Received: 30 May 2023 | Accepted: 11 August 2023

DOI: 10.1002/csc2.21085

Crop Science

SPECIAL SECTION: INTERNATIONAL YEAR OF MILLETS

Characterization of finger millet global germplasm diversity panel for grain nutrients content for utilization in biofortification breeding

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Assigned to Associate Editor O.P. Yadav.

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Funding information

Department of Agriculture, Government of Karnataka; CGIAR Genebank Platform, Coordinated by Crop Trust

Abstract

Finger millet (*Eleusine coracana* L.) is a versatile dryland crop known for its high calcium (Ca) content. Estimating the variability for grain nutrients in diverse germplasm is important for developing biofortified cultivars. A finger millet diversity panel consisting of 310 accessions and four controls was evaluated in two rainy seasons at International Crops Research Institute for the Semi-Arid Tropics, Hyderabad, India, to assess variability for grain nutrient content and its association with agronomic traits and identify promising accessions. Inductively coupled plasma optical emission electrometry was used to analyze grain nutrients content, and the protein content was estimated from the total nitrogen content of the finger millet grains using the sulfuric acid–selenium digestion method. Highly significant variability was found for all the grain nutrients and was significantly influenced by the genotype, environment, and their interactions. Grain nutrients showed a significant relationship between the 2 years ($R^2 = 0.06$ for phosphorus to 0.60 for Ca, $p \geq 0.001$). A nonsignificant correlation between grain yield and Ca was noticed among accessions within landraces, breeding lines, and accessions from Asia, while this correlation was significantly negative among accessions from Africa and in the entire set. The estimated percent daily values indicated that the consumption of 100 g of finger millet grains could potentially contribute to the recommended dietary allowance of up to 49% Ca,

Abbreviations: %DV, percent daily values; REML, Restricted Maximum Likelihood; RDA, Recommended Dietary Allowance.

52% magnesium, 23% protein, 23% iron, and 26% zinc. This study provides valuable insights into the variability in the finger millet germplasm, and identified grain nutrient dense accessions, that could be used in finger millet improvement to develop the biofortified cultivars.

1 | INTRODUCTION

Finger millet (*Eleusine coracana* L.) is an important dryland crop grown in Asia and Africa where its grains are used as food, while stover is used as fodder. The characteristic features such as nutrient-dense grains, high water use efficiency, climate resilience, and excellent grain storage quality made finger millet an ideal staple food crop in semi-arid regions of the world (Gimode et al., 2016; Gupta et al., 2017; Mgonja et al., 2007; Puranik et al., 2017; Vetriventhan et al., 2020). Finger millet is also known as a "crop for the poor" or "famine crop," which gives a reasonable yield even under low input agriculture (Gupta et al., 2017; National Research Council, 1996). Finger millet is also gaining importance in Europe and the United States where it has the potential for use in a variety of foods such as porridge, bread, biscuits, pasta, instant baby food, and composite flour (Upadhyaya et al., 2011).

Several studies have shown that finger millet contains more nutrients than the major cereals (Gupta et al., 2017; Kumar et al., 2016; Sood et al., 2019; Upadhyaya et al., 2011; Vetriventhan et al., 2020), and it is termed as "future smart food" by the Food and Agriculture Organization (FAO) (FAO, 2018). Finger millet is the richest source of calcium (Ca) (364 ± 58 mg/100 g), which is many fold higher than rice (raw, brown; 10.91 ± 1.79 mg/10 g), wheat (whole, 39.36 ± 5.65 mg/100 g), maize (8.91 ± 0.61 mg/100 g), and pearl millet (27.6 ± 2.16 mg/100 g) and also three times more than in milk (121 ± 3 mg/100 g in buffalo milk, 118 ± 2.9 mg/100 g in cow milk) (Anitha et al., 2021; Antony Ceasar et al., 2018; Kumar et al., 2016; Longvah et al., 2017; Puranik et al., 2017; Shobana et al., 2013; Vetriventhan et al., 2020). The Ca retention from finger millet is 19.6%, which is almost equal to 19.7% retention from rice; however, because of the high Ca content in finger millet, the Ca retention from finger millet-based diet is 4.4 times higher compared to the rice-based diet (Anitha et al., 2021). Ca bioavailability in finger millet in general is about 28.6% upon cooking, which is similar to milk (32.1%), and it could be increased considerably through different processing methods (Anitha et al., 2021). This makes finger millet the most suitable crop to reduce Ca-related health issues in the human population globally. In addition, finger millet also contains high dietary fiber (10%–18%), balance protein (6%–13%), minerals (2.5%–3.5%), phytates (0.48%), tannins (0.61%), phenolic compounds (0.3%–3%), and so on. (Chandra et al., 2016; Devi et al., 2014). The dietary fiber content of finger millet (10%–18%) is comparable to that of wheat and maize, but higher than in polished and brown rice (Gopalan et al., 2009; Rodríguez et al., 2020; Shobana et al., 2013). The protein content of finger millet is 6%–13%, which is better balanced with sulfur-containing amino acids, namely, methionine and cystine, as well as lysine, threonine, and valine content than in rice and other millets (Rodríguez et al., 2020; Saleh et al., 2013; Sharma et al., 2017; Shobana et al., 2013). It is also high in iron content; thus, it has been promoted in Africa to reduce the risk of anemia (Tripathi & Platel, 2010; Udeh et al., 2017). It is also enriched in polyunsaturated fatty acids and contains both water soluble and liposoluble vitamins. Millets also contain phytates, polyphenols, tannins, trypsin inhibitory factors, and dietary fiber, which are considered nutraceuticals (Devi et al., 2014; Chandra et al., 2016).

Globally, about 3.8 million tons of finger millet grains are produced annually (Gebreyohannes et al., 2021). The important finger millet growing countries in Eastern and Southern Africa are the sub-humid regions of Ethiopia, Kenya, Tanzania, Zambia, Malawi, the Democratic Republic of the Congo, Uganda, and Zimbabwe, while in South Asia, the crop is widely cultivated in India, Nepal, Bhutan, and Sri Lanka (Vetriventhan et al., 2020). India stands first in the world in finger millet area (1.2 million ha) and production (2 million tons), followed by Ethiopia (0.46 million ha and 1.13 million tons) (Gebreyohannes et al., 2021) (https://www.indiastat.com/). In India, the average productivity has increased from 649 kg ha^{-1} (1950–1951) to 1724 kg ha^{-1} (2019–2020) (https://www.indiastat.com/). Although there is an increase in yield potential over decades of finger millet improvement, focused breeding for improving grain nutrients is still lagging. Finger millet core collection characterized for grain iron (Fe), zinc (Zn), Ca, and protein content revealed a large variability (mean Fe 29.3 mg kg^{-1}, Zn 19.9 mg kg^{-1}, protein 7.3% and Ca 2.85 g kg^{-1}) and the range value (Fe, 21.71–65.23 mg kg^{-1}, Zn 16.58–25.33 mg kg^{-1}, Ca 1.84–4.89 g kg^{-1} and protein 6.00%–11.09%) (Upadhyaya et al., 2011). With the growing demand for healthier food products in this modern world with a rapidly increasing population rate, finger millet can bring conventional healthcare to the market in an economical way. Besides, the crop is receiving attention from the nutraceutical industry, due to its immense potential for therapeutic attributes (Kumar et al., 2016). The International Crops Research Institute for the Semi-Arid

Tropics (ICRISAT) established a finger millet product profile (blueprint of varietal development) in which nutrition traits are classified as futuristic traits while Ca as target traits. To meet this requirement, studying genetic variation using as much germplasm as possible is a prerequisite. Thus, this study was framed to characterize the grain nutrients content in 310 finger millet germplasm which represents the finger millet global collection conserved at the ICRISAT Genebank in India. The objectives of this study were to (i) assess the finger millet accessions for grain nutrients content; (ii) study the association of grain nutrient traits with agronomic traits among landraces, breeding lines, and germplasm from Asia and Africa and (iii) identify the finger millet accessions with superior single and multiple grain nutrient content for use in the finger millet breeding program.

Core Ideas

- Finger millet is a highly versatile dryland crop renowned for its remarkable calcium content.
- The study highlights significant variability in the grain nutrients content of finger millet germplasm.
- The promising nutrients dense accessions identified are a valuable resource for finger millet improvement.
- Consuming 100 g of finger millet grains could potentially contribute up to 49% of the Recommended Dietary Allowance of calcium.

2 | MATERIALS AND METHODS

2.1 | Plant material and experimental details

The genetic material for this study consists of 310 finger millet accessions and four checks, namely, GPU 26, KMR 204, MR 6, and VL 149. These varieties were chosen to represent different maturity durations, early (VL 149, <100 days), medium (GPU 26 and KMR 204, 100–120 days), and late (MR 6, >120 days). These 314 finger millet accessions included the mini core collection (Upadhyaya et al., 2010), trait-specific sources identified in the core collection (Upadhyaya et al., 2006), newly acquired germplasm, elite breeding and advance lines, and released cultivars conserved at the ICRISAT Genebank. These 314 accessions originated from 23 different countries, representing the four geographical regions in the world: Africa (160 accessions), Asia (136 accessions), Europe (six accessions), North America (three accessions), and nine accessions with unknown origin. The set included all four races of finger millet: *vulgaris* (202 accessions), *plana* (48), *elongata* (31), *compacta* (28), and their subraces and a few unclassified (5). Besides, it comprised landraces (264 accessions) and breeding lines (50 accessions). The passport data details of the 314 finger millet accessions are presented in Table S1.

The experiment was conducted in an alpha-lattice design with three replications for two consecutive years (2018 and 2019 rainy seasons) in the alfisols at ICRISAT, Patancheru, Telangana, India (17.53°N latitude, 78.27°E longitude, and 545 m above MSL) to evaluate the germplasm for agronomic and grain nutrient traits. Sowing was done in the third week of July in both years. Each accession was planted in a single row of 4 m in length with a spacing of 60 cm between rows (plot size 2.4 m^2) and ∼10 cm between plants. Fertilizers were applied at the rate of 100 kg ha^{-1} of diammonium phosphate as a basal dose and 100 kg ha^{-1} of urea as a top dressing. Crop-specific agronomic and plant protection measures were provided as needed. There was an average rainfall of 568 mm in 2019 and 852 mm in 2019, with 54% and 73% of that rainfall occurred during the crop growing season from July to December, respectively. The minimum temperature ranged from 10.5 to 24.4˚C in 2018 and 12.4 to 24.0˚C in 2019. The maximum temperature varied from 23.4 to 33.6˚C in 2018 and 23.6 to 33.2˚C in 2019 during the crop growth period.

2.2 | Data collection

2.2.1 | Morpho-agronomic traits

Data on days to 50% flowering, 100-seed weight, grain yield, and grain color were recorded. Based on grain color, finger millet accessions were classified into dark brown, light brown, copper brown, reddish-brown, and white color. Days to 50% flowering, grain yield, and grain color were recorded on a plot basis. The 100-seed weight was estimated from the bulked seeds of each accession. The grain yield per plot was converted into kg/ha.

2.2.2 | Grain nutrient determination

Harvesting and threshing of finger millet were done manually. For nutrient analysis, 10 g of grain samples from each replication of 314 finger millet accessions were taken from both years. The samples were cleaned and washed with distilled water for a few seconds to remove the dust and metal contamination and dried in the oven for 2 h at 40˚C. The cleaned, well-dried whole grain samples were analyzed in the Charles Renald Analytical Laboratory in ICRISAT, Patancheru, India. The grain samples were kept in a hot air oven at 55˚C for

2 h before grinding to a fine powder using a steel blade coffee grinder and weighing of sample before digestion to avoid moisture interference. The samples (0.3 g) were digested using nitric acid-hydrogen peroxide mixture on an automated block digestor (SCP Science), followed by analyzing the digests for the estimation of Fe, Zn, Ca, magnesium (Mg), copper (Cu), sulfur (S), and potassium (K) content on inductively coupled plasma optical emission spectroscopy (Wheal et al., 2011). S and K contents were estimated for only one year (2019). The estimation of total nitrogen and phosphorus (P) content was done by digesting the grain samples (0.15 g) with sulfuric acid–selenium digestion mixture on a block digestor (FOSS), followed by analyzing the digests on a continuous flow autoanalyzer (Skalar SAN++). The protein content was calculated by multiplying the total nitrogen content (N%) with a conversion factor of 6.25 (Sahrawat et al., 2002). The grain nutrient content was expressed in mg kg^{-1} except for protein which was expressed in percentage.

2.3 | Statistical analysis

The significance between the accessions and the years for various traits was determined using the Restricted Maximum Likelihood (REML) procedure in GenStat 20th edition (http://www.genstat.co.uk) for individual years and pooled data of the 2 years, considering year as fixed and treatment, block, and replication as a random factors. The significance of environmental (years) effects was tested using Wald's statistics (Wald, 1943). Best linear unbiased predictors (Schönfeld & Werner, 1986) were obtained for each accession in the individual years and pooled for both years and were used for all downstream analyses. The broad-sense heritability (h^{2}b) was estimated for each trait and categorized as low (<0.30), medium (0.30–0.60), or high (>0.60) (Vetriventhan et al., 2021). Comparison of mean performance on regions (only for Asia and Africa), races, and biological status were performed using the Newman–Keuls test (Keuls, 1952; Newman, 1939), in the R package "*agricolae*" (de Mendiburu, 2023). The linear regression (R^2) between the 2 years was performed using the "*stats*" package ("*lm*" function) in R (R Core Team, 2018). The correlation coefficients among 12 traits and their significance were estimated in the R software using the "*corrplot*" package (Wei et al., 2017). Gower's phenotypic distance matrix was estimated and hierarchical clustering was done following Ward.D2 method (Murtagh & Legendre, 2014) using the R package "*vegan*" (Oksanen et al., 2022) and "*cluster*" (Maechler et al., 2019), and the cluster mean values were tested following the Newman–Keuls procedure. Promising finger millet accessions for grain nutrient traits were identified based on per se performance based on pooled data of both years.

2.4 | Estimating percent daily value

Percent daily values (%DV) for finger millet grain nutrients were calculated based on the amount of a particular nutrient present in 100 g of finger millet grain that contributes to the Recommended Dietary Allowance (RDA) of the nutrients for an Indian adult male and female per 100 g of consumption (ICMR-NIN, 2020). RDA accounts for bioavailability, and it is considered a wide range of age groups (ICMR-NIN, 2020). The %DV was calculated by using the following formula:

$$\%\text{DV} = (\text{Amount of nutrient per 100g of grain}/\text{RDA}) \times 100.$$

The %DV of major nutrients for men and women are 19 and 29 mg/day for Fe, 17 and 13 mg/day for Zn, 1000 mg/day for Ca and P, 54 and 46 g/day for protein, 440 and 370 mg/day for Mg, 3 mg/day for Cu, and 3510 mg/day for potassium (ICMR-NIN, 2020).

3 | RESULTS

3.1 | REML variance component analysis

The REML-based variance component analyses revealed a highly significant genotypic variance ($\sigma^2{}_{g}$) in the individual years and pooled data, indicating the presence of significant variability for the grain nutrients and agronomic traits studied. Variance due to genotype × environment interactions ($\sigma^2{}_{g\times e}$) and environment effects by Wald's statistics showed a significant effect on all the traits under study (Table 1), indicating the interaction between genotype and environment for the expression of the phenotype of the studied traits.

3.1.1 | Variability parameters and heritability (h^{2}b)

A wide range of variability was found for agronomic and grain nutrients traits in both the years and in the pooled data of the two years. The grain nutrients and agronomic traits differed significantly between the 2 years except for days to 50% flowering (Table 2). The relationship between the grain nutrient content in finger millet evaluated during the 2018 and 2019 rainy seasons is presented in Figure 1. All nutrient contents showed a significant relationship between the 2 years. Based on pooled data, agronomic traits, namely, days to 50% flowering varied from 51 to 97 days (average 74 days) and produced grain yield of 945–3532 kg ha^{-1} (average 2214 kg ha^{-1}). The 100-seed weight of finger millet germplasm varied from 0.17 to 0.41 g with an average of 0.26 g. Grain nutrient traits showed significant variability. The grain Fe

TABLE 1 Variance due to genotype (σ^2g) and genotype and environment interaction (σ^2ge) for agronomic and grain nutrient traits among 314 finger millet accessions.

Trait	2018 σ^2g	2019 σ^2g	Pooled σ^2g	Pooled σ^2ge	Pooled Wald's statistics for year
Days to 50% flowering	89.01**	54.10**	66.00**	5.52**	8.85*
Grain yield (kg ha^{-1})	483,310**	213,483**	180,001**	68,490**	572.36**
100-Seed weight (g)	0.0009923**	0.0012473**	0.0010347**	0.0008**	1205.81**
Protein (%)	0.37**	0.76**	0.27**	0.27**	71.64**
Iron (mg kg^{-1})	19.01**	14.84**	11.52**	5.44**	1683.99**
Zinc (mg kg^{-1})	9.01**	6.01**	5.98**	1.30*	2416.01**
Calcium (mg kg^{-1})	145,203**	126,726**	22,033**	217,880**	1655.84**
Magnesium (mg kg^{-1})	10,968**	12,424**	8048**	3501**	446.75**
Copper (mg kg^{-1})	0.83**	0.56**	0.60**	0.10**	1160.73**
Sulphur (mg kg^{-1})	NR	6843**	NR	NR	NR
Phosphorus (mg kg^{-1})	0.0002**	0.0003**	0.0001061**	0.00007*	472.95**
Potassium (mg kg^{-1})	NR	0.0024**	NR	NR	NR

Abbreviation: NR, not recorded.

* and ** significant at $p \leq 0.05$ and 0.01 probability levels, respectively.

varied from 20.44 to 42.76 mg kg^{-1} and Zn from 17.45 to 34.39 mg kg^{-1}, with the average mean value of 30.70 mg kg^{-1} and 25.68 mg kg^{-1}. Similarly, the protein content varied from 7.27% to 10.74%, with an average of 8.95%. The grain Ca content of finger millet ranged from 2986.92 to 4869.20 mg kg^{-1} (mean 3965.48 mg kg^{-1}). Similarly, a wide range was found for Mg (1332.52–1908.54 mg kg^{-1}), Cu (4.04–8.68 mg kg^{-1}), and S (1061.07–1489.58 mg kg^{-1}) with an average value of 1624.33 mg kg^{-1}, 6.00 mg kg^{-1}, and 1275.96 mg kg^{-1}. The total P and K content ranged from 2894.69 to 3457.79 mg kg^{-1}, 3093.20 to 5551.21 mg kg^{-1} and the mean of 3133.83 mg kg^{-1} (P) and 4332.10 mg kg^{-1} (K), respectively.

The h^{2}b of grain nutrient content in finger millet germplasm varied from low to high, that is, 0.25–0.72 in 2018 and 0.20–0.76 in 2019 (Table 2). In pooled data, h^{2}b ranged from 0.67 to 0.87, and all traits had high heritability. On the other hand, all the agronomic traits showed high heritability >0.68 in both the years and for pooled data.

3.2 | Comparison of mean grain nutrient values among races, regions, and biological status

Comparisons of mean values among races, regions, and biological status were performed for agronomic and grain nutrients traits (Table 3; Figure 2A-C). Races differed significantly for Ca, Cu, K, days to 50% flowering, and 100-seed weight. The Ca content of races *elongata* and *plana* significantly differed from that of races *vulgaris* and *compact*. Race *compacta* had high Cu (6.26 mg kg^{-1}) than the other three races but significantly differed from race *elongata* (5.74 mg kg^{-1}). For K, race *compacta* (4331.35 mg kg^{-1}), *plana* (4391.67 mg kg^{-1}), and *vulgaris* (4356.45 mg kg^{-1}) were superior and differed significantly from race *elongata* (4074.88 mg kg^{-1}). Among regions, mean values of accessions from Africa (160 accessions) and Asia (136 accessions) were compared, while accessions from Europe, North America, and unknown origin were not included because of the small sample size (<10 accessions). Mean comparison between accessions from Africa and Asia revealed significant differences for traits such as Fe, Zn, Ca, Mg, P, and days to 50% flowering. For the aforementioned traits, African accessions had the highest nutrient content except Fe and flowered 7 days later than Asian accessions (71 days). Landraces were superior in Zn and Ca content, whereas breeding lines were early in flowering (5 days) and high in Cu content, grain yield, and 100-seed weight. However, traits such as grain protein and S content did not vary among races, regions, and biological status.

3.2.1 | Variability on the grain color

Finger millet grain color was recorded for all 314 accessions. Light brown (55%) was the predominant grain color, followed by reddish-brown (25%), dark brown (8%), copper brown (7%), and white (5%) (Table 4). Analysis was performed to find the relationship between grain color and grain nutrient content in finger millet (Table 4). Except for Fe and Cu, all other nutrients did not vary between grains of different colors. For Fe, reddish brown accessions (31.64 mg kg^{-1}) had significantly higher iron content than light brown accessions

TABLE 2 Mean, range, and heritability on agronomic and grain nutrient traits of 314 finger millet accessions.

Trait	Year	Mean	Range	Heritability (H^2b)	CV%	SED	LSD ($p \leq$ 0.05)
Days to 50% flowering	2018	74 ± 0.53a	50–99	0.98	1.94	1.18	2.31
	2019	75 ± 0.41a	53–97	0.96	2.13	1.30	2.56
	Pooled	74 ± 0.47	51–97	0.95	2.08	1.27	2.49
Grain yield (kg ha^{-1})	2018	2666 ± 36.73a	615–4416	0.73	16.03	349	685
	2019	1865 ± 24.18b	731–3331	0.68	16.85	256.53	503.58
	Pooled	2214 ± 23.70	945–3532	0.70	23.35	422.08	828.55
100-Seed weight (g)	2018	0.24 ± 0.002b	0.16–0.36	0.76	7.25	0.01	0.03
	2019	0.28 ± 0.002a	0.17–0.44	0.78	6.74	0.02	0.03
	Pooled	0.26 ± 0.002	0.17–0.41	0.92	7.04	0.02	0.03
Protein (%)	2018	9.20 ± 0.03a	7.63–10.82	0.43	7.50	0.56	1.11
	2019	8.71 ± 0.04b	5.75–10.77	0.50	9.93	0.71	1.39
	Pooled	8.95 ± 0.03	7.27–10.74	0.67	9.90	0.72	1.42
Iron (mg kg^{-1})	2018	35.93 ± 0.22a	24.75–46.22	0.56	10.81	3.17	6.23
	2019	25.48 ± 0.2b	17.06–38.53	0.59	12.52	2.60	5.11
	Pooled	30.70 ± 0.20	20.44–42.76	0.69	12.28	3.08	6.04
Zinc (mg kg^{-1})	2018	29.46 ± 0.15a	21.11–36.43	0.56	9.00	2.17	4.25
	2019	21.89 ± 0.12b	15.84–31.75	0.56	9.96	1.78	3.49
	Pooled	25.68 ± 0.13	17.45–34.39	0.76	10.50	2.20	4.32
Calcium (mg kg^{-1})	2018	4281.72 ± 20.12a	3315.34–5367.09	0.70	5.52	193.00	378.67
	2019	3649.24 ± 19.1b	2652.22–4725.44	0.76	5.43	161.90	317.65
	Pooled	3965.48 ± 19.74	2986.92–4869.20	0.87	5.97	111.64	219.04
Magnesium (mg kg^{-1})	2018	1697.70 ± 5.01a	1407.30–1984.08	0.47	6.61	91.66	179.92
	2019	1550.99 ± 5.73b	1294.51–1935.35	0.62	5.58	70.69	138.77
	Pooled	1624.33 ± 5.08	1332.52–1908.54	0.68	6.76	89.60	175.88
Copper (mg kg^{-1})	2018	6.60 ± 0.05a	4.65–8.72	0.72	8.55	0.46	0.91
	2019	5.39 ± 0.04b	3.33–8.41	0.71	8.78	0.39	0.76
	Pooled	6.00 ± 0.04	4.04–8.68	0.86	8.93	0.44	0.86
Sulphur (mg kg^{-1})	2018	NR	NR	NR	NR	NR	NR
	2019	1275.96 ± 3.83	1061.07–1489.58	0.41	7.71	80.37	157.76
	Pooled	NR	NR	NR	NR	NR	NR
Phosphorus (mg kg^{-1})	2018	2960.07 ± 0.0004b	2692.16–3230.25	0.25	8.24	0.02	0.04
	2019	3307.62 ± 0.001a	2932.03–3653.00	0.20	9.66	0.03	0.05
	Pooled	3133.83 ± 0.0008	2894.69–3457.79	0.67	9.96	0.03	0.05
Potassium (mg kg^{-1})	2018	NR	NR	NR	NR	NR	NR
	2019	4332.10 ± 0.004	3093.20–5551.21	0.75	6.51	0.02	0.05
	Pooled	NR	NR	NR	NR	NR	NR

Note: Mean values followed by different letters represent significant differences at the $p \leq 0.05$ probability level.
Abbreviation: CV, coefficient of variation; LSD, least significant difference; NR, not recorded; SED, standard error difference.

(30.18 mg kg^{-1}). White seeded accessions had the highest Cu content (6.45 mg kg^{-1}) and significantly differed from dark brown (5.61 mg kg^{-1}), copper brown (5.73 mg kg^{-1}), and reddish-brown (5.91 mg kg^{-1}) seeded accessions (Figures S1–S3). When we grouped accessions into two categories, colored (dark brown, reddish brown, and copper brown) and white accessions, except for Cu, the remaining accessions did not differ significantly among colored and white grain colors. In the case of Cu, white seeds (6.45 mg kg^{-1}) had a significantly higher value than colored seeds (5.96 mg kg^{-1}).

TABLE 3 Mean comparison of agronomic and grain nutrient traits in finger millet among races, regions, and biological status.

Trai	Race				Region		Biological status	
	***ccompacta* (28)**	***elongata* (31)**	***plana* (48)**	***vulgaris* (202)**	**Africa (160)**	**Asia (136)**	**Breeding lines (50)**	**Landrace (264)**
DF	75 ± 1.82ab	78 ± 1.43a	78 ± 0.95a	73 ± 0.56b	77 ± 0.52a	71 ± 0.72b	70 ± 1.14b	75 ± 0.5a
GY	2191 ± 72.32a	2122 ± 103.8a	2241 ± 53.04a	2214 ± 28.9a	22126 ± 29.73a	2235 ± 40.94a	2463 ± 49.28a	2165 ± 25.67b
Swt	0.25 ± 0.004b	0.25 ± 0.006b	0.27 ± 0.005a	0.26 ± 0.002ab	0.26 ± 0.002a	0.26 ± 0.002a	0.28 ± 0.003a	0.26 ± 0.001b
Protein	8.95 ± 0.12a	8.94 ± 0.1a	8.75 ± 0.07a	9.01 ± 0.04a	8.9 ± 0.04a	9.01 ± 0.05a	8.94 ± 0.07a	8.95 ± 0.03a
Fe	30.56 ± 0.53a	30.09 ± 0.67a	29.5 ± 0.55a	31.07 ± 0.24a	30.27 ± 0.29b	31.21 ± 0.28a	31.19 ± 0.45a	30.61 ± 0.22a
Zn	25.74 ± 0.35a	25.23 ± 0.43a	25.79 ± 0.47a	25.73 ± 0.15a	26.13 ± 0.2a	25.07 ± 0.19b	24.88 ± 0.28b	25.83 ± 0.15a
Ca	3905.04 ± 69.84b	4075.99 ± 70.73a	4111.84 ± 49.01a	3917.018 ± 23.6b	4134.35 ± 23.35a	3742.63 ± 24.92b	3746.16 ± 38.73b	4004.53 ± 21.56a
Mg	1606.74 ± 18.58a	1589.38 ± 20.56a	1633.42 ± 12.28a	1629.68 ± 6.04a	1646.17 ± 7.12a	1595.01 ± 7.3b	1622.39 ± 10.71a	1624.71 ± 5.71a
Cu	6.26 ± 0.16a	5.74 ± 0.12b	6.07 ± 0.12ab	5.97 ± 0.05ab	6.05 ± 0.06a	5.92 ± 0.07a	6.29 ± 0.1a	5.94 ± 0.05b
S	1277.33 ± 12.16a	1254.4 ± 11.29a	1275.4 ± 9.07a	1281.02 ± 4.88a	1282.98 ± 5.52a	1268.19 ± 5.73a	1263.45 ± 8.03a	1278.39 ± 4.29a
P	3127.24 ± 0.001a	3112.90 ± 0.001a	3154.65 ± 0.001a	3132.96 ± 0.001a	3148.22 ± 0.001a	3115.71 ± 0.001b	3125.88 ± 0.001a	3135.37 ± 0.001a
K	4331.35 ± 0.008a	4074.88 ± 0.008b	4391.67 ± 0.007a	4356.45 ± 0.003a	4353.45 ± 0.004a	4309.96 ± 0.004a	4416.14 ± 0.005a	4315.80 ± 0.003a

Note: Mean values followed by different letters represent significant differences at the $p \leq 0.05$ probability level.

Abbreviations: Ca, calcium (mg kg^{-1}); Cu, copper (mg kg^{-1}); DF, days to 50% flowering; Fe, iron (mg kg^{-1}); GY, grain yield (kg ha^{-1}); K, potassium (mg kg^{-1}); Mg, magnesium (mg kg^{-1}); protein (%); Swt, 100-seed weight (g); P, phosphorus (mg kg^{-1}); S, sulfur (mg kg^{-1}); Zn, zinc (mg kg^{-1}).

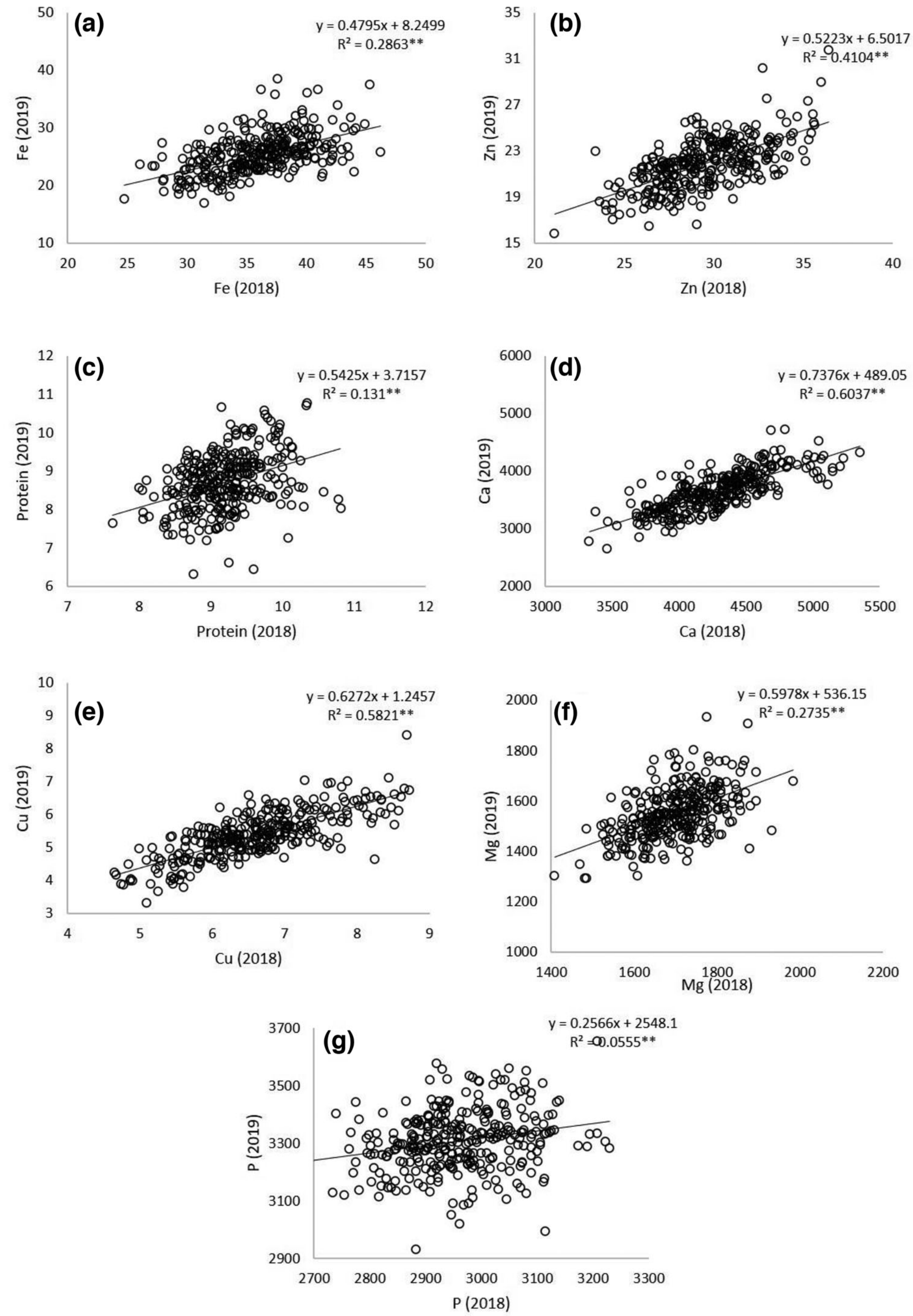

FIGURE 1 Relationship between grain nutrients of finger millet germplasm, evaluated during 2018 and 2019 rainy seasons at International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), Hyderabad, India.

3.3 | Correlation among grain nutrients and agronomic traits

Based on a pooled analysis of the 2 years of data, the correlation coefficients were estimated to determine the relationship between grain nutrients and agronomic traits (Table 5). Among grain nutrients, Ca is the most important nutrient in finger millet, which had a significant and positive association with Zn, Mg, Cu, S and P was and negatively correlated with K. Ca had a nonsignificant association with protein and Fe. Grain protein content had a positive and significant association with Fe, Zn, Mg, Cu, S, and P, and a nonsignificant correlation with Ca and K. Likewise, Zn, Mg, Cu, S and P showed a significant and positive association with all other nutrients, except for Cu and S with K that showed a nonsignificant association. The associations between S and P, and

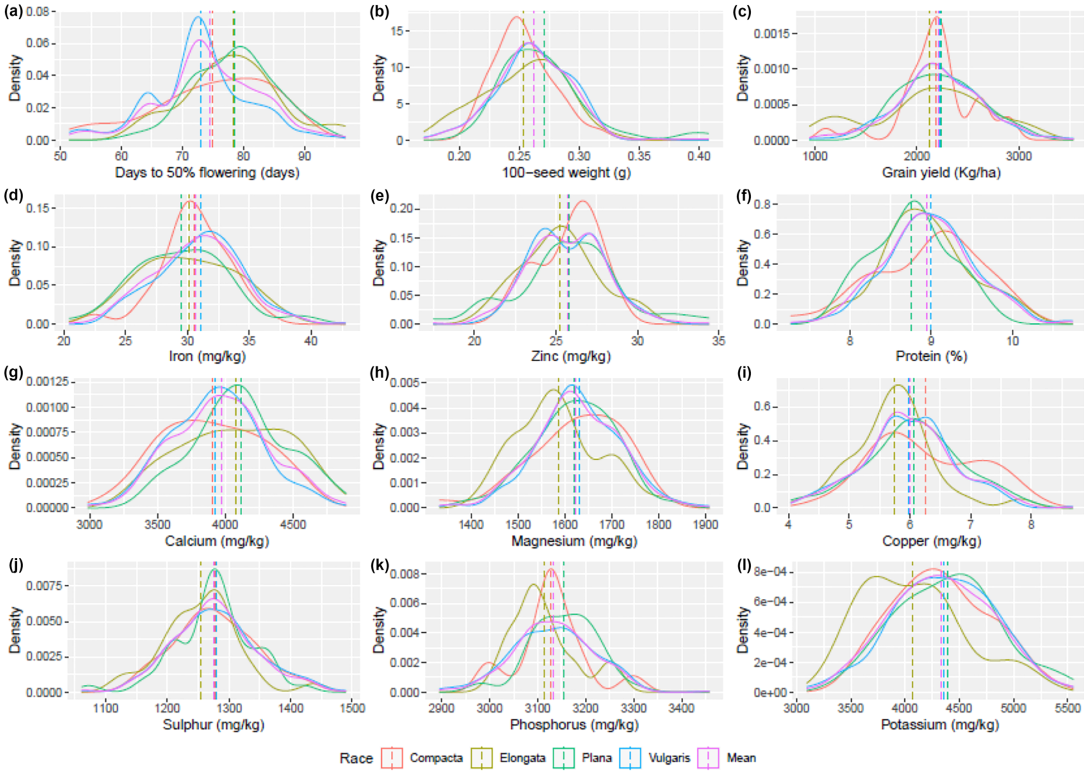

FIGURE 2 Upper panel Distribution of agronomic (a–c) and grain nutrient (d–l) traits in races of 314 finger millet accessions. Middle Panel Distribution of agronomic (a–c) and grain nutrient (d–l) traits in region of 314 finger millet accessions. Lower panel Distribution of agronomic (a–c) and grain nutrient (d–l) traits in the biological status of 314 finger millet accessions.

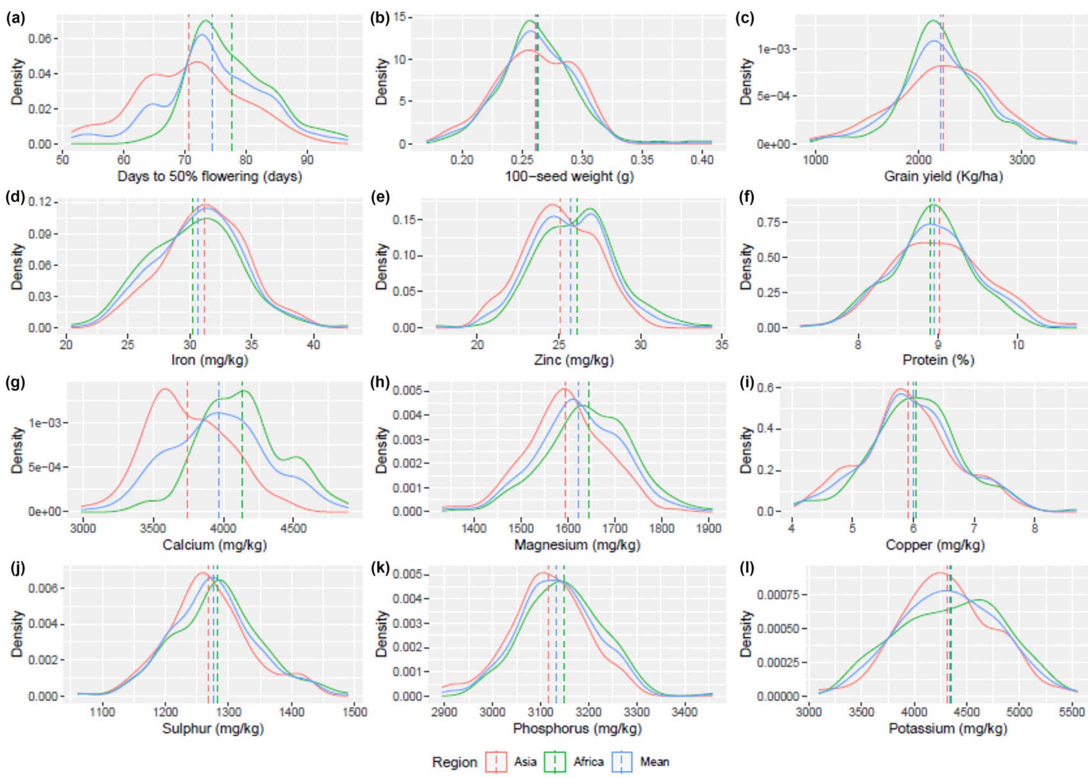

FIGURE 2 Continued

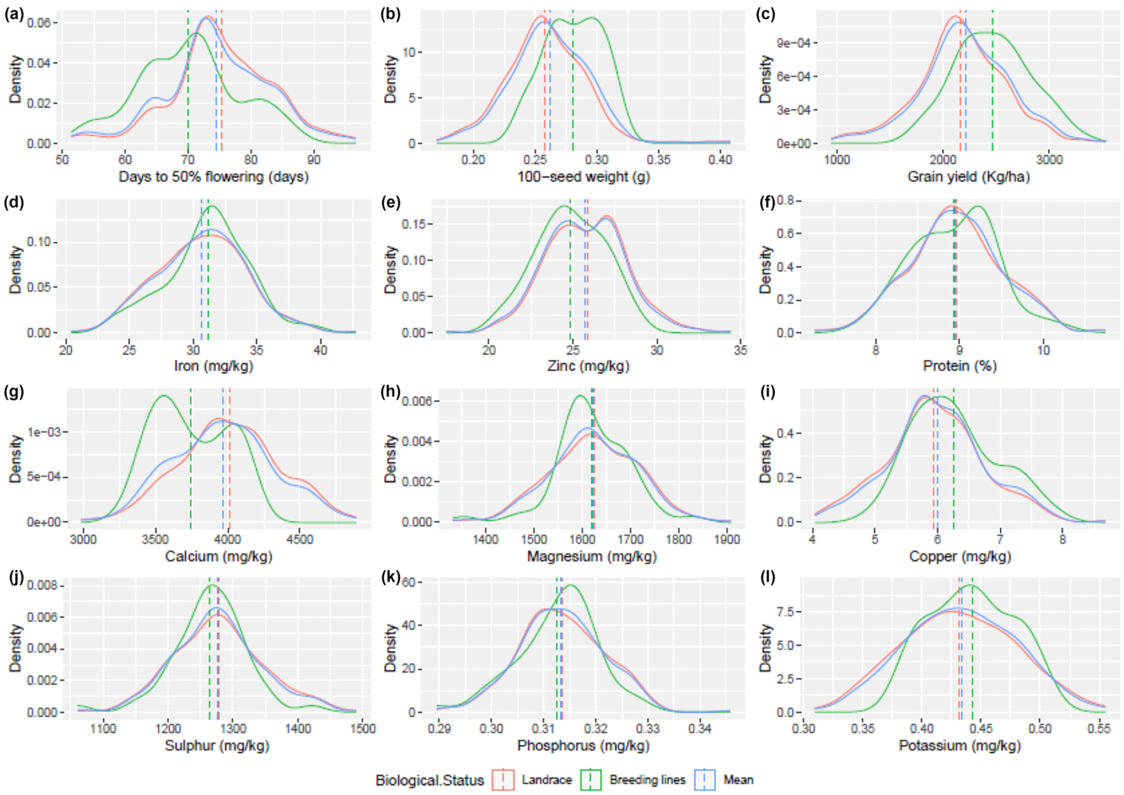

FIGURE 2 Continued

TABLE 4 Comparison of means for agronomic and grain nutrient traits in finger millet grain color.

Trait	Dark brown (24)	Light brown (172)	Copper brown (21)	Reddish brown (80)	White (17)
DF	73 ± 1.94b	75 ± 0.55b	75 ± 2.23b	72 ± 0.98b	80 ± 1.66a
GY	2001 ± 104.28bc	2334 ± 30.43a	1874 ± 87.86c	2155 ± 39.91bc	1992 ± 80.68bc
Swt	0.25 ± 0.01b	0.27 ± 0.01a	0.24 ± 0.01b	0.26 ± 0.01ab	0.25 ± 0.01b
Protein	8.99 ± 0.11a	8.89 ± 0.04a	9.14 ± 0.12a	9.05 ± 0.07a	8.87 ± 0.18a
Fe	30.79 ± 0.61ab	30.18 ± 0.26b	30.85 ± 0.78ab	31.64 ± 0.4a	31.28 ± 0.79ab
Zn	26.17 ± 0.53a	25.59 ± 0.18a	25.53 ± 0.6a	25.57 ± 0.26a	26.59 ± 0.56a
Ca	3942.75 ± 79.61a	3983.58 ± 22.74a	4035.6 ± 83.92a	3900.42 ± 42.84a	3995.36 ± 131.9a
Mg	1619.94 ± 23.19a	1629.34 ± 6.27a	1627.32 ± 18.29a	1617.78 ± 10.41a	1607.08 ± 30.15a
Cu	5.61 ± 0.18b	6.08 ± 0.05ab	5.73 ± 0.18b	5.91 ± 0.08b	6.45 ± 0.29a
S	1256.19 ± 16.86a	1280.81 ± 4.83a	1277.94 ± 16.11a	1272.13 ± 7.58a	1270.49 ± 20.43a
P	3117.56 ± 0a	3136.51 ± 0a	3137.47 ± 0a	3126.80 ± 0a	3158.19 ± 0a
K	4309.67 ± 0.01a	4354.08 ± 0a	4185.71 ± 0.01a	4309.89 ± 0.01a	4426.72 ± 0.01a

Note: Mean values followed by different letters represent significant differences at the $p \leq 0.05$ probability level.
Abbreviations: Ca, calcium (mg kg^{-1}); Cu, copper (mg kg^{-1}); DF, days to 50% flowering; Fe, iron (mg kg^{-1}); GY, grain yield (kg ha^{-1}); K, potassium (mg kg^{-1}); Mg, magnesium (mg kg^{-1}); protein (%); Swt, 100-seed weight (g); P, phosphorus (mg kg^{-1}); S, sulfur (mg kg^{-1}); Zn, zinc (mg kg^{-1}).

P and K were positively significant. An association between grain nutrients and agronomic traits revealed a significant and positive association between grain yield with Cu, days to 50% flowering with Ca, and 100-seed weight with Cu and K. Negative correlations were observed between days to 50% flowering with protein, Fe, S, P and K; grain yield with protein, Zn, Ca, and S; and 100-seed weight with protein, Zn, S, and P.

The correlation coefficients were also estimated separately among breeding lines, landraces, and germplasm from Africa and Asia, and varied considerably among different groups (Tables 6 and 7). For example, correlations between

TABLE 5 Correlation among grain nutrient and agronomic traits in 314 finger millet accessions.

Trait	GY	Swt	Protein	Fe	Zn	Ca	Mg	Cu	S	P	K
DF	0.026	0.044	−0.396***	−0.339***	0.032	0.494***	−0.064	−0.009	−0.201***	−0.127*	−0.161**
GY		0.442***	−0.204***	−0.038	−0.318***	−0.136*	0.043	0.161**	−0.220***	−0.071	−0.006
Swt			−0.185***	−0.055	−0.323***	−0.072	0.036	0.203***	−0.137*	−0.129*	0.120*
Protein				0.556***	0.311***	0.042	0.261***	0.318***	0.449***	0.468***	−0.085
Fe					0.501***	0.002	0.205***	0.318***	0.288***	0.247***	−0.006
Zn						0.255***	0.293***	0.190***	0.364***	0.254***	0.136*
Ca							0.459***	0.238***	0.163**	0.284***	−0.148**
Mg								0.412***	0.292***	0.464***	0.157**
Cu									0.178**	0.325***	0.054
S										0.311***	0.085
P											0.182**

Abbreviations: Ca, calcium (mg kg^{-1}); Cu, copper (mg kg^{-1}); DF, days to 50% flowering; Fe, iron (mg kg^{-1}); GY, grain yield (kg ha^{-1}); K, potassium (mg kg^{-1}); Mg, magnesium (mg kg^{-1}); protein (%); Swt, 100-seed weight (g); P, phosphorus (mg kg^{-1}); S, sulfur (mg kg^{-1}); Zn, zinc (mg kg^{-1}).
*, **, and *** significant at $p \leq 0.05$, 0.01, and 0.001 probability levels, respectively.

TABLE 6 Correlation coefficients among grain nutrient and agronomic traits of breeding lines ($n = 50$; upper diagonal) and landraces ($n = 264$; lower diagonal) of finger millet germplasm.

Trait	DF	GY	Swt	Fe	Zn	Protein	Ca	Mg	Cu	S	P	K
DF		0.51***	0.46***	−0.49***	0.06	−0.73***	0.57***	−0.05	0.31*	−0.28*	−0.43**	0.03
GY	0.03		0.37**	−0.23	0.05	−0.51***	0.15	−0.14	−0.02	−0.37**	−0.18	0.1
Swt	0.07	0.41***		−0.09	−0.05	−0.38**	0.01	−0.09	0.09	−0.25	−0.45**	−0.13
Fe	−0.31***	−0.03	−0.07		0.45***	0.55***	−0.28*	0.18	−0.05	0.25	0.17	−0.04
Zn	−0.01	−0.34***	−0.32***	0.53***		0.18	0.16	0.57***	0.25	0.21	0.17	0.02
Protein	−0.36***	−0.16**	−0.17**	0.56***	0.33***		−0.31*	0.26	−0.08	0.51***	0.55**	−0.04
Ca	0.45***	−0.09	0.01	0.06	0.23***	0.08		0.44**	0.37**	0.06	−0.13	−0.04
Mg	−0.07	0.07	0.06	0.21***	0.26***	0.26***	0.48***		0.39**	0.35*	0.25	0.05
Cu	−0.02	0.15*	0.18**	0.37***	0.21***	0.38***	0.29***	0.42***		0.24	−0.03	−0.23
S	−0.22***	−0.19***	−0.11	0.30***	0.38***	0.44***	0.16*	0.28***	0.19**		0.39**	−0.05
P	−0.09	−0.04	−0.08	0.26**	0.26***	0.45***	0.34***	0.50***	0.39***	0.30***		0.18
K	−0.17**	−0.04	0.12*	−0.01	0.17**	−0.09	−0.14*	0.17**	0.07	0.11	0.19**	

Abbreviations: Ca, calcium (mg kg^{-1}); Cu, copper (mg kg^{-1}); DF, days to 50% flowering; Fe, iron (mg kg^{-1}); GY, grain yield (kg ha^{-1}); K, potassium (mg kg^{-1}); Mg, magnesium (mg kg^{-1}); protein (%); Swt, 100-seed weight (g); P, phosphorus (mg kg^{-1}); S, sulfur (mg kg^{-1}); Zn, zinc (mg kg^{-1}).
*, **, and *** significant at $p \leq 0.05$, 0.01, and 0.001 probability levels, respectively.

agronomic and grain nutrient traits in the landraces indicated that days to 50% flowering with K and 100-seed weight with Zn showed a significantly negative correlation, while these correlations were nonsignificant in the breeding lines (Table 6). Among breeding lines, days to 50% flowering had a significant and positive association with Cu; and 100-seed weight had a significantly negative correlation with P; however, these relationships were nonsignificant in landraces. Similarly, in Asian accessions, correlations between days to 50% flowering with Fe, protein, Mg, and Cu; and 100-seed weight with S were significantly negative; grain yield and 100-seed weight with Mg, Cu, and K were significantly positive, while these correlations were nonsignificant in the African germplasm (Table 7). Among germplasm from Africa, negative and significant correlations were observed between grain yield with Ca, and P; and 100-seed weight with protein and P, while these were nonsignificant in germplasm from Asia. A correlation between grain yield and Ca showed a nonsignificant association in the landraces, breeding lines, and Asian population, while the relationship showed a significant and negative association in the African population.

Among grain nutrient traits, a significant and positive correlation was observed for Fe with Mg, Cu, S, and P; protein

TABLE 7 Correlation coefficients among grain nutrient and agronomic traits of finger millet accessions from Africa (n = 160; lower diagonal) and Asia (n = 136; upper diagonal).

Trait	DF	GY	Swt	Fe	Zn	Protein	Ca	Mg	Cu	S	P	K
DF		0.15	−0.02	−0.54**	−0.08	−0.66***	0.19*	−0.35***	−0.23**	−0.38***	−0.43***	−0.22**
GY	−0.12		0.55**	0	−0.27**	−0.22**	0.06	0.17*	0.30***	−0.24**	0.08	0.14
Swt	0.04	0.38***		0.1	−0.26**	−0.09	−0.14	0.17*	0.34***	−0.19*	0.04	0.26**
Fe	−0.12	−0.09	−0.18*		0.43***	0.65***	0.04	0.33***	0.31***	0.31***	0.35***	0.02
Zn	−0.05	−0.39***	−0.43***	0.61***		0.33***	0.13	0.24**	0.11	0.28***	0.1	−0.06
Protein	−0.02	−0.18*	−0.27***	0.49***	0.34***		0.13	0.40***	0.33***	0.60***	0.54***	−0.08
Ca	0.52***	−0.38***	−0.11	0.11	0.19*	0.15		0.46***	0.24**	0.14	0.27**	−0.20*
Mg	−0.04	−0.03	−0.08	0.18*	0.24**	0.21**	0.33***		0.49***	0.27**	0.52***	0.23**
Cu	0.15	0.06	0.08	0.34***	0.20*	0.34***	0.24**	0.35***		0.27**	0.36***	0.12
S	−0.16*	−0.22**	−0.11	0.32***	0.41***	0.34***	0.13	0.28***	0.05		0.28**	−0.06
P	−0.03	−0.20*	−0.31***	0.22**	0.29***	0.49***	0.19*	0.37***	0.23**	0.28***		0.20*
K	−0.20*	−0.14	−0.01	−0.01	0.23**	−0.11	−0.21**	0.1	0.01	0.18*	0.17*	

Abbreviations: Ca, calcium (mg kg^{-1}); Cu, copper (mg kg^{-1}); DF, days to 50% flowering; Fe, iron (mg kg^{-1}); GY, grain yield (kg ha^{-1}); K, potassium (mg kg^{-1}); Mg, magnesium (mg kg^{-1}); protein (%); Swt, 100-seed weight (g); P, phosphorus (mg kg^{-1}); S, sulfur (mg kg^{-1}); Zn, zinc (mg kg^{-1}).
*, **, and *** significant at $p \leq 0.05$, 0.01, and 0.001 probability levels, respectively.

with Mg and Cu; Ca with S, and P; Mg with P and K; Cu with S and P; and P with K in landraces, while these associations were nonsignificant in breeding lines (Table 6). Among regions, the correlations between Cu and S, Mg, and K were significant and positive in Asian germplasm, and these associations were nonsignificant in African germplasm. Likewise, Zn showed a significantly positive correlation with all other nutrients in African germplasm, whereas in Asian lines, only protein, Mg, and S had a positive association with Zn (Tables 6 and 7).

3.4 | Cluster analysis

The cluster analysis of finger millet accessions using both agronomic and grain nutrient traits grouped them into four distinct clusters (Figure 3). The number of accessions in each group varied from 30 in Cluster 3 to 115 in Cluster 2 (Table S2). Cluster 1 represents the majority of accessions from Africa (87%), while Clusters 3 and 4 represent accessions from Asia (67% in Cluster 3 and 80% in Cluster 4) with a few exceptions. However, Cluster 2 represents accessions from both Asia (54%) and Africa (43%). The mean values of each cluster have significantly differed for all traits and are provided in Table S2. Clusters 1 and 4 had higher cluster mean values for most of the traits than other clusters.

3.5 | Trait-specific sources

The top 10 promising nutrient-dense accessions for each grain nutrient trait and accessions with multi-nutrient traits were identified based on pooled data of both the seasons. The top 10 selected accessions had values higher than the check values. All these top-10 nutrient-dense accessions flowered in between 58 and 97 days, produced grain yield up to 1134–2963 kg ha^{-1}, and had 0.18–0.31 g per 100-seed weight (Table 8). For instance, promising top 10 nutrient-specific accessions had 37.36–42.76 mg kg^{-1} Fe, 30.10–34.39 mg kg^{-1} Zn, 4618.46–4888.52 mg kg^{-1} Ca, 10.02%–10.74% protein, 1790.01–1908.54 mg kg^{-1} Mg, 7.49–8.68 mg kg^{-1} Cu, 1421.32–1489.58 mg kg^{-1} S, 3278.40–3457.79 mg kg^{-1} P, and 5222.10–5551.20 mg kg^{-1} K. The means and ranges of the promising accessions were above the overall mean value and higher than values observed in checks, namely, GPU 26, KMR 204, MR 6, and VL 149, except for phosphorous which include KMR 204. In addition, the top 10 multiple nutrient-dense accessions were identified, which originated from five countries, namely, India, Zambia, Uganda, Kenya, and Malawi (Table 9). Of these 10 multi-nutrient sources, two accessions, IE 2872 (Zn, Ca, Mg, S, P) and IE 2875 (Zn, Ca, Mg, Cu, K), were good sources for five nutrients, while four accessions, namely, IE 817 (Fe, protein, P), IE 2008 (Fe, protein, S), IE 3935 (Fe, Zn, protein), and IE 5433 (Mg, S, K) had high values for three-grain nutrients. The four accessions IE 3973 (Mg, S), IE 6473 (Fe, Zn), IE 7386 (Fe, Zn), and IE 2760 (Cu and Mg) were good sources of two nutrients, and all these 10 accessions were landraces.

3.6 | %DV of finger millet accessions

The %DV per 100 g of grain per day had been estimated for the 314 finger millet accessions, and promising accessions were

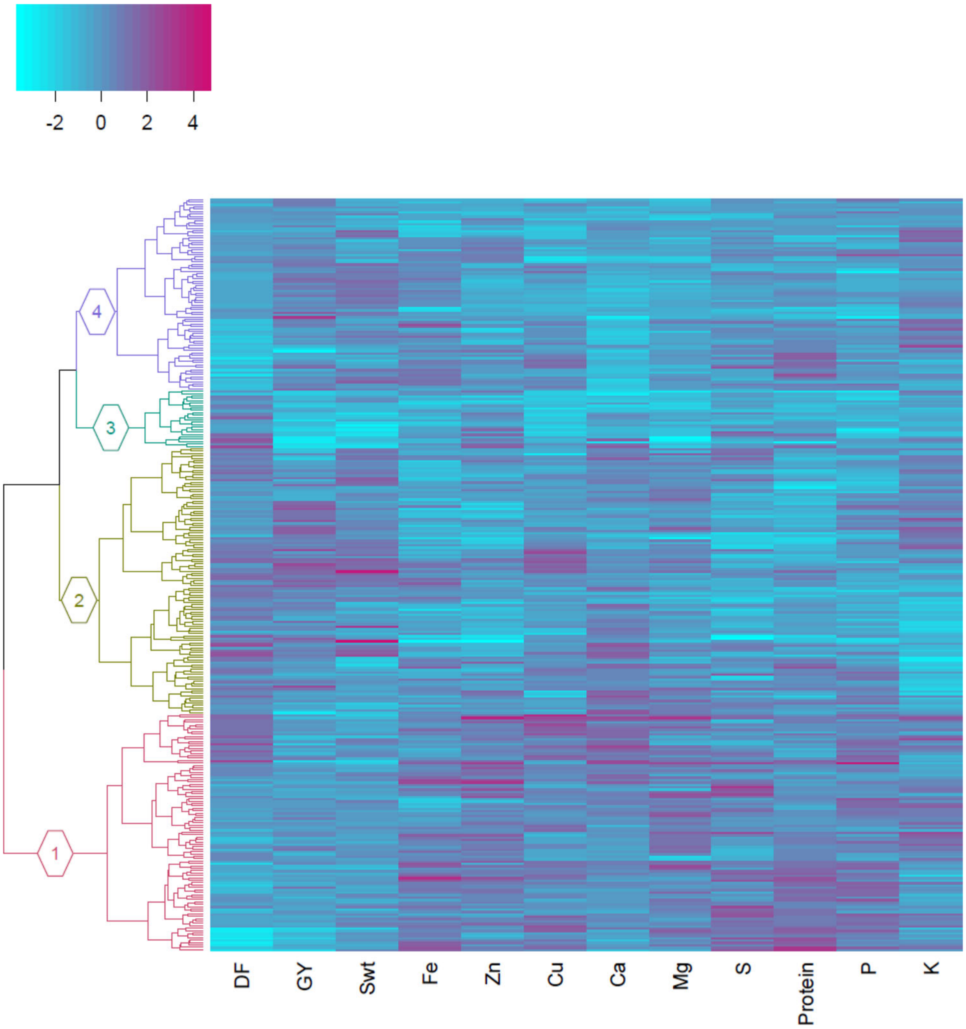

FIGURE 3 Dendrogram depicting the clustering of 314 finger millet accessions based on Gower's distance matrix along with the Ward.D2 clustering method and heatmap showing the grain nutrient content and agronomic traits in each accession of the cluster. Abbreviations: Ca, calcium (mg kg^{-1}); Cu, copper (mg kg^{-1}); DF, days to 50% flowering; Fe, iron (mg kg^{-1}); GY, grain yield (kg ha^{-1}); K, potassium (mg kg^{-1}); Mg, magnesium (mg kg^{-1}); protein (%); Swt, 100-seed weight (g); P, phosphorus (mg kg^{-1}); S, sulfur (mg kg^{-1}); Zn, zinc (mg kg^{-1}).

selected for each nutrient (Table S3). Consumption of 100 g of finger millet grains can potentially contribute to the recommended dietary allowance of up to 7%–23% Fe, 10%–26% Zn, 13%–23% protein, 30%–49% Ca, 30%–52% Mg, 20%–43% Cu, 29%–35% P, and 9%–16% K.

4 | DISCUSSION

Highly significant variability was found for all the grain nutrients. Cluster analysis grouped accessions into four major clusters, largely based on the region of origin (Clusters 1, 3, and 4), while Cluster 2 represents accessions from both Africa and Asia. Clusters were significantly different for flowering time, seed weight, and grain nutrients content. Accessions in Clusters 1 and 4 had higher values for most of the nutrient traits; therefore, the selection of parents from these two diverse nutrients dense clusters for use in the hybridization program could capture diverse favorable traits that contribute to higher heterosis. Table S1 contains details of accessions along with grain nutrient content and cluster number. Though, the grain nutrients showed a significant relationship between the 2 years ($R^2 = 0.06$ for P to 0.60 for Ca, $p \geq 0.001$), but are significantly influenced by the genotype, environment, and their interactions. Therefore, assessing the grain nutrient stability across different growing environments and soil types is very much needed to breed for nutrient-rich finger millet varieties (Vetriventhan & Upadhyaya, 2019). In general, like yield attributes, grain nutrients content is highly influenced by genotype, environment, and genotype × environmental interactions, reported by many studies in different crops, namely, maize (Oikeh et al., 2004), sorghum (Badigannavar et al., 2016; Phuke et al., 2017), pearl millet (Govindaraj et al., 2020; Pucher et al., 2014; Pujar et al., 2020), kodo millet

TABLE 8 Top 10 finger millet accessions with the high value of each grain nutrient traits.

Trait	Nutrient range in the selected accessions	Top promising accessions
Fe	37.36−42.76 mg kg^{-1}	IE 9, IE 817, IE 956, IE 2008, IE 2055, IE 3935, IE 4115, IE 6473, IE 6645, IE 7386
Zn	30.10−34.39 mg kg^{-1}	IE 2872, IE 2875, IE 3025, IE 3443, IE 3723, IE 3935, IE 4115, IE 4192, IE 6473, IE 7386
Protein	10.02%−10.74%	IE 501, IE 510, IE 817, IE 2008, IE 2030, IE 2608, IE 3935, IE 4698, IE 4734, IE 6013
Ca	4618.46−4888.52 mg kg^{-1}	IE 2568, IE 2756, IE 2869, IE 2872, IE 2875, IE 3814, IE 4134, IE 6537, IE 6546, IE 8599
Mg	1790.01−1908.54 mg kg^{-1}	IE 954, IE 2689, IE 2760, IE 2872, IE 2875, IE 3443, IE 3973, IE 4218, IE 5433, IE 6533
Cu	7.49−8.68 mg kg^{-1}	IE 2760, IE 2875, IE 2911, IE 2957, IE 3132, IE 3157, IE3428, IE4700, IE 5367, IE 6957
S	1421.32−1489.58 mg kg^{-1}	IE 2008, IE 2030, IE 2416, IE 2430, IE 2872, IE 3973, IE 4073, IE 4192, IE 4866, IE 5433
P	3278.40−3457.79 mg kg^{-1}	IE 817, IE 2416, IE 2872, IE 2957, IE 3663, IE 3788, IE 4218, IE 6655, IE 6964, IE 7508
K	5222.10−5551.20 mg kg^{-1}	IE 2581, IE 2875, IE 3758, IE 3788, IE 4110, IE 4497, IE 4656, IE 4817, IE 5433, IE 6082

Abbreviations: Ca, calcium (mg kg^{-1}); Cu, copper (mg kg^{-1}); Fe, iron (mg kg^{-1}); GY, grain yield (kg ha^{-1}); K, potassium (mg kg^{-1}); Mg, magnesium (mg kg^{-1}); protein (%); Swt, 100-seed weight (g); P, phosphorus (mg kg^{-1}); S, sulfur (mg kg^{-1}); Zn, zinc (mg kg^{-1}).

(Vetriventhan & Upadhyaya, 2019), and little millet (Vetriventhan et al., 2021).

Millets include two major millets (sorghum and pearl millet) and several minor or small millets that are packed with high grain nutrients. Finger millet is renowned for its remarkable Ca content, surpassing that of staple cereals and other millets by several folds. But this nutritionally important crop had only a few characterization studies on other grain nutrient traits. In this study, Fe, Zn, Ca, and protein content were well within the range reported in a previous study (Upadhyaya et al., 2011), but the mean was slightly higher indicating the level of diversity captured in the smaller subset and would give ample scope for the effective utilization of finger millet germplasms in the development of micronutrient dense cultivars. Among the small millets, the mean Fe, Zn, and protein content in finger millet are comparable with nutrient content in kodo millet (Fe, 25.5–27.6 mg kg^{-1}; Zn, 23–25 mg kg^{-1}; protein, 8%–8.5%) (Vetriventhan & Upadhyaya, 2019) but lower than in proso millet (Fe, 54 mg kg^{-1}; Zn, 36 mg kg^{-1}; protein −14%) (Vetriventhan & Upadhyaya, 2018) and little millet (Fe, 31–33 mg kg^{-1}; Zn, 28.5–29.6 mg kg^{-1}; protein −11%) (Vetriventhan et al., 2021). The mean Fe (38.2 mg kg^{-1}), Cu (6.4 mg kg^{-1}), and Mg (2034.9 mg kg^{-1}) were higher, while Zn (20.9 mg kg^{-1}) and protein (8.4%) were lower in sorghum grain than in finger millet (Badigannavar et al., 2016). Likewise, in pearl millet, the mean Fe (70–75 mg kg^{-1}) and Zn (46–53 mg kg^{-1}) content were double the value of in finger millet mean value (Govindaraj et al., 2020; Pujar et al., 2020). However, in pearl millet Cu (5.7 mg kg^{-1}) and Mg (1335.1 mg kg^{-1}) content were lower than in finger millet, while K content (4174.4 mg kg^{-1}) in finger millet is comparable with pearl millet (Govindaraj et al., 2020). Overall, the Ca content in finger millet is manyfold (17−27 times) higher than in other millets, namely, sorghum (230.3 mg kg^{-1}), pearl millet (172.6 mg kg^{-1}), kodo millet (189.6–213.3 mg kg^{-1}), little millet (145–190 mg kg^{-1}), and proso millet (165 mg kg^{-1}).

There are two major grain colors, namely, brown and white present in finger millet. Brown is the predominant grain color in finger millet while the intensity of brown color varies with germplasm from light brown to dark brown. Among these two types, white grain types are reported to have high protein, low fiber, low tannin, and higher consumer acceptability, especially by the non-traditional/urban millet consumer or to blend with wheat or rice (Chaudhari et al., 2012; Ojulong et al., 2021). Available literature indicates that the white finger millet contains higher protein than the brown-seeded finger millet cultivar, and white-seeded finger millet is reported to be devoid of tannin, while the red finger millet contains 2.5% (Rao, 1994). Ojulong et al. (2021) indicated a slight increase in grain nutrient content with increasing color intensity in the core collection of finger millet indicating that dark brown finger millet is likely to have more nutrients than white grain finger millet. Among the nutrients investigated in this study, except for Cu, all other nutrients do not differ significantly between white and brown colored seeds, while slightly higher Zn, Ca, P, and K are noticed in white seeded finger millet. But the differences were nonsignificant; thus, selection based on seed color may not be the desired parameters for grain nutrient improvement as reported in pearl millet (Govindaraj et al., 2018). However, breeding opportunities for nutritional traits, though, can be achieved without compromising regional and consumer preferences, including color. The finger millet races also had a nonsignificant difference in grain nutrient traits

TABLE 9 Finger millet accessions with high values of multiple grain nutrient traits.

Accessions	Cluster No.	Fe	Zn	Protein	Ca	Mg	Cu	S	P	K	DF	GY	Swt	Region	Country	Biological type	Seed color
IE 817	4	**38.60**	27.47	**10.63**	4042.16	1629.76	7.27	1372.32	**3289.86**	4939.28	64	1956	0.25	Asia	India	Landrace	Reddish brown
IE 2008	4	**38.62**	29.43	**10.06**	3873.12	1603.14	6.13	**1429.51**	3156.96	3850.68	69	2148	0.26	Asia	India	Landrace	Reddish brown
IE 2872	1	36.70	**32.01**	9.78	**4888.52**	**1846.58**	5.54	**1452.29**	**3457.79**	3878.26	82	1836	0.21	Africa	Zambia	Landrace	White
IE 2875	1	32.78	**34.39**	9.44	**4826.94**	**1908.54**	**7.88**	1368.47	3224.01	**5316.44**	86	1758	0.23	Africa	Zambia	Landrace	Reddish brown
IE 3935	1	**42.76**	**30.66**	**10.06**	3984.63	1599.28	6.87	1350.30	3214.02	4249.35	71	2050	0.25	Africa	Uganda	Landrace	Light brown
IE 3973	1	32.73	29.00	9.06	4280.26	**1823.76**	6.48	**1435.69**	3144.59	3989.73	72	2003	0.25	Africa	Uganda	Landrace	Dark brown
IE 5433	1	33.01	26.84	9.44	3936.33	**1800.73**	5.71	**1440.81**	3266.38	**5551.21**	75	2473	0.26	Africa	Kenya	Landrace	Light brown
IE 6473	1	**39.30**	**32.71**	8.97	4569.98	1697.44	5.96	1354.95	3209.86	4583.25	75	1846	0.24	Africa	Uganda	Landrace	Light brown
IE 7386	1	**38.99**	**31.84**	8.74	4320.42	1605.89	6.66	1330.70	3120.10	4582.18	69	2097	0.28	Africa	Kenya	Landrace	Light brown
IE 2760	1	31.53	26.82	9.02	4371.13	**1790.01**	**7.49**	1274.97	3185.17	4402.80	85	2223	0.25	Africa	Malawi	Landrace	Light brown

Note: Bold values indicate higher levels of multiple nutrients.

Abbreviations: Ca, calcium (mg kg^{-1}); Cu, copper (mg kg^{-1}); DF, days to 50% flowering; Fe, iron (mg kg^{-1}); GY, grain yield (kg ha^{-1}); K, potassium (mg kg^{-1}); Mg, magnesium (mg kg^{-1}); protein (%); Swt, 100-seed weight (g); P, phosphorus (mg kg^{-1}); S, sulfur (mg kg^{-1}); Zn, zinc (mg kg^{-1}).

except for Ca and Cu, as reported in kodo millet where races did not differ for grain nutrient content (Vetriventhan & Upadhyaya, 2019). However, race *nana* in little millet had high Fe, Zn, and protein content than race *robusta* (Vetriventhan et al., 2021), and in proso millet, race *ovatum* had significantly higher Fe, Zn, Ca, and protein than other races (Vetriventhan & Upadhyaya, 2018). But in contrast, grain nutrient contents by geographical origin indicated that accessions from Africa had significantly higher nutrient content than those from Asia for Zn, Ca, and Mg. However, Puranik et al. (2020) reported that finger millet lines with high Ca in the Asian subpopulation but high Zn content in the African population. It implies that the use of accessions from Africa should be considered during nutrient enhancement targeting breeding programs in finger millet. In biological status, except for Ca, Zn, and Cu, all other nutrients did not differ between breeding lines and landraces.

The magnitude and strength of correlations depend upon the population used in the study. If the population is more homogenous, it gives better estimates of correlation (Upadhyaya et al., 2021). Since the performance of finger millet germplasm for most grain nutrient traits differed based on regions and biological status, we performed correlation coefficients separately among landraces, breeding lines, and African and Asian accessions and compared their results to gain knowledge on any effect of regions and biological status on grain nutrient traits (Upadhyaya et al., 2021). Overall, Ca, Fe, Zn, Mg, Cu, P, and K showed a nonsignificant correlation with grain yield in the breeding lines, while Fe, Ca, Mg, P, and K showed a nonsignificant association with grain yield among landraces, indicating that simultaneous selection for these nutrient traits could be possible without compromising grain yield in finger millet germplasm. Ca content was significantly and positively associated with days to 50% flowering in the entire diversity set, as well as among the breeding lines, landraces, and accessions from Asia and Africa. Grain yield was also significant and positively associated with maturity duration among the breeding lines, while this association was nonsignificant in the entire diversity panel, landraces, and accessions from Africa and Asia. This indicates that both grain yield and Ca content can be simultaneously improved in different maturity durations, making it a potential crop for developing biofortified varieties. Most of the correlations among grain nutrients in the landraces were significant and positive but nonsignificant in breeding lines. It suggests that improvement in finger millet cultivars through breeding programs mainly focused on improving the grain yield (Puranik et al., 2020), and landraces hold the opportunity to improve the grain nutrient content in finger millet cultivars.

Identification of high nutrient-dense accessions offers a wider scope in releasing as a variety through direct selection from germplasm, use as parental lines in hybridization, or introgression breeding program for enhancement of grain nutrient content. From our study, the top 10 promising accessions for each nutrient were identified based on the per se performance. The top 10 multi-nutrient accessions identified originated from five countries (India, Kenya, Uganda, Malawi, and Zambia) indicating their geographical diversity of nutrient-dense sources. This data set could also be used to set up the baseline value for Fe, Zn, and Ca improvement for breeding biofortified cultivars in finger millet. The clustering results help to choose the diverse lines that would be used in the future grain nutrient improvement program.

Ca plays a crucial role in maintaining bone health and preventing osteoporosis. Young children, pregnant and nursing women, and the elderly population are at the highest risk of Ca malnutrition and osteoporosis. Osteoporosis is characterized by low bone mass, deterioration of bone tissue, and disruption of bone microarchitecture, which leads to compromised bone strength and an increase in the risk of fractures. Ca is also essential for several basic regulatory body functions such as the contraction and relaxation of muscles, the transmission of nerve impulses, coagulation of blood, activation of enzymatic reactions, stimulation of hormonal secretion, and so on. Worldwide, osteoporosis causes more than 8.9 million fractures annually, resulting in an osteoporosis fracture every 3 s. The disease affects approximately 21.2% and 6.3% of women and men over the age of 50, respectively, indicating about 500 million men and women worldwide may be affected (https://www.osteoporosis.foundation/facts-statistics). A systematic review of global dietary Ca intake among adults showed that across 74 countries, the average national dietary Ca intake ranges from 175 to 1233 mg/day. Many countries in Asia have an average dietary Ca intake of <500 mg/day, while those in Africa and South America mostly have low Ca intake between about 400–700 mg/day (Balk et al., 2017). Finger millet is naturally a Ca-rich crop compared to any other cereal and has the potential to enhance further through breeding and genomics technologies. The estimates on %DV of finger millet indicated that the consumption of finger millet could potentially contribute up to 49% Ca of RDA per 100 g of grains which is several-fold higher than Ca content in brown rice (2%DV), maize (2%DV), pearl millet (1%DV), little millet (3% DV), and milk and cheese (20%DV) (Górska-Warsewicz et al., 2019; Vetriventhan et al., 2021; Yankah et al., 2020) and higher than all other cereals. About 28.6% of Ca is bioavailable in finger millet and can be increased with certain processing such as germination, malting, and fermentation (Anitha et al., 2021). Apart from Ca, finger millet is also a good source of several minerals, and it contributes %DV of up to 23% Fe, 26% Zn, 23% protein, 52% Mg, 43% Cu, 35% P, and 16% K of RDA per 100 g of grains. This %DV was higher than in rice (Fe 10.6% DV, Zn 16.8% DV, protein 13.4% DV), wheat (Fe 20.6% DV, Zn 8.8% DV, protein 21.1% DV), and maize (Fe 15.9% DV, Zn 22.7% DV, protein 16.7% DV) but comparatively lower than little millet (28% Fe, 36.8% Zn, and 27.4% protein) (Longvah et al., 2017; Saleh et al., 2013; Vetriventhan et al., 2021). This suggests that daily consumption of finger millet improves bone health which offers lactose-intolerant people an alternative Ca source. Finger millet has a storehouse for various neutraceutical properties such as antioxidant, anti-ageing, anti-carcinogenic, anti-diabetogenic, anti-hyperlipidemic, and cardio-protective properties (Kumar et al., 2016). Thus, breeding Ca-rich finger millet cultivars and integration of this crop into global biofortification programs can potentially contribute to alleviating Ca deficiency-related health issues such as osteoporosis and malnutrition.

5 | CONCLUSION

Finger millet is a staple food for millions of people in Asia and Africa; hence, adding to biofortification target crop breeding investment list will benefit several millions of people. So far, little attention has been given to grain nutrient traits in global finger millet improvement programs. The present study provides insight into the genetic variability present in the diverse germplasm collections and identified the top 10 accessions for higher grain nutrients and also accessions which are rich in multiple nutrients. These diverse nutrients dense germplasm could be used in finger millet improvement program to develop and disseminate the biofortified cultivars. The consumption of finger millet could potentially contribute up to 49% Ca, 52% Mg, 43% Cu, 35% P, 26% Zn, 23% protein, 23% Fe, and 16% K of RDA per 100 g of grains for humans. There is a need for large-scale high throughput phenotyping platforms such as X-Ray Fluorescence Spectroscopy and Near-Infrared Spectroscopy for rapid grain nutrients assessment and genomics studies to scoop genes-based markers to fast-track the trait deployment process. The incorporation of identified finger millet accessions and mega varieties that are higher in nutrition will reduce the cost of household nutrition interventions and contributes to transforming the agri-food system sustainably.

AUTHOR CONTRIBUTIONS

Chinnadurai Backiyalakshmi: Data curation; methodology; software; writing–original draft; writing–review and editing. **Chakrapani Babu**: Supervision; writing–review and editing. **Santosh Deshpande**: Funding acquisition; investigation; writing–review and editing. **Mahalingam Govindaraj**: Methodology; writing–review and editing. **Rajeev Gupta**: Supervision; writing–review and editing. **Rajaprakasam Sudhagar**: Supervision; writing–review and editing. **Dagunapur Naresh**: Data curation; formal analysis; methodology; writing–review and editing. **Seetha Anitha**: Investigation; validation; writing–review and editing. **Ovais Peerzada**: Resources. **Sobhan Sajja**: writing–review and editing. **Kuldeep Singh**: writing–review and editing. **Mani Vetriventhan**: Conceptualization; data curation; formal analysis; funding acquisition; investigation; methodology; project administration; resources; software; supervision; validation; visualization; writing–original draft; writing–review and editing.

ACKNOWLEDGMENTS

The authors are thankful to Ramesh Reddy, Shanku Reddy, Raju Jadhav, and Manish Reddy for their help in field trials. The authors also duly acknowledged Charles Renald Analytical Laboratory, ICRISAT, Hyderabad, for their support in the Grain nutrient trait analysis. We acknowledge the funding support by the Department of Agriculture, Government of Karnataka for the project Genomics-Assisted Breeding for High Yielding and Climate-Resilient Finger Millet (ragi) Varieties/Hybrids and Promotion of Best Suitable Cultivars for Food and Nutritional Security in the Karnataka State of India, and the CGIAR genebank platform coordinated by Crop Trust for this study.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

All the required data are provided as Supporting Information tables. Researchers can approach the corresponding author for any additional information required.

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How to cite this article: Backiyalakshmi, C., Babu, C., Deshpande, S., Govindaraj, M., Gupta, R., Sudhagar, R., Naresh, D., Anitha, S., Peerzada, O., Sajja, S., Singh, K., & Vetriventhan, M. (2023). Characterization of finger millet global germplasm diversity panel for grain nutrients content for utilization in biofortification breeding. *Crop Science*, 1–20. https://doi.org/10.1002/csc2.21085