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ORIGINAL ARTICLE

Genetic diversity of under-utilized indigenous finger millet genotypes from Koraput, India for crop improvement

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Abstract

Phenotyping and genetic assessment of germplasm provide information about trait variability, which helps for effective breeding programs. In the present study, 12 indigenous finger millet genotypes from Koraput, India and three high-yielding improved genotypes were used for elucidation of genotypic variability of photosynthetic traits and genetic diversity using 36 SCoT (Start codon targeted polymorphism) markers. Significant variations were noticed in the CO_2 photosynthetic rate (P_N), stomatal conductance (g_s), transpiration rate (E), internal CO_2 concentration (Ci), water use efficiency and carboxylation efficiency among the genotypes. Significant variations of stomatal traits, pigment content, PS II activity and dry matter accumulation were also observed. The major morpho-physiological traits such as stomatal conductance, dry matter accumulation, shoot length and stomata per leaf area are played a pivotal role and are the major determinants of phenotypic diversity. The positive association of photosynthesis with dry matter accumulation indicates that some of the genotypes remarkably have more photosynthetic rate along with better plant biomass accumulation and can be used in future crop improvement program. Further, SCoT markers were polymorphic and revealed moderately high level of genetic diversity and provided information on population structure among the finger millet genotypes. The SCoT primers, SCoT-14, SCoT-18 SCoT-20 and SCoT-23 showed the higher PIC value and marker index, and potentiality for exploring the genetic diversity of studied millet genotypes. Based on the genetic similarity analysis it is revealed that some of the indigenous finger millet genotypes such as *Jhana*, *Lala*, *Kurkuti*, *Ladu*, *Bhadi* and *Taya* showed highest genetic disimilarity with modern high yielding genotype and can be considered as the potential genetic resources for breeding program.

Keywords Chlorophyll fluorescence · Finger millet · Gas exchange · Stomatal traits · SCoT marker · Genetic diversity

Abbreviations

CE	Carboxylation efficiency
Ci	Internal CO_2 concentration
CV	Coefficient of variance
DMA	Dry matter accumulation
Dwt	Dry weight
ETR	Electron transfer rate
Fo	Minimum fluorescence yield obtained with dark-adapted leaf
Fm	Maximum fluorescence yield obtained with dark-adapted leaf
Fv/Fm	Maximal photochemical efficiency of PS II
Fwt	Fresh weight
g_s	Stomatal conductance
LA	Leaf area
LSD	Least significance difference
MSI	Membrane stability index
NPQ	Non-photochemical quenching
P_N	Photosynthetic rate
RL	Root length
RWC	Relative water content
SL	Shoot length

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qP Photochemical quenching
WUE Water use efficiency
Y(II) Yield of PSII photochemistry

Introduction

Millets are a diverse group of small-grained cereal and one of the important staple food crops grown around the world (Singh and Sharma 2018). Unique attributes of millet such as ability to adapt under severe and adverse climate condition, least agro-input requirement and with the exceptional nutritional quality makes them crucial plant genetic resources for agriculture (Gupta et al. 2017). Finger millet is [*Eleusine coracana* (L.) Gaertn.] widely cultivated in arid and semi-arid regions of Africa and South Asia under rainfed conditions (Mukami et al. 2019). Finger millet is one of the important small millet belongs to *Poaceae* family and commonly known as "*Ragi*" and "*Mandia*" in India (Babu et al. 2017; Sakamma et al. 2018). It has been estimated that about 3.38 million hectares of global area are under finger millet cultivation with a production of 3.76 million tons of grain (FAO 2007; Babu et al. 2017). In India, finger millet ranks third next to sorghum and pearl millet as most important millet crop is grown on 1.27 million hectares (Mha) of cultivated land with an annual production of 1.89 million tons (Mt) (FAO 2007). Finger millet grains are rich in methionine and tryptophan, total aromatic amino acids, and high calcium content with superior nutritional qualities, therefore plays a significant role in nutritional security (Panda et al. 2019; Mukami et al. 2019). The crop cultivation under diverse eco-geographical zones globally signifies high genetic variations of finger millet, which could be the basis for future breeding program for climate resilient crop improvement (Assefa et al. 2013). Morphologically finger millet showed huge variations, which need to be captured at DNA level for detection of genetic diversity. Despite its economic and nutritional importance, breeding and selection of finger millet with improved traits are currently limited by the lack of adequately characterized germplasm both at in the physiological and molecular level. The dearth of knowledge regarding population structure has significantly contributed to the genetic erosion of millets. Extensive genetic diversity has been observed, especially among the genotypes for many agronomic traits. However, this diversity has not yet been tapped for crop improvement. Therefore, information on genetic diversity of finger millet is essential for their efficient utilization in the crop improvement programs.

Photosynthesis forms an integral part of the plant metabolism and balance sheet of growth and development, which is known to be regulated by internal and environmental parameters (Gupta et al. 2002; Panda et al. 2018). Previous reports suggested that the global crop production requires alteration of the primary photosynthetic process of the crops to cope up with the changing climatic scenario (Kondamudi et al. 2016; Panda et al. 2018). The increase in photosynthetic efficiency and growth in crop plants led to an increase in grain yield. Extensive studies on variations of traits associated with photosynthesis have been reported in rice, wheat and other cereal crops and were used successfully in the breeding programs (Kondamudi et al. 2016; Haritha et al. 2017; Panda et al. 2018). However, the photosynthetic efficiency in finger millets has been little studied and there is a dearth of knowledge on photosynthetic variants among traditional and modern finger millet genotypes.

Traditional genotypes possess genetic variability and adapted to local climatic condition and soil quality. Assessment of genetic variation among genotypes might help understand evolutionary relationship and pattern of genetic diversity for conservation of valuable resources as well as efficient use in the crop improvement program (Bashir et al. 2015). Currently, molecular markers have been used as an efficient tool to assess the genetic variation and relatedness among cultivars. Various molecular markers such as RAPD, RFLP, AFLP, ISSR and SSR, etc. have been used in the genetic diversity analysis in different crop species (Ramakrishnan et al. 2016). Each marker system has certain advantages and disadvantages compared to each other and influenced by crop varieties (Collard and Mackill 2009). The start codon targeted polymorphism (SCoT) marker is one of the novel marker systems is based on a short-conserved region in the plant genes flanking the ATG start codon (Collard and Mackill 2009). Earlier some attempts have been made to use molecular markers for assaying genetic diversity to estimate the relationship among African and Asian finger millet germplasm (Dida et al. 2007). For instance, genetic diversity of extensive collection of global finger millet accessions (Babu et al. 2014), genotypes from Indians (Rajendran et al. 2016) and millets of world-wide (Ramakrishnan et al. 2016; Kumar et al. 2016; Wakista et al. 2017) were assessed. However, there is a deficiency of documented information on genetic structure and diversity of indigenous finger millets of India and SCoT marker-based genetic diversity in finger millets is yet to be carried out.

Koraput is one of the tribal-dominated districts of Odisha in India (18° 14′ to 19° 14′ N latitude and 82° 05′ to 83° 25′ E longitude) and is recently declared as one of the agro-biodiversity hot spots in India (Mishra and Chaudhury 2012). Large numbers of finger millet genotypes have been reported from Koraput and conserved in different national and base collection centres. The indigenous finger millet genotypes cultivated by traditional farmers might contain considerable genetic diversity and could serve as potential

genetic resources for future crop improvement programs. For proper utilization and incorporation useful traits from these genotypes for future crop improvement program, information on genetic structure and diversity is of utmost importance. Therefore, the present study aims to evaluate genotypic variability in morpho-physiological traits and genetic diversity in selected indigenous finger millets of Koraput.

Materials and methods

Plant material and growth condition

The experiment was conducted by taking 12 indigenous finger millet genotypes from Koraput, India namely *Jhana*, *Lala*, *Kurkuti*, *Ladu*, *Bati*, *Bhadi*, *Taya*, *Limca*, *Chilli*, *Biri*, *Sili janha* and *Dasara* along with three high yielding improved varieties such as *Arjuna*, *Chilika* and *Bhairabi* (Table 1). These indigenous genotypes possess many primitive features and the tribal farmers are being grown to suit their local circumstances. The seeds were obtained from MS Swaminathan Research Foundation (MSSRF), Koraput, India.

Uniformly sized matured seeds of each genotype were selected and kept at 48 ± 2 °C for 5 days to break the seed dormancy. The seeds were directly sown in plastic pots (45 cm in diameter) having two kg of farm soil and farmyard manure in a ratio of 3:1. The seedlings were thinned after 10 days of germination and ten plants per pots were kept for further studies. Each pot was provided with 190 mg single super phosphate (P_2O_5) and 50 mg murate of potash (K_2O). N-fertilizer in the form urea at 1 g per pot was applied after 10, 30 and 50 days of sowing. Plants were regularly irrigated with tap water and subjected to natural solar radiations, with daily maximum photosynthetic photon flux density, air temperature and relative humidity being about 1360 ± 20 µmol m^{-2} s^{-1}, 31.6 ± 2 °C and 65–70%, respectively throughout the experiment. The experiments were conducted with three replications in each variety.

Measurement of plant growth parameters

The seedling growth parameters of finger millets were estimated by measuring shoot and root length, fresh weight and dry weight of seedling during the flowering stage. The shoot and root dry mass of each replication were measured after drying at 80 °C until a constant weight recorded. The dry matter accumulation (DMA) was determined by the following formula:

$$\mathrm{DMA}(\%) = [\text{Dry weight}/\text{Fresh weight}] \times 100$$

The leaf area (LA) was measured in 2nd leaf of each finger millet seedlings by measuring the length and breadth of leaf and the leaf area was calculated by following equation (Yoshida et al. 1976):

$$\text{Leaf area}\left(\mathrm{cm}^2\right) = 0.67 \times \text{Length} \times \text{Breath}$$

Table 1 List of analyzed finger millets germplasm with their origin, days of maturation and yield potential

Sl. No.	Variety	Origin	Days of maturation	Yield (q/ha)[a]
1	Jhana	Local genotypes of Koraput	110–125	18.0
2	Lala	Local genotypes of Koraput	100–110	16.0
3	Kurkuti	Local genotypes of Koraput	115–125	21.2
4	Ladu	Local genotypes of Koraput	110–120	17.2
5	Bati	Local genotypes of Koraput	115–125	19.8
6	Bhadi	Local genotypes of Koraput	110–115	20.2
7	Taya	Local genotypes of Koraput	115–120	20.5
8	Arjuna	Pure line selection from OUAT, Bhubaneswar, Odisha	80–85	26
9	Chilika	Hybrid variety (GE 68 × GE 156) from OUAT, Berhampur, Odisha	115–120	26.5
10	Limca	Local genotypes of Koraput	110–120	23.0
11	Chilli	Local genotypes of Koraput	110–120	19.2
12	Biri	Local genotypes of Koraput	90–100	14.5
13	Silli jhana	Local genotypes of Koraput	100–110	19.2
14	Dasara	Local genotypes of Koraput	80–90	18.5
15	Bhairabi	Mutant of Budha Mandia from OUAT, Bhubaneswar, Odisha	105–110	27.5

[a]Yield data was collected from MS. Swaminathan Research Foundation, Jeypore, India

Measurement of leaf gas exchange, chlorophyll fluorescence and stomatal traits

Leaf gas exchange was measured in matured leaves during flowering stage using an open system photosynthetic gas analyzer (CI-304, CID, USA). The parameters such as photosynthetic rate (P_N), transpiration rate (E), internal CO_2 concentration (Ci) and stomatal conductance (g_s) were recorded under normal ambient environmental condition. The leaf water use efficiency (WUE) and carboxylation efficiency (CE) were calculated as per the formula previously described by Panda et al. (2018).

The same leaves which were used for gas exchange measurements were used for chlorophyll fluorescence measurement during flowering stage using a portable chlorophyll fluorometer (JUNIOR-PAM, WALZ, Germany). Minimal fluorescence (Fo), maximal fluorescence (Fm), variable fluorescence (Fv = Fm − Fo) and Maximum photochemical efficiency of PSII (Fv/Fm) were measured in 20 min of dark-adapted sample (Maxwell and Johnson 2000). In light-adapted leaves at a PPFD of 400 µmol m^{-2} s^{-1}, steady-state fluorescence yield (Fs), maximal fluorescence (Fm′) and minimal fluorescence (Fo′) were measured. Quenching value due to non-photochemical dissipation of absorbed light energy (NPQ) and the coefficient for photochemical quenching (qP) was also calculated (Maxwell and Johnson 2000).

The stomatal traits such as stomatal density (SD), stomatal size (SS) and stomatal index (SI) were measured in the flag leaf of each finger millet seedlings following the method of Radoglou and Jarvis (1990). Briefly, the leaves were collected and abaxial epidermal side of the leaf was cleaned by tissue paper, smeared with nail varnish carefully and after that thin film was peeled off from the leaf surface, mounted on a glass slide. The stomatal traits such as Numbers of stomata (s) and stomatal size (SS) were counted under a trinocular microscope (Olympus model No. MIPS-3 MP CAMERA, Japan).

Measurement of SPAD index photosynthetic pigments

The same leaves which were used for measurement of the gas exchange and chlorophyll fluorescence were used for measurement of SPAD chlorophyll index using the Minolta SPAD 502 chlorophyll meter (Konica Minolta Sensing, Inc., Osaka, Japan) (Shrestha et al. 2012). The photosynthetic pigments such as chlorophyll and carotenoid were estimated by using 100 mg fresh leaves of finger millets dipped in 10 ml of 80% cold acetone, and kept dark inside a refrigerator (4 °C) for 48 h. The total chlorophyll and carotenoid were measured spectrophotometrically by taking absorbance at 665 nm, 445 nm and 470 nm. The chlorophyll a, chlorophyll b, total chlorophyll and carotenoid contents were calculated by using the equation of (Arnon 1949) and (Lichtenthaler and Wellburn 1983), respectively.

Measurement of leaf relative water content (RWC) and membrane stability index (MSI)

For the measurement of RWC the terminal leaflet of each finger millet genotype were collected and immediately weighed, and recorded as leaf fresh weight (LFW). After weighing the leaflet was poured in distilled water and left in dark for 48 h. After 48 h of incubation, the leaves were again weighed to measure the leaf turgid weight (LTW) was recorded and then the leaf was placed in an oven at 70°c for 48 h to know the leaf dry weight (LDW). The relative water content (RWC) of the leaf was calculated according to the equation of González and González-Vilar (2001).

$$\mathrm{RWC}(\%) = [(\text{Leaf fresh weight} - \text{Leaf dry weight})/(\text{Leaf turgid weight} - \text{Leaf dry weight})] \times 100$$

The membrane stability index (MSI) was measured by utilizing, leaf sample (0.1 g) of each finger millet genotype in two sets of test tubes and the leaves were dipped in 10 ml of distilled water in the test tube. Test tubes of one set kept in 40 °C in a water bath for 30 min and another set were incubated at 100 °C in boiling water bath for 15 min. Then the electrical conductivity of the water containing the leaf samples were measured as C1 at 40 °C and C2 at 100 °C separately. After that, MSI was calculated as per the following equation of Mishra et al. (2019):

$$\mathrm{MSI}(\%) = (1 - \mathrm{C1}/\mathrm{C2}) \times 100$$

Molecular profiling of finger millet genotypes through SCoT markers

For molecular marker analysis, 20–30 seeds of each genotype were shown in a Hyco tray at temperature 25 °C. About 3–4 g fresh leaf samples were collected after 25 days of sowing and leaf were stored at − 70 °C. Total genomic DNA was extracted from lyophilized leaves following a modified CTAB-based procedure (Sharma et al. 2011; Singh et al. 1999). The quality of DNA was checked on 1% agarose gel and with a UV–VIS 2450 spectrophotometer (Shimadzu, Japan). The genotyping was carried out by taking 36 SCoT primers. Detailed sequence information of SCoT markers was presented in Table S1. The SCoT primers were used in the study, according to primers developed by Collard and Mackill (2009).

SCoT marker analysis

The typical PCR mix for SCoT marker contained 50 ng genomic DNA in 1 × reaction buffer, 1.5 mM $MgCl_2$, 10 pmol primers and 1 U Taq DNA polymerase (Biotools, Spain) in 20 µl reaction volume. PCR amplification conditions were as follows: 94 °C for 5 min followed by 35 cycles of 94 °C (30 s)/48–50 °C (30 s)/72 °C (60 s) and a final extension at 72 °C for 10 min. All PCR reactions were performed in a Gene Amp PCR 9700 Thermal Cycler (Applied Biosystems, USA). The amplification products were resolved on 1.5% agarose gels. The amplified fragments were scored manually for their presence (denoted as '1') or absence (denoted as '0') for each primer. The Jaccard's similarity matrix was subjected to the unweighted pair group method of arithmetic averages clustering to construct the phonetic dendrogram using NYSys software (version 2.2). The marker attributes of each SCoT primer combination was assessed by evaluating polymorphism information content (PIC), marker index (MI) and resolving power (RP).

The PIC was computed using the following equation (Roldan-Ruiz et al. 2000)

$$PIC_i = 2f_i(1 - f_i)$$

where PIC_i is the polymorphic information content of the marker i, f_i is the frequency of the amplified allele (band present) and $1 - f_i$ is the frequency of the null allele. PIC was averaged over the fragments for each primer combination.

The MI was calculated using the following formula (Roldan-Ruiz et al. 2000):

$$MI = PIC \times EMR$$

where effective multiplex ratio (EMR) is the total number of polymorphic loci/fragments per primer.

The resolving power (RP) of each primer combination was calculated using the following formula (Prevost and Wilkinson 1999):

$$RP = \Sigma I_b$$

where I_b represents band informativeness expressed as $I_b = 1 - (2 \times |5 - p|)$, where, p is the fraction of the total accessions in which the band is present.

Data analysis

Morpho-physiological traits were analyzed by analysis of variance (ANOVA) using CropStat-7.2 software (International Rice Research Institute, Philippines). The statistical significance of the parameter means was carried out by the least significance difference (LSD) test. The standard deviations and correlation analysis were carried out by Microsoft Excel 2007. The genetic variability of finger millet genotypes was estimated by genotypic variance and phenotypic variance as per Steel (1997). The phenotypic coefficient of variation and genotypic coefficient of variation was calculated according to the formula of Burton and Devane (1953). Broad sense heritability of all traits was calculated according to the formula as described by Falconer et al. (1996) and the genetic advance was determined as described by Johnson et al. (1955). The principal component analysis (PCA) and cluster analysis were carried out by using PAST-3 (Palaeontological Statistics) software.

Results

Variations of morpho-physiological traits

Variations of growth parameters viz. shoot length (SL), root length (RL), fresh weight (Fwt), dry weight (Dwt) and dry matter accumulation (DMA) of different finger millet genotypes were presented in Table 2. The range of SL and RL ranged from 35.55 to 77 cm and 13.75 to 28 cm, respectively. Some indigenous finger millets such as *Kurkuti*, *Sili jhana*, *Bhadi* and *Dasara* showed significantly ($P < 0.05$) higher SL and RL compared to other millets. Further, fresh weight (Fwt), dry weight (Dwt) and dry matter accumulation (DMA) significantly varied ($P < 0.05$) among the studied finger millet genotypes (Table 3). The range of Fwt, Dwt and DMA in different finger millets was varied from 2.63 to 5.36 g $Plant^{-1}$, 0.68 to 1.75 g $Plant^{-1}$ and 20.31 to 34.85%, respectively. The DMA was significantly higher in *Jhana* and *Ladu* compared to other millets and high yielding genotypes. The leaf area in studied finger millet genotypes ranges from 6.49 to 17.50 cm^2. The leaf area was significantly higher in *Bhairabi* followed by *Sili jhana*, *Taya* and *Jhana* and lowest was observed in Limca genotypes (Table 3). Physiological parameters such as relative water content (RWC) and membrane stability index (MSI) was significantly varied ($P < 0.05$) among the studied finger millet genotypes. The range of RWC and MSI was varied from 75.94 to 91.81% and 57.94 to 86.61%, respectively among the studied finger millets. Some of the indigenous finger millets viz. *Ladu* and Limca showed significantly higher RWC compared to other millets, whereas MSI was highest in *Sili jhana*.

Variations of photosynthetic traits

Variations in the photosynthetic traits in traditional finger millet varieties were studied by gas-exchange measurements and significant ($P < 0.05$) variation was observed among studied finger millet genotypes (Table 3). There

Table 2 Growth and physiological parameters in different finger millet genotypes

Variety	SL (cm)	RL (cm)	Fwt (g Plant^{-1})	Dwt (g Plant^{-1})	DMA (%)	LA (cm^2)	RWC (%)	MSI (%)
Jhana	56.00 ± 1.48c	25.15 ± 0.91a	4.98 ± 0.43a	1.75 ± 0.05a	34.85 ± 0.87a	13.69 ± 1.10a	82.81 ± 0.87a	72.88 ± 2.15b
Lala	55.65 ± 0.49c	23.85 ± 1.33b	4.63 ± 0.33a	1.06 ± 0.08b	22.95 ± 0.96c	9.35 ± 0.90b	82.91 ± 0.52a	68.96 ± 2.009b
Kurkuti	74.00 ± 2.24a	23.50 ± 1.12b	5.11 ± 0.12a	1.04 ± 0.05b	20.31 ± 0.30c	9.34 ± 0.95b	75.94 ± 1.95b	75.00 ± 2.71b
Ladu	61.25 ± 2.47b	13.75 ± 1.06c	2.98 ± 0.03ab	0.87 ± 0.09b	30.03 ± 0.92b	12.82 ± 1.07a	87.37 ± 0.65a	68.69 ± 3.67b
Bati	55.00 ± 1.41c	25.50 ± 1.82a	3.75 ± 0.17a	0.93 ± 0.08b	24.87 ± 0.53c	11.61 ± 1.01b	78.63 ± 0.16b	68.32 ± 3.39b
Bhadi	75.50 ± 0.70a	28.00 ± 1.41a	5.09 ± 0.11a	1.15 ± 0.03a	22.44 ± 0.63c	7.83 ± 0.22c	80.02 ± 1.87b	71.13 ± 0.42b
Taya	63.75 ± 2.42b	22.20 ± 1.81a	2.89 ± 0.09b	0.68 ± 0.04b	23.47 ± 0.76c	13.99 ± 0.11a	82.57 ± 0.73a	73.71 ± 3.23b
Arjuna	35.55 ± 1.31e	23.35 ± 1.56b	3.29 ± 0.21a	0.93 ± 0.09b	27.88 ± 0.53c	11.22 ± 0.56b	79.45 ± 1.83b	57.94 ± 2.91c
Chilika	43.10 ± 3.11d	23.85 ± 1.61b	2.63 ± 0.16b	0.78 ± 0.08	27.65 ± 0.76c	8.22 ± 0.84b	77.55 ± 1.31b	59.74 ± 2.55c
Limca	63.50 ± 0.70b	27.35 ± 0.91a	3.99 ± 0.15a	0.87 ± 0.01b	21.86 ± 0.85c	6.49 ± 0.53b	91.81 ± 0.89a	69.78 ± 0.30c
Chilli	63.50 ± 2.77b	26.85 ± 0.49a	5.36 ± 0.47a	1.10 ± 0.08ab	20.69 ± 0.54c	8.90 ± 0.62b	82.61 ± 0.90a	75.59 ± 2.37b
Biri	68.00 ± 1.07ab	24.50 ± 2.12a	3.70 ± 0.37a	0.78 ± 0.03b	21.04 ± 0.89c	11.59 ± 0.14b	85.64 ± 2.30a	76.14 ± 1.60b
Sili jhana	75.50 ± 0.70a	18.20 ± 0.56c	4.10 ± 0.37a	0.91 ± 0.10b	22.51 ± 0.67c	15.40 ± 1.01a	78.85 ± 1.32b	86.61 ± 1.26a
Dasara	77.00 ± 1.31a	18.00 ± 1.36c	3.42 ± 0.14a	0.95 ± 0.04b	27.93 ± 0.52b	8.41 ± 0.80c	81.45 ± 1.78b	70.78 ± 1.72b
Bhairabi	69.00 ± 2.82b	20.30 ± 1.25b	4.43 ± 0.34a	0.94 ± 0.09b	21.12 ± 0.83	17.50 ± 0.78a	78.29 ± 2.31b	70.42 ± 0.58b
Mean	62.69	22.96	4.02	0.98	24.71	11.09	81.73	71.05
LSD ($P < 0.05$)	7.85	3.53	2.40	0.63	2.69	5.46	9.70	9.32
CV (%)	5.8	13.3	27.8	30.1	7.0	23.0	7.3	6.1

Data are the mean of three replications ± SD. Means followed by a common letter in the same column are not significantly different at the 5% level by *Fisher's* least significance difference (LSD) test

SL shoot length (cm), *RL* root length (cm), *Fwt* fresh weight (g Plant^{-1}), *Dwt* dry weight (g Plant^{-1}), *DMA* dry matter accumulation (%), *LA* leaf area (cm^2), *RWC* relative water content (%), *MSI* membrane stability index (%), *CV* coefficient of variance

Table 3 Leaf photosynthetic characteristics and leaf pigments in different finger millet genotypes

Variety	P_N (μmol CO_2 m^{-2} s^{-1})	E (mMol H_2O m^{-2} s^{-1})	g_s (mMol H_2O m^{-2} s^{-1})	Ci (mMol m^{-2} s^{-1})	WUE (P_N/E)	CE (P_N/Ci)	SPAD (rel.)	Chlorophyll (mg g^{-1} fwt)	Carotenoid (mg g^{-1} fwt)
Jhana	19.18 ± 0.19a	3.87 ± 0.09a	77.64 ± 1.52a	146.80 ± 11.88c	4.96 ± 0.14a	0.14 ± 0.003a	21.90 ± 0.28b	0.22 ± 0.01c	0.06 ± 0.0005b
Lala	15.42 ± 0.12b	3.30 ± 0.05a	57.07 ± 1.70c	157.35 ± 11.52c	4.68 ± 0.01b	0.10 ± 0.003b	20.20 ± 1.13b	0.34 ± 0.005a	0.09 ± 0.004a
Kurkuti	10.43 ± 0.14c	2.71 ± 0.12a	52.21 ± 1.21c	162.65 ± 18.2c	3.96 ± 0.16b	0.08 ± 0.002c	23.70 ± 0.14a	0.22 ± 0.003c	0.06 ± 0.006b
Ladu	11.63 ± 0.18c	3.38 ± 0.13a	52.95 ± 1.42c	216.65 ± 22.09a	3.55 ± 0.23c	0.08 ± 0.005c	19.65 ± 0.35c	0.33 ± 0.004a	0.09 ± 0.003a
Bati	13.97 ± 0.51b	3.85 ± 0.08a	64.25 ± 0.87b	238.65 ± 25.67a	3.60 ± 0.40c	0.07 ± 0.003c	22.50 ± 0.28a	0.29 ± 0.005b	0.08 ± 0.005c
Bhadi	11.40 ± 0.79c	3.15 ± 0.11a	47.00 ± 0.31d	192.70 ± 16.58b	3.63 ± 0.24c	0.06 ± 0.01c	20.05 ± 0.07b	0.20 ± 0.02c	0.05 ± 0.004b
Taya	17.61 ± 0.93a	3.06 ± 0.12a	39.69 ± 1.41d	226.80 ± 19.79a	5.86 ± 0.32a	0.08 ± 0.01c	20.80 ± 0.09b	0.27 ± 0.004b	0.07 ± 0.003b
Arjuna	15.32 ± 0.88b	3.45 ± 0.07a	64.97 ± 1.72b	234.70 ± 15.19a	4.45 ± 0.27b	0.07 ± 0.0004c	20.65 ± 0.90b	0.24 ± 0.0005b	0.03 ± 0.001c
Chilika	15.37 ± 0.85b	3.52 ± 0.02a	63.27 ± 0.91b	217.85 ± 13.22a	4.36 ± 0.15b	0.07 ± 0.002c	21.75 ± 1.19b	0.20 ± 0.01c	0.06 ± 0.003b
Limca	12.64 ± 0.77b	3.83 ± 0.14a	63.59 ± 1.47b	227.15 ± 26.96a	3.35 ± 0.26c	0.06 ± 0.01c	20.55 ± 0.21b	0.23 ± 0.0008c	0.06 ± 0.001b
Chilli	15.08 ± 0.53b	3.73 ± 0.11a	64.06 ± 0.87b	167.10 ± 21.90	4.09 ± 0.37c	0.09 ± 0.002b	21.45 ± 0.21b	0.23 ± 0.001b	0.06 ± 0.0003b
Biri	13.74 ± 0.74b	3.69 ± 0.15a	69.38 ± 1.32b	206.30 ± 26.89b	3.81 ± 0.41b	0.07 ± 0.001c	22.35 ± 0.21b	0.24 ± 0.01b	0.07 ± 0.004a
Sili jhana	14.66 ± 0.22b	3.33 ± 0.08a	73.91 ± 1.16a	219.25 ± 15.48a	4.42 ± 0.31b	0.07 ± 0.003c	23.40 ± 0.28a	0.35 ± 0.005a	0.09 ± 0.004a
Dasara	18.88 ± 0.72a	3.30 ± 0.09a	94.35 ± 1.22a	248.85 ± 19.20a	5.72 ± 0.09a	0.08 ± 0.003c	24.25 ± 0.21a	0.35 ± 0.01a	0.09 ± 0.004a
Bhairabi	13.99 ± 0.67b	3.89 ± 0.03a	43.52 ± 0.62d	213.10 ± 12.30a	3.60 ± 0.24c	0.07 ± 0.005c	22.50 ± 0.28a	0.30 ± 0.009b	0.06 ± 0.004b
Mean	14.62	3.47	63.19	205.06	4.27	0.08	21.71	0.27	0.07
LSD ($P < 0.05$)	3.31	1.07	11.75	36.84	1.03	0.01	1.82	0.05	0.03
CV (%)	13.8	14.4	16.1	31.1	16.7	17.2	3.9	9.3	9.2

Data are the mean of three replications ± SD. Means followed by a common letter in the same column are not significantly different at the 5% level by *Fisher's* least significance difference (LSD) test

P_N: Photosynthetic rate (μmol CO_2 m^{-2} s^{-1}); g_s: stomatal conductance (mMol H_2O m^{-2} s^{-1}); Ci: internal CO_2 concentration (mMol m^{-2} s^{-1}); WUE: water use efficiency (P_N/E); CE: carboxylation efficiency (P_N/Ci); Chlorophyll (mg g^{-1} fwt); Carotenoid (mg g^{-1} fwt); CV: coefficient of variance

Table 4 Leaf chlorophyll fluorescence parameters in different finger millet genotypes

Variety	Fo (rel.)	Fm (rel.)	Fv/Fm (ratio)	Y(II) (rel.)	ETR (rel.)	qP (rel.)	NPQ (rel.)
Jhana	63.5 ± 4.43a	217.0 ± 7.94a	0.709 ± 0.01a	0.169 ± 0.01a	49.850 ± 2.38a	0.532 ± 0.01a	0.567 ± 0.14c
Lala	56.0 ± 6.07a	152.0 ± 8.28a	0.630 ± 0.02a	0.227 ± 0.001a	40.050 ± 0.21b	0.520 ± 0.03a	1.182 ± 0.11b
Kurkuti	49.0 ± 2.82a	143.5 ± 7.77a	0.658 ± 0.03a	0.212 ± 0.002a	37.300 ± 2.35b	0.454 ± 0.002a	1.198 ± 0.12b
Ladu	59.0 ± 5.31a	186.0 ± 5.31a	0.681 ± 0.07a	0.227 ± 0.003a	39.950 ± 2.79b	0.501 ± 0.03a	1.641 ± 0.06a
Bati	64.5 ± 0.70a	203.0 ± 0.78a	0.683 ± 0.003a	0.214 ± 0.007a	37.650 ± 0.07b	0.434 ± 0.01a	1.261 ± 0.08b
Bhadi	57.0 ± 4.24a	194.0 ± 8.08a	0.700 ± 0.005a	0.277 ± 0.005a	48.850 ± 3.94a	0.571 ± 0.04a	1.377 ± 0.11a
Taya	66.0 ± 4.14a	227.5 ± 6.16a	0.712 ± 0.002a	0.286 ± 0.007a	50.450 ± 2.48a	0.547 ± 0.03a	1.286 ± 0.01b
Arjuna	61.5 ± 6.60a	173.5 ± 7.99a	0.646 ± 0.002a	0.203 ± 0.003a	35.750 ± 0.63b	0.444 ± 0.004a	1.189 ± 0.05b
Chilika	50.5 ± 2.12a	159.5 ± 0.70a	0.684 ± 0.01a	0.276 ± 0.01a	48.700 ± 2.96a	0.546 ± 0.003a	1.105 ± 0.16b
Limca	64.0 ± 4.14a	202.0 ± 859a	0.684 ± 0.002a	0.204 ± 0.02a	35.900 ± 3.35b	0.407 ± 0.01b	1.143 ± 0.14b
Chilli	60.0 ± 5.72a	198.5 ± 4.84a	0.700 ± 0.004a	0.252 ± 0.005a	44.450 ± 2.99a	0.505 ± 0.007a	1.343 ± 0.15a
Biri	67.0 ± 4.07a	205.5 ± 7.64a	0.672 ± 0.02a	0.191 ± 0.01a	33.700 ± 2.26b	0.424 ± 0.03a	1.529 ± 0.09a
Sili jhana	70.5 ± 4.94a	220.5 ± 5.77a	0.681 ± 0.01a	0.170 ± 0.01a	29.900 ± 2.12c	0.351 ± 0.002b	1.280 ± 0.11b
Dasara	68.0 ± 5.48a	226.0 ± 9.79a	0.700 ± 0.01a	0.255 ± 0.004a	44.900 ± 3.65a	0.504 ± 0.02a	1.113 ± 0.15b
Bhairabi	72.5 ± 3.36a	228.0 ± 5.45a	0.679 ± 0.02a	0.181 ± 0.006a	36.850 ± 1.31b	0.416 ± 0.01a	1.284 ± 0.06a
Mean	61.9	195.8	0.681	0.223	40.950	0.477	1.286
LSD ($P < 0.05$)	29.34	56.45	0.178	0.094	6.44	0.15	0.56
CV (%)	14.6	13.4	5.4	19.8	18.7	14.7	20.5

Data are the mean of three replications ± SD. Means followed by a common letter in the same column are not significantly different at the 5% level by *Fisher's* least significance difference (LSD) test

Fo: minimum fluorescence yield obtained with dark-adapted leaf; Fm: maximum Chl fluorescence yield obtained with dark-adapted leaf; Fv/Fm: maximal photochemical efficiency of PS II; NPQ: non-photochemical quenching; qP: photochemical quenching; Y(II): yield of PSII photochemistry; ETR: electron transfer rate; CV: coefficient of variance

Table 5 Variation in stomatal traits and leaf area in different finger millet genotypes

Variety	Stomata density (no. mm^{-2})	Total stomata no. (Million LA^{-1})	Stomata size (μm^2)	Stomatal index (SI)
Jhana	43.74 ± 3.83a	603.66 ± 69.46a	2079.40 ± 66.96b	30.30 ± 1.28a
Lala	43.74 ± 3.83a	404.87 ± 43.22b	2177.02 ± 19.61b	29.29 ± 1.01a
Kurkuti	43.74 ± 3.83a	399.93 ± 2.84b	2198.11 ± 127.58b	23.30 ± 0.31b
Ladu	31.24 ± 3.83b	427.43 ± 56.21b	2109.04 ± 42.47b	23.14 ± 1.60b
Bati	31.24 ± 3.83b	376.10 ± 76.75b	2285.44 ± 18.46b	23.14 ± 1.76b
Bhadi	49.99 ± 0.001a	391.22 ± 11.36b	2128.53 ± 67.98b	29.67 ± 1.55a
Taya	43.74 ± 3.83a	612.45 ± 68.60a	1926.86 ± 10.71b	27.92 ± 0.91a
Arjuna	31.24 ± 3.83b	353.03 ± 56.76b	2543.10 ± 74.53a	21.83 ± 0.56b
Chilika	37.49 ± 0.001b	308.23 ± 92.90b	2672.35 ± 73.28a	22.14 ± 1.60b
Limca	25.00 ± 0.001c	162.11 ± 13.26bc	19,234.91 ± 866.8b	26.79 ± 2.52a
Chilli	37.49 ± 0.001b	333.61 ± 61.10b	2249.84 ± 60.80b	28.64 ± 1.92a
Biri	37.49 ± 0.001b	434.59 ± 5.32b	2036.10 ± 180.26b	28.64 ± 1.92a
Sili jhana	37.49 ± 0.001b	577.28 ± 72.97a	2128.60 ± 34.28b	24.04 ± 1.35b
Dasara	49.99 ± 0.001a	620.36 ± 40.26a	1830.65 ± 28.58b	24.26 ± 1.03b
Bhairabi	38.74 ± 1.76b	378.77 ± 61.29b	2870.11 ± 24.37a	22.79 ± 2.52b
Mean	38.83	432.24	4686.67	26.66
LSD ($P < 0.05$)	7.13	186.91	519.18	2.05
CV (%)	15.5	30.9	5.2	7.1

Data are the mean of three replications ± SD. Means followed by a common letter in the same column are not significantly different at the 5% level by *Fisher's* least significance difference (LSD) test

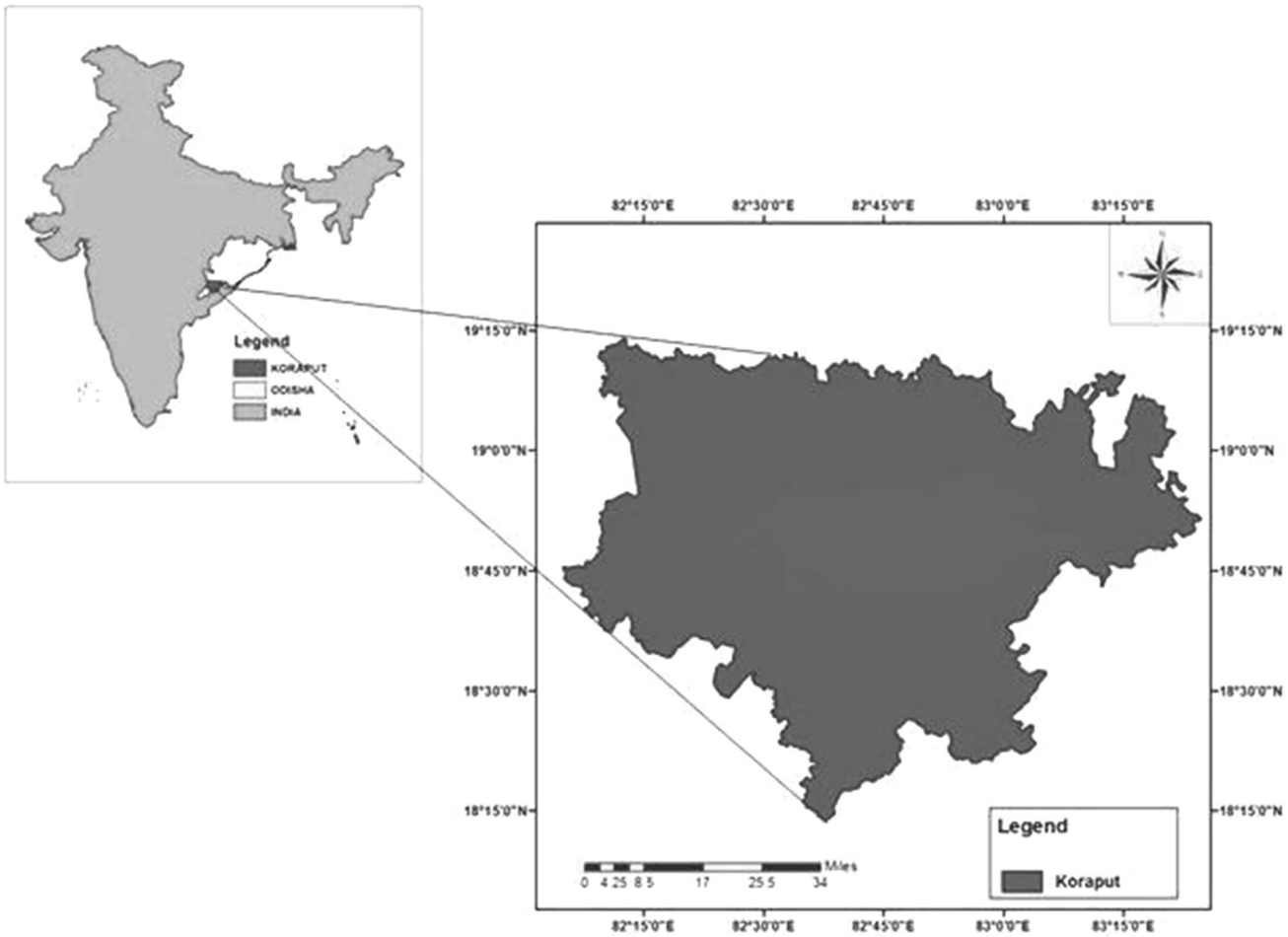

Fig. 1 Map showing Koraput district of Odisha, India, where the local genotypes of finger millets were collected for the study

were significant differences between indigenous and modern high-yielding finger millets for photosynthetic rate (P_N). The range of P_N varied from 10.43 to 19.18 µmol CO_2 m^{-2} s^{-1} among the studied finger millet genotypes. Some indigenous finger millets such as *Jhana*, *Taya* and *Dasara* showed significantly ($P < 0.05$) higher P_N compared to modern high-yielding finger millets genotypes. Similarly, stomatal conductance (g_s) was also significantly varied among the studied finger millet genotypes. Among the finger millet genotypes, the transpiration rate (E) was not significantly ($P < 0.05$) different. The stomatal conductance (g_s) was ranged from 39.69 to 94.35 mMol H_2O m^{-2} s^{-1} among the finger millet genotypes and some indigenous finger millets such as *Jhana*, *Sili jhana* and *Dasara* showed significantly ($P < 0.05$) higher g_s compared to modern high-yielding finger millets genotypes. The internal CO_2 concentration (Ci) was significantly varied from 146.80 to 248.85 mMol m^{-2} s^{-1} among the studied finger millet genotypes and highest Ci was observed in *Dasara* genotypes. Further, water-use efficiency (WUE, P_N/E) and carboxylation efficiency (CE, P_N/Ci), among tested finger millet genotypes significantly ($P < 0.05$) varied (Table 3). The range of WUE and CE was varied from 3.35 to 5.86 and 0.06 to 0.14, respectively among the tested finger millet genotypes.

Significant variations of leaf chlorophyll content and SPAD index was observed among the studied finger millet genotypes (Table 3). The range of SPAD index was varied from 19.65 to 24.25 and highest SPAD index was observed in *Dasara* compared to other genotypes (Table 3). The chlorophyll and carotenoid content significantly varied among the studied finger millet genotypes and the value of chlorophyll and carotenoid ranged from 0.20 to 0.35 mg g^{-1} fwt and 0.03 to 0.09 mg g^{-1} fwt, respectively.

The range of Fo, Fm and Fv/Fm was varied from 49.0 to 72.5, 143.5 to 228.0 and 0.630 to 0.712, respectively among the studied finger millets (Table 4). The value of Fo, Fm and Fv/Fm were not significantly ($P < 0.05$) different among traditional and modern high yielding finger millet genotypes. However, significant ($P < 0.05$) variation of ETR, qP and NPQ was found among traditional and

Table 6 Relationship between leaf photosynthetic parameters and stomatal traits in finger millet genotypes

Parameters	P_N	g_s	CI	WUE	CE	Fv/Fm	qp	NPQ	Chl	CAR	DMA	LA	SS	SI
g_s	0.635**													
CI	0.062^{ns}	0.327^{ns}												
WUE	0.833**	0.276^{ns}	0.051^{ns}											
CE	0.525**	0.014^{ns}	− 0.738**	0.414*										
Fv/Fm	0.344^{ns}	-0.098^{ns}	0.142^{ns}	0.250^{ns}	0.125^{ns}									
qp	0.273^{ns}	-0.215^{ns}	-0.314^{ns}	0.396*	0.399*	0.322^{ns}								
NPQ	− 0.456**	-0.333^{ns}	0.374*	− 0.383*	− 0.621**	-0.113^{ns}	-0.272^{ns}							
Chl	0.160^{ns}	-0.035^{ns}	0.281^{ns}	0.141^{ns}	-0.053^{ns}	-0.235^{ns}	-0.259^{ns}	0.503**						
CAR	0.099^{ns}	-0.180^{ns}	0.210^{ns}	0.090^{ns}	-0.042^{ns}	0.006^{ns}	-0.202^{ns}	0.459**	0.874**					
DMA	0.544**	0.408*	0.031^{ns}	0.365*	0.484**	0.230^{ns}	0.396*	− 0.550**	-0.039^{ns}	-0.121^{ns}				
LA	0.195^{ns}	-0.275^{ns}	0.065^{ns}	0.100^{ns}	0.124^{ns}	0.089^{ns}	-0.343^{ns}	0.292^{ns}	0.488**	0.432*	0.074^{ns}			
SS	− 0.425*	0.095^{ns}	0.116^{ns}	− 0.369*	-0.250^{ns}	-0.072^{ns}	− 0.388*	0.054^{ns}	-0.249^{ns}	-0.132^{ns}	-0.280^{ns}	-0.251^{ns}		
SI	0.451*	− 0.454*	− 0.525**	-0.031^{ns}	0.449*	0.356*	0.496**	-0.133^{ns}	-0.159^{ns}	0.079^{ns}	0.003^{ns}	-0.034^{ns}	0.189^{ns}	
SD	0.416*	-0.097^{ns}	-0.351^{ns}	0.560**	0.346^{ns}	0.238^{ns}	0.557**	-0.109^{ns}	-0.003^{ns}	0.076^{ns}	0.030^{ns}	-0.035^{ns}	− 0.437*	0.277^{ns}

P_N: Photosynthetic rate; g_s: stomatal conductance; Ci: internal CO_2 concentration; WUE: water use efficiency (P_N/E); CE: carboxylation efficiency (P_N/Ci); SD: stomatal density; SLA: total stomata no.; SI: stomatal index; SS: stomatal size, Fv/Fm: maximum photochemical efficiency of PS II, qP: photosynthetic quenching; NPQ: non photosynthetic quenching; Chl: chlorophyll; CAR: carotenoid; LA: leaf area

*$P < 0.05$, **$P < 0.01$, *ns* non significant

Table 7 Genetic variability parameters such as range, mean, standard error (SE), genotypic variation (σ^2_G), phenotypic variation (σ^2_P), genotypic coefficient of variation (GCV), phenotypic coefficient of variation (PCV), heritability in broad sense (h^2_{bs}), genetic advance (GA) and genetic advance as percentage of the mean (GAM) for different traits of indigenous finger millets of Koraput, Odisha

Traits	Range	Mean ± SE	σ^2_G	σ^2_P	GCV (%)	PCV (%)	h^2_{bs} (%)	GA	GAM
P_N	10.43–19.18	14.62 ± 0.55	4.56	6.59	14.61	17.55	69.25	3.66	25.04
E	2.7–3.89	3.47 ± 0.09	0.10	0.12	9.25	9.78	89.57	0.63	18.04
g_s	39.6–94.35	63.19 ± 1.22	176.10	227.50	21.00	23.87	77.41	24.05	38.06
CI	146.8–248.85	205.06 ± 8.31	− 998.50	1036.50	12.00	15.70	96.33	63.89	31.16
WUE	3.34–5.86	4.27 ± 0.20	0.34	0.60	13.72	18.10	57.41	0.91	21.41
CE	0.05–0.14	0.08 ± 0.005	0.01	0.03	8.00	24.11	14.29	0.01	7.09
Fo	49.0–72.50	61.93 ± 1.76	5.55	46.20	3.80	10.97	12.01	1.68	2.72
Fm	143.5–228.00	195.77 ± 6.33	423.00	769.00	10.51	14.17	55.01	31.42	16.05
Fv/Fm	0.63–0.71	0.68 ± 0.01	0.05	0.01	8.00	10.38	40.00	0.06	8.56
YII	0.16–0.29	0.22 ± 0.01	0.01	0.02	31.76	55.00	33.33	0.08	37.77
ETR	29.9–50.45	40.95 ± 1.68	12.75	42.15	8.72	15.85	30.25	4.05	9.88
qp	0.35–0.57	0.48 ± 0.02	0.04	0.05	8.12	13.26	37.50	0.05	10.25
NPQ	0.56–1.88	1.29 ± 0.07	0.05	0.08	17.73	22.26	63.41	0.37	29.08
Chl	0.19–0.35	0.27 ± 0.01	0.03	0.05	18.27	18.84	94.00	0.10	36.49
CAR	0.03–0.09	0.07 ± 0.00	0.02	0.07	10.28	23.00	20.00	0.01	9.48
SPAD	19.65–24.25	21.71 ± 0.36	1.91	1.95	6.37	6.43	98.15	2.82	13.00
Fwt	2.63–5.36	4.02 ± 0.23	0.16	0.78	9.78	21.95	19.87	0.36	8.99
Dwt	0.67–1.75	0.98 ± 0.06	0.02	0.06	13.46	25.13	28.69	0.15	14.85
DMA	20.30–34.85	24.71 ± 1.09	16.45	17.90	16.42	17.12	91.90	8.01	32.42
SL	35.55–77.00	62.69 ± 3.14	141.40	148.10	18.97	19.41	95.48	23.94	38.18
RL	13.75–28.00	22.96 ± 1.01	10.75	15.35	14.28	17.07	70.03	5.65	24.62
LA	6.48–17.50	11.09 ± 0.81	6.50	9.75	22.99	28.16	66.67	4.29	38.67
RWC	75.93–91.81	81.73 ± 1.07	0.30	17.25	3.00	5.08	1.74	0.15	0.18
MSI	57.94–86.61	71.05 ± 1.74	35.85	45.25	8.43	9.47	79.23	10.98	15.45
SS	1830–20,366	4686 ± 1588	378,196	378,489	13.12	13.13	99.92	1266.3	27.02
SI	21.82–30.30	26.66 ± 0.64	4.40	6.15	7.87	9.30	71.54	3.65	13.71
SD	24.99–49.99	38.83 ± 1.77	33.05	51.20	14.81	18.43	64.55	9.51	24.51
SLA	162–678	432.24 ± 35	9254	18,201	22.26	31.21	50.84	141.3	32.69

modern high yielding finger millet genotypes. Some indigenous finger millets such as *Jhana*, *Bhadi*, *Chilli* and *Dasara* showed higher ETR compared to modern high-yielding finger millets genotypes. The value of qP and NPQ ranged from 0.351 to 0.571 and 0.567 to 1.641, respectively among the studied genotypes. However, the value of NPQ was significantly higher in high-yielding varieties as compared to indigenous finger millets (Table 4).

There were significant ($P < 0.05$) variations of stomatal density (SD), stomata number (SLA), stomatal size (SS) and stomatal index (SI) was found among the studied finger millet genotypes (Fig. S2). The value of SD, SLA, SS and SI was varied from 25.00 to 49.99 no. mm^{-2}, 162.11to 620.36 million LA^{-1}, 1830.65 to 19,234.91 μm^2 and 21.83 to 30.30, respectively among the studied finger millet genotypes (Table 5). Some indigenous finger millets such as *Jhana*, *Lala*, *Kurkuti*, *Bhadi* and *Dasara* showed higher SD, SLA and SI compared to modern high-yielding finger millets genotypes, whereas SS was significantly higher in high-yielding finger millets genotypes except *Limca* (Fig. 1).

Relationship between leaf photosynthetic parameters with stomatal traits and dry matter accumulation

Relationship between photosynthetic and stomatal traits in finger millet genotypes was studied by multiple correlation analysis (Table 6). The results showed that a strong positive correlation between P_N with g_s, WUE, CE and DMA (r = 0.635**, 0.833**, 0.525** and 0.544**, respectively, $P < 0.01$) was observed whereas, leaf P_N was negatively correlated with NPQ (r = − 0.456**, respectively, $P < 0.01$). The stomatal traits such as SD and SI was

positively correlated with leaf P_N (r = 0.451*, 0.416*, respectively, $P < 0.05$), whereas SS was negatively correlated with leaf P_N (r = − 0.425*, $P < 0.05$). The leaf P_N in different finger millets was not significantly correlated with leaf area and leaf chlorophyll content.

Genetic variability of morpho-physiological traits

The extent of variability for various morpho-physiological traits in studied finger millet genotypes was evaluated in terms of phenotypic variances (σ^2_P), genotypic variances (σ^2_G), phenotypic coefficient of variation (PCV) and genotypic coefficient of variation (GCV) (Table 7). The GCV was less than that of PCV and low differences were observed between the two for all the studied traits (Table 7). The highest values of GCV and PCV were recorded in traits such as g_s, CE, LA, YII, and SLA in different finger millets (Table 7). In the present study, the broad-sense heritability was varied from 1.74 to 99.9 among the studied morpho-physiological traits (Table 7). The genetic advance as a percentage of means (GAM) among the studied traits ranged from 0.01 to 1266.3%. High GAM, along with high heritability, was observed in g_s, CI, Chlorophyll, DMA, SL and SLA (Table 7).

Cluster analysis by Bray–Curtis paired linkage revealed the percent of similarity in different morpho-physiological traits among different finger millet genotypes (Fig. 2). The dendrogram is showing the similarity forming three major clusters. The cluster I included *Arjuna* and *Dasara* genotypes having more than 91% similarity. The cluster II included 7 genotypes such as *Bati*, *Limca*, *Biri* and *Sili jhana* in one sub-cluster and *Chilika*, *Jhana*, and *Chilli* in another sub-cluster having 92% similarity. The cluster III included *Bhadi Taya*, *Bhairabi*, *Kurkuti*, *Ladu* and *Lala* with similarity 89%.

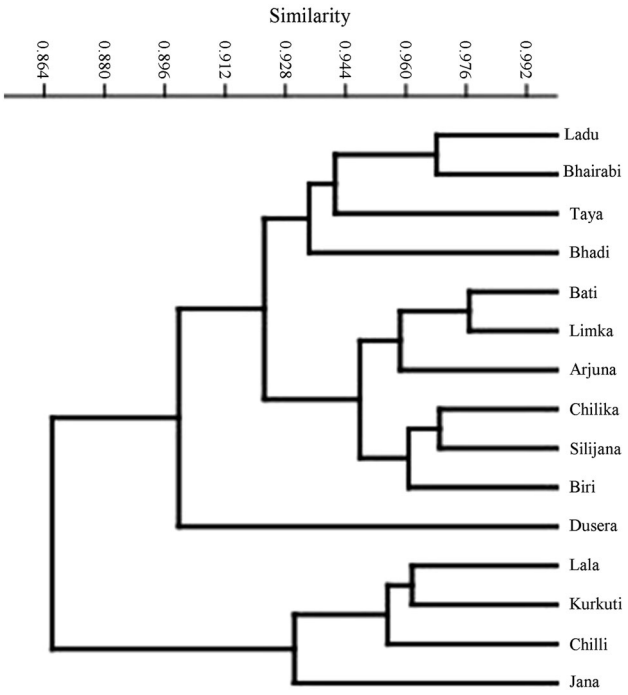

Fig. 2 Dendrogram showing Bray–Curtis similarity index of different finger millets based on morpho-physiological traits

Molecular genotyping of finger millet genotypes based on SCoT markers

Molecular profiling of the studied finger millet genotypes was carried out by taking 36 SCoT markers. The details of primer and their sequence information were presented in Table S1. Different banding pattern, in the forms of variation in molecular weight of each amplified products for each marker against studied finger millet genotypes, are given in Fig. S3. A representative SCoT profile using primer SCoT7 was shown in Fig. 3. The present investigation used a total of 36 SCoT primers to examine genetic polymorphism, out of total used primers, 33 SCoT primers produced unambiguous and reproducible banding profile with product size ranged from 250 to 2000 bp but 3 SCoT primers such as SCoT-31, SCoT-32 and SCoT-34 failed to amplify the studied millet genotypes. A total of 184 bands were generated by using 33 SCoT primers with an average of 5.57 bands per primer. The number of locus amplified by each primer ranged from 3 to 9 (Table 8). The highest number of fragment (9) was amplified by two primers (SCoT-3 and SCoT-14), whereas lowest number of bands (3) was reported in three primers (SCoT-22, SCoT-28, SCoT-35). A total of 48 polymorphic bands were generated with an average of 1.45 per marker among the studied finger millet genotypes and out of 36 primers 21 primers showed polymorphic bands. The polymorphism percentage with SCoT markers ranged from 11.11 to 100% among the

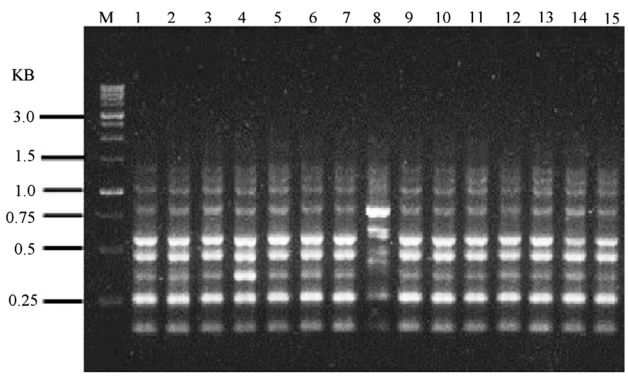

Fig. 3 Representative SCoT profile using primer SCoT7 of 15 Finger millet genotypes. Lane numbers are the same as the serial numbers of the genotypes mentioned in Table 1. Lanes M is the 1 kb ladder used as size markers

Table 8 Total amplified band, polymorphic band, polymorphism (%), polymorphic information index (PIC) and MI of different SCoT markers

Sl no.	Primer	Total band	Polymorphic band	% polymorphism	PIC	MI	RP
1	SCoT1	5	0	0.00	0.00	0.00	0.00
2	SCoT2	6	1	16.67	0.07	0.07	0.53
3	SCoT3	9	1	11.11	0.02	0.02	0.13
4	SCoT4	7	0	0.00	0.00	0.00	0.00
5	SCoT5	4	0	0.00	0.00	0.00	0.00
6	SCoT6	4	0	0.00	0.00	0.00	0.00
7	SCoT7	9	3	33.33	0.04	0.12	0.40
8	SCoT8	6	5	83.33	0.10	0.52	0.27
9	SCoT9	8	1	12.50	0.05	0.05	0.40
10	SCoT10	4	0	0.00	0.00	0.00	0.00
11	SCoT11	5	1	20.00	0.09	0.09	0.67
12	SCoT12	7	2	28.57	0.13	0.27	1.60
13	SCoT13	6	0	0.00	0.00	0.00	0.00
14	SCoT14	9	4	44.44	0.20	0.81	3.07
15	SCoT15	7	2	28.57	0.07	0.15	0.40
16	SCoT16	6	1	16.67	0.04	0.04	0.27
17	SCoT17	7	3	42.86	0.16	0.48	1.73
18	SCoT18	5	5	100.00	0.29	1.44	2.00
19	SCoT19	6	5	83.33	0.18	0.90	1.47
20	SCoT20	4	3	75.00	0.22	0.67	1.87
21	SCoT21	4	1	25.00	0.11	0.11	0.67
22	SCoT22	3	0	0.00	0.00	0.00	0.00
23	SCoT23	7	3	42.86	0.17	0.52	2.00
24	SCoT24	4	0	0.00	0.00	0.00	0.00
25	SCoT25	7	2	28.57	0.04	0.07	0.27
26	SCoT26	5	1	20.00	0.02	0.02	0.13
27	SCoT27	5	1	20.00	0.10	0.10	0.93
28	SCoT28	3	0	0.00	0.00	0.00	0.00
29	SCoT29	5	0	0.00	0.00	0.00	0.00
30	SCoT30	5	1	20.00	0.06	0.06	0.40
31	SCoT33	5	1	20.00	0.05	0.05	0.27
32	SCoT35	3	1	33.33	0.11	0.11	0.40
33	SCoT36	4	0	0.00	0.00	0.00	0.00
Total		184	48	806.1	2.3	6.674	19.88
Mean		5.57	1.45	24.4	0.071	0.202	0.602

studied primer and the highest polymorphism was obtained in SCoT-18 marker. The level of polymorphism among the 15 studied millet genotypes was obtained by evaluating the polymorphism information content (PIC) values for each primer. The PIC value ranged from 0.02 to 0.29, with an average of 0.071 per primer. Among all the SCoT primers, SCoT-14, SCoT-18 SCoT-20 and SCoT-23 showed the higher PIC value, which implies the potentiality for exploring the genetic diversity of studied millet genotypes. The marker index (MI) was varied from 0.02 to 1.44 among the studied markers and the highest MI was obtained in SCoT-18 markers. Resolving power (RP) ranges from 0.13 (SCoT 3) to 3.07 (SCoT 14), as shown in Table 8. Jaccard's similarity coefficient calculated the pair-wise genetic similarity and it ranged from 0.872 to 0.981 among the 15 finger millet genotypes (Table 9). The maximum genetic similarity (Jc = 0.981) was between variety *Bhadi* and *Taya*; both, are local landraces from Koraput, Odisha. On the other hand, the minimum genetic similarity (Jc = 0.872) was found between variety *Arjuna* (pure-line selection from OUAT, Bhubaneswar Odisha) and *Jhana* (local landraces from Koraput).

The dendrogram was constructed among 15 genotypes of finger millet using binary data that was based on neighbour-joining. Cluster analysis grouped all genotypes in two major clusters I and II. Cluster I included four

Table 9 Genetic similarity between the studied finger millet genotypes on the basis of SCoT marker data

Variety	Jhana	Lala	Kurkuti	Ladu	Bati	Bhadi	Taya	Arjuna	Chilika	Limca	Chilli	Biri	Sili jhana	Dasara	Bhairabi
Jhana	1.000														
Lala	0.971	1.000													
Kurkuti	0.929	0.934	1.000												
Ladu	0.933	0.939	0.944	1.000											
Bati	0.902	0.896	0.937	0.919	1.000										
Bhadi	0.922	0.939	0.933	0.927	0.943	1.000									
Taya	0.918	0.946	0.939	0.920	0.925	0.981	1.000								
Arjuna	0.872	0.876	0.895	0.898	0.902	0.899	0.906	1.000							
Chilika	0.924	0.917	0.933	0.938	0.935	0.956	0.950	0.878	1.000						
Limka	0.928	0.933	0.950	0.929	0.928	0.961	0.968	0.904	0.956	1.000					
Chilli	0.887	0.880	0.932	0.924	0.948	0.919	0.926	0.915	0.937	0.944	1.000				
Biri	0.908	0.913	0.943	0.925	0.943	0.962	0.968	0.896	0.929	0.941	0.935	1.000			
Sili jhana	0.882	0.887	0.919	0.925	0.939	0.932	0.938	0.919	0.910	0.932	0.952	0.939	1.000		
Dasara	0.921	0.926	0.919	0.914	0.932	0.950	0.943	0.897	0.918	0.935	0.917	0.950	0.946	1.000	
Bhairabi	0.888	0.892	0.909	0.889	0.931	0.925	0.920	0.887	0.913	0.924	0.918	0.925	0.906	0.938	1.000

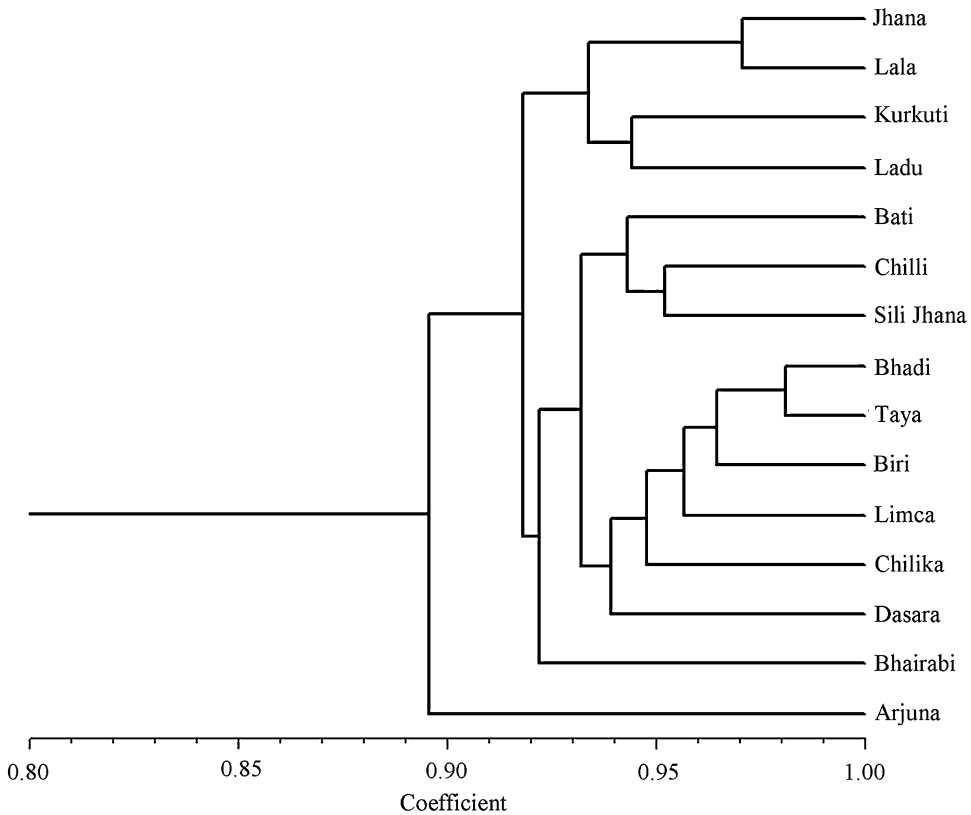

Fig. 4 Dendrogram showing the Jaccard's similarity index between the finger millet genotypes based on ScoT marker amplified products

genotypes all were local landraces of Koraput while cluster II was further subdivided into two sub-clusters IIA and IIB. Cluster IIA included three genotypes namely *Bati*, *Chilli* and *Sili Jhana* were from local landraces of Koraput while cluster IIB included seven genotypes from genotype *Chilika* is a hybrid from OUAT, Berhampur and *Bhairabi* is a mutant *Bhudha Mandia* from OUAT while remaining five genotypes were from local landrace from Koraput. The

most distinct genotype namely, *Arjuna*, which is pure line selection from OUAT, Bhubaneswar, was not grouped in any of the two clusters (Fig. 4).

Discussion

The Koraput district of Odisha is one of the centres of diversity for many food crops and forest species and harbouring rich genetic diversity of millets (Mishra et al. 2012). These millet genotypes may serve as a valuable genetic resource for future crop improvement to meet the demands of food security. Although, indigenous finger millet genotypes have less productivity it provides a great opportunity that ensures food security and livelihood of poor farming communities due to their tolerance capacity to biotic and abiotic stresses. This is the first study on genetic diversity and population structure of different indigenous finger millet genotypes originated from various regions of Koraput.

There was remarkable variation of shoot length (SL), root length (RL), fresh weight (Fwt), dry weight (Dwt) and dry matter accumulation (DMA) was observed among the studied finger millet genotypes. Some indigenous finger millets such as *Kurkuti*, *Sili jhana* and *Dasara* showed remarkably superior growth parameters compared to modern high yielding millet genotypes. Such diversity among the millet genotypes might be related to their genetic origin, genetics of the species and geographical sources where they are grown. These results of morphological variations of millet genotypes were also consistent with the previous report of global collections of millets (Babu et al. 2014) and millets of India (Das et al. 2007). The leaf relative water content (RWC) is important parameters for study of water status of the plant (Lafitte et al. 2002). Some of the indigenous finger millets such as *Ladu* and *Limca* showed significantly higher RWC and *Sili jhana* showed maximum membrane stability index (MSI) compared to other millets, Which suggested that these genotypes may have better shielding mechanism to protect membrane damage and sustain better leaf turgor under prevalent environmental conditions (Chakraborty et al. 2002; Swapna and Shyalaraj 2017).

Variations in the photosynthetic traits in indigenous finger millets genotypes were studied by gas-exchange measurements, chlorophyll fluorescence and stomatal traits and the results were compared with the modern high-yielding genotypes. Some indigenous finger millets such as *Jhana*, *Taya* and *Dasara* showed superior photosynthetic rate, stomatal conductance, water-use efficiency (WUE, P_N/E) and carboxylation efficiency (CE, P_N/Ci) compared to modern high-yielding finger millets genotypes. The leaf photosynthesis is regulated by various internal and environmental parameters (Shi et al. 2005). The variation observed in photosynthetic traits among the genotypes might be related to their origin and genetics of the varieties. In the present study, leaf photosynthetic rate of millet genotypes was lower than the previous reports (Shankar et al. 1990; Subrahmanyam 2000). The lower values of photosynthetic rate may be due to high temperatures during measurements. In an earlier study of Xie et al. (2011) reported that there is a decline in photosynthesis and grain yield, with atmospheric air temperature higher than 35 °C. Results of the present study indicated that indigenous genotypes showed better photosynthetic efficiency but unable to increase grain yield, because the increase in leaf photosynthesis may not necessarily lead to increase in grain yield as reported in different millets (Subrahmanyam 2000) and rice (Gu et al. 2013). The results suggested that the indigenous finger millets associated with high leaf photosynthetic rate, which can contribute this trait for crop improvement despite their other disadvantageous phenotypes (Subrahmanyam 2000; Vikram et al. 2016). Leaf chlorophyll content is an important plant pigment regulates the photosynthetic process by absorbing solar energy from the environment, as they indicate the light-harvesting capacity of plants (Panda et al. 2018). Some indigenous finger millets such as *Jhana*, *Taya* and *Dasara* showed better chlorophyll and carotenoid status in comparison to modern high-yielding finger millets genotypes.

In addition, Chl fluorescence measurement helps to assess the intrinsic photosynthetic performance of plants, which provides essential information regarding the function of PSII under prevalent environmental conditions (Batra et al. 2016). The F_0, Fm, F_v/F_m, YII, NPQ, and qP is widely used Chl fluorescence parameters in plant physiology studies (Murchie and Lawson 2013). There were no significant differences in values of Fo, Fm, Fv/Fm and Y (II) observed among studied finger millet varieties (Table 4). However, some indigenous finger millets such as *Jhana*, *Lala*, *Bhadi*, *Chilli* and *Dasara* showed maximum ETR and showed better photochemical activity in the prevalent environmental condition as compared to the other genotypes.

Stomata are the key player in plants which regulates the exchange of CO_2 and water vapour between atmosphere and surrounding (Buckley 2005; Kondamudi et al. 2016). The stomatal traits such as stomatal size, number and density controls the leaf gas exchange in plants (Panda et al. 2018). However, very little information is available on the relationship between leaf gas exchange and stomatal traits in finger millet (Subrahmanyam 2000). Some indigenous finger millets such as *Jhana*, *Lala*, *Kurkuti*, *Bhadi* and *Dasara* showed better stomatal traits and showed adaptive mechanism to cope with changing

environment compared to modern high-yielding finger millet genotypes (Subrahmanyam 2000).

Based on the result of multiple correlations, the rate of photosynthesis (P_N) was not significantly influenced by leaf pigments (Chl and carotenoid contents) and leaf area. A strong positive correlation between P_N with g_s, CE and WUE, were observed. This result indicated that the observed variations in P_N in different millets genotypes were not based on pigment content or leaf area, but related to the leaf CE and WUE as has been reported earlier in rice and other crops (Yeo et al. 1994; Kiran et al. 2013; Haritha et al. 2017). Further, leaf P_N showed a significant positive correlation with DMA ($P < 0.05$), which supports the previous reports in other crops (Evans 2013; Puteh et al. 2014) for increased biomass in plants is associated with higher photosynthetic rate. The findings also suggested that the number and density of stomata in the leaf are the major regulating factor for leaf photosynthesis than the shape and size in millets. This results consistent with the earlier finding in different plant species (Chandra and Das 2000; Giuliani et al. 2011).

Based on genetic variability study, high PCV and GCV values were recorded in the traits such as g_s, CE, LA, YII, and SLA in different finger millets. This indicates the existence of substantial variability for such characters based on which selection of finger millet genotype may be useful. These characters showing ample variation are efficient for selection in a breeding program (Mohapatra et al. 2017). The GCV was less than that of PCV and low differences were observed between them for all the morphological traits in the studied finger millets. This indicates that environment least influence high contribution of genotypic effect for phenotypic expression of these traits and above characters. In the present study, high GAM along with high heritability was observed in g_s, CI, Chlorophyll, DMA, SL and SLA parameters. It indicates that these characters would be beneficial as a base for selection in finger millet improvement.

This is the first report of SCoT marker-based genetic diversity and population structure in finger millet genotypes of Koraput. SCoT marker technique used in the current study is simple, low cost, fast, effective and highly reproducible. In the present investigation, a set of 36 SCoT primers were used to examine genetic polymorphism, out of the total, 33 SCoT primers produced unambiguous and reproducible banding profile with 250–2000 bp product size but 3 SCoT primers such as SCoT-31, SCoT-32 and SCoT-34 failed to amplify the studied millet genotypes. Significant level of polymorphism were detected as reported in the present study complies with earlier investigations using some of these SCoT primers in rose (Henuka et al. 2015) and Grape (Guo et al. 2012). It was observed that all the markers used in the present study showed polymorphism at various loci which may be useful in breeding for improving the genotypes of finger millets and as well as for the identification of the appropriate genotypes suitable for specific environmental conditions. Among all the SCoT primers, SCoT-14, SCoT-18 SCoT-20 and SCoT-23 showed the higher PIC value and marker index, which implies the potentiality for exploring the genetic diversity of studied millet genotypes. Based on the genetic similarity analysis it is revealed that some of the indigenous finger millet genotypes such as *Jhana*, *Lala*, *Kurkuti*, *Ladu*, *Bhadi* and *Taya* showed highest genetic disimilarity with modern high yielding genotype *Arjuna*. The mean genetic distance among the studied varieties was 0.934, which indicates that a very low level of genetic diversity among the studied finger millet genotypes. The low level of genetic diversity might be due to the similar origin, ecotype and speciation as millets were collected only from, Koraput.

Conclusion

Significant variability was observed for leaf photosynthetic traits in studied finger millets of Koraput, which need conservation and sustainable utilization for future crop improvement programs. The major morpho-physiological traits such as stomatal conductance, dry matter accumulation, shoot length and stomata per leaf area are played a pivotal role and are the significant determinants of phenotypic diversity among studied finger millet genotypes. The positive association of photosynthesis with dry matter accumulation indicates that some of the genotypes remarkably have more photosynthetic rate along with better plant biomass accumulation. These parameters might be instrumental for superior phenotypic selection of finger millet improvement program. Further, SCoT markers were polymorphic and revealed a moderate level of genetic diversity and provided information on population structure among the finger millet genotypes. Based on the genetic similarity analysis it is revealed that some of the indigenous finger millet genotypes such as *Jhana*, *Lala*, *Kurkuti*, *Ladu*, *Bhadi* and *Taya* showed highest genetic dissimilarity with modern high yielding genotype *Arjuna*. These genotypes can be considered as the potential genetic resources for a breeding program. The information generated in this study will be valuable for breeding and conservation of finger millet genotypes. Further research is aim to elucidate the marker-trait association mapping and yield evaluation in field condition in these genotypes and could be used in finger millet breeding program.

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Author contributions NHS and DP designed the experiments, cultivated the plants and performed the measurement of morphological traits. NHS, PKB and KL performed the measurement of physiological and biochemical traits. SSS and SKL performed the molecular profiling. DP analyzed the data and wrote the paper. All authors read and provided helpful discussions for the manuscript.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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