The accessions were evaluated in the following locations in Kenya: Alupe – sub-humid Lake Victoria zone, 1189 meters above sea level (masl), 0°28’N and 34°7’E; Lanet – cool highland, 1920 masl, 0°30’S and 36°0’E; Kiboko – dry lowland, 960 masl, 2°20’S and 37°45’E; and Mtwapa – near sea level humid coast, 21 masl, 4°25’S and 39°44’S. These locations represent the finger millet production agro-ecologies in east Africa. At all four locations, the accessions were planted in an augmented design comprising 20 blocks of 26 plots each. Each check entry was planted once in each block to obtain an estimate of error and of blocking effects. The entries were sown in single row plots, 4 m in length at inter-row spacing of 0.40 m. Seed was drilled in furrows (2.5-3 cm deep) and plants were thinned two weeks after emergence to one plant per hill after every 0.10 m. At planting, a basal application of Double Ammonium Phosphate fertilizer (18:46:0) was applied at a rate of 20 kg N and 20 kg $P_2O_5ha^{-1}$. After thinning, the trials were top-dressed with Urea (46% N) at a rate of 20 kg N ha^{-1}. Data were collected on 22 traits based on the descriptors for finger millet (IBPGR 1985).Data were taken on five randomly selected plants in each plot and the means of the five plants from each plot were used for statistical analysis except for grain yield and 1000 grain mass which were done on plot basis. Blast disease data were recorded only at Alupe location (a blast hot spot) where natural blast occurrence is high.

Data analysis

REML

Quantitative data were analysed using the augmented random model of residual maximum likelihood (REML) (Federer and Wolfinger 2003) in SAS (SAS 2008) as follows:

$$Yij = \mu + \alpha i + \beta j + \varepsilon ij$$

where:
Yij = Observation of i^{th} entry in j^{th} block.
αi = i^{th} entry effect.
βj = j^{th} block effect.
εij = Random error component

The block effects were estimated from the repeated check means and then removed from the means of the test entries (Federer and Wolfinger 2003). A two way location (random) by accessions (fixed) analysis was performed. An estimate of the error variance over locations was obtained by computing the average effective error variance at each location and then averaging these over locations as suggested by Cochran and Cox (1957).

Correlation and path coefficient analyses

Phenotypic and genotypic correlation coefficients were calculated in SAS (SAS 2008) according to Kwon and Torrie (1964) as follows:

Phenotypic correlations:

$$r_p = COV_P(X1,X2)/\surd V_P(X1)*V_P(X2)$$

where: r_p = phenotypic correlation, X1 is independent variable and X2 is dependent variable, V_P and COV_P are the phenotypic variance and phenotypic covariance, respectively.

Genotypic correlations coefficients:

$$r_g = COV_G(X1,X2)/\surd V_G(X1)*V_G(X2)$$

where: r_g = genotypic correlation, V_G and COV_G are the genotypic variance and genotypic covariance, respectively.

Genotypic path coefficients were calculated according to Dewey and Lu (1959) to determine direct and indirect effects of the yield components on grain yield ha^{-1}:

$$r_{ij}P_{ij} + \sum r_{ik}p_{kj}$$

where: r_{ij} = mutual association between independent trait *i* and dependent trait *j*;P_{ij} = direct effect of independent trait *i* on dependent trait *j* as measured by the corresponding path coefficient; and $\sum r_{ik}p_{kj} =$ summation of the components of the indirect effect of independent trait *i* on dependent trait *j* via all other independent traits *k*.

Estimation of residual effect:

$$\sqrt{(1 - R^2)}$$

where: $R^2 = \sum P_{ij}r_{ij}$, and P_{ij} and r_{ij} are as before. Scales for path coefficients have been suggested by Lenka and Mishra (1973) where 0.00-0.09 is negligible association effects, 0.01-0.19 is low, 0.20-0.29 is moderate, 0.30-0.99 is high and >1.0 is very high. Blast score data were not used in path analysis.

Phenotypic, genotypic and environmental coefficients of variation and broad sense heritability

Phenotypic coefficient of variation (PCV), genotypic coefficients of variation (GCV) and environmental coefficients of variation (ECV) were calculated according to Burton (1952) using combined data across the four locations:

$$PCV = \frac{\sqrt{\sigma_p^2}}{\bar{x}} \text{ x } 100$$

where: σ_p^2 = phenotypic variance; and $\bar{x}$ = phenotypic trait population mean;

$$GCV = \frac{\sqrt{\sigma_g^2}}{\bar{x}} \text{ x } 100$$

where:σ_g^2 =genotypic variance; and $\bar{x}$ phenotypic trait population mean;

$$ECV = \frac{\sqrt{\sigma_e^2}}{\bar{x}} \text{ x } 100$$

where: σ_e^2= random error variance.

Shivasubramanian and Menon (1973) classified PCV and GCV scales as 0-10% low, 10-20% moderate and >20% high.

Broad-sense heritability per location was estimated according to Hanson et al. (1956):

$$H^2 = (\sigma_g^2/\sigma_p^2) \text{ x } 100$$

where: σ_g^2 = genotypic variance; and σ_p^2 = phenotypic variance.

Broad sense heritability was calculated for the combined analysis across locations data:

$$H^2 = \sigma_g^2/(\sigma_g^2 + \sigma_{Gl}^2/l + \sigma_e^2/rl$$

where: σ_{Gl}^2 is variance due to genotype x location interaction, *l* and *r* are the numbers of environments and replications per environment, respectively.

Robinson et al. (1949) classified heritability values as 0-30% low, 31-60% medium and >61% high.

RESULTS

Correlation coefficients for blast severity with selected yield components

For the data collected at Alupe, negative and significant ($P \leq 0.01$) Spearman's rank correlations were recorded between days to flowering and: leaf blast (r_p = -0.265); neck blast (r_p = -0.440); and finger blast (r_p = -0.167). Similar correlations were recorded between grain yield and: leaf blast (r_p = -0.278); neck blast (r_p = -0.134); and finger blast (r_p = -0.347) (Table 1). All the three blast types were also significantly ($P \leq 0.01$) negatively correlated with leaf blade length and finger width. Tall accessions had lower blast scores as reflected by the negative correlations between plant height and the three blast types. Similarly high blast levels reduced threshing percent as evidenced by the negative correlations ($P<0.01$) between threshing percent and the three blast types. There was some moisture stress during the end of the crop reproductive phase hence low humidity and this could have reduced the prevalence

Table 1. Spearman's rank correlation coefficients for blast severity with selected finger millet yield components at Alupe.

Blast type	Days to flower	Grain yield	Plant height	Leaf blade width	Leaf blade length	Finger width	Finger length	Grains per spikelet	1000 grain mass	Threshing %
Leaf blast	-0.265***	-0.278***	-0.106***	-0.105*	-0.178***	-0.110**	0.140*	-0.155***	0.007ns	-0.140***
Neck blast	-0.440***	-0.134***	-0.058*	-0.048ns	-0.078*	-0.106***	0.048ns	-0.023ns	0.099ns	-0.081**
Finger blast	-0.167***	-0.347***	-0.153***	-0.102**	-0.246***	-0.153***	0.0064ns	-0.233***	0.08ns	-0.157***

***- Significant at P<0.001, **- Significant at P<0.01, *-Significant at P<0.05, ns-Non significant

of the blast pathogen and blast reaction of late maturing genotypes.

Phenotypic and genotypic correlation coefficients were determined between 19 quantitative traits across locations excluding score data (Table 2). Low but significant ($P \leq 0.01$) positive phenotypic correlations were recorded between grain yield and finger width ($r_p = 0.134$), peduncle length ($r_p = 0.272$), panicle exertion ($r = 0.281$), grains per spikelet ($r_p = 0.255$) and threshing percent ($r_p = 0.459$) (Table 2). The same trend was recorded in genotypic correlations but with higher correlation values between grain yield and finger width ($r_g = 0.876$), peduncle length ($r_g = 0.517$), panicle exertion ($r_g = 0.571$), grains per spikelet ($r_g = 0.623$) and threshing percent ($r_g = 0.677$). The highest significant ($P \leq 0.01$) phenotypic correlation was recorded between peduncle length and panicle exertion ($r_p = 0.853$). The highest significant ($P \leq 0.01$) positive genotypic correlation was recorded between finger width and 1000 grain mass ($r_g = 1.000$). The phenotypic and genotypic correlations between grain yield and days to flowering were both negative at $r_p = -0.357$ and $r_g = -0.450$, respectively. Very high significant ($P \leq 0.01$) negative genotypic correlations were recorded between productive tillers and: 1000 grain mass ($r_g = -1.000$); flag leaf blade width ($r_g = -1.000$); leaf sheath width ($r_g = -0.927$); and finger width ($r_g = -0.768$).

For the 18 quantitative traits, direct and indirect path coefficients on grain yield were estimated (Table 3). The path coefficients revealed that threshing percent (2.864), leaf blade width (2.523), leaves per plant (1.229), leaf blade length (1.119), grains per spikelet (0.760), leaf sheath length (0.601), and finger length (0.448) had high positive direct effects on grain yield. Negative direct effects were contributed by leaf sheath width (-2.938), plant height (-1.545), finger length (-1.260) and days to flowering (-1.183). Indirect genotypic effects of traits on grain yield through other traits were high. Some of the traits that had positive direct effects recorded overall negative effects on grain yield due to their negative indirect effects on grain yield through other traits and vice versa. Finger length which had a positive direct effect (0.448) on grain yield had an overall negative effect (-0.098) on grain yield due to its high indirect negative effects via leaf sheath width (-0.945), flag leaf blade width (-0.318), finger width (-0.439) and plant height (-0.457). Leaves per plant with a positive direct effect (1.229) on grain yield gave a negative overall effect contributed by its high indirect negative effects via days to flowering (-0.962), leaf sheath width (-0.529) plant height (-0.425), and threshing percent (-0.547). Traits which had negative direct effects on grain yield but with an overall positive effect included leaf sheath width, flag leaf blade length, finger width, peduncle length, panicle exertion, and plant height as a result of high indirect positive effects via other traits. The efficiency of the genotypic path coefficients was high with $R^2 = 0.935$ and a low residual of 0.255.

Phenotypic, genotypic and environmental coefficients of variation

For the 19 quantitative traits estimates of PCV, GCV and ECV across locations were determined (Table 4). The PCV estimates were higher than GCV estimates for all the traits. High PCV estimates were recorded for fingers per panicle, flag leaf blade length, finger length, peduncle length, number of leaves per plant, leaf sheath length, plant height, leaf blade length, grains per spikelet, days to flowering and number of productive tillers per plant. There were no high GCV estimates but medium estimates were recorded for finger length, peduncle length, number of leaves per plant, threshing percent and number of productive tillers per plant. The ECV estimates were relatively low ranging from 2.4% for grain yield to 23.8% in peduncle length.

Heritability

At Alupe, H^2 estimates ranged from 0.0% for threshing percent to 92.4% for days to flowering and at Lanet the lowest H^2 estimate recorded was for flag leaf width (3.6%) and the highest for finger length (81.4%) (Table 4). At Kiboko, leaf blade width (7.6%) and days to flowering (88.4%) had the lowest and highest H^2 estimates, respectively while at Mtwapa, 1000 grain mass (19.2%) and leaf blade width (91.8%) had the lowest and highest

Table 2. Phenotypic and genotypic (bold) correlation coefficients between 19 quantitative traits of finger millet based on data combined across four locations4.4.2 Genotypic path coefficients.

Trait	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	19
1	1.000 **1.000**	-0.248 **-0.417**	-0.028 **0.056**	0.022 **0.180**	0.036 **0.140**	-0.326 **-0.532**	-0.021 **-0.059**	0.022 **0.135**	0.023 **0.039**	-0.111 **-0.663**	-0.405 -0.571	0.4620 **0.813**	-0.371 **-0.516**	-0.063 **0.138**	-0.085 **-0.200**	-0.111 **-0.410**	-0.001 **-0.373**	-0.210 **-0.420**	-0.357 **-0.450**
2		1.000 **1.000**	0.169 **0.087**	0.366 **0.401**	0.060 **-0.068**	0.335 **0.502**	0.060 **0.033**	0.072 **-0.050**	0.109 **0.189**	0.114 **0.216**	0.155 **0.386**	-0.078 **-0.360**	0.063 **0.315**	0.334 **0.503**	-0.015 **-0.297**	0.092 **0.223**	0.044 **0.089**	0.036 **0.323**	0.127 **0.144**
3			1.000 **1.000**	0.504 **0.795**	0.362 **0.752**	-0.072 **-0.587**	0.344 **1.000**	0.156 **0.090**	0.192 **0.322**	0.185 **0.851**	-0.011 **-0.281**	0.134 **0.180**	0.024 **-0.014**	0.152 **0.146**	-0.231 **-0.927**	0.130 **0.502**	0.078 **0.102**	0.081 **0.451**	0.160 **0.215**
4				1.000 **1.000**	0.278 **0.679**	-0.101 **-0.389**	0.317 **0.776**	0.073 **-0.046**	0.293 **0.432**	0.163 **0.643**	0.034 **-0.036**	0.184 **0.111**	0.095 **0.194**	0.411 **0.556**	-0.215 **-0.792**	0.151 **0.429**	0.092 **0.075**	0.093 **0.385**	0.210 **0.214**
5					1.000 **1.000**	-0.124 **-0.369**	0.328 **0.763**	0.186 **0.218**	0.090 **0.267**	0.170 **0.380**	-0.130 **-0.275**	0.107 **0.190**	-0.053 **-0.125**	0.054 **0.224**	-0.135 **-0.962**	0.077 **0.126**	0.051 **0.266**	0.001 **0.018**	0.064 **0.081**
6						1.000 **1.000**	-0.185 **-0.581**	0.077 **0.061**	-0.069 **-0.198**	-0.037 **-0.270**	0.405 **0.698**	-0.206 **-0.475**	0.109 **0.361**	0.142 **0.028**	0.180 **0.502**	0.036 **-0.299**	-0.059 **-0.329**	0.016 **-0.028**	0.135 **0.175**
7							1.000 **1.000**	0.097 **0.132**	0.173 **0.443**	0.231 **0.441**	-0.017 **-0.207**	-0.001 **0.059**	0.060 **0.008**	0.061 **0.060**	-0.128 **-1.000**	0.074 **0.338**	0.095 **0.375**	0.002 **0.357**	0.023 **0.235**
8								1.000 **1.000**	0.014 **-0.049**	-0.064 **-0.394**	-0.153 **-0.230**	0.141 **0.166**	-0.206 **-0.280**	-0.004 **-0.129**	-0.027 **-0.116**	-0.026 **-0.213**	-0.028 **-0.264**	-0.09 **-0.273**	-0.01 **-0.192**
9									1.000 **1.000**	0.185 **0.349**	-0.04 **-0.087**	0100 **0.157**	-0.02 **-0.024**	0.201 **0.296**	-0.13 **-0.377**	0.185 **0.564**	0.062 **0.391**	0.009 **-0.059**	0.058 **-0.098**
10										1.000 **1.000**	0.007 **0.326**	-0.010 **-0.207**	0.034 **0.525**	0.073 **0.186**	-0.027 **-0.768**	0.160 **1.000**	-0.013 1.000	0.029 **0.912**	0.134 **0.876**
11											1.000 **1.000**	-0.267 **-0.479**	0.853 **0.910**	0.385 **0.305**	0.141 **0.459**	0.112 **0.401**	-0.022 **-0.360**	0.161 **0.462**	0.272 **0.517**
12												1.000 **1.000**	-0.260 **-0.416**	0.226 **0.275**	-0.077 **-0.261**	0.064 **0.058**	0.008 **0.333**	-0.086 **-0.191**	-0.004 **-0.174**
13													1.000 **1.000**	0.384 **0.369**	0.084 **0.291**	0.109 **0.605**	0.018 **-0.366**	0.187 **0.560**	0.281 **0.571**
14														1.000 **1.000**	-0.020 **-0.237**	0.121 **0.264**	0.039 **-0.084**	0.097 **0.179**	0.252 **0.119**
15															1.000 **1.000**	-0.004 **-0.398**	-0.070 **-1..000**	-0.071 **-0.290**	0.140 **0.098**
16																1.000 **1.000**	-0.026 **-0.429**	0.037 **0.476**	0.255 **0.623**
17																	1.000 **1.000**	0.100 **0.416**	0.078 **-0..294**
18																		1.000 **1.000**	0.459 **0.677**

1-Days to flowering, 2-Leaf sheath length, 3-Leaf sheath width, 4-leaf blade length, 5-Leaf blade width, 6-Flag leaf blade length, 7-Flag leaf blade width, 8-Fingers/panicle, 9-Finger length, 10-Finger width, 11-Peducnle length, 12-Leaves/plant, 13-Panicle exertion, 14-Plant height, 15-Productive tillers/plant, 16-Grains/spikelet, 17-1000 grain mass, 18-Threshing%, 19-Grain yield.

Table 3. Genotypic path coefficients showing direct (diagonal) and indirect genetic effects of 18 quantitative traits on grain yield.

	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**Overall path coefficients**
1	**-1.183**	-0.251	-0.165	0.201	0.352	0.378	0.042	-0.043	0.018	0.836	0.242	0.999	0.084	-0.213	-0.019	-0.312	-0.216	-1.202	-0.450
2	0.493	**0.601**	-0.257	0.449	-0.172	-0.357	-0.024	0.016	0.085	-0.273	-0.163	-0.442	-0.051	-0.777	-0.028	0.169	-0.052	0.926	0.144
3	-0.067	0.053	**-2.938**	0.889	1.898	0.417	-0.727	-0.029	0.144	-1.073	0.119	0.221	0.002	-0.225	-0.086	0.381	-0.059	1.293	0.215
4	-0.213	0.241	-2.336	**1.119**	1.713	0.276	-0.557	0.015	0.194	-0.810	0.015	0.136	-0.032	-0.858	-0.073	0.326	-0.044	1.102	0.214
5	-0.165	-0.041	-2.210	0.759	**2.523**	0.262	-0.547	-0.069	0.120	-0.479	0.117	0.234	0.020	-0.347	-0.089	0.096	-0.154	0.052	0.081
6	0.629	0.301	1.724	-0.435	-0.931	**-0.711**	0.417	-0.019	-0.089	0.341	-0.295	-0.584	-0.059	-0.043	0.046	-0.227	0.190	-0.081	0.175
7	0.070	0.020	-2.979	0.868	1.926	0.413	**-0.717**	-0.042	0.198	-0.556	0.087	0.073	-0.001	-0.093	-0.096	0.257	-0.217	1.023	0.235
8	-0.160	-0.030	-0.266	-0.051	0.549	-0.043	-0.095	**-0.316**	-0.022	0.497	0.097	0.204	0.046	0.199	-0.011	-0.162	0.152	-0.781	-0.192
9	-0.046	0.114	-0.945	0.483	0.674	0.141	-0.318	0.016	**0.448**	-0.439	0.037	0.192	0.004	-0.457	-0.035	0.429	-0.226	-0.169	-0.098
10	0.785	0.130	-2.502	0.719	0.960	0.192	-0.316	0.125	0.156	**-1.260**	-0.138	-0.254	-0.086	-0.287	-0.071	0.809	-0.697	2.611	0.876
11	0.676	0.232	0.825	-0.041	-0.695	-0.497	0.148	0.073	-0.039	-0.410	**-0.423**	-0.589	-0.148	-0.472	0.043	0.304	0.208	1.322	0.517
12	-0.962	-0.216	-0.529	0.124	0.48	0.338	-0.043	-0.052	0.070	0.261	0.203	**1.229**	0.068	-0.425	-0.024	0.044	-0.192	-0.547	-0.174
13	0.610	0.189	0.042	0.218	-0.314	-0.256	-0.006	0.089	-0.011	-0.662	-0.385	-0.511	**-0.163**	-0.570	0.027	0.460	0.211	1.604	0.571
14	-0.163	0.302	-0.428	0.622	0.566	-0.020	-0.043	0.041	0.133	-0.234	-0.129	0.338	-0.060	**-1.545**	-0.022	0.200	0.048	0.513	0.119
15	0.237	-0.178	2.724	-0.886	-2.426	-0.357	0.746	0.037	-0.169	0.967	-0.194	-0.321	-0.047	0.366	**0.093**	-0.303	0.640	-0.830	0.098
16	0.485	0.134	-1.474	0.48	0.317	0.212	-0.242	0.067	0.253	-1.340	-0.169	0.071	-0.098	-0.407	-0.037	**0.760**	0.248	1.364	0.623
17	-0.442	0.054	-0.300	0.084	0.672	0.234	-0.269	0.083	0.175	-1.521	0.152	0.409	0.060	0.130	-0.103	-0.326	**-0.578**	1.192	-0.294
18	0.496	0.194	-1.326	0.431	0.045	0.020	-0.256	0.086	-0.026	-1.149	-0.195	-0.235	-0.091	-0.276	-0.027	0.362	-0.240	**2.864**	0.677

1-Days to flowering, 2-Leaf sheath length, 3-Leaf sheath width, 4-leaf blade length, 5-Leaf blade width, 6-Flag leaf blade length, 7-Flag leaf blade width, 8-Fingers/panicle, 9-Finger length, 10-Finger width, 11-Peduncle length, 12-Leaves/plant, 13-Panicle exertion, 14-Plant height, 15-Productive tillers/plant, 16-Grains/spikelet, 17-1000 grain mass, 18-Threshing%; R2 = 0.935; Residual effect = 0.2552

Table 4. Genotypic, phenotypic and environmental coefficients of variation and heritability of 19 quantitative traits in finger millet.

Trait	Means across locations	GCV across locations	PCV across locations	ECV across locations	H^2 (%) Alupe	H^2 (%) Lanet	H^2 (%) Kiboko	H^2 (%) Mtwapa	H^2 (%) across locations
1	7.94	9.57	25.02	8.02	52.5	73.5	72.6	68.2	83.0
2	10.53	8.71	26.50	8.25	38.3	70.3	76.7	65.2	77.8
3	2.59	1.64	11.70	7.44	14.6	54.8	33.6	19.2	68.5
4	4.08	17.61	54.56	5.00	72.2	65.1	54.4	72.2	66.0
5	6.85	15.50	56.19	7.85	78.1	81.4	82.1	66.7	65.1
6	19.91	17.57	79.20	23.77	76.1	63.9	69.3	63.3	64.2
7	9.56	2.12	11.58	4.39	63.8	58.6	59.0	55.0	61.6
8	14.32	16.72	72.43	11.36	79.0	47.9	69.9	58.7	59.8
9	11.31	7.50	35.48	5.41	78.6	72.3	60.9	63.5	56.7
10	84.51	8.92	57.78	6.04	79.1	71.9	64.6	75.3	45.3
11	48.00	2.68	24.93	3.00	58.8	45.6	60.3	53.4	35.6
12	71.34	10.27	16.68	8.50	0.0	80.6	31.5	44.7	35.2
13	5.60	1.45	21.73	9.60	61.2	38.0	47.3	36.2	34.2
14	1.59	0.70	7.35	1.31	60.7	60.0	56.6	50.7	34.2
15	2.38	0.94	10.11	2.36	54.2	78.4	44.6	68.4	34.0
16	84.31	8.04	72.86	21.99	92.4	77.0	88.4	80.6	33.9
17	1.17	0.54	8.14	1.92	73.2	3.6	16.3	68.4	27.1
18	1.33	0.65	11.41	2.48	72.2	48.2	7.6	91.8	23.6
19	1.15	0.25	11.35	2.14	65.5	50.0	22.9	44.1	10.0

GCV-Genotypic coefficient of variation, PCV-Phenotypic coefficient of variation, ECV-Environment coefficient of variation, H2-Broad-sense heritability; 1-Fingers per panicle, 2-Flag leaf blade length, 3-1000 grain mass, 4-Productive tillers per plant, 5-Finger length, 6-Peduncle length, 7-Panicle exertion, 8-Leaves per plant, 9-Leaf sheath length, 10-Plant height, 11-Leaf blade length, 12-Threshing percent, 13-Grains per spikelet, 14-Leaf sheath width, 15-Grain yield, 16-Days to flowering, 17-Flag leaf blade width, 18-Leaf blade width, 19-Finger width.

H^2estimates,respectively. Heritability estimates across locations were lower than for individual locations. The highest H^2 estimate across locations was recorded for fingers per panicle (83.0%) while the lowest (10.0%) was recorded for finger width. High H^2 estimates($\geq$60%) were recorded for fingers per panicle (83.0%), flag leaf blade length (77.8%), 1000 grain mass(68.5%), productive tillers per plant (66.0%), finger length (65.1%), peduncle length (64.2%) and panicle exertion(61.6%). Number of leaves per plant, plant height, days to flowering, leaf blade length, grains per spikelet, leaf sheath length and width and threshing percent had moderate H^2 estimates (33.9-59.8%).

DISCUSSION

Associations between traits

For effective simultaneous improvement of the key traits in crop productivity it is necessary to determine the magnitude of associations between the traits. In this study, the rank, phenotypic and genotypic correlation coefficients indicated the magnitude and direction (positive or negative) of the associations between the traits. Spearman's rank correlation analysis of the Alupe data revealed significant ($P \leq 0.01$) negative correlations between all blast types (leaf, neck and finger) with days to flowering and grain yield implying that early genotypes suffered more blast damage leading to reduced grain yield. These findings agree with those of Dida and Devos (2006) and Takan et al. (2004). The high positive correlations among leaf, neck and finger blast lend support to the conclusions of Pande (1992). The negative correlations between finger blast and grains per spikelet and threshing percent indicated that higher blast scores contributed to fewer and lighter grains per spikelet and low threshing percent leading to low grain yields. These are similar findings to those of Sreenvasaprasad et al. (2005) and Pande et al. (1995). Leaf blast reduces the photosynthetic capacity of the plant, whereas early neck blast reduces or completely impairs the flow of nutrients to the panicle and finger blast reduces or completely impairs grain filling (Rath and Mishra 1975). Low blast scores in tall accessions could be due to their higher clearance from the ground (inoculum levels are likely to be higher near the ground due to debris and rain drops splashes), or due to the negative correlation between days to flowering and blast since most of the tall plants were late flowering and flowered in lower humidity when rainfall was less than earlier in the season.

Across locations, the genotypic correlations were higher than phenotypic correlations for most of the traits studied indicative of the inherently strong genetic relationships among the traits once the non-heritable influence of the environment was removed. This was also reported by Chaudhari and Acharya (1969) and Wolie and Desalegn (2011). However, the same authors found grain yield to be positively correlated with finger width, peduncle length, panicle exertion, grains per spikelet, and threshing percent. Days to flowering had high negative genotypic and phenotypic correlations with the key yield related traits of finger width, peduncle length, panicle exertion grains per spikelet, and threshing percent, corroborating results reported by Bezawelataw et al. (2006). Late maturing accessions, therefore, had narrower fingers, shorter peduncles, shorter exertions, fewer grains per spikelet and poorer threshing percent. These high negative correlations negated the positive effects of higher number of leaves per plant in late maturing plants and hence this trait did not translate into higher grain yield. The negative association between plant height and number of productive tillers per plant in this study was also reported by Sonnad et al. (2008). However, Suyambulingam and Jebarani (1977) reported positive significant correlations between plant height and finger length and number of fingers per panicle. Finger width recorded the highest positive genotypic correlations ($r_g = 1.00$) with grains per spikelet, 1000 grain mass ($r_g = 1.00$) and threshing percent ($r_g = 0.91$) but had high negative genotypic correlation with productive tillers per plant ($r_g = -0.77$) which agrees with the findings of Bezawelataw et al. (2006) save for threshing percent which had negative correlation with threshing percent. Therefore, many tillers will give many panicles but with narrow fingers hence fewer grains. The negative genotypic correlation between grains per spikelet and 1000 grain mass (-0.429) could be from the high competition for assimilates between the two traits as was also reported by Dewey and Liu (1959).

Path coefficients

The highest direct positive effects on grain yield were contributed by number of leaves per plant, leaf blade length, leaf blade width, leaf sheath blade length, finger length, grains per spikelet, and threshing percent. When compared to the path coefficient scales suggested by Lenka and Mishra (1973) where 0.00-0.09 is negligible, 0.0 1-0.19 low, 0.2 0-0.29 moderate, 0.30-0.99 high and >1.0 very high, threshing percent (2.864), leaf blade width (2.523), number of leaves per plant (1.229) and leaf blade length (1.119) had very high direct effects whereas grains per spikelet (0.760), leaf sheath length (0.601) and finger length (0.448) had high direct effects. Productive tillers per plant had a positive but low direct effect (0.093) on grain yield. This means that accessions with a high number of long, wide leaves and long fingers with many grains and a high grain to panicle ratio will give more grain yield per unit area. The high yields achieved by accessions with a high number of long and wide leaves could be attributed to their high capacity to intercept more light thereby increasing photosynthesis (Dewey and Lu 1959). By implication this would require a strong source-sink relationship. Dependence of grain yield on sink size in finger millet was reported by Subedi and Budhathoki (1996). Although plant height had a negative direct effect on grain yield, it had an overall positive effect due to positive indirect effects via leaf blade length and width, leaves per plant and threshing percent. In pearl millet (*Pennisetumglaucum* (L.) R.Br) though, Chaudhry et al. (2003) found positive direct effects of plant height on grain yield. Threshing percent has been found to be useful as a selection criterion for terminal drought tolerance in pearl millet and is used to indirectly select for grain yield (Bidinger and Mukuru 1995). The results of this study confirm the value of threshing percent in yield selection based on its very high direct positive effects on yield. The negative direct effects of days to flowering on grain yield were contributed largely via the number of leaves per plant and 1000 grain mass. Late accessions generally had lower 1000 grain mass probably due to limited moisture at grain filling. High leafiness may also result in excessive shading such that photosynthesis is not optimal for the given leaf area.

In previous studies in finger millet, positive direct effects on grain yield have been reported by: Bendale et al. (2002) and Ganapathy et al. (2011) from finger length; Dhanakodi (1988) from number of leaves per plant and leaf length; and Bezawelataw et al. (2006) from number of leaves per plant. Positive direct effects of grains per spikelet on grain yield detected in this study were also reported by Lule et al. (2012) in finger millet and El-din et al. (2012) in sorghum (*Sorghum bicolor* (L.) Moench). Negative direct effects of plant height and days to flowering on grain yield in finger millet have been reported by Wolie and Dessalagn (2011) and from plant height in wheat by Pandey et al. (2012). However, Bezawelataw et al. (2006) reported positive direct effects from 1000 grain mass and negative direct effects from grains per spikelet. Although Ravikumar and Seetharam (1993) and Sonnad et al. (2008) reported positive direct effects of productive tillers per plant on grain yield, this study found a negligible direct effect (0.093) which could be attributed to the negative indirect effects of this trait via leaf blade length and threshing percent on grain yield.

Finger length had negative indirect contribution via leaf sheath width, finger width, and plant height. These traits should therefore be used with caution when selecting for grain yield. Number of fingers per panicle had negative direct effects on grain yield. This means that as the number of fingers increases grain yield decreases which means there is competition for assimilate between number of fingers and grains per finger and grain mass. This however contradicts findings of Priyadharshini et al. (2011) and Ganapathy et al. (2011) who reported direct positive effects.

Grain yield is influenced by many independent traits and understanding the nature and magnitude of the association of these traits with grain yield and among themselves is vital for effective selection for grain yield. Findings of this study show that threshing percent, leaf blade width, number of leaves per plant, leaf blade length, grains per spikelet, leaf sheath length and finger length had high positive direct effects on grain yield and could be ideal traits to select for in finger millet for grain yield improvement. Simultaneous selection for the improvement of those traits with strong positive direct effects and those with strong positive indirect effects on grain yield would obviously be the best approach. However, the constraints imposed by negative trait associations must also be taken into consideration when selecting for any components of yield individually. The magnitude of other component traits may often compensate downwards in order to allow for an increased proportion of the fixed pool of assimilate to be partitioned to the improved component trait (Slafer et al. 1996). For example, high direct effects on grain yield were recorded from grains per spikelet but this was negatively correlated with 1000 grain mass meaning that more grains per spikelet will use more assimilate at the expense of grain fill leading to low mass grain^{-1}and ultimately reduced yield. In essence selection for a trait must be in sympathy with selection for the other trait so that an optimum level maximizes the net effect of the system (Yan and Wallace 1995).

The variability in grain yield in finger millet was well captured by the 18 traits studied based on the very low residual effect obtained (0.255) and a high coefficient of determination ($R^{2=}$0.935) for path coefficients.

Phenotypic and genotypic coefficients of variation

Phenotypic coefficient of variation and GCV estimates are useful in obtaining a measure of the genetic variability in the expression of the target traits. Higher GCV than PCV estimates would suggest that the phenotypic expression of the trait is more influenced by genes than the environment whereas higher PCV estimates would mean the trait is more influenced by the environment. From the results, PCV estimates across the locations were orders of magnitude higher than GCV estimates across the locations for all traits indicating a considerable influence of the environment. However, in fingers per panicle, flag leaf blade length, finger length, number of leaves per plant, leaf sheath length, productive tillers per plant, plant height and threshing percent, the effects of the environment were relatively lower than those for the other traits as evidenced by the lower ECV estimates. Likewise, the relatively closer estimates of PCV and GCV in threshing percent suggest low environmental effects for this trait and thus high heritability. Improvement of these traits should, therefore, be achievable through selection. In Ethiopia, Bezawelataw et al. (2006) reported on the strong influences of both genes and environment in most of the finger millet traits he studied owing to the high PCV and GCV estimates obtained. In India though, Ganapathy et al. (2011) found high PCV and GCV only in productive tillers per plant. Lule et al. (2012) reported low PCV in days to flowering with low GCV in grains per spikelet and finger width while Nandini et al. (2010) found a small difference between PCV and GCV for fingers per panicle.

Heritability

Although heritability estimates across locations/environments are usually lower than the component single location estimates (Falconer 1981,Mudler and Bijma 2005), as was found in this study, they provide a more realistic estimate for genetic gain predictions in the absence of narrow sense heritability which is based on the additive effects of genes only . For single location data GxE interaction effects are confounded with genotypic effects. They are mathematically entangled and cannot be separated unless the genotypes are tested at least in two locations and consequently the magnitude of the heritability estimates is inflated. High H^2 across locations were recorded in fingers per panicle, flag leaf blade length, 1000 grain mass, productive tillers per plant, finger length, panicle exertion, and peduncle length indicating that these traits are influenced more by genetic than environmental effects. Because of their high $H^2$and finger millet being highly inbred and breeds true to type, improvement of these traits through selection should theoretically be achieved quickly. High H^2 was also reported by Daba (2000), Sumathi et al. (2007), Gananapathy et al. (2011), Priyadharshini (2011) and Lule et al. (2012) in fingers per panicle and finger length with Sumathi et al. (2007) also reporting high H^2 in 1000grain mass.

Low H^2 in number of productive tillers per plant, finger width and grain yield implies high environmental effects on expression of these traits. Low H^2 has also been reported by Patnaik (1968) for productive tillers per plant. Satish et al. (2007) and Kadam et al. (2008) found high $H^2$for grain yield. Trait H^2 estimates varied between locations with the lowest estimates in nine traits recorded at Kiboko, a dry lowland location with limited and erratic rainfall. This was not surprising since the degree of genetic influence on trait development is dependent on the environment (Robinson et al. 1949) and, as reported by Falconer (1981), H^2 increases with reduced variability in test conditions and vice versa. Rosielle and Hamblin (1981) also found H^2 in grain yield to be correlated with the availability of water and Eid (2009) found low H^2 in drought stress conditions in wheat.

In inbred lines, dominance effects diminish rapidly with inbreeding and the genotypic variance components estimated provide estimates of additive genetic variance (Hallauer and Miranda 1998). Finger millet being a highly self-pollinating crop means that each line will be highly inbred with most of the genotypic variance component estimate being due to additive genetic variance. Traits which recorded high H^2 in this study (number of fingers per panicle, flag leaf sheath length, 1000 grain mass, finger length, productive tillers per plant, peduncle length, panicle exertion) would be presumed to be under strong additive genetic control hence can be improved through selection. Similar findings of high H^2 estimates in finger millet traits were reported by John (2006) for fingers per panicle; Bezawelatawet al. (2006) for finger length; Satish et al. (2007) and Nandini et al. (2010) for fingers per panicle and finger length; and Lule et al. (2012) for finger length and 1000 grain mass. Finger width had low H^2 estimates an indication of high environmental effects on this trait hence very slow progress through direct selection is expected. The slow rate of progress in yield improvement in breeding programs is more often due to its low heritability (though moderate in this study) rendering direct selection difficult. Using traits with high heritability that have positive direct effects on yield and are highly correlated with yield would increase the rate of improvement in yield in selection programmes. In this regard, although grains per spikelet recorded moderate heritability it had high correlation with and high positive direct effects on grain yield, and therefore it could potentially be a useful trait for indirectly selecting for yield improvement.

CONCLUSION

Considerable opportunity exists for finger millet improvement to address the different biotic and abiotic stresses in varied agro-ecologies owing to the ample variability recorded in the quantitative traits. This variability could be utilized in direct selection and for hybridization. Genotypic correlations were higher than phenotypic correlations for most traits. Grain yield was significantly ($P \leq 0.01$) genotypically positively correlated with grains per spikelet, threshing percent, peduncle length and panicle exertion. These traits could be used to indirectly select for grain yield. Key yield components with positive and strong direct effects on grain yield such as threshing percent, number of leaves per plant, leaf blade length, grains per spikelet, leaf sheath length and finger length can be used in indirect selection for grain yield, a complex trait with low heritability. But due consideration should also be given to traits with strong indirect effects on grain yield during selection, taking into account the fixed amount of assimilate available to be partitioned among the components of yield. Though there were high environmental influences on most traits, the high broad-sense heritability estimates recorded in fingers per panicle, flag leaf sheath length, 1000 grain mass, finger length, peduncle length, panicle exertion, number of leaves per plant and leaf sheath length indicate the potential for their improvement through selection.

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