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Studies on Photosynthetic Rate, Anatomical Characters, and Grain Yield in Finger Millet Genotypes

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Author's contribution

The sole author designed, analysed, interpreted and prepared the manuscript.

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ABSTRACT

Finger millet (*Eleusine coracana* L. Gaertn.) yield improvement has been achieved through development of blast resistant varieties and adoption of appropriate management practices. However, yield improvement is approaching stagnation and further improvement could be possible by inclusion of physiological traits in addition to yield *per se*. In this direction, nine selected genotypes for high net assimilation were compared with popular Cv. GPU-28 for photosynthetic, anatomical, and yield contributing traits to identify a better genotype and physiological traits associated with grain yield. Results revealed that the photosynthetic rate did not differ significantly between genotypes, but influenced the grain yield through increased earhead size and harvest index. Path analysis showed a direct positive effect of photosynthetic rate, transpiration rate, mean earhead size and productive tillers towards grain yield. The photosynthetic rate was positively associated with leaf lamina thickness and vein frequency. Therefore, for finger millet yield improvement, traits like photosynthetic rate/ transpiration rate and mean earhead size with 3 to 4 tillers could be selected. Variety, GPU-28 which is widely cultivated had better photosynthetic traits and grain yield attributes, this variety can be used as important baseline check for both photosynthetic rate and grain yield in finger millet yield improvement programmes.

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1. INTRODUCTION

Finger millet is a C_4 crop [1,2] suitable for rainfed areas and; cultivated in arid and semi-arid regions of more than 25 countries, the prominent are India and Africa. Finger millet grain is nutritionally rich in protein (7.3%), carbohydrates (72.6%), calcium (352 mg/100g), iron (5.47 mg/100g), dietary fibre (18%), zinc, magnesium, potassium, with low glycemic index and anti-nutritional factors like phytic acid and tannins [3-11]. Ninety per cent of finger millet cultivation is confined to rainfed areas in India [12], with an area of 1.19 m ha and production of 2.0 million tones contributed mainly from the state of Karnataka by 58 % production [13,14]. Owing to its suitability to rainfed conditions and nutritional superiority, yield improvement over the years was achieved though development of blast resistant varieties with adoption of improved management practices. However, the yield improvement is approaching a plateau [15]. Therefore, to break the yield stagnation, additional inclusion of physiological traits could be appropriate than yield *per se* alone. In addition, selection of genotypes superior to Cv. GPU-28 (popular variety) from among the selected germplasm accessions, would have direct benefit to farming community. In this direction, yield improvement through enhanced partitioning of biomass to reproductive structures (harvest index) has been reported in major cereals like rice, wheat and maize [16]. Therefore, the objective of this study was to assess the physiological traits associated with grain yield and to identify accessions better over the popularly cultivated variety, GPU-28.

2. MATERIALS AND METHODS

2.1 Crop Management

Experiment was conducted at the field Unit, AICRP (Small Millets), Zonal Agricultural Research Station, University of Agricultural Sciences, GKVK, Bengaluru-65 during *kharif*, 2008. The location is situated at 12º58¹ North latitude and 77º35¹ East longitude at an altitude of 930 meter above the MSL and has red sandy loam soil. Ten selected genotypes (GE-1034, GE-1013, GE-4248, Indaf-9, GPU-28, GE-844, GE-4222, GE-619, GE-4999 and GE-3454) including the popular variety (GPU-28, Germ Plasm Unit) were sown directly in the field on 28th July 2008 and thinned to single plant per hill within 20 days after sowing (DAS). Experiment was planned in randomized block design with 10 genotypes in three replications. Each replication had 12 rows of 1.4 m length in the spacing of 30 cm between rows and 10 cm between plants. The gross plot size was 11.56m^2. Crop was raised under rainfed conditions with two protective irrigations (10 mm each) during 25 days of rain free period. The fertilizer dose was 50:40:25 kg ha^{-1} (N: P: K respectively) was applied. The entire dose of P and K; and half dose of nitrogen were applied at the time of sowing. The remaining N was supplied at 40 days after sowing. Two hand weedings were taken within 30 DAS.

2.2 Data Collection on Physiological Characters

At the time of flowering, physiological traits *viz.*, gas exchange parameters, specific leaf weight (SLW) and anatomical characters were measured. Gas exchange parameters *viz.*, stomatal conductance, transpiration rate and internal CO_2 concentration were measured using Infrared Gas Analyzer (IRGA) (LI 6400) at 11.00 AM on fully expanded 3rd leaf from the apex. Using these basic parameters, A/gs, A/Ci and Ci/gs were computed. The same leaf was used to measure SLW by taking leaf length x leaf width x 0.75 to arrive at leaf area; these leaves were oven dried to constant weight and; calculated the SLW by dividing the leaf dry weight (mg) with its leaf area in cm^2. For leaf vein frequency, middle portion of the leaf was cut into cross sections to thinnest possible (< 0.5 mm) and such sections were placed in potassium iodide solution for dyeing and then observed under microscope with 10 x magnification for vein number and interveinal distance measurements [17]. The leaf vein frequency was computed as total number of veins divided by the leaf width to arrive at number of veins / cm.

2.3 Data Collection on Yield Attributes

The yield attributes *viz.*, productive tillers, mean earhead weight and test weight were measured at the time of harvest. Grain yield and straw weight were recorded in net plot area of 3 x 3 (9 m^2). The productive tiller number, threshing ratio and other parameters were recorded in 1.0 meter row length of 10 plants.

2.4 Statistical Analysis

The data was statistically analyzed in RCBD using OPSTAT [18]. Pearson correlations were drawn between traits and the direct and indirect effects of each trait towards grain yield were also computed. Further, step wise regression was followed using MS excel for identifying the important traits contributing to photosynthetic rates or grain yield.

3. RESULTS AND DISCUSSION

Grain yield of finger millet is mainly determined by the above ground biomass accumulation and partitioning of biomass to reproductive parts [19-22]. The biomass production in turn depends on physiological processes, mainly the light interception by the crop canopy cover, and the photosynthetic rate and; the yield attributing traits [23,24].

3.1 Photosynthetic Traits

Photosynthetic rate is an important physiological process under rainfed conditions for biomass production and grain yield [25] and genotypic differences exists for photosynthetic rate [23-24]. In the present study, photosynthetic rate did not differ significantly between the genotypes (Table 1), as the genotypes evaluated were selected for high net assimilation rate (DM/LAD) from the previous experiments. The relationship between DM/LAD (previous experiment) and photosynthetic rate (present experiment) was significant and positive (r = 0.650*). Furthermore, finger millet being a C_4 species would maintain higher photosynthetic rate [1,2,26]. However, photosynthetic rate associated traits differed significantly between genotypes (Table 1) which is supported by earlier studies [23]. The stomatal conductance (g_s) differed significantly between genotypes, but no genotype was significantly superior to GPU-28 (0.239 m $m^{-2}s^{-1}$). With respect to transpiration rate, lower transpiration rates could be ideal for survival of crop under rainfed conditions but it reduces the crop productivity hence, the water use efficiency (A/g_s) could be a better trait, and was highest in Cv. GPU-28 (Table 1). Among the gas exchange parameters, GPU-28 recorded highest photosynthetic rate, mesophyll efficiency (C_i/g_s) and better stomatal conductance, internal CO_2 concentration, transpiration rate and carboxylation efficiency compared to other genotypes, therefore, GPU-28 is a photosynthetically efficient variety.

Correlations among the gas exchange parameters show that, photosynthetic rate is poorly related to stomatal conductance (r = 0.175^{NS}) and transpiration rate (r= 0.087^{NS}; Table 2) which is contradictory to a strong positive association reported earlier [23,27,28]. Poor relationship in the present study could be because; the genotypes are high net assimilation types. The stomatal conductance and transpiration rate are significantly and positively related each other (r = 0.955**; Table 2) and; similar relationships has been reported earlier [23,29]. Higher the stomatal conductance, higher is the water loss, which is not a desirable trait under rainfed situations, therefore, higher stomatal efficiency (A/g_s) could be apt. Furthermore, photosynthetic rate is positively and significantly related with carboxylation efficiency (A/C_i; r= -0.681**) and mesophyll efficiency (C_i/g_s; r = -0.640*) followed by SLW (r = 0.495^{NS}) suggests the importance of these traits in higher assimilate production. The mesophyll CO_2 concentration (C_i) was significantly related to stomatal efficiency (r = -0.793**) and carboxylation efficiency (r = -0.917**). Therefore, it suggests that RuBisCo activity could be preferred in addition to gas exchange rate as finger millet is a C_4 plant, which has CO_2 concentrating mechanism [30].

Furthermore, the path analysis (Table 3) shows that, transpiration rate (1.845) has a major direct effect on grain yield followed by photosynthetic rate directly (0.567). The stomatal conductance has indirect positive effect on grain yield through transpiration rate (1.763). These results suggest that transpiration dependent photosynthetic rate is an important physiological trait under protective rainfed conditions for achieving higher grain yield of finger millet.

3.2 Anatomical Features

Leaf anatomical features are important in determining the photosynthetic rate especially under rainfed situations. Higher the SLW, higher will be the mesophyll packing, high photosynthetic rate and WUE. The SLW had positive relationship with photosynthetic rate (r= 0.495^{NS}, Table 2). The photosynthates produced at source should be efficiently translocated to reproductive parts for higher yields. Hence, the vein number per unit leaf width is important to for translocation and a positive association between photosynthetic rate and vein number was observed (r= 0.341^{NS}; Table 2). Therefore, large number of veins is desirable for higher translocation of photosynthates from source to sink [31]. Amongst the genotypes, Cv. GPU-28 has relatively higher specific leaf weight (SLW) and highest vein number per unit leaf width (Table 1) as also evidenced by others [32]. This suggests that, GPU-28 has higher mesophyll area, with higher photosynthetic rate and translocation efficiency to result in higher grain yield. The path analyses show that, vein number has positive direct influence (0.131) on grain yield; while SLW had positive indirect influence through photosynthetic rate on grain yield (0.281).

3.3 Yield Attributes

Grain yield and yield attributing parameters differed significantly between the genotypes (Table 4). Grain yield was highest in Cv. GPU-28 (3.465 kg $9m^{-2}$) and on par with Cv. GE-1034 (3.183 kg $9m^{-2}$). Higher grain yield in GPU-28 was due to higher mean earhead weight (6.70 g), test weight (3.23 g/ 1000 seeds) as also observed by Gupta in 2011 [29] followed by higher harvest index (0.37) and threshing ratio (0.89). The productive tillers (30 per meter row length of 10 plants) and straw weight (6.543 kg $9m^{-2}$) were moderate in Cv. GPU-28. The productive tiller number varies with the genotype, for instance Co-15 has 8.5 tillers/ hill but has small earhead size of 2.83g [28]. Similar genotypic variations for ear size have been reported earlier [19, 20, 24].

Correlations (Table 5) show that the grain yield was significantly and positively associated with harvest index (r = 0.814**) and mean ear weight (r = 0.771**). Similarly, significant positive association between harvest index and mean ear weight with grain yield has been reported [33-34]. Poor relationship between number of productive tillers and yield was observed (r = 0.164^{NS}) implies the lesser influence of productive tillers on grain yield and; compensation between productive tiller number and mean earhead weight (r = -0.370^{NS}). In the present study average tiller number was 3.4 per hill, which could be optimum [35]. Several reports show a positive relationship between productive tiller number and grain yield [20, 28, 36]. The straw weight was negatively associated with mean earhead weight (r = 0.597*) suggests that optimum biomass may be advantageous for grain yield. Further, the harvest index and mean earhead weight are highly significant and positive (r = 0.786**) suggests the higher partitioning of assimilates to earhead. These results indicate that, with protective irrigation, under rainfed condition, mean earhead weight could be important to increase the grain yield further followed by tiller number by closer spacing 7.5 cm between plants [37].

Relationship between physiological traits and yield attributes are presented in Table 6. Photosynthetic rate has direct moderate influence on grain yield (r = 0.358^{NS}; Table 6).

Table 1. Genotypic variation in photosynthetic and anatomical traits in finger millet genotypes

Genotypes	A	g_s	C_i	T	A/g_s	Ci/g_s	A/C_i	SLW	IVD	VF
GE-1034	24.7	0.196	142.7	6.06	126.3	751.1	0.174	5.67	17.1	60.0
GE-1013	24.4	0.196	183.5	6.01	128.1	948.6	0.135	6.40	16.2	66.0
GE-4248	22.4	0.178	148.7	5.52	126.7	859.1	0.152	5.71	22.9	52.0
Indaf-9	26.1	0.214	150.8	6.18	122.6	710.3	0.174	6.50	18.7	51.3
GPU-28	26.1	0.239	164.7	7.04	109.9	689.5	0.160	6.15	21.7	68.0
GE-844	22.4	0.272	204.5	7.55	82.4	756.1	0.110	6.41	18.5	64.0
GE-4222	22.6	0.230	204.3	6.98	98.7	900.7	0.113	5.52	23.4	41.3
GE-619	24.1	0.191	151.5	5.36	125.7	798.8	0.160	6.85	24.2	53.7
GE-4999	20.2	0.193	185.3	6.09	104.0	989.2	0.110	5.60	21.0	52.7
GE-3454	22.1	0.183	137.8	5.58	120.9	758.1	0.162	5.97	20.9	58.7
Mean	**23.5**	**0.209**	**167.4**	**6.23**	**114.5**	**816.2**	**0.145**	**6.08**	**20.5**	**56.8**
SEm ±	NS	0.013	5.96	0.36	6.15	52.2	0.013	0.29	0.35	1.52
CD @ 5 %	NS	0.036	17.0	1.04	17.5	148.7	0.037	0.87	1.01	4.50
C.V. (%)	14.8	13.2	8.66	14.2	13.1	15.5	19.7	8.37	4.70	4.56

Note: A: Photosynthetic rate (u mol. $m^{-2}s^{-1}$), g_s: Stomatal conductance (mol. $m^{-2}s^{-1}$), Ci: Internal CO_2 concentration (ppm), T: Transpiration rate (m mol. $m^{-2}s^{-1}$), A/g_s: Water Use Efficiency, C_i/g_s: Mesophyll efficiency, A/C_i: Carboxylation efficiency, SLW: Specific leaf weight (mg.cm-2), IVD: Interveinal distance (u) and vein number per total leaf width. SEm±: Standard error of mean, CD: Critical difference and C.V.: Coefficient of variation

Table 2. Correlation between photosynthetic and anatomical traits in finger millet

Trait	A	g_s	C_i	T	A/g_s	Ci/g_s	A/C_i	SLW	IVD
g_s	0.175								
C_i	-0.341	**0.658**							
T	0.087	**0.955**	**0.729**						
A/g_s	0.398	**-0.822**	**-0.793**	**-0.843**					
Ci/g_s	**-0.640**	-0.346	0.473	-0.198	-0.036				
A/C_i	**0.681**	-0.420	**-0.917**	-0.510	**0.764**	**-0.658**			
SLW	0.495	0.187	-0.107	-0.074	0.049	-0.375	0.269		
IVD	-0.270	-0.134	-0.052	-0.176	-0.086	0.062	-0.080	-0.113	
VF	0.341	0.229	-0.090	0.190	0.038	-0.337	0.184	0.371	-0.554

Note: A: Photosynthetic rate (u mol. $m^{-2}s^{-1}$), g_s: Stomatal conductance (mol. $m^{-2}s^{-1}$), C_i: Internal CO_2 concentration (ppm), T: Transpiration rate (m mol. $m^{-2}s^{-1}$), A/g_s: Water Use Efficiency, C_i/g_s: Mesophyll efficiency, A/C_i: Carboxylation efficiency, SLW: Specific leaf weight (mg.cm-2), IVD: Interveinal distance (u), VF: Veinal frequency (number of veins per total leaf width) . Values in bold are significant at 5 % (0.632) and % (0.765) level

Table 3. Path co-efficient analysis among photosynthetic traits towards grain yield in finger millet

Trait	A	g_s	T	IVD	VF	SLW	"r"
Photosynthetic rate (A)	**0.567**	-0.261	0.161	0.016	0.046	-0.171	0.358
Stomatal conductance (gs)	0.099	**-1.498**	1.763	0.008	0.031	-0.065	0.339
Transpiration rate (T)	0.049	-1.431	**1.845**	0.010	0.026	0.025	0.526
Interveinal distance (IVD)	-0.153	0.201	-0.324	**-0.060**	-0.075	0.039	-0.372
Vein frequency (VF)	0.193	-0.343	0.351	0.033	**0.135**	-0.128	0.247
Specific leaf weight (SLW)	0.281	-0.280	-0.136	0.007	0.050	**-0.346**	-0.424

Residual: 0.13; r: Correlation coefficient

Table 4. Genotypic variations in yield and yield attributes in finger millet

Genotypes	Grain Yield (Kg $9m^{-2}$)	Straw yield (Kg $9m^{-2}$)	TDM (Kg $9m^{-2}$)	HI	Grain yield (qha^{-1})	1000 seed wt. (g)	PT / mrl	Th. ratio	MEW (g)
GE-1034	3.183	5.787	8.970	0.393	35.37	2.54	37.3	0.87	5.30
GE-1013	3.097	5.990	9.087	0.393	34.41	2.61	33.3	0.87	5.27
GE-4248	2.931	6.805	9.736	0.290	32.56	3.13	38.0	0.86	4.61
Indaf-9	2.678	5.533	8.211	0.383	29.75	2.77	31.7	0.93	6.07
GPU-28	3.465	6.543	10.008	0.370	38.50	3.23	30.0	0.89	6.70
GE-844	2.665	6.663	9.328	0.357	29.61	3.03	28.7	0.94	5.71
GE-4222	3.068	7.010	10.078	0.353	34.09	2.77	42.0	0.92	4.51
GE-619	1.591	7.173	8.765	0.227	17.68	3.10	37.0	0.90	2.80
GE-4999	2.436	7.187	9.623	0.337	27.07	2.35	37.3	0.88	4.46
GE-3454	2.028	8.237	10.264	0.237	22.53	2.93	24.7	0.87	4.25
Mean	**2.714**	**6.693**	**9.407**	**0.334**	**30.16**	**2.85**	**34.0**	**0.89**	**4.97**
SEm ±	0.125	0.484	NS	0.013	1.398	0.04	3.55	0.01	0.34
CD @ 5 %	0.360	1.399	NS	0.040	4.040	0.11	10.5	0.04	0.99
C.V. (%)	7.990	12.52	10.44	0.510	7.990	2.23	17.6	2.34	11.2

Note: TDM: Total dry matter at harvest, HI: Harvest index, PT/mrl: Productive tiller number per meter row length of 10 plants, Th ratio: Threshing ratio and MEW: Mean ear weight

Table 5. Correlation amongst yield attributes in finger millet

Trait	Grain yield	Straw yield	TDM	HI	1000 seed wt.	No. of PT	Threshing ratio
Straw yield	-0.582						
TDM	0.165	**0.706**					
HI	**0.814**	**-0.809**	-0.272				
1000 Seed wt.	-0.083	0.236	0.214	-0.429			
No. of Prod. tillers	0.164	-0.197	-0.096	0.117	-0.319		
Threshing ratio	-0.080	-0.201	-0.313	0.221	0.165	-0.079	
Mean earhead wt.	**0.771**	-0.597	-0.052	**0.786**	0.042	-0.370	0.227

Note: Values in bold are significant at 5 % (0.632) and % (0.765) level
TDM: Total dry matter, HI: Harvest index, No. of Prod. tillers: Number of productive tillers

Table 6. Pearson correlation coefficients between physiological traits and yield attributes in finger millet

Parameter	A	g_s	C_i	T	A/g_s	Ci/g_s	A/C_i	SLW	IVD	VF
Straw weight	**-0.667**	-0.212	-0.029	-0.218	-0.197	0.175	-0.256	-0.191	**0.611**	-0.188
Harvest index	0.392	0.450	0.400	0.583	-0.199	0.010	-0.139	-0.167	**-0.678**	0.239
Prod. Tillers	-0.167	-0.229	0.225	-0.128	0.085	0.550	-0.241	-0.411	0.339	**-0.651**
Mean earhead wt	0.505	0.560	0.152	**0.635**	-0.235	-0.419	0.093	-0.038	-0.542	0.484
Threshing Ratio	0.165	**0.785**	0.513	**0.655**	**-0.650**	-0.308	-0.300	0.383	0.032	-0.220
Test wt.	0.296	0.269	-0.196	0.105	-0.047	-0.574	0.263	0.400	0.493	0.196
Grain yield	0.358	0.339	0.260	0.526	-0.107	-0.034	-0.052	-0.424	-0.372	0.242

Note: A: Photosynthetic rate (u mol. $m^{-2}s^{-1}$), g_s: Stomatal conductance (mol. $m^{-2}s^{-1}$), C_i: Internal CO_2 concentration (ppm), T: Transpiration rate (m mol. $m^{-2}s^{-1}$), A/g_s : Water Use Efficiency, C_i/g_s: Mesophyll efficiency, A/C_i: Carboxylation efficiency, SLW: Specific leaf weight (mg.cm^{-2}), IVD: Interveinal distance (u) and vein number per total leaf width. Values in bold are significant at 5 % (0.632) and % (0.765) level

Table 7. Path co-efficient analyses amongst yield attributes towards grain yield in finger millet

Trait	Test Wt.	Prod. tillers	Mean earhead wt.	Thresh. ratio	Straw wt.	"r"
Test weight	**0.066**	-0.161	0.043	0.049	0.018	-0.083
Prod. Tillers	-0.021	**0.505**	-0.383	0.024	0.040	0.165
Mean earhead wt.	0.003	-0.187	**1.034**	-0.068	-0.010	**0.771****
Threshing ratio	0.011	-0.040	0.235	**-0.301**	0.016	-0.080
Straw weight	0.014	0.234	-0.121	-0.055	**0.086**	0.158

Residual: 0.088; r = Correlation coefficient

Similar moderate influence of photosynthetic rate on grain yield has been reported earlier [23, 29]. Photosynthetic rate also related positively with mean earhead weight (r = 0.505^{NS}), and harvest index (r = 0.392^{NS}; Table 6); implying that photosynthates were translocated to earhead. However, the photosynthetic rate is not a major limitation under optimal condition; rather it is sink associated traits like earhead size [38-39]. Transpiration rate showed a direct relationship with grain yield (r = 0.526^{NS}), threshing ratio (r = 0.655*) and mean ear weight (r = 0.635*) implies that higher transpiration rate increases the photosynthetic rate thus higher translocation, larger earhead and grain yield. This is supported by positive significant relationship between vein number and mean ear weight (r = 0.484^{NS}), which helps in higher translocation to ear and thus grain yield. Negative relationship between SLW and grain yield (r -0.424^{NS}) implies that during *kharif* season, when protective irrigation is provided, large leaf lamina area could be preferred than thicker leaf. Path analysis among independent yield attributing traits (Table 7) clearly depicts that mean earhead weight (1.034) has major direct positive influence on grain yield followed by productive tiller number (0.505) and; emphasize that, mean earhead weight is more important followed by productive tillers in determining the grain yield of finger millet under protective rainfed conditions. Hence, the mean earhead may be considered in selection process with a mean productive tiller of 3-4 per hill.

4. CONCLUSION

Overall, under rainfed conditions with 2 to 3 protective irrigations, stomatal limitation is not a major constraint in finger millet as it is a C_4 plant. The mean earhead weight is an important determinant of grain yield. The Cv. GPU-28 has better photosynthetic traits and grain yield and be used as a check variety while screening germplasm for grain yield or photosynthetic traits.

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COMPETING INTERESTS

Author has declared that no competing interests exist.

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