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Approaches for enhancing grain yield of finger millet (*Eleusine coracana*)

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Abstract

Finger millet is gaining importance as a food crop with the increasing emphasis on nutritional aspects and drought resilience. However, yield improvement has stagnated. Therefore, popular varieties have been examined for the purpose of whether direct selection for grain yield can be continued or an alternate trait-based approach using the germplasm is necessary. Direct selection for grain yield over the ruling variety, cv. GPU-28 (Germplasm Unit) has not been satisfactory. The path analysis has revealed a high direct effect of mean ear weight on grain yield followed by a moderate direct effect of photosynthetic rate and leaf area index. Furthermore, backward stepwise regression analysis revealed that among the independent traits, the mean ear weight made a significant contribution (60.8%) towards grain yield, followed by the photosynthetic rate (39.2%). The regression equation predicts the inclusion of mean ear weight by 1.0 g extra (as in GE-2672) to cv. GPU-28 will increase grain yield by 4.74%. The trait-specific genotypes are superior to the cv. GPU-28 were GPU-67 (photosynthetic rate) and GE-2672 (mean ear weight) and they could be used as donors for yield improvement. Future selection would aim for genotypes having 70–75 days for flowering with 4−5 productive tillers and mean ear weight of more than 8−9 g/ear. The possible approaches for enhancing grain yield are also discussed.

Keywords: biomass, LAI, mean ear weight, photosynthetic rate, yield prediction

Introduction

Millets are widely cultivated in arid and semi-arid regions of the world as a source of food and fodder (Dwivedi *et al*., 2012). Finger millet is a C_4 species (Ueno *et al*., 2006) that has both drought resilience features as well as nutritional importance. The grain has a high concentration of mineral nutrients and fibre with minimum anti-nutritional factors like phytic acid and tannins. Moreover, finger millet has better health benefits compared to major cereals (Wondimu, 2001; Devi *et al*., 2014; Chandra *et al*., 2016; Kumar *et al*., 2016; Netravati *et al*., 2018). About 3.5 billion people in the world are at risk of calcium deficiency (Kumssa *et al*., 2015) and finger millet could be a better option to provide nutritional security in developing countries in Asia and Africa (Puranik *et al*., 2017). Finger millet also serves as the best cattle feed (Baath *et al*., 2018) because of its superior quality with 61% digestible nutrients (NRC, 1996).

Globally, the finger millet occupies the fourth place after sorghum, pearl millet and foxtail millet in terms of importance (Dida *et al*., 2007). The total millet area and production in the world is 33.49 million hectares with 31.74 million tonnes, respectively. In India, it is 9.22 million hectares with 11.63 million tonnes during 2018 (http://fao.org). Finger millet accounts for 8 to 12% of the area and 11% production of the food grains in the world (Bennetzen *et al*., 2003; http://exploreit.icrisat.org/profile/smallmillets/187). In India, finger millet is grown in 1.19 million hectares with a production of 2.0 million tonnes (Sakamma *et al*., 2018), and in East Africa (Uganda, Tanzania, Kenya) it is ∼0.7 million hectares (Mgonja *et al*., 2007).

Finger millet productivity has been increased over the years, by breeding and selection based on yield *per se*. In finger millet yields are reported higher (1661 kg/ha) than

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major millets like sorghum (998 kg/ha) and pearl millet (1237 kg/ha) (Sakamma *et al.*, 2018; http://www.indiaagristat.com). In India, more than 140 varieties were released and cv. GPU-28 is considered one of the popular varieties (Krishne Gowda *et al.*, 2009; Swetha, 2011; Gowda *et al.*, 2014). However, worldwide, the average farm yield is 400–800 kg/ha (Uganda, Tenywa *et al.*, 1999), 1661 kg/ha (India, Sakamma *et al.*, 2018) and 2260 kg/ha (Ethiopia, Degu *et al.*, 2009). The yield improvement has reached a plateau (Swetha, 2011). Recent reports show that the farm yield potential of finger millet is >3000 kg/ha (Mgonja *et al.*, 2007; Sakamma *et al.*, 2018). This could be possible by the selection of germplasm lines for specific traits contributing to grain yield (Ojo *et al.*, 2006; Upadhyaya *et al.*, 2007, Bharathi *et al.*, 2013; Patil, 2016). The yield improvement in cereals can be achieved through enhanced partitioning of biomass to grain (Wilson *et al.*, 2008; Fischer and Edmeades, 2010; Swetha, 2011). Therefore, the genotypes were evaluated for morpho-physiological traits and yield attributes and proposed possible approaches to enhance the grain yield of finger millet.

Material and methods

Experimental site

The field experiment was conducted at the field unit, AICRP on Small Millets, Zonal Agricultural Research Station, University of Agricultural Sciences, GKVK, Bengaluru, India situated at 12°58´N latitude and 77°35´E longitude at an altitude of 930 m above the mean sea level (MSL).

Crop management

Thirty-one genotypes including popular varieties were evaluated in completely randomized block design with three replications. Each replication had an area of 3.1 m row length × 0.9 m width (three rows). The crop was sown directly on 17 August 2009, with a spacing of 30 cm between rows and 10 cm between plants. Thinning was performed twice within 15 days after sowing (DAS) to maintain one seedling per hill. The recommended dose of 50:40:25 nitrogen, phosphorus and potassium (NPK) (kg/ha) fertilizer was applied in a split dose. Half of the recommended dose of nitrogen (N) and a full dose of P and K were given as basal dose at the time of sowing. The remaining 50% N was provided as top dressing at 40 DAS. Manual weeding was undertaken twice within 30 DAS. The crop was raised as a rainfed crop in the monsoon season. Besides, three protective irrigations (10 mm each) were provided during rain-free period. (from 03 October 2009 to 28 October 2009, coincided with ear emergence).

Collection of data

At the time of flowering, five plants (0.5 m row length) were harvested to measure the leaf area and biomass. From these plants, sample leaf area was measured by length × width × 0.75 (factor for leaf shape) in randomly selected 10 leaves and their dry weight was measured to arrive at a specific leaf area (SLA). SLA was computed by dividing the leaf area with its leaf dry weight (cm^2/mg). Total leaf area was calculated by multiplying the total leaf dry weight of five plants with SLA. The leaf area index (LAI) was computed by dividing the leaf area of five plants by spacing for five plants. Leaf anatomical characters were recorded in the leaf next to the flag leaf. Thin transverse sections were stained with potassium – iodide solution and observations on leaf thickness, leaf width and leaf vein frequency (LVF) were made under 10 × (1 ocular unit = 9.01 um) (Nanja Reddy *et al.*, 1996). During the same period, gas exchange parameters were measured using IRGA (LI 6400) at 11.00 AM. At the time of harvest, yield and yield attributes were recorded.

Data analysis

The data were statistically analysed for analysis of variance (ANOVA) in randomised completely block design (RCBD) using OPSTAT (Sheoran *et al.*, 1998). Furthermore, correlation and path analysis were followed to measure the relationship between traits and their contribution respectively to grain yield. Furthermore, using Microsoft Excel Toolpak, stepwise multiple linear regressions (MLRs) (stepwise backward regression) were followed to identify significant traits associated with grain yield. In stepwise regression, non-significant parameters were eliminated one by one to obtain the significant traits contributing to grain yield. For such contributing traits, the data were transformed to unity, MLR was followed and the contribution of each trait was computed by dividing the regression co-efficient of each trait by the sum of the regression coefficients.

Results

Selection of genotypes for grain yield

The genotypes showed significant variations for physiological, anatomical and yield parameters (Table 1). None of the genotypes was significantly superior to the cv. GPU-28 for grain yield (351 g/m^2). The grain yield was in the range of 359 to 392 g/m^2 in GPU-66, GPU-67, GE-1013, GE-1034 and GE-1293 (Table 1). The mean grain yield of nine cultivated varieties (321.2 g/m^2) was significantly superior over the mean yield of 22 germplasm accessions (275.1 g/m^2; Table 2).

Table 1. Genotypic variation in physiological, anatomical and yield attributes in finger millet

Variety	DFF	LAI	A	LT	DMF	PDM	Ped. Len.	LVF	FL	PT	MEW	Th.	TEW	DMH	HI	GY
GPU-26	66	1.88	14.3	263	529.3	275.7	19.2	58.2	5.95	2.3	5.03	0.68	400	805	0.33	270
GPU-28	73	2.39	17.4	284	495.3	420.7	22.0	50.5	7.17	2.1	7.79	0.78	450	916	0.38	351
GPU-45	60	2.61	17.2	286	477.3	391.7	22.5	49.4	5.4	2.1	6.41	0.68	421	869	0.33	285
GPU-48	66	2.55	13.1	299	574.7	162.3	20.0	54.3	6.08	1.9	6.61	0.71	400	737	0.38	283
GPU-66	74	2.95	23.5	223	642.7	275.3	23.2	56.6	7.33	2.1	6.51	0.78	505	918	0.43	392
GPU-67	75	3.22	26.4	315	545.3	327.7	13.5	53.5	5.44	2.7	6.15	0.82	468	873	0.44	383
PR-202	74	2.68	24.4	284	413.3	293.7	17.0	52.2	5.23	3.8	5.43	0.81	322	707	0.37	260
MR-6	79	2.86	17.2	223	740.0	272.0	21.3	54.5	8.51	2.0	7.79	0.76	425	1012	0.32	322
L-5	76	2.64	17.4	248	631.3	368.7	17.4	61.3	6.86	2.4	8.02	0.71	488	1000	0.35	345
GE-113	67	2.60	20.7	290	526.7	22.3	18.8	62.6	6.82	2.2	5.74	0.79	220	549	0.32	175
GE-449	81	3.74	18.9	212	831.3	214.7	21.8	56.7	7.2	1.8	7.52	0.78	370	1046	0.28	290
GE-619	79	2.21	23.5	194	539.3	352.7	23.8	55.4	6.2	3.3	3.49	0.72	313	892	0.25	226
GE-714	68	2.57	24.7	243	532.0	93.0	19.0	61.0	5.18	2.5	4.33	0.81	296	625	0.38	240
GE-996	76	2.96	23.2	173	699.3	295.7	22.3	73.8	7.01	1.9	4.44	0.82	353	995	0.29	291
GE-1013	74	2.72	21.0	270	620.0	282.0	21.0	53.4	7.9	2.0	7.85	0.79	474	902	0.42	376
GE-1033	74	2.18	15.9	214	528.7	225.3	22.9	63.3	7.54	2.3	5.17	0.75	371	754	0.37	278
GE-1034	68	1.82	22.2	272	551.3	322.7	19.6	54.1	7.23	2.3	9.46	0.84	444	874	0.43	372
GE-1293	73	3.16	18.3	187	772.7	349.3	20.5	67.3	6.81	2.0	5.80	0.77	468	1122	0.32	359
GE-1453	66	2.88	21.2	236	621.3	248.7	21.0	61.0	6.59	2.4	5.18	0.74	418	870	0.36	311
GE-1687	73	3.68	8.5	221	739.3	277.7	22.3	69.0	7.52	2.0	6.68	0.74	400	1017	0.29	297
GE-2672	79	3.34	11.8	252	859.3	1.7	18.7	57.0	8.26	2.0	8.99	0.84	330	861	0.32	277
GE-2858	79	2.88	9.3	221	650.7	296.3	21.1	63.0	6.26	1.9	6.60	0.82	285	947	0.25	234
GE-3069	79	3.63	13.0	198	966.7	13.3	19.4	60.4	7.65	2.3	6.74	0.72	345	980	0.25	247
GE-3434	81	2.99	18.6	227	613.3	175.7	16.8	63.8	7.02	2.7	6.77	0.58	362	789	0.27	209
GE-3457	79	3.26	8.8	209	601.3	390.7	20.0	58.5	5.71	2.5	5.84	0.68	395	992	0.27	268
GE-4149	81	3.15	22.6	286	840.7	126.3	18.0	56.9	5.83	2.0	6.17	0.77	343	967	0.28	266
GE-4732	73	2.96	14.5	293	640.7	171.3	18.9	53.2	5.15	1.8	7.53	0.79	302	812	0.29	238
GE-4777	73	2.28	15.3	268	652.0	170.0	14.0	50.2	6.85	1.9	7.49	0.71	377	822	0.33	269
GE-4999	93	2.21	7.1	221	580.0	301.0	20.9	59.0	5.48	3.5	4.57	0.73	271	881	0.23	199
GE-5192	76	1.46	17.5	200	457.3	388.7	18.4	57.6	7.41	1.5	8.42	0.88	367	846	0.38	322
GE-5252	74	1.85	18.2	236	496.7	400.3	21.7	55.8	8.35	1.6	8.83	0.86	359	897	0.35	308
Mean	75	2.72	17.6	243	624.4	255.1	19.9	58.2	6.71	2.3	6.56	0.76	379	880	0.33	288
SEm ±		0.15	0.26	4.8	41.2	14.7	0.56	1.2	0.16	0.2	0.86	0.01	22.9	50.7	0.01	16
CD 5 @		0.42	0.73	14.0	120.0	43.0	1.6	3.4	0.71	0.5	2.43	0.04	65.0	143	0.03	44
CV (%)		9.63	2.56	11.0	11.7	12.1	6.4	4.2	6.4	12	12.6	3.11	10.5	10.0	5.7	9.3

DFF: Days to 50% flowering, LAI: leaf area index, A: Photosynthetic rate (μMol/m^2/s^1), LT: Leaf thickness (um), DMF: Biomass at flowering (g/m^2), PDM: Post-anthesis biomass (g/m^2), Ped. Length: Peduncle length (cm), LVF: Leaf vein frequency (No. cm^{-1} leaf width), FL: Finger length (cm), PT: Productive tillers/hill, MEW: Mean earhead weight (g/ear), Th: Threshing ratio, TEW: Total ear weight/unit land area (g/m^2), DMH: Total dry matter at harvest (g/m^2); HI: Harvest index, GY: Grain yield (g/m^2).

Table 2. Differences in grain yield in response to varieties/selected germplasm, duration, total ear weight and threshing ratio in finger millet

Genotype/ Classification	Respective units	Number of genotypes	Grain yield (g/m^2)
Varieties/ Accessions (Days)			
(a) Varieties	71	9	321.2^b
(b) Accessions	76	22	275.1^a
Duration group (Days)			
(a) Short duration	66	7	276.5$^{a, b}$
(b) Medium duration	74	11	319.2^b
(c) Long duration	80	13	268.9^a
Total ear weight (g/m^2)			
(a)	268.0^a	4	212.0^a
(b)	359.4^b	17	270.5^b
(c)	456.1^c	10	349.6^c
Threshing ratio			
(a)	0.66^a	4	258.0^a
(b)	0.73^b	9	272.8^a
(c)	0.78^c	9	307.7^b
(d)	0.82^c	7	293.9^b
(e)	0.87^d	2	315.0^b

Note: Different superscript letters indicates the significant difference

Selection of specific trait: possible approaches to enhance grain yield

Primary traits

Primarily, the grain yield can be calculated as the product of the crop duration × ear weight/unit land area × threshing ratio (Fig. 1).

Crop duration: Medium duration genotypes (74 days to 50% flowering, DFF) gave higher grain yield (319.2 g/m^2) as compared to short duration (66 DFF; 276.5 g/m^2) and long duration (80 DFF; 268.9 g/m^2) genotypes (Table 2). This was confirmed through a negative correlation between DFF and grain yield ($r = -0.223^{ns}$; online Supplementary Table S1) with a negligible direct effect of DFF on grain yield (0.02; online Supplementary Table S2). Six out of 9 released varieties were of medium duration (Table 1).

Ear weight per unit land area: Grain yield is the product of total ear weight (TEW) per unit land area and its threshing ratio (Fig. 1). The mean TEW of nine cultivated varieties was significantly high (431.0 g/m^2) as compared to the mean of 22 accessions (357.4 g/m^2 (Table 1). With an increase in TEW significant increase in yield was observed (Table 2). The TEW had a significant positive correlation to grain yield ($r = 0.903^{**}$; online Supplementary Table S1) and influenced the grain yield with a high direct positive effect (0.70) and lower indirect positive effect through biomass at harvest (0.10) and harvest index (0.14) (online Supplementary Table S2).

Threshing ratio: Genotypes differed significantly in threshing ratio with a large genotypic variation from 0.68 to 0.88. Genotypes, GPU-67, GE-1034, GE-5192 and GE-5252 had a significantly higher threshing ratio of 0.85 as compared to GPU-28 (0.78) but the grain yields were similar (Table 1). Furthermore, the threshing ratio of nine cultivated varieties (0.75) and 22 germplasm accessions (0.77) were similar, but cultivated varieties had higher grain yield as compared to germplasm accessions (Table 1). A higher threshing ratio above 0.78 did not show higher grain yield (Table 2) although the threshing ratio was positively correlated to grain yield ($r = 0.325^{ns}$; online Supplementary Table S1) and the threshing ratio influenced the grain yield with a high direct positive effect (0.31) (online Supplementary Table S2).

Contribution of primary traits towards grain yield: Considering the crop duration, threshing ratio and TEW towards grain yield, the MLR, showed an equal contribution by TEW (49.1%) and threshing ratio (48.3%) with the least contribution (2.6%) by days to flowering (Table 3). Applying MLR equation to GPU-28, the contribution towards yield was 2.2% by DFF, 44.8% by threshing ratio and 53.0% by TEW (Table 3). An increase in threshing ratio from 0.78 to 0.82 in GPU-28 estimated to increase the grain yield by 4.1%, while an increase in total ear weight from 450 to 500 g/m^2 would increase the grain yield by 11.1% with an unaltered contribution by DFF and an increase in both these parameters would increase the yield by 15.4% (Table 3).

Secondary independent traits

Mean ear weight: Total ear weight (TEW) is the product of independent traits namely, mean ear weight (MEW) and the number of productive tillers (PTs) (Fig. 1). None of the genotypes was significantly superior to GPU-28 (7.79 g/ear) in ear weight. However, accessions GE-1034, GE-2672 and GE-5252 had 1.0 g higher mean ear weight than cv. GPU-28 (Table 1). The mean ear weight had a positive correlation to total ear weight ($r = 0.328^{ns}$) but negatively with PT number ($r = -0.559^{**}$; online Supplementary Table S1). The mean ear weight was significantly and positively correlated with the finger length ($r = 0.564^{**}$). The mean ear weight <6.52 g decreased grain yield significantly (Table 4).

PT number: Five genotypes were significantly superior to GPU-28 with more than 2.6 tillers per plant. But all these genotypes except GPU-67 had lower grain yield as compared to GPU-28 (Table 1). PTs had no significant correlation with total ear weight ($r = -0.213^{ns}$) and grain yield

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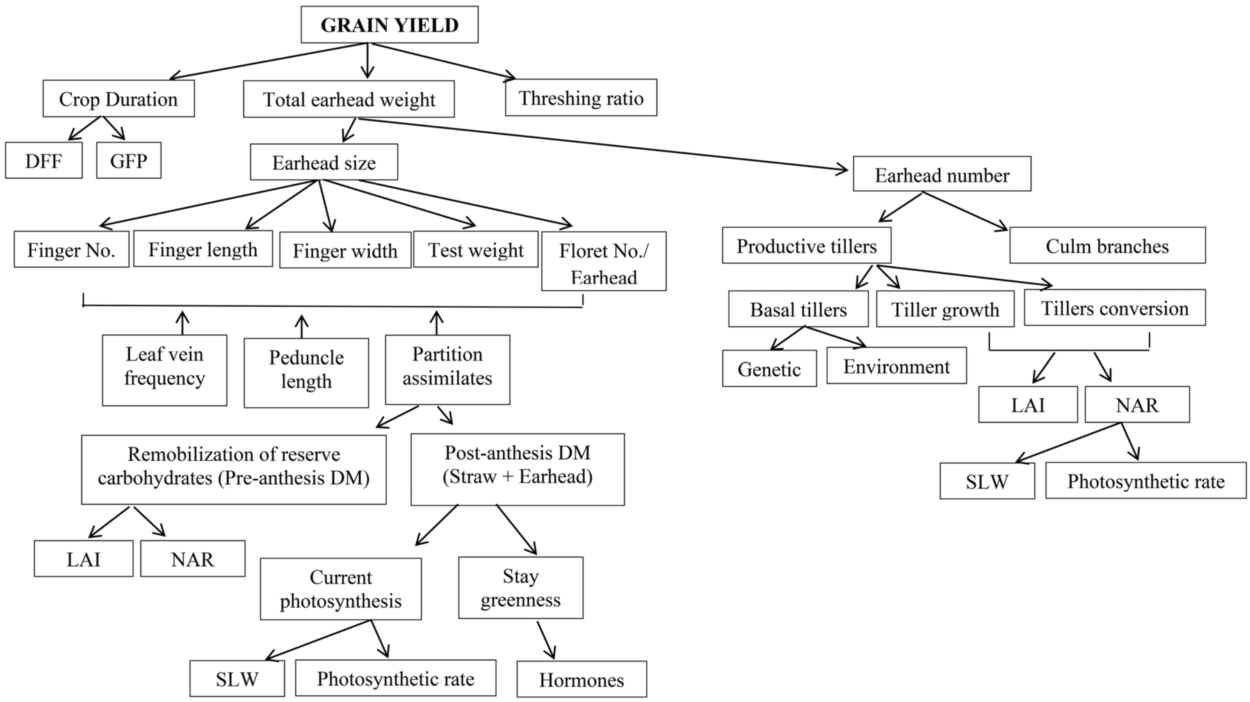

Fig. 1. Approaches to enhance grain yield in finger millet (DFF: Days to 50% flowering, GFP: Grain filling period, LAI: Leaf area index, NAR: Net assimilation rate, SLW: Specific leaf weight)

Table 3. Possible contribution (%) of primary yield contributing parameters on grain yield in finger millet

Traits (values for GPU-28)	For all genotypes	For GPU-28	With higher threshing (0.82)	With higher TEW (500 g/m^2)	Threshing ratio + TEW
DFF (73 d)	2.6	2.2	2.2	2.2	2.1
Threshing ratio (0.78)	48.3	44.8	46.0	42.2	43.5
TEW (450 g/m^2)	49.1	53.0	51.8	55.6	54.4
Total	100.0	100.0	100.0	100.0	100.0
Actual grain yield	288.0	351.0	351.0	351.0	351.0
Computed GY with MLR	286.0	349.7	364.8	388.5	403.6
% increase in GY	–	–	4.1	11.1	15.4
$Y = -308.7 + 0.21$ DFF + 377.8 Th. ratio + 0.77 TEW, MLR = 0.999***					

($r = -0.312^{ns}$; online Supplementary Table S1). An increase in PT per plant to 3.53 decreased the grain yield significantly (Table 4).

Contribution of secondary traits towards grain yield: The mean ear weight had a high direct positive effect (0.385) on grain yield. Furthermore, MLR between MEW and PT towards grain yield ($y = 216.5 + (-10.42$ PT) + 14.56 MEW, MLR = 0.446*), the mean ear weight showed a positive effect on total ear weight (78.8%), but PTs showed a negative effect (22.2%) (data not shown).

Physiological traits

LAI, photosynthetic rate and leaf anatomical traits: The mean ear weight and PTs are dependent on basic physiological components namely, the LAI, photosynthetic rate and translocation of photosynthates to sinks. Fifteen genotypes had significantly higher LAI over the GPU-28 (2.39, LAI), but not the corresponding grain yield (Table 1). An increase in LAI > 1.75 did not increase the grain yield significantly. The genotypes with LAI of < 1.75 were relatively monoculm and had a higher grain yield of

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Table 4. Differences in grain yield in response to varieties/selected germplasm, duration, total ear weight and threshing ratio in finger millet

Genotype/ Classification	Respective units	Number of genotypes	Grain yield (g/m^2)
Mean ear weight (g/head)			
(a)	4.21	4	239.0[a]
(b)	5.46	7	274.4[a,b]
(c)	6.52	9	288.4[b,c]
(d)	7.66	6	307.7[c]
(e)	8.74	5	324.8[c]
Productive tillers (Number/hill)			
(a)	1.88	14	295.1[a]
(b)	2.35	14	294.7[a]
(c)	3.53	3	228.3[b]
LAI			
(a)	1.75	4	318.0[a]
(b)	2.64	19	278.1[a]
(c)	3.40	8	298.4[a]
Photosynthetic rate (uM $m^{-2}s^{-1}$)			
(a)	8.4	4	249.5[a]
(b)	16.2	16	286.8[b]
(c)	23.2	11	292.7[b]
Leaf thickness (uM)			
(a)	188.0	4	280.8[a]
(b)	223.9	13	286.8[a]
(c)	281.7	14	292.7[a]
Leaf vein frequency (No. cm^{-1})			
(a)	54.9	20	297.9[a]
(b)	64.2	11	271.5[a]

Note: Different superscript letters indicates the significant difference

318.0 g/m^2 (Table 4). LAI had a positive correlation with pre-anthesis biomass production ($r = 0.732^{***}$; online Supplementary Table S1) but not with the grain yield. The photosynthetic rate was significantly higher in 15 genotypes over the GPU-28 (17.4 µMol/m^2/s) and has a positive correlation towards grain yield ($r = 0.330^{ns}$) and harvest index ($r = 0.533^{**}$; online Supplementary Table S1). The photosynthetic rate showed an indirect lower positive effect on grain yield through TEW (0.14) and harvest index (0.13) (online Supplementary Table S2). The leaf thickness had a negative correlation with the dry matter at harvest ($r = -0.496^{**}$) but positive with HI ($r = 0.454^{*}$). An increase in leaf thickness did not influence grain yield (Table 4). The anatomical parameter, LVF had a significant negative correlation with MEW (r= −0.368*) and HI ($r = -0.356^{*}$).

Among the traits associated with the grain yield, independent traits contributing significantly towards grain yield were identified based on backward stepwise regression ($y = 52.1 + 1.65$ photosynthetic rate + 5.81 mean ear weight, MLR = 0.60**) (data not shown).

Selection of genotypes for specific traits

Genotypes superior over the cv. GPU-28 for selected traits contributing to grain yield are presented in Table 5. Genotype, GPU-67 was superior for photosynthetic rate (26.4 µM/m^2/s) and GE-2672 for MEW (8.99 g).

Discussion

Finger millet yield improvement was achieved by targeting the grain yield directly. Of the 140 varieties that have been released so far (Gowda *et al.*, 2014), cv. GPU-28 is considered as a stable, blast-resistant popular variety cultivated in >60% of finger millet area in India (Krishne Gowda *et al.*, 2009). In this study, none of the genotypes was significantly superior to cv. GPU-28 for yield attribute. It appears that direct selection of the genotype, based on the higher grain yield would be difficult. Hence, it could be apt to select genotypes for specific traits contributing to grain yield. In this direction, yield improvement of cereals through enhanced harvest index has been reported (Wilson *et al.*, 2008; Fischer and Edmeades, 2010; Swetha, 2011). Selection/improvement of varieties better than cv.GPU-28 would be highly useful at the farm level, for which existing genetic diversity for yield attributing traits can be exploited (Upadhyaya *et al.*, 2007; Bharathi *et al.*, 2013; Patil, 2016).

The primary traits associated with the grain yield of finger millet are, the crop duration × ear weight/ unit land area × threshing ratio (Fig. 1). One of the primary characteristics of a genotype is the crop duration. Crop duration in finger millet is mainly determined by the days to flowering (DFF) with relatively unaltered post-anthesis period (Udaya Kumar *et al.*, 1986). It has a positive correlation to grain yield (Owere *et al.*, 2015; Kandel *et al.*, 2019). However, in the present study and way back in 1969 a non-significant negative correlation between duration and grain yield are reported (Chaudhari and Acharya, 1969; Ashok *et al.*, 2016). Furthermore, long-duration varieties will be caught up with end season stress and prone to lodging. Therefore, finger millet genotypes selection could be aimed at medium-duration with 70–75 DFF and 110–115 days to maturity.

The threshing ratio is the ratio of grain to the ear weight. The threshing ratio is generally very low in the case of wild races (18.1%) as against 79.6% in cultivated genotypes (Anon, 2015; online Supplementary Fig. S1). Among cultivated varieties, genetic variability for the threshing ratio is

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Table 5. Trait specific superior genotypes compared to Cv. GPU-28 in finger millet

Trait	GPU-28	SD of all genotypes	Trait value (GPU-28 + SD)	Genotypes with > trait value
MEW	7.79	1.47 (1SD)	9.26	GE-2672, GE-1034
DMF	495.3	129.8 (2SD)	754.9	GE-1293, GE-449, GE-4149, GE-2672, GE-3069
PDM	420.7	536.9 (1SD)	NS	–
A	17.4	5.2 (1SD)	22.6	GE-996, GPU-66, GE-619, PR-202, GE-714, GPU-67
LAI	2.39	1.12 (2SD)	3.51	GE-2672, GE-3069, GE-1687, GE-449
PT	2.1	1.04 (2SD)	3.14	GE-619, GE-4999, PR-202
GY	351	55.7 (1SD)	406.7	GPU-67

Note: MEW: Mean ear weight (g/ear), DMF: Dry matter at flowering (g/m^2), PDM: post-anthesis biomass ((g/m^2), A: Photosynthetic rate ($\mu M\ m^2/s^1$), LAI: Leaf area index, PT: Productive tillers per hill, GY: Grain yield (g/m^2), SD: Std. Deviation.

narrow (0.74 to 0.79) but reports elicit a positive relationship with grain yield (Prasanna Kumar and Naveen Kumar, 2012; Kumari *et al.*, 2018; online Supplementary Table S1). In the present study, threshing ratio did not differ between cultivated varieties and germplasm accessions and; genotypes with a higher threshing ratio > 0.78 (GPU-28) did not produce higher grain yield. Furthermore, genotypes with a higher threshing ratio would be vulnerable to shattering and bird damage (naked types; online Supplementary Fig. S1). Therefore, the optimum threshing ratio could be nearly 0.80 to 0.85 in the selection process. The MLR and path analysis for these three parameters towards grain yield also showed that the total ear weight (TEW) is a better trait than the threshing ratio and DFF (Table 3).

The total ear weight in turn is the product of ear number and mean ear weight (Fig. 1). Of these, mean ear weight (MEW) was prominent with a positive correlation ($r = 0.439^*$; online Supplementary Table S1) and a moderate indirect effect on grain yield through total ear weight (online Supplementary Table S2; Lenka and Mishra, 1973). Mean ear weight was the major selection criterion for higher finger millet yield during the 1970s, when tiller number per plant was not a limitation (Krishnamurthy, 1971). Farmer participatory trials also showed that farmers choose large ear size for higher grain yield (Ojulong *et al.*, 2017). In the present study, none of the genotypes possess significantly higher mean ear weight as compared to cv. GPU-28 (7.79 g/ear), implying that GPU-28 has a better MEW (Table 1). However, MLR (using MEW and PT) showed the possibilities for enhancing the grain yield of cv. GPU-28 by 4.74% through an increase in MEW by 1.0-g/ear^1 using the specific genotype like GE-2672 or GE-5252 possessing relatively higher MEW. The MEW can be improved through its component traits, the finger number, finger length, finger width (Owere *et al.*, 2015; Kumari *et al.*, 2018), test weight and the number of seeds/ear head (Fig. 1). Such ear components would be in turn determined by the photosynthesis-associated characters like partitioning of assimilates, LVF and peduncle length (Fig. 1). Short peduncle length is expected to have rapid translocation of assimilates. Accordingly, a negative ($r = -0.189^{ns}$) correlation between peduncle length and MEW was observed in the present study (online Supplementary Table S1). Furthermore, thicker leaves (higher SLW) are expected to have higher mesophyll volume with less leaf area and high water use efficiency suitable to rainfed areas (Sastry *et al.*, 1982) and; leaf thickness showed a positive correlation with MEW ($r = 0.240^{ns}$). Higher LVF is expected to result in higher translocation rates but, in the present study, it was negatively related ($r = -0.368^*$) suggesting that higher LVF might reduce the photosynthetic lamina area as genotypic variability for leaf width could be narrow. The mean ear weight was dependent upon finger length ($r = 0.564^{**}$).

The PTs per unit area which is responsible for ear number was reported to increase with higher planting and showed a positive correlation with grain yield (Mujahid *et al.*, 2020). However, a poor relationship between PT per plant and total ear weight in the present study (online Supplementary Table S1) was due to compensation between these two parameters. A similar, negative relationship between PTs per plant and grain yield has been reported earlier (Goswami *et al.*, 2015; Ashok *et al.*, 2016; Nanja Reddy, 2020). In the present study, photosynthates might have been utilized for maintenance of stems instead of translocation to ear, hence, under rainfed conditions, it could be apt to have an optimum number of PTs (3 to 4), while under adequate input conditions PT number has a positive influence and could go up to eight per hill depending on the variety (Mujahid *et al.*, 2020). Therefore, the optimum PTs could be between 2.1 and 3.2 per hill, for rainfed conditions, above which the grain yield would be dependent more on MEW.

To achieve the required yield components like mean ear weight, two principal physiological parameters, the leaf area index (LAI) and photosynthetic rate are important. LAI was reported to have a positive relationship with grain yield

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(Subramanyam, 2000; Nanja Reddy *et al.*, 2019). In the present study, although LAI was high in many genotypes, but the yield did not increase correspondingly, probably the reserved photosynthates might not have remobilized to ear, in contrast, the low LAI types showed higher grain yield. Hence, for rainfed situations, the low LAI with higher WUE and stay green types could be appropriate (Sastry *et al.*, 1982). However, an increase in LAI of shy tillering genotypes like GE-5252 through increased plant density can be explored to increase the grain yield of finger millet. Photosynthetic rate showed an indirect lower positive effect on grain yield through total ear weight and harvest index (online Supplementary Table S2). In addition to leaf photosynthesis, ear photosynthesis is also important in finger millet which contributes up to 41% (Tieszen and Imbamba, 1978). Therefore, the selection of genotypes with a longer grain filling period and stay green leaf could be a better option for higher current photosynthesis and grain yield.

Among several yield associated parameters, independent traits which had a direct positive effect on grain yield were the mean ear weight followed by photosynthetic rate and leaf area index (online Supplementary Table S3). Among these, the photosynthetic rate is an instantaneous measurement and already high in cv. GPU-28, therefore, selection for higher mean ear weight could be a suitable trait.

Supplementary material
The supplementary material for this article can be found at https://doi.org/10.1017/S1479262121000265.

Data
Transparent.

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Author contributions
YANR formulated and conducted the experiment and wrote the manuscript. JG provided the germplasm and guided in conducting the experiment and; KTKG advised in formulating, initiation and advised in conduct of the experiment.

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Conflict of interest
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