

Trait specific genetic resources to break the yield plateau in finger millet (*Eleusine coracana* L.).

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Abstract

Previously, most breeding efforts were aimed at direct selection for grain yield, and the yield improvement of finger millet in the last two decades is showing a declining trend. Hence, breeding efforts need to be prioritized for trait based improvement. Therefore, to select genetic resources for traits linked to grain yield, selected accessions and popular varieties were evaluated under field conditions in the rainy season of two consecutive years. Data were analyzed for ANOVA, correlations, path effects, and multiple regressions to identify the best-contributing traits for grain yield. The independent parameters, mean ear-head weight (MEW), ear-head number/ plant (ENo.), and threshing percentage were the highest contributors to grain yield. The genotypes for higher mean ear-head weight (GE-4683, 10.31 g, and GE-4596, 10.22 g), and productive tillers (RAU-8, 126.4 m⁻², and PR-202, 104.7 m⁻²) were selected over the popular cv. GPU-28 (7.59g average ear-weight and 72.7 PT m⁻², respectively). Theoretical incorporation of higher MEW and ear-head number/plant from the identified lines into cv. GPU-28 predicted an increased grain yield of 17.8% and 29.5%, respectively, indicating the possibility of enhancing grain yield of finger millet. These selected donors can also be used in developing Multi-parent advanced generation inter-cross (MAGIC) population.

Highlights

- Finger millet yield improvement is plateau, and further improvement is possible by trait introgression through development of multi-parent advanced generation inter-cross (MAGIC) population.
- Major yield contributing traits are mean ear-head weight and productive tillers that contribute to grain yield by 17.8% and 29.5%.
- The donors selected for higher mean ear-head weight are GE-4683, GE-4596, and for higher productive tillers are, RAU-8, PR-202, PES-110 compared to the popular variety, GPU-28.

1. Introduction

Millet, including the finger millet, are gaining importance due to their higher capacity to adapt to weather-related conditions. According to <http://exploreit.icrisat.org>, finger millet accounts for 12% of the millet area, cultivated in more than 25 nations in Africa and Asia. In India, finger millet was grown on 1.004 million hectares producing 1.755 million metric tonnes in 2019–2020. Compared to major rainfed millets, the sorghum (989 kg/ha) and pearl millet (1374 kg/ha), the finger millet productivity is considerably high with 1747 kg/ha (<http://www.indiaagristat.com>). As a result, finger millet is more appropriate for drought-prone areas in semi-arid regions (Thilakarathna and Raizada, 2015; Wafula et al., 2016; Puranik et al., 2017; Nanja Reddy et al., 2021a) and is grown as a rainfed crop in more than 90% of finger millet area under cultivation (Davis et al., 2019). Additionally, finger millet has many dietary advantages with high calcium, iron, amino acids, fibre, and polyphenols (Upadhyaya et al., 2011; Chandra et al., 2016; Badigannanavar and Ganapathi, 2018; Hiremath et al., 2018; Hassan et al., 2021). Livestock

prefers finger millet fodder (straw or haulm) because it contains more than 60% digestible nutrients (Baath et al., 2018).

Considering such advantages, breeding efforts have accelerated the productivity from 1.5 to 2.0 t/ha (Cv. H-22 in 1919) to 4.0 to 4.5 t/ha (in popular varieties like GPU-28 released in 1998) on research stations and innovative farmer's fields (Gowda et al., 2014). The success was attributed to the blast resistance and improved partitioning of the biomass towards grain (Megha et al., 2023). One of the most successful and popular varieties in varietal improvement was GPU-28, which has 2.5 productive tillers per hill with an average ear weight of 7.5 g/ear (Nanja Reddy et al., 2019). Finger millet yield improvement became a declining trend in the last twenty years (Adugna et al., 2011; Megha et al., 2023) because the selection was mainly towards yield only. Choosing additional yield-contributing traits would increase the grain yield further (Nanja Reddy et al., 2021b). Therefore, it would be appropriate to identify the germplasm accessions for characters associated with grain yield. Such donors can be utilized in breeding programmes to achieve targeted higher grain yield in the background of popular varieties with blast resistance, through development of Multi-parent advanced generation inter-cross (MAGIC) population. Hence, the present study of the identification of genotypes for yield contributing traits compared to cv. GPU-28 would be relevant for further yield improvement.

2. Material and Methods

Field experiments had been carried out in red-sandy loam soils in the wet seasons over two consecutive years at the All-India Coordinated Small Millets Improvement Project, University of Agricultural Sciences, GKVK, Bengaluru, India. The experiment was conducted in a completely randomized block design with 30 medium (105–110 days) to long-duration (115 days) genotypes with three replications. Every genotype had a plot size of 0.9 m width x 2.0 m long (3 rows of 2 m long each) in 2010, and it was 1.5 m width x 4.5m long (5 rows of 4.5 m long) in 2011. Sowing was done, on 07-07-2010, and 22-07-2011, and seedlings were thinned within 20 days after sowing (DAS) to have one seedling per hill. The distance between rows was 30 cm, and between hills within a row was 10 cm. Fifteen days before sowing, the organic matter (FYM @ 7.5t/ha) was incorporated into the soil. The recommended fertilizer dose for finger millet is 50:40:25 kg nitrogen, phosphorus, and potassium per hectare. At the time of sowing, half of the nitrogen, full of P and K, were applied, and remaining 50% N was applied at 40 DAS. Manual weeding was under taken to keep the field weed free. When the rainfall did not occur continuously for 15 days irrigation was given. Observations at crop harvest were recorded from 30 hills constituting one square meter ground area. The parameters (traits) recorded were the number of ear-heads, straw-weight, grain yield, and above-ground dry matter (TDM). The threshing percentage ((grain yield/total ear weight) x 100), and mean ear-head weight (total ear-weight divided by total ear-head number), were calculated.

The parameters associated with grain yield were identified with the help of a regression equation using pooled data over two years. Pooling of data over seasons/ years will be applicable only if the variances between the two seasons/years are homogeneous. If the variances are not homogeneous, the original observations shall be normalized to bring equal variances among the two years/ seasons. Since the data

pertaining to the two years in the present study, F-test using Microsoft Excel software (<https://www.lexjansen.com>) was carried out, to check the homogeneity of variances for each parameter between years. The F-ratio (F-statistic) was computed by dividing the larger variance by the smaller, and the F-critical values were taken from the statistical tables at $P < 0.05$ at 29 degrees. The parameters with a lower F-statistic to that F-critical value indicate that the variances are similar (not significantly different), and such parameters considered directly for the pooling of data for combined analysis. But, the F-statistic was higher than the F-critical for the number of ears/ hill and threshing percentage, therefore, each observation of these parameters was divided by the error mean sum of squares (MSSe) of that respective experiment analyzed in RCBD and obtained normalized values. The normalized values were used for combined analysis using OPSTAT statistical software (Sheoran et al., 1998). The coefficient of variation for each trait was calculated as $CV (\%) = (\text{Square root of error mean sum of squares in combined analysis} / \text{the mean of all observations}) \times 100$.

To check for the extent of the relationship between the traits, Pearson's correlations, was performed using the Microsoft Excel ToolPak. The path analysis was performed using OPSTAT software to check for the direct and indirect effects of parameters on grain yield. The direct and indirect effects were classified based on a scale, of 0.00–0.09 (negligible), 0.10–0.19 (low), 0.20–0.29 (moderate), 0.30–0.99 (high), and > 1.0 (very high) (Lenka and Misra, 1973). Furthermore, the contribution of each or combination of traits to grain yield was measured by considering the residual values in the path analysis. The lower residual value indicates that the selected parameters through path coefficient analysis were appropriate (Amein et al., 2020). The traits contributing to grain yield were selected using multiple linear regressions (MLR) in stepwise backward selection, using the Microsoft Excel ToolPak. In stepwise backward regression, the MLR was drawn considering all the traits, and removed the parameters one by one that has $P > 0.05$, till the significant parameters with $P < 0.05$ only remains. Using the identified significant parameters the final MLR equation was arrived. By employing the derived MLR equation, yield predictions were made and compared with the actual grain yields. Furthermore, the values of the specific parameter (10.31g of mean ear-weight of GE-4683 or 126.4 ear-heads per m^{-2} of cv. RAU-8) was incorporated in the final MLR equation, to arrive at the predicted grain yield of popular variety, GPU-28.

3. Results

3.1 Genotypic variability for yield contributing parameters

Before pooling the data for combined analysis of ANOVA, the F-test for homogeneity of variances for all the traits between the two years was performed. The F-ratios (statistic) were less than the F-critical for all the parameters except the ear-head number per square metre and the threshing percentage (Table 1). The traits, mean ear-head weight, dry straw (haulm) weight, total dry matter (TDM), harvest index (HI), and grain yield had similar variances, and less influenced by the environment. The ear-head number and threshing percentage had a higher F-ratio than the F-critical, depicts the higher influence of environmental conditions on these traits, hence for these traits the data was normalized before proceeding to the

combined analyses (Table 1). In the combined (pooled) analysis the mean ear-head weight, and grain yield did not differ statistically between the years, whereas, the other parameters differed statistically between years, genotypes, and their interactions (Table 2; Suppl. Tables 1, 2 & 3). The mean and variability statistics showed a higher genetic variability (Table 2). With respect to grain yield, none of the genotypes was statistically superior to the cv. GPU-28 (Suppl. Table 1). But, the mean ear-weight was higher (> 10 g/ear) in germplasm accessions GE-4596 and GE-4683 than in cv. GPU-28 (7.59 g.ear⁻¹). A higher ear-head number (> 100 m⁻²) was observed in cv. PES-110, PR-202, and RAU-8 compared to the popular cv. GPU-28 (72.7 m⁻²). Except for a few accessions (GE-3609, GE-3510, GE-4683), the majority of genotypes had a higher threshing percentage of $> 80\%$, and it was higher (84.5%) in cv. GPU-28 (Suppl. Table 2).

Note for table 1: (1) F-test two sample for variances was followed using Excel tool pack, data analysis, (2) When the F-statistic values (calculated) are less than the F-critical (Statistical table value), the variances are statistically not differed significantly (in other words the variances are similar) and (3) F-statistic values in parenthesis are derived from weighed observations (each original value /Msse of ANOVA).

Table 1
Test of homogeneity for variances between years for yield and yield contributing parameters in finger millet genotypes

Statistic	Year	EHNo. (No.m ⁻²)	MEW (g)	Threshing (%)	Str. wt (gm ⁻²)	TDM (gm ⁻²)	HI	Grain Yield (gm ⁻²)
Variance	2010	644.8	4.90	43.8	9859	20229	0.002	4297
Variance	2011	191.2	3.32	6.17	15830	29872	0.002	6859
F-critical		1.86	1.86	1.86	1.86	1.86	1.86	1.86
F-statistic		3.37 (1.24) ^{ns}	1.42 ^{ns}	7.10 (1.81) ^{ns}	1.61 ^{ns}	1.48 ^{ns}	1.31 ^{ns}	1.60 ^{ns}

Table 2
Pooled mean and variability statistics in finger millet genotypes in comparison with cv. GPU-28

	F-test	F-test	Across genotypes						GPU-28
Character	for traits	for genotypes	Mean	Min.	Max.	SD	Variance	CV (%)	Mean
Grain yield (gm^{-2})	NS	*	399.3	288.5	548.3	67.3	4376	13.0	463.2
Mean ear weight (g)	NS	*	7.06	3.43	10.3	1.97	3.75	8.5	7.59
Ear number (No.m^{-2})	*	*	74.9	53.4	126.4	18.3	325.2	13.8	72.7
Threshing (%)	*	*	81.1	68.3	86.8	4.39	18.6	2.6	84.8
Straw weight (gm^{-2})	*	*	586.4	388.3	778.2	98.2	9322	14.8	597.2
Total dry matter (gm^{-2})	*	*	1079	815.9	1323	131.8	16791	12.3	1145
Harvest index	*	*	0.373	0.290	0.445	0.044	0.002	8.64	0.41
NS: Statistically Non-significant; *: Statistically significant at $P < 0.05$									

3.2 Contribution of specific traits to grain yield

Pearson correlations revealed that the grain yield was positively and significantly related to dependent (biomass and harvest index) and independent traits (mean ear weight and threshing percentage). The mean ear-head weight and ear-head number were negatively related to each other (Table 3). Among the independent traits, the mean ear-head weight showed a very high direct positive effect (1.364) on grain yield, followed by a higher effect of ear-head number (0.902) and a moderate influence of threshing percentage (0.298). The lower residual value of 0.127 of path analysis further confirmed that the mean ear-head weight could be the best trait for increasing finger millet yield (Table 4). A lower residual value in path analysis indicates a higher contribution of parameters towards the grain yield. The highest contribution to grain yield was predicted by mean ear-head weight (42.6%), followed by threshing percentage (23.0%), and ear-head number (3.9%). The combination of ear-head number and mean ear-head weight increased the contribution to 77.5% (Table 5). The mean ear-head weight, ear-head number, and threshing percentage collectively increased the contribution to 86.7%, with a low residual value of 0.133. Further addition of straw weight to these three traits increased the contribution by only 0.6% (Table 5).

Table 3

Pearson correlation coefficients between yield contributing traits and grain yield in finger millet genotypes in pooled data

Parameters	MEW	EH No	Th%	Str	TDM	HI	GY
MEW	1.000						
EH No	-0.817	1.000					
Th%	0.061	0.093	1.000				
Str	0.105	-0.078	0.175	1.000			
TDM	0.466	-0.176	0.244	0.832	1.000		
HI	0.400	-0.044	0.474	-0.521	-0.043	1.000	
GY	0.653	-0.191	0.476	0.215	0.696	0.680	1.000
TDM: Total dry matter at harvest, HI: Harvest index, Str. wt.: Straw weight, ENo.: Ear number, MEW: Mean ear weight, Thr. %: Threshing percentage, GY: Grain yield, correlation values of > 0.361* and > 0.463** are significant at 5% and 1% respectively.							

Table 4

Direct and indirect effects of independent yield contributing traits on grain yield in finger millet

Character	MEW	EH No.	Th %	Str	Correlation coefficient with grain yield
Mean ear weight (MEW)	1.364	-0.740	0.020	0.009	0.653**
Ear number per hill (EHNo.)	-1.118	0.902	0.025	-0.006	-0.197*
Threshing percentage (Th%)	0.091	0.076	0.298	0.015	0.479**
Straw weight (Str.)	0.144	-0.064	0.053	0.082	0.215*
Residuals: 0.127					

Table 5
Contribution of yield attributing traits towards grain yield of finger millet in pooled data

Parameters (Grain yield Vs other traits)	Residual	Contribution (%)	% Increase
1) Total dry matter (g m ⁻²)	0.516	48.4	
2) Harvest index	0.536	46.4	
3) Mean ear-head weight (MEW) (g ear ⁻¹)	0.574	42.6	
4) Threshing percentage (Thr. %)	0.770	23.0	
5) Straw weight (Str. Wt.; gm ⁻²)	0.954	4.6	
6) Ear-head number (ENo.; No. m ⁻²)	0.961	3.9	
7) Mean ear-head weight + Ear number	0.225	77.5	34.9
8) Mean ear-head weight + Threshing percent	0.383	61.7	38.7
9) Mean ear-head weight + Straw weight	0.552	44.8	40.2
10) Mean ear-head weight + ENo. + Straw weight	0.208	79.2	1.70
11) Mean ear-head weight + ENo. + Thr. %.	0.133	86.7	9.20
12) MEW + ENo. + Thr. % + Str. Wt.	0.127	87.3	0.60
Foot note: GY: Grain yield, HI: Harvest index, EH No.: Ear number, Thr. %: Threshing percentage, MEW: Mean ear weight, TDM: Total dry matter at harvest, Str. wt.: Straw weight.			

3.3 Yield prediction by specific traits

To predict the grain yield using the selected traits, a multiple linear regression (MLR) model was computed ($Y = -589.1 + (49.5 * MEW) + (3.56 * \text{Ear-head number}/ m^{-2}) + (4.59 * \text{Th. \%})$). The relationship between observed and predicted grain yield using MLR was statistically significant, with 8.85% deviation between observed and expected grain yield (Fig. 1). The grain yield, ear-head number, and harvest index of popular cultivars are already high over the germplasm accessions (Fig. 2). The superior genotypes/ accessions for mean ear-head weight (GE-4683 and GE-4596), and ear-head number per hill (RAU-8, PR-202, PES-110) were selected in comparison with cv. GPU-28 (Table 6). In the MLR equation, theoretical incorporation of a higher ear-head number of cv. RAU-8 into cv. GPU-28 predicted a 29.5% increase in grain yield, and with the mean ear-head weight of accession, GE-4683, it was 17.8% (Table 7). The mean threshing percentage of cv. GPU-28 (84.8%) is already high.

Table 6
Superior genotypes for selected traits in comparison with ruling variety, GPU-28

Mean ear weight (g)	Ear/ PT (No. m ⁻²)	Threshing (%)
GE-4683 (10.31)	RAU-8 (126.4)	GPU-67 (86.8)
GE-4596 (10.22)	PR-202 (104.7)	GPU-76 (86.3)
MR-1 (9.95)	GE-4999 (102.6)	PES-110 (85.5)
GPU-28 (7.59)	GPU-28 (72.7)	GPU-28 (84.8)

Table 7
Selected traits with multiple linear regression by forward selection of traits

Parameter	Coefficient	T-statistic	Prob.	Observed yield of GPU-28 (gm ⁻²)	Expected increase in grain yield of GPU-28 by trait introgression
Adj. R ²	0.846				
Intercept	-589.1				
Mean ear weight (g/ear)	49.5	10.50	***	483.3	569.3 (17.8%)
Ear-number (No.m ⁻²)	3.56	7.06	***	483.3	625.8 (29.5%)
Threshing (%)	4.59	4.00	***	483.3	443.8 (NS)
Straw weight (g. m ⁻²)			NS		
Y= -589.1 + (49.5 * MEW) + (3.56 * PT/ Ear number) + (4.59 * Th.%)					

4. Discussion

To fulfil the food requirements of the growing population, plant breeding efforts and management practices have progressed the grain yield in important food crops like rice, wheat, and maize (Fischer and Edmeades, 2010) and finger millet (Adugna et al., 2011; Megha et al., 2023). Finger millet contributes to a lesser share of the country-wide food production in India, but it has significance in nutritional superiority, drought resilience, and regional food security, with a positive response to additional irrigation and fertilizers (Thilakaratna and Raizada, 2015). However, in the last two decades, finger millet productivity is decreasing (Adugna et al., 2011; Saxena et al., 2018; Megha et al., 2023). Therefore, to increase the grain yields further, donor lines with higher yield contributing traits are necessary (Nanja Reddy et al., 2021b),

and one of the principal approaches for developing donor lines is the utilization of genetic resources (Upadhyaya et al., 2007). Utilization of distinct donors in hybridization for particular traits, developing the MAGIC population, and the selection of transgressive segregants would increase productivity further (Upadhyaya et al., 2007).

4.1 Genotypic variability for yield contributing parameters

In identification of donor lines for a specific character, the prerequisites are the availability of germplasm, genetic variability for specific traits, heritability, and stability over the locations/ seasons (Upadhyaya et al., 2007). In the present study, the genotypes were stable across the seasons for most of the traits including grain yield with lower F-ratios (statistic) than the F-critical value, and thus appropriate in the selection of donors (Table 1; Lule et al., 2012). In the combined analysis, the genotypes were stable for mean ear-head weight, and grain yield with no significant differences between the years. Hence, the genotypes have been utilized to identify superior donors over the popular variety, GPU-28 (Table 2; Suppl. Table 1). The existing wide genetic variability for other parameters was effective in selecting genotypes for specific superior traits. In particular, Acc. GE-4596 and GE-4683 had higher mean ear-head weight and cv. PES-110, PR-202, and RAU had higher ear-head numbers compared to cv. GPU-28. The popular variety, GPU-28, is a shy tillering variety with 2.5 tillers per hill with relatively a higher mean ear-head weight (Nanja Reddy et al., 2019). Hence, incorporating higher productive tillers of selected donors into the background of GPU-28 would increase finger millet productivity.

4.2 Contribution of specific traits to grain yield

Although genetic variability exists for yield-contributing traits and selection could be possible, the nature and extent of interrelationships between the characters will provide additional support in the selection of trait-specific donors (Akhtar et al., 2011). Pearson correlations revealed that the grain yield was positively and significantly correlated to both the dependent and independent traits. The correlations suggest that mean ear-head weight would be a better trait for yield improvement, as mean ear-head weight and ear-head number are strongly and negatively correlated (Table 3; Owere et al., 2015; Mujahid et al., 2020; Chaithra and Nanja Reddy, 2023). In addition, dividing the correlation influence of traits into direct and indirect effects by path analysis will be more meaningful in selecting yield-contributing characters and provides a better understanding of their association with grain yield (Dhavaleshvar et al., 2019). In the present study, among the independent traits, the mean ear-head weight followed by ear-head number showed a higher direct effect on grain yield with a lower residual effect (Table 4; Chaithra and Nanja Reddy, 2023). Furthermore, the mean ear-head weight, ear-head number, and threshing percentage collectively contributed to the grain yield by 86.7%, with a low residual value of 0.133 (Table 5; Nanja Reddy et al., 2021b), and hence, these traits are collectively appropriate for selecting the donors in finger millet, that can be used in development of MAGIC population.

4.3 Yield prediction by specific traits

The relationship between observed and predicted grain yield using MLR was statistically significant, suggesting that the model is appropriate. However, the grain yield of popular cultivars is already high over the germplasm accessions (Fig. 2). Therefore, direct selection for a given location or across locations directly for the grain yield is not advisable (Simion, 2020; Nanja Reddy et al., 2021b). Hence, trait-specific donor selection could be a better approach for improving the grain yield of finger millet, using the available genetic resources for independent traits such as mean ear-head weight, and productive tillers (Owere et al., 2015; Kandel et al., 2019). Furthermore, the theoretical model predicted a 29.5% and 17.8% increase in grain yield of cv. GPU-28 with incorporation of higher ear-head number, or mean ear-head weight of selected donors respectively (Table 7; Ojulong et al., 2017; Krishna et al., 2021; Nanja Reddy et al., 2021b; Nanja Reddy, 2023). The trait, higher productive tillers per plant could be better because the cv. GPU-28 has relatively a higher mean ear-head weight. However, both can be used in development of MAGIC population.

5. Conclusions

Finger millet improvement could be possible by improving the ear-head size, and productive tillers per hill of a popular cultivar. However, the incorporation of traits depends on the background of the variety that needs improvement. For instance, a genotype with a shy tillering should be improved for a higher productive tiller number, and a high tillering genotype for a large ear-head size. Furthermore, using the identified genetic resources for multiple traits a MAGIC population can be developed to achieve higher grain yield of finger millet.

Declarations

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Figures

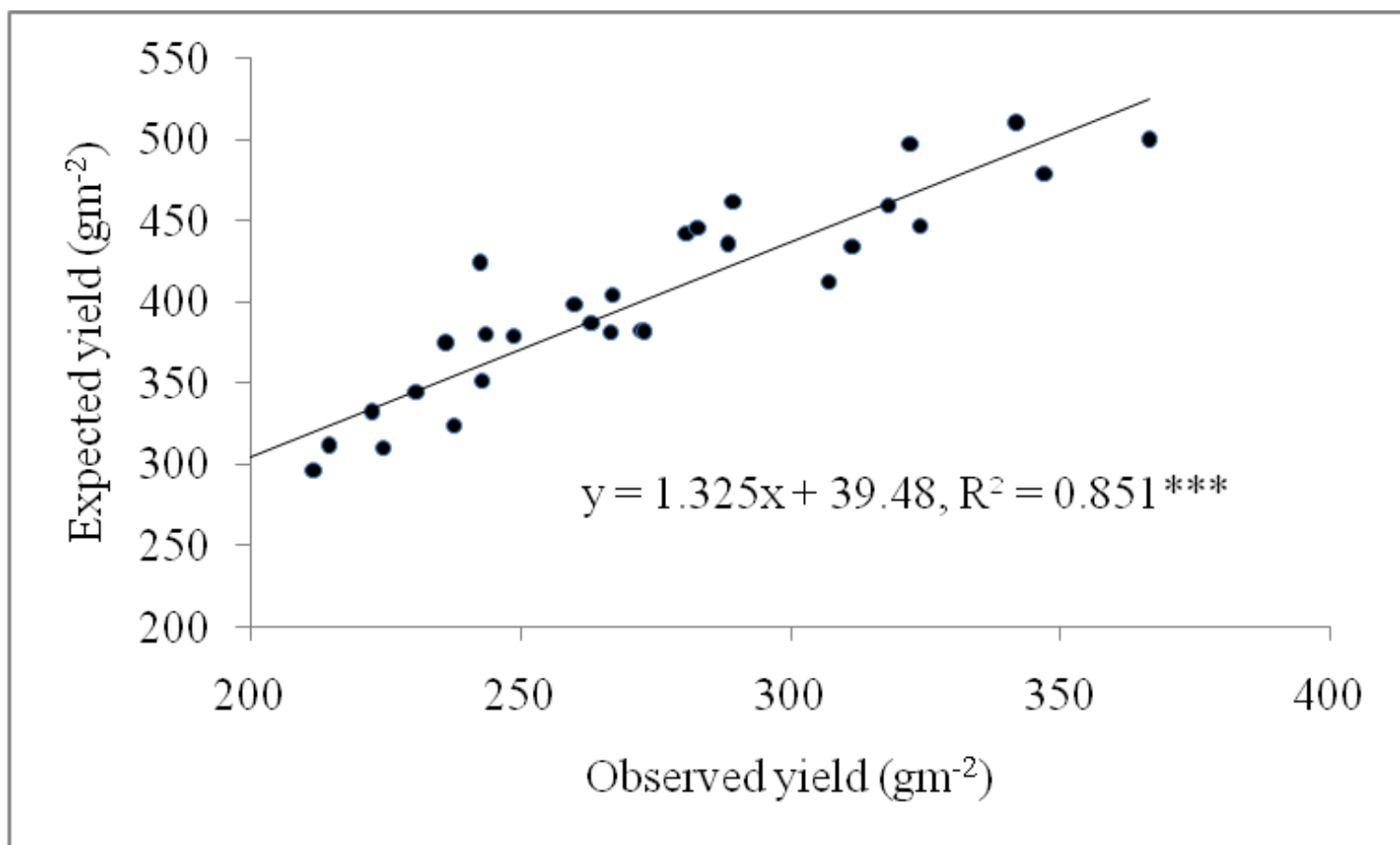


Figure 1

Relationship between observed and expected grain yield using three variables in regression model

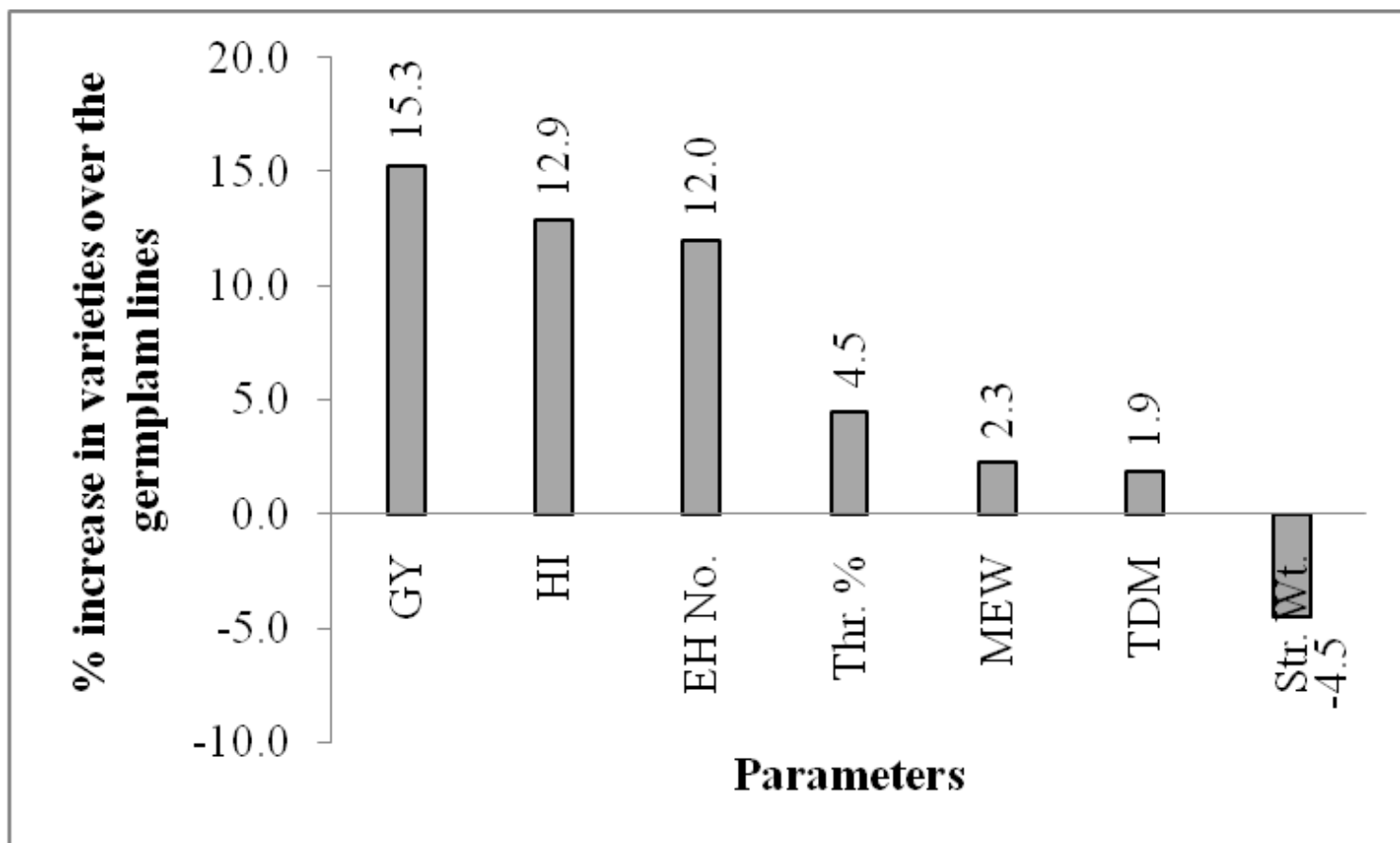


Figure 2

Performance of varieties over the germplasm accessions in finger millet in pooled data (varieties, 11 and germplasm, 19)