Indonesian Journal of Agricultural Science
Vol. 22 No. 2 December 2021: 66–76
DOI: http//dx.doi.org/10.21082/ijas.v.22.n2.2021.p.66–76

GENETIC ANALYSIS OF QUALITATIVE AND QUANTITATIVE TRAITS AMONG PROGENIES OF ENSET CLONES ORIGINATED FROM SOUTHERN ETHIOPIA

Analisis Genetik Karakter Kualitatif dan Kuantitatif Beberapa Keturunan Klon Enset dari Ethiopia Bagian Selatan

Abraham Bosha and Mesfin Kebede Gessese*

Wolaita Sodo University, College of Agriculture, PO Box 138 Wolaita Sodo, SNNPR, Ethiopia

** Correspondence author: mesfin04@yahoo.com*

Submitted 04 April 2021; Revised 13 July 2021; Accepted 04 August 2021

ABSTRACT

The present cultivated enset (*Ensete ventricosum*) clonal landraces in Ethiopia originated from few wild progenitors. However, enset has a mixed mode of reproduction in which, the wild enset reproduces sexually through seeds, while cultivated enset is generally propagated vegetatively. The objectives of this study were to determine the genetic structure of enset cultivars through genetic analysis of qualitative morphological traits and estimate their genetic variability by evaluating the quantitative agronomic traits data generated from progenies of cultivated and wild enset genotypes. Hence, seeds collected from six cultivated and four wild enset genotypes were used for this study. Data on four qualitative and six quantitative morphological traits were recorded from the progenies of the 10 enset genotypes. Progenies of seven enset genotypes segregated in a 3:1 segregation ratio while progenies of the remaining genotypes segregated differently for the qualitative traits considered. With regard to the quantitative traits, the progenies of the 10 enset genotypes differed significantly for five of the six traits except pseudostem length. The cultivated clones, in general performed better than that of the wild types. Moderate heritability (h^2_b) estimates and high genetic advances were obtained for leaf length (0.38, 62.0%), pseudostem circumference (0.35, 78.5%), and plant height (0.30, 19.1%) indicating selection for these traits indirectly improves economic yield of enset clones. This study demonstrated the possibility of creating genetic variation through selfing the existing enset genotypes for traits of interest and making improvements either through selection or crossing the elite types to develop novel enset cultivars.

[Keywords: *Ensete ventricosum*, trait inheritance, progenies, selfing, genetic analysis]

ABSTRAK

Kultivar enset (Ensete ventricosum) *yang saat ini dibudidayakan di Etiopia berasal dari beberapa tetua liar. Enset memiliki cara reproduksi campuran, yakni enset liar bereproduksi secara seksual melalui biji, sedangkan enset yang dibudidayakan umumnya diperbanyak secara vegetatif. Penelitian ini bertujuan untuk mengetahui struktur genetik kultivar enset melalui analisis genetik sifat morfologi kualitatif dan memperkirakan keragaman genetiknya dengan mengevaluasi data kuantitatif sifat agronomis dari keturunan enset budidaya dan enset liar. Oleh karena itu, benih yang dikumpulkan dari enam genotipe enset budidaya dan empat enset liar digunakan untuk penelitian ini. Data empat sifat morfologi kualitatif dan enam sifat kuantitatif diperoleh dari keturunan 10 genotipe enset. Keturunan dari tujuh genotipe enset terpisah dengan rasio segregasi 3:1, sementara keturunan dari tiga genotipe yang tersisa terpisah secara berbeda untuk sifat kualitatif yang diteliti. Untuk sifat kuantitatif, keturunan dari 10 genotipe enset berbeda nyata untuk lima dari enam sifat kecuali panjang batang semu. Enset yang dibudidayakan secara umum memiliki kinerja yang lebih baik dibandingkan dengan tipe liar. Perkiraan heritabilitas (h^2_b) sedang dan kemajuan genetik tinggi untuk panjang daun (0,38, 62,0%), lingkar batang semu (0,35, 78,5%), dan tinggi tanaman (0,30, 19,1%) memperlihatkan bahwa seleksi untuk sifat-sifat tersebut secara tidak langsung meningkatkan hasil klon enset. Studi ini menunjukkan kemungkinan untuk menciptakan variasi genetik melalui selfing genotipe enset yang ada untuk sifat-sifat yang diinginkan dan melakukan perbaikan baik melalui seleksi maupun persilangan tipe elit untuk mengembangkan kultivar baru enset.*

[Kata kunci: *Ensete ventricosum*, pewarisan sifat, keturunan, selfing, analisis genetik]

INTRODUCTION

Enset is considered mainly as an African crop that currently provides the staple food for one-fifth of Ethiopian population (Yemataw et al. 2017; Borell et al. 2019). It is a large perennial monocarpic herbaceous plant, similar in form to the related bananas of the genus Musa (Zerfu et al. 2018). Unlike to *Musa* species that has n = 7, 10, and 11 set of chromosomes with various ploidy levels, enset is a diploid plant with chromosome number 2n = 18 with no record of polyploidy (Diro and Van Staden 2003). Ensete is geographically distributed in the wild in many parts of Sub-Saharan Africa and Asia with about 6–7 species (Simmonds 1962; Pursglove 1972) in which *Ensete ventricosum* species is cultivated only in its native indigenous farming systems of south and south-western Ethiopia (Brandt et al. 1997). The highlands of southern part of the country form the geographical center of the crop cultivation (Vavilov and Rodin 1997) and the various ethnic groups in this region recognize and exploit many enset landraces.

The enset planting is complex, supports a denser population than any other farming system (Brandt et al. 1997). The crop has been domesticated

and is cultivated for food, animal feed, and fiber (Bezuneh et al. 1967), ensuring food security for about 20% of the human population in Ethiopia that depend on enset as one of the staple food sources. It is Ethiopia's most important root crop, a traditional staple crop in the densely populated parts of the country (Jacob 2004). This multipurpose culture crop has been used as source of large quantities of carbohydrate-rich food (Bosha et al. 2016), animal forage, fiber production, construction materials, as well as ornamental plant (Hölscher and Schneider 1998). Moreover, products from enset are used in different forms in traditional medicine and a starch for textile, adhesive and paper industries is being produced (Diro and van Staden 2005; Temesgen et al. 2014).

The present cultivated enset in Ethiopia originated from few wild progenitors. However, enset has a mixed mode of reproduction in which, the wild enset reproduces sexually through seeds, while cultivated enset is generally propagated vegetatively. Naturally, vegetative propagation results in the genetic fixation, which could lead to loss of clones owing to diseases and abiotic stress resistant due to selection pressures, or changes in land use systems. The wild Musaceae family have always been known for their broad genetic base and carry several desirable genes (Vuylsteke et al. 1995) which breeders should look in the future.

Seed propagation of enset might be one of the options to create variation and allow breeders to select the clones with desired traits with the knowledge of enset seed germination and seedling growing techniques to breed enset efficiently (Karlsson et al. 2012; Bosha et al. 2016). So far, maintenance of the existing germplasm in the wild populations, as well as introduction of genes from wild or related species into the cultivated clones is useful to improve environmental stress tolerance, e.g., disease resistance and crop adaptation could have a major impact on future food security of Ethiopia.

Genetic diversity study on available enset genotypes either from molecular and phenotypic data may help to understand the extent of the variation in the species (Amare and Daniel 2016; Biswas et al. 2020). The source of variation in enset crop lacks to pin point either due to cross pollination (recombination) or entirely due to ancestors' inherent genetic make-up. The information generated from such researches explain the variation is due to the individual genetic constitutes which can help the breeders to design exploitation of genetic diversity in the species as a whole but not able to provide information how much is the breeder can create variation. Unlike to most vegetatively propagated species that are known to be polyploidy in nature and have homogenous plants in their clones with heterozygous loci in their genome, little is known about the genetic structure of the diploid species of *E. ventricosum* that produces morphologically uniform, homogenous plants when multiplied by vegetative propagation.

The improvement of cross pollinated crops exploits the variation within and between the family that can be manipulated by planned hybridization or recombination breeding (Shelton and Tracy 2015). However, before suggesting the possibility of applying recombination breeding to exploit the within and between family variations, it is necessary to understand the extent of phenotypic variation inherited to the progenies since the extent of variation within a seed cohort is not known. Morphological comparisons of genotypes within seed cohorts can help much to understand the extent of genetic variation achieved through seed propagation. Generating such information is needed to launch crossing program and selection of clones from natural outcrosses to develop new enset cultivars (Bosha et al. 2016). The objectives of this study were to determine the inheritance of four qualitative morphological traits, and estimate variability of quantitative agronomic traits of 10 enset genotypes originated from South Ethiopia.

MATERIALS AND METHODS

Description of the Study Area

The study was conducted in Wolaita Sodo University field research station located in Wolaita Sodo town, Wolaita zone, SNNPR region, 315 km away from Addis Ababa. The specific location of the experimental area lies at elevation of 1891 m above sea level (asl) and its geographic coordinates are $37^0$45'08" E longitudes and 6^0 50'00" N latitude. Wolaita zone covers an altitude range of 800 to 3.500 m asl. The area experiences bimodal type of rainfall. The shortest rainy season stretches from March to April and the main rainy season extends from June to September. The 12-year average annual rainfall data (2003 to 2015 cropping years) was 1.580 mm. Minimum and maximum average annual temperature was 12.7 ^{0}C and 23.7 ^{0}C, respectively, and the major soil type of the area was reported to be Nitosols (Fanuel et al. 2017) having well drained sandy loam texture class with low organic carbon content (Hailu et al. 2017).

Plant Material

Progenies of the mother plants of clonal landraces of enset cultivated in Wolaita zone and wild plants of enset genotypes collected from natural forests found in Dawuro and Keffa areas were used in this study. The enset genotypes used in this study consisted of six cultivated landraces and four wild plants (Table 1). The progenies of each genotype were generated from seeds of the respective mother plants.

Design and Layout of the Field Experiment

Each of the progenies of the mother plants (the 10 genotypes) was planted in a single row of 16 plants using a nested design with four replications. The spacing was 3 m between plants and 4 m between rows planted on a 12 m x 9 m plot size having 16 plants per plot. All the management practices such as weeding, hoeing, mulching, watering, and fertilizer application were properly and uniformly applied to all plots using the recommended practices of enset cultivation as described in Blomme et al. (2018) and Borell et al. (2020).

Data Collection

The data included both qualitative and quantitative characters were recorded from this study. Data for qualitative parameters were collected from all available plants in each plot. While for quantitative character data were collected from a sample of four plants per plot. List of qualitative and quantitative characters observed from this study are shown in Table 2.

Table 1. Ten enset genotypes used in this study and description of their collection site.

Enset clone	Collection site	Collected area altitude (m asl)	Geographical location	Annual temperature average (^{0}C)	Annual rainfall average (mm)	Soil type
Arkia	Sodo Zuria	1924	06^{0}53'36.3''N 37^{0}43'36.9''E	22	1340	Clay
Banga	Sodo Zuria	1920	06^{0}53'32.0''N 37^{0}43'30.1''E	21	1340	Clay
Gefetanuaw 2	Sodo Zuria	1912	06^{0}53'32.4''N 37^{0}43'34.7''E	20	1340	Clay
Wild 15	Waka	2369	07^{0}03'33.2''N 37^{0}0.9'59.8''E	26	1500	Silt loam
Alageena	Sodo Zuria	1924	06^{0}53'25.1''N 37^{0}43'38.7''E	22	1340	Clay
Wild 9*	WSU	1886	06^{0}49'55.4''N 37^{0}45'4.6''E	21	1630	Silt loam
Gefetanuwa 1	Sodo Zuria	1936	06^{0}53'12.7''N 37^{0}43'43.8E	20	1340	Clay loam
Wild 11*	WSU	1886	06^{0}49'55.4''N 37^{0}45'4.6''E	21	1630	Silt loam
Wild 10*	WSU	1886	06^{0}49'55.4''N 37^{0}45'4.6''E	21	1630	Silt loam
Gamo Gofa 71	Areka	1785	07°04'02'' N, 37°41'22'', E	20	1400	Silt loam

*Mother plants originating from seeds collected in the wild, around Jimma (N 07°40'43'', E36°50'19'', 1739 m asl) and grown at Areka Research Centre until seed ripening (Karlsson et al. 2013a); WSU = Wolaita Sodo University.

Table 2. Morphological traits measured from 10 enset genotypes tested at Wolaita Sodo University in 2020 crop year

Character	Qualitative categories and quantitative measurement
Pseudostem color	1 = light green, 2 = deep green, 3 = greenish black, 4 = light red, 5 = dark red, 6 = reddish yellow
Petiole color	1 = light green, 2 = deep green, 3 = yellowish green, 4 = light red, 5 = dark red, 6 = reddish yellow
Midrib color	1 = light green, 2 = deep green, 3 = greenish yellow, 4 = greenish red, 5 = light red, 6 = dark red, 7 = dark brown
Leaf color	1 = light green, 2 = deep green, 3 = light red, 4 = dark red, 5 = purple
Plant height	cm
Pseudostem length	cm
Pseudostem circumference	cm
Leaf length	cm
Leaf width	cm
Leaf number per plant	Counted leaf number per plant

Data Analysis

Chi-Squared Test

Chi-squared (χ^2) analyses were conducted to test the goodness of fit of the observed segregation to the theoretically expected ratios for a given genetic model to determine the number of genes involved in the inheritance of the qualitative characters. The formula for calculating the Chi-squared analysis was described by Cochran (1952) as shown below:

$$\chi^2 = \Sigma\frac{(O-E)^2}{E}$$

Where, Σ is summation of the chi-squared values of the alleles, O is observed values, and E is expected values.

For a recombinant inbred (RI) population, a 1:1 ratio is expected for a single gene. However, for an F_2 (2nd filial generation) population, a single dominant gene is expected to segregate in a 3:1 ratio, and for a co-dominant single gene the expected genetic ratio was 1:2:1.

Analysis of Variance of Quantitative Characters

Analysis of variance (ANOVA) of quantitative characters was computed using nested design for each quantitative character in order to estimate the variability among genotypes for each trait. The ANOVA was constructed by considering the experimental units (the four enset plants within each genotype) as factor B nested within levels of factor A (the 10 genotypes) (Sokal and Rolf 1969). The differences between treatment means were compared using least significant difference (LSD) test at 5% significance level when the ANOVA showed the presence of significant differences among genotypes.

Variability Analysis

The genotypic and phenotypic variances of agronomic traits at each location were estimated using the following formula as previously described by Burton and Devane (1953).

Genotypic variance (σ_g^2):

$$\sigma_g^2 = \frac{MSg - MS}{r}$$

Where, MSg is mean square due to genotypes, MSe is environmental variance (error mean square), and r is number of replications.

Phenotypic variance (σ_p^2):

$$\sigma_p^2 = \sigma_g^2 + \text{MSe}$$

Phenotypic coefficient of variations (PCV) and genotypic coefficient of variation (GCV) were estimated using the following formula (Burton and DeVane 1953).

$$\text{PCV} = \frac{\sqrt{phenotypic\ variance}}{population\ mean\ for\ character} x10$$

$$\text{GCV} = \frac{\sqrt{genotypic\ variance}}{population\ mean\ for\ character} x100$$

Estimation of Heritability in Broad-Sense (h^2_b) and Genetic Advance (GA)

Broad-sense heritability (h^2_b) was calculated as the ratio of the genotypic variance to that of the phenotypic variance, using the following formula as previously described by Allard (1960).

$$h^2_b = \frac{\sigma^2 g}{\sigma^2 p} x100$$

Where, h^2_b is heritability (in broad-sense), σ_g^2 is genotypic variance, and σ^2p is phenotypic variance.

Genetic Advance

Genetic advance (GA) was computed using the formula adopted from Johnson et al. (1955) and Allard (1960) as shown in the following formula.

$$GA5\% = (k)\ (\sigma_p) \times (h^2_b)$$

Where, GA5% is genetic advance at 5% selection intensity, K is the selection intensity (K = 2.06 at 5% selection intensity), σ_p is the phenotypic standard deviation, and h^2_b is heritability in broad sense.

Genetic advance as percent of mean: $GAM5\% = \frac{GA}{\mu}$

Where, GAM5% is genetic advance as percent of mean at 5% selection intensity, GA is genetic advance, and μ is mean value of the trait.

RESULTS

Variation for Qualitative Morphological Traits

Enset plant is usually propagated vegetatively through corms. Plants propagated through corms are genetically uniform, hence they are said to be clones. However, most asexually (vegetatively) reproducing plants when propagated through seeds (sexually) their progenies show genetically diverse genotypes. Similarly, the enset progenies considered in this study demonstrated genetic diversity in both qualitative and quantitative traits as they were propagated through seeds obtained from each of the ten mother plants. The data for all four qualitative traits showed single gene segregation confirmed by chi-squared analyses for single gene (non-significant for $\chi^2 < 3.841$ at P = 0.05 and 1 d.f.) at F_2 generation with genetic ratio of 3:1 for the eight landraces (Table 3). On the other hands, the cultivated landrace Gefetanuwa 1 did not show segregation for all qualitative traits, while Gefetanuwa 2 segregated for a single gene with genetic ratio of recombinant inbred lines of 1:1 at P = 0.05 and 1 d.f. (Table 3). The three qualitative traits; pseudostem color, petiole color, and mid-rib color exhibited segregation for two distinct types of color classes for each trait (Table 3). However, leaf color showed segregation only in three progenies of the landrace cultivars (Banga, Gefetanuwa 1, and Gamo Gofa 71), while the rest seven landrace progenies exhibited deep green leaf color with no segregation. The wild landrace Erpha15 (Wild 15) segregated monogenically (3 deep green: 1 light red) only for pseudostem color, while petiole color, midrib color, and leaf color did not show segregation and all the progenies showed greenish brown, light red, and deep green colors, respectively.

Variation for Quantitative Morphological Traits

Analyses of Variances of Quantitative Agronomic Traits

Univariate analysis of variance computed for the quantitative agronomic traits showed significant differences (P<0.05) among the enset genotypes except for pseudostem length that displayed non-significant mean square for genotypes (Table 4). This study demonstrated the presence of significant variations among the genotypes for the agronomic traits that improvement can be made for the traits considered through selection and breeding efforts. Leaf length exhibited highly significant (P<0.01) difference between the genotypes (Table 4) indicating that this trait is the most varied among the quantitative traits under study.

Mean Performances of Enset Genotypes

Estimated mean performances of the 10 enset genotypes for the sixth agronomic morphological traits are presented in Table 5. The result showed presence of significant differences for five of the traits viz. leaf length, leaf width, leaf number per plant, plant height, and pseudostem circumference at 5% probability level that further confirmed by mean comparison tests using the respective LSD values. The mean data indicated that mainly the wild genotypes had inferior performances compared to that of the cultivated clonal landraces with the exception of the genotype Wild 15 that showed average performances in all the traits evaluated (Table 5). The genotype Wild 15 performed better than Alageena and Gamo Gofa 71 clones for majority of agronomic traits and also ranked second next to Arkia for traits such as leaf width, leaf number per plant, pseudostem length, and plant height. The cultivated clonal landrace Arkia was the top performer for majority of traits except for pseudostem length on which Wild 15 was the top performer, whereas

Table 3. Chi-squared test of the segregation ratio of four morphological characters of enset progenies derived from 10 enset clones tested at Wolaita Sodo University in 2020 crop year.

Enset clones	Pseudostem color		Petiole color		Midrib color		Leaf color	
	Ratio tested	χ^2 test [a]	Ratio tested	χ^2 test [a]	Ratio tested	χ^2 test [a]	Ratio tested	χ^2 test [a]
Arkia	3 green: 1 dark-red	0.0 [ns]	1 light-green: 3 red-purple	0.33[ns]	1 light-green: 3 red	0.33[ns]	All deep-green	-
Banga	3 dark-red: 1 green-black	0.33 [ns]	1 light-green: 3 dark-red	0.33 [ns]	1 light-green: 3 brown-red	0.33 [ns]	1 light-green: 3 dark-green	0.33 [ns]
Gefetanuwa 2	1 light-green: 1 reddish-brown	0.52 [ns]	1 light-green: 1 green-red	0.52 [ns]	1 light-green: 1 greenish brown	0.52 [ns]	1 light-green: 1 deep-green	0.52 [ns]
Wild 15	3 deep-green: 1 light-red	0.67 [ns]	All greenish brown	-	All light-red	-	All deep-green	-
Alageena	All red	-	All brown-red	-	All red	-	All deep-green	-
Wild 9	3 green: 1 dark-red	0.09 [ns]	1 red: 3 dark-brown	0.81 [ns]	1 light-red: 3 dark-brown	0.81[ns]	All deep-green	-
Gefetanuwa 1	all red		all greenish-red		all red brown		all deep green	
Wild 11	1 deep-green: 3 red-green	0.33 [ns]	1 light-red: 3 greenish-red	1.33 [ns]	1 light-red: 3 dark brown	1.33 [ns]	All deep-green	-
Wild 10	1 light-green: 3 dark-red	0.00 [ns]	1 purple: 3 greenish-red	0.00 [ns]	3 light red: 1 dark brown	0.00 [ns]	All deep-green	-
Gamo Gofa 71	1 light-green: 3 red	0.18 [ns]	1 light-green: 3 red green	0.18 [ns]	1 green: 3 red	0.18 [ns]	1 light-green: 3 deep-green	0.18 [ns]

[a] The null hypothesis of the test was that the trait is segregated in a 3:1 and a 1:1 ratios as shown in Table 3.
Table value of x^2 at P = 0.05 and 1 df is 3.841.
*, ** and [ns] indicate significant at 5%, significant at 1% levels, and non-significant difference, respectively.

Table 4. Mean squares for the different sources of variation and their corresponding coefficient of variation (CV) for the six quantitative traits of 10 enset genotypes tested at Wolaita Sodo University in 2020 crop year.

Traits	Replications (Df=3)	Enset clones (Df=9)	Error (Df=27)	CV (%)
Leaf length	11923	13234**	3789	17.9
Leaf width	170.9	423.4*	164.8	18.2
Leaf number per plant	10.445	18.10*	7.405	22.6
Plant height	31444	29588*	10672	19.3
Pseudostem circumference	427.2	1431.7*	454.2	27.3
Pseudostem length	6519	4368[ns]	2206	24.6

*Significant at p = 0.05, **Highly significant at p = 0.01, Df = degree of freedom, CV (%) = coefficient of variation, ns = non-significant.

Table 5. Mean performances of the 10 enset genotypes and their studied traits tested at Wolaita Sodo University in 2020 crop year.

Genotypes	LL	LW	LN	PH	PSC	PSL
Wild 11	276.3[a]	54.23[a]	9.67[a]	445[a]	48.38[a]	168.8
Wild 10	282.8[a]	64.35[ab]	9.90[a]	451.8[a]	59.63[ab]	169.0
Wild 9	317[abc]	71.78[abc]	10.35[a]	533[ab]	80.55[b]	216.0
Wild 15	391.9[cd]	80.03[bc]	12.92[ab]	631.1[b]	76.45[ab]	239.2
Alageena	292[ab]	58.58[a]	10.45[a]	447.7[a]	63.25[ab]	155.7
Gamo Gofa 71	303.9[abc]	69.58[ab]	12.10[a]	449.6[a]	82.23[b]	145.8
Banga	348.9[abcd]	67.50[ab]	12.30[a]	534.9[ab]	81.0[b]	186.0
Gefetanuwa 1	374.5[bcd]	70.95[abc]	13.2[ab]	557.7[ab]	81.68[b]	183.2
Gefetanuwa 2	411.9[d]	78.90[bc]	12.6[a]	622.8[b]	89.1b[c]	210.9
Arkia	436.5[d]	88.80[c]	16.8[b]	673.5[b]	118.2[c]	237.0

Means followed by the same letter are not significantly different at p < 0.05.
LL = leaf length, LW = leaf width, LN = leaf number per plant, PH = plant height, PSC = pseudostem circumference, PSL = pseudostem length

Wild 11 was the least (Table 5). The enset genotypes showed unique performances with respect to pseudostem length although statistically was not significant; for instance, the least performing genotypes Wild 11 and Wild 10 performed better than the cultivated ones Alageena and Gamo Gofa 71 suggesting that the wild enset genotypes can also contribute to the improvement of *kocho* yield apart from quality traits and stress tolerance.

Estimates of Variance Components

The results of estimated variance components, phenotypic coefficients of variation (PCV) and genotypic coefficients of variation (GCV), broad sense heritability (h_b^2), genetic advance (GA), and genetic advance as percentage of mean (GAM%) were calculated for the six traits investigated using the ANOVA computed between the tested genotypes and presented in Table 6.

Table 6. Estimates of variability parameters for six traits of the 10 enset genotypes tested at Wolaita Sodo University in 2020 crop year.

Traits	Mean	σ^2_g	σ^2_p	σ^2_e	GCV	PCV	h^2_b	GA5%	GAM5%
Leaf lenght	343.6	2361.25	6150.3	3789	14.14	22.82	0.38	62.02	18.05
Leaf weight	70.5	64.65	229.45	164.8	11.40	21.49	0.28	8.79	12.47
Leaf number per plant	12.03	2.67	10.08	7.41	13.59	26.39	0.27	1.735	14.42
Plant height	535	4729	15401	10672	12.85	23.20	0.31	78.50	14.67
Peudostem circumference	78	244.38	698.58	454.2	20.04	33.88	0.35	19.05	24.42
Peudostem lenght	191.1	540.5	2746.5	2206	12.17	27.42	0.20	21.24	11.11

σ^2_g = genetic variance, σ^2_p = phenotypic variance, σ^2_e = environmental variance, GCV = genotypic coefficient of variance, PCV = phenotypic coefficient of variance, h^2_b = heritability in broad sense, GA5% = genetic advance at 5% selection intensity, and GAM5% = genetic advance as percentage of the mean at 5% selection intensity.

Phenotypic and Genotypic Coefficient of Variation

Both the PCV and GCV values computed for the six traits ranged from 21.49 to 33.88 and 11.40 to 20.04 for leaf width and pseudostem circumference, respectively (Table 6). The values of PCV were generally higher than the corresponding values of GCV for all traits studied indicating that the influence of environmental differences across years was significant, particularly annual climatic (weather) changes were important. High PCV was observed along with moderate GCV values for all the six traits studied.

Broad Sense Heritability

Broad sense heritability (h^2_b), which is an estimate of the total contribution of the genetic variance to that of the total phenotypic variance ranged from 0.197 (pseudostem length) to 0.38 (leaf length). The heritability value estimates were moderate for half of the traits; namely, leaf length, plant height, and pseudostem circumference which might be due to the presence of relatively higher genotypic variations among the enset genotypes and less effect of environmental influences on the expression of these traits. The remaining three traits (leaf width, leaf number per plant, and pseudostem length) exhibited low estimate of heritability (Table 6) implying that the environmental influence in the expression of these traits was higher compared to that of the genetic variation between the genotypes.

Genetic Advance

The genetic advance percent of means (GAM) expressed ranged from 11.11% for leaf length to 24.42% for pseudostem circumference. This refers to the improvement of the characters in genotypic value for the new population compared to the base population in one cycle of selection, which is in the range of 11.11% to 24.42% at 5% selection intensity. High GAM was observed for pseudostem circumference (24.42%) whereas moderate GAM was obtained for the rest of the traits that showed that there is a huge potential for improving the enset yield through selection and breeding using the available enset germplasm (Table 6).

DISCUSSION

Enset is a perennial crop mainly cultivated in the highlands of southern and southwestern parts of Ethiopia, particularly in densely populated areas of the country (Yemataw et al. 2014; Zerfu et al. 2018) such as, Gurage, Silte, Wolaita, Gedeo, Sidama, and Gamo Gofa zones. It is a staple food for nearly one-fifth of the country's population. The crop represents 65% of the total crop production in the southern regions of Ethiopia. The major food types produced from matured enset plant are *kocho, bulla* and *amicho* (Zerfu et al. 2018). Kocho is fermented starch processed from scraped leaf sheaths and corms; it constitutes the major product of enset. Several food recipes can be prepared from this product depending on the cultures; *kitta* (leavened bread), *burseme*, *kocho frfir*, etc. Bulla is a liquid, which is obtained when leaf sheaths and corms are pulverized. The liquid starch is dried to make white powder. Bulla is usually used to make porridge. Amicho is prepared from pieces of corm/rhizomes of enset plant and boiled and eaten similar to the other root crops (Brandt et al. 1997; Borell et al. 2020). The by products of enset can be used for fiber production that can be further processed to make different products; bags, ropes, twines, cordage, and mat.

Though enset has several benefits to the society, little progress has been made in terms of improving the crop through selection and breeding works to develop improved cultivars. So far only six cultivars, Zerietta (Ashura), Mesena (Eskuris), Kelisa (Wellanchie), Endale (Manduluka), Yanbule (Digomerza), and Gewada (Henuwa), were released by Areka Agricultural Research Center. The released cultivars were developed by clonal selection method by screening from available collections (cultivated clonal landraces) obtained from farmers of the region.

Since enset is a flowering plant that can produce viable seeds, it is possible to develop cultivars through hybridization and selection methods. It is known that the genetic structures of cross-pollinated and vegetatively propagated plant species are highly heterozygous in nature. Hence, it is possible to generate a variable base population upon selfing a clonal variety. Cultivated landraces of enset clones are propagated vegetatively through corms/suckers whereas wild enset plants are disseminated through seeds (Birmeta et al. 2004). Hence, wild plants of enset could be in different/various filial generations (F_1, F_2, F_3, etc.) since they are propagated through seeds; furthermore, enset plant is by nature a cross-pollinated plant as well as capable of multiplying through vegetative means.

In the current study, cultivated clonal plants and wild enset plants were used to study the genetic structures of the genotypes. The findings of our study indicated that progenies of clonal landrace cultivar Gefetanuwa 2 segregated with 1:1 genetic ratio for a single gene for the qualitative traits; viz a viz, pseudostem, midrib, petiole, and leaf colors. Therefore, the result justified that the mother plant Gefetanuwa 2 was different from F_1 that could be either F_4 or F_5 plant. While the other cultivated clonal landrace Gefetanua 1 didn't show segregation for all progenies of the mother plant implying this clone could be a selection from recombinant inbred lines. The wild plant selection Wild 15 (Erpha) segregated monogenically with genetic ratio of 3:1 only for pseudostem color, while it did not segregate for the rest three qualitative traits. On the other hand, the cultivated clonal cultivars segregated monogenically with a 3:1 genetic ratio confirming the mother plants were an F_1 (first filial) generation. Progenies of the enset genotypes showed differences in the diversity of colors for the qualitative morphological traits (pseudostem color, petiole color, midrib color, and leaf color). Petiole color and midrib color each exhibited 10 different types of colors; the pseudostem showed 8 different types of colors while the leaf color exhibited only 3 types of colors. Compared to the mother plants which had 5–6 phenotypes, the 3–4 additional phenotypes were displayed in the progenies for the qualitative traits except leaf color.

The progenies of the mother plants also demonstrated the potential for developing high genetic diversity for establishing a base population in the F_2 for quantitative (breeding) traits following selfing of the clones of both the cultivated and wild genotypes. The progenies of the 10 enset genotypes differed significantly for five of the six metric (quantitative) traits except pseudostem length. Generally the cultivated clones performed better than the wild types; however, one of the wild types (Wild 15) showed outstanding performance for majority of the traits following the cultivated cultivar Arkia that excelled all the rest. The variance components computed for the five traits showed the presence of higher level of variations among the genotypes that could be enough to improve the yield and other desirable traits through selection. The PCV and GCV values for the traits fall in the range of moderate to high level of variation as indicated by Deshmukh et al. (1986) where, the GCV and PCV values were considered low if it is <10%, moderate (10–20%), and high (>20%). The relatively higher values of PCV compared to the respective values of GCV indicate the influence of environmental variation in the performance of the traits that is common for quantitative yield traits as they are usually controlled by many genes with minor effects and additive in nature.

The estimated values of broad-sense heritability and the respective genetic advance indicated that it is possible to improve the enset yield and other associated traits through selection. According to Dabholkar (1992), moderate values of heritability were scored for majority of enset yield traits followed by high values of genetic advance as percent of the mean value of each trait. High values of genetic advance indicate the involvement of additive gene action in the genetic make-up of the quantitative traits. Johnson et al. (1955) reported that heritability estimates along with genetic gain would be more satisfying than heritability solitary in predicting the consequential effect of selection to choose the best individual plant. Hence, this study demonstrated that it is possible to create genetic variation through selfing of the existing clones of the farmers' cultivated enset landraces as well as wild types for qualitative and quantitative traits of interest and make improvements and develop new cultivars either through selection or crossing the elite types and evaluate the F1s and release the best performing novel clones to farmers.

CONCLUSIONS

The progenies obtained from the 10 enset genotypes showed genetic variability in both qualitative and quantitative traits. Eight of the 10 genotypes were clones of F_1 hybrids whereas the two mother plants were clones of recombinant inbred lines (F_5, F_6 or above). The moderate h^2_b along with high GA estimated for leaf length, plant height, and pseudostem circumference indicated the presence of huge potential to improve the economic yield of enset through selection and hybridization. Therefore, it can be concluded that this work generated important information in enset breeding for quality and yield improvement.

ACKNOWLEDGEMENTS

The authors thank Wolaita Sodo University for maintaining the germplasm in its research farm plots. We thank technical staff members of the Department of Horticulture, College of Agriculture.

REFERENCES

Allard, R.W. (1960) *Principles of Plant Breeding*. New York, USA, John Willey and Sons, Inc.

Amare, S. & Daniel, F. (2016) Diversity of enset landraces (Ensete ventricosum (Welw) Cheesman) in Aleta Chuko District, Sidama Zone, South Nation Nationality People and Regional State, Ethiopia. *Journal of Plant Science*. 4 (1), 1–7.

Bezuneh, T., Feleke, A. & Beyie, R. (1967) The cultivation of genus Ensete in Ethiopia. *Soil and Crops Science Society of Florida*. 27, 133–141.

Birmeta, G., Nybom, H. & Bekele, E. (2004) Distinction between wild and cultivated enset (*Ensete ventricosum*) gene pools in Ethiopia using RAPD markers. *Hereditas*. [Online] 140 (2), 139–148. Available from: doi:10.1111/J.1601-5223.2004.01792.X.

Biswas, M.K., Darbar, J.N., Borrell, J.S., Bagchi, M., Biswas, D., Nuraga, G.W., Demissew, S., Wilkin, P., Schwarzacher, T. & Heslop-Harrison, J.S. (2020) The landscape of microsatellites in the enset (*Ensete ventricosum*) genome and web-based marker resource development. *Scientific Reports*. [Online] 10 (1), 1–11. Available from: doi:10.1038/s41598-020-71984-x.

Blomme, G., Jacobsen, K., Tawle, K. & Yemataw, Z. (2018) Agronomic practices with a special focus on transplanting methods for optimum growth and yield of enset [*Ensete ventricosum* (Welw.) Cheesman] in Ethiopia. *Fruits*. [Online] 73 (6), 349–355. Available from: doi:10.17660/TH2018/73.6.5.

Borrell, J.S., Biswas, M.K., Goodwin, M., Blomme, G., Schwarzacher, T., Heslop-Harrison, J.S., Wendawek, A.M., Berhanu, A., Kallow, S., Janssens, S., Molla, E.L., Davis, A.P., Woldeyes, F., Willis, K., Demissew, S. & Wilkin, P. (2019) Enset in Ethiopia: a poorly characterized but resilient starch staple. *Annals of Botany*. [Online] 123 (5), 747–766. Available from: doi:10.1093/AOB/MCY214.

Borrell, J.S., Goodwin, M., Blomme, G., Jacobsen, K., Wendawek, A.M., Gashu, D., Lulekal, E., Asfaw, Z., Demissew, S. & Wilkin, P. (2020) Enset-based agricultural systems in Ethiopia: A systematic review of production trends, agronomy, processing and the wider food security applications of a neglected banana relative. *Plants People Planet*. [Online] 2 (3), 212–228. Available from: doi:10.1002/PPP3.10084.

Bosha, A., Dalbato, A.L., Tana, T., Mohammed, W., Tesfaye, B. & Karlsson, L.M. (2016) Nutritional and chemical properties of fermented food of wild and cultivated genotypes of enset (Ensete ventricosum). *Food Research International*. [Online] 89, 806–811. Available from: doi:10.1016/J.FOODRES.2016.10.016.

Brandt, A.., Anita, S., Hiebsch, C., McCabe, J.T., Endale, T., Mulugeta, D., Gizachew, W.-M., Gebre, Y., Masayoshi, S. & Shiferaw, T. (1997) *The 'Tree against Hunger' Enset Based Agricultural Systems in Ethiopia*. Washington DC, American Association for the Advancement of Science.

Burton, G.W. & DeVane, E.H. (1953) Estimating Heritability in Tall Fescue (*Festuca Arundinacea*) from Replicated Clonal Material1. *Agronomy Journal*. [Online] 45 (10), 478–481. Available from: doi:10.2134/AGRONJ1953.00021962004500100005X.

Cochran, W.G. (1952) The X2 test of goodness of fit. *The Annals of Mathematical Statistics*. [Online] 23 (3), 315–345. Available from: doi:10.1214/AOMS/1177729380.

Dabholkar, A.R. (1992) *Elements of Biometrical Genetics*. New Delhi, Concept Publishing Company.

Deshmukh, S., Basu, M. & Reddy, P. (1986) Genetic variability, character association and path coefficients of quantitative traits in Virginia bunch varieties of groundnut. *Indian Journal of Agricultural Sciences*. 56 (12), 816–821.

Diro, M. & Van Staden, J. (2003) In vitro regeneration of Ensete ventricosum from zygotic embryos of stored seeds. *South African Journal of Botany*. [Online] 69 (3), 364–369. Available from: doi:10.1016/S0254-6299(15)30319-7.

Hailu, G., Ali, M., Nigussie, D. & Derbew, B. (2017) Profitability of potato (*Solanum tuberosum* L.) as affected by NP nutrition and variety in Southern Ethiopia. *Journal of Horticulture and Forestry*. [Online] 9 (2), 9–16. Available from: doi:10.5897/JHF2017.0479.

Hölscher, D. & Schneider, B. (1998) Phenylphenalenones from Ensete ventricosum. *Phytochemistry*. [Online] 49 (7), 2155–2157. Available from: doi:10.1016/S0031-9422(98)00423-3.

Jacob, G. (2004) *Field Exchange Jul 2004: Enset - The 'false banana' as food security in Ethiopia*.2004 [Online] Available from: https://reliefweb.int/report/ethiopia/field-exchange-jul-2004-enset-false-banana-food-security-ethiopia.

Johnson, H.W., Robinson, H.F. & Comstock, R.E. (1955) Estimates of Genetic and Environmental Variability in Soybeans. *Agronomy Journal*. [Online] 47 (7), 314–318. Available from: doi:10.2134/AGRONJ1955.00021962004700070009X.

Karlsson, L., Tamado, T., Dalbato, A. & Mikias, Y. (2012) Sexual and asexual reproduction of enset as tools to increase agro-biodiversity and agricultural productivity.In: Workeneh, S., Dechassa, N., Zewdu, T. & Bekele, H. (eds.) *Book of Abstracts of the International Conference on Biodiversity Conservation and Ecosystems Services for Climate Change Mitigation and Sustainable Development, Haramaya University, Ethiopia, December 20–22, 2012.* Haramaya, UNDP and Haramaya University, p.38.

Pursglove, J. (1972) *Tropical Crops: Monocotylodons*. New York, USA, Halsted Press Division, Wiley.

Shelton, A.C. & Tracy, W.F. (2015) Recurrent Selection and participatory plant breeding for improvement of two organic open-pollinated sweet corn (*Zea mays* L.) Populations. *Sustainability*. [Online] 7 (5), 5139–5152. Available from: doi:10.3390/SU7055139.

Simmonds, N.. (1962) *The Evolution of the Bananas*. London, Butler and Tanner Ltd.

Sokal, R.R. & Rohlf, F.J. (1969) *Biometry, The Principles and Practice of Statistics in Biological Research*. Folkestone, W. H. Freeman and Company Ltd.

Vuylsteke, D., Ortiz, R., Ferris, S. & Swennen, R. (1995) `PITA-9': A Black-sigatoka-resistant hybrid from the `False Horn' plantain gene pool. *HortScience*. [Online] 30 (2), 395–397. Available from: doi:10.21273/hortsci.30.2.395.

Yemataw, Z., Chala, A., Ambachew, D., Studholme, D.J., Grant, M.R. & Tesfaye, K. (2017) Morphological Variation and Inter-Relationships of Quantitative Traits in Enset (*Ensete ventricosum* (welw.) Cheesman) Germplasm from South and South-Western Ethiopia. *Plants*. [Online] 6 (4), 56. Available from: doi:10.3390/PLANTS6040056.

Zerfu, A., Gebre, S.L., Berecha, G. & Getahun, K. (2018) Assessment of spatial distribution of enset plant diversity and enset bacteria wilt using geostatistical techniques in Yem special district, Southern Ethiopia. *Environmental Systems Research*. [Online] 7 (1), 1–13. Available from: doi:10.1186/S40068-018-0126-9.

Appendix 1 chi-squared analysis of pseudostem color of the enset genotypes evaluated at WSU

Enset clones	Pseudostem color			
Arkia	color	observed	expected	chi-square (3:1)
	green	12	12	0.0
	dark red	4	4	0.0
	Total	16	16	0.0
Banga	color	observed	expected	chi-square (1:3)
	greenish black	3	4	0.25
	dark red	13	12	0.08
	Total	16	16	0.33
Gefetanuwa(2)	color	observed	expected	chi-square (1:1)
	light green	7	8.5	0.265
	reddish brown	10	8.5	0.265
	Total	17	17	0.529
Wild 15 (Erpha)	color	observed	expected	chi-square (3:1)
	deep green	15	13.5	0.167
	light red	3	4.5	0.5
	Total	18	18	0.667
Alageena	color	observed	expected	chi-square (1:3)
	greenish black	4	4	0.0
	red	12	12	0.0
	Total	16	16	0.0
Wild 9	color	observed	expected	chi-square (3:1)
	green	9	8.25	0.068
	dark red	24	24.75	0.023
	Total	33	33	0.091
	color	observed	expected	chi-square
Gefetanuwa (1)	red	17		
Wild 11	color	observed	expected	chi-square (1:3)
	deep green	3	4	0.25
	red	13	12	0.08
	Total	16	16	0.33
Wild 10	color	observed	expected	chi-square (1:3)
	light green	4	4	0.0
	dark red	12	12	0.0
	Total	16	16	0.0
Gamogofa 71	color	observed	expected	chi-square (1:3)
	light green	5	4.25	0.132
	red	12	12.75	0.044
	Total	17	17	0.176

Appendix 2 chi-squared analysis of petiole color of the enset genotypes evaluated at Wolaita Sodo University.

Genotypes	Petiole Color			
Arkia	Color	observed	expected	chi-square (1:3)
	light green	5	4	0.25
	red-purple	11	12	0.08
	Total	16	16	0.33
Banga	Color	observed	expected	chi-square (1:3)
	light green	5	4	0.25
	light-dark red	11	12	0.08
	Total	16	16	0.33
Gefetanuwa(2)	Color	observed	expected	chi-square (1:1)
	light green	7	8.5	0.265
	greenish red	10	8.5	0.265
	Total	17	17	0.529

Wild 15 (Erpha)	Color	observed	expected	chi-square
	greenish brown	18		
	Color	**observed**	expected	chi-square (1:3)
Alageena	light green	4	4	0.0
	brown-red	12	12	0.0
	Total	16	16	0.0
Wild 9	Color	observed	expected	chi-square (1:3)
	Red	6	8.25	0.613
	dark brown	27	24.75	0.205
	Total	33	33	0.818
Gefetanuwa-1	Color	observed	expected	chi-square (1:3)
	greenish red	17		
Wild 11	Color	observed	expected	chi-square (1:3)
	light red	6	4	1.0
	greenish red	10	12	0.3
	Total	16	16	1.3
Wild 10	Color	observed	expected	chi-square (1:3)
	Purple	4	4	0.0
	greenish red	12	12	0.0
	Total	16	16	0.0
Gamogofa 71	Color	observed	expected	chi-square (1:3)
	light green	4	4.25	0.132
	Red	13	12.75	0.047
	Total	17	17	0.179

Appendix 3 chi-squared analysis of midrib color of the enset genotypes evaluated at Wolaita Sodo University

Enset clones	Midrib Color			
Arkia	Color	observed	expected	chi-square (1:3)
	Light green	5	4	0.250
	red	11	12	0.083
	Total	16	16	0.333
Banga	Color	observed	expected	chi-square (1:3)
	light green	5	4	0.25
	brown-red	11	12	0.08
	Total	16	16	0.33
Gefetanuwa(2)	Color	observed	expected	chi-square (1:1)
	light green	10	8.5	0.265
	greenish brown	7	8.5	0.265
	Total	17	17	0.529
Wild 15 (Erpha)	Color	observed	expected	chi-square
	light red	18		
Alageena	Color	observed	expected	chi-square (1:3)
	light green	4	4	0.0
	red	12	12	0.0
	Total	16	16	0.0
Wild 9	Color	observed	expected	chi-square (1:3)
	light red	6	8.25	0.61
	dark brown	27	24.75	0.20
	Total	33	33	0.81
Gefetanuwa-1	Color	observed	expected	chi-square (1:3)
	red-brown	17		

Wild 11	Color	observed	expected	chi-square (1:3)
	light red	6	4	1.0
	dark brown	10	12	0.3
	Total	16	16	1.3
Wild 10	Color	observed	expected	chi-square (3:1)
	light red	12	12	0.0
	dark brown	4	4	0.0
	Total	16	16	0.0
Gamogofa 71	Color	observed	expected	chi-square (1:3)
	green	4	4.25	0.132
	red	13	12.75	0.047
	Total	17	17	0.179

Appendix 4 chi-squared analysis of leaf color of the enset genotypes evaluated at Wolaita Sodo University

Enset clones	Leaf Color			
Arkia	Color	observed	expected	chi-square (1:3)
	deep green	16		
Banga	Color	observed	expected	chi-square (1:3)
	light green	5	4	0.250
	dark green	11	12	0.083
	Total	16	16	0.333
Gefetanuwa (2)	Color	observed	expected	chi-square (1:1)
	light green	7	8.5	0.265
	deep green	10	8.5	0.265
	Total	17	17	0.529
Wild 15 (Erpha)	Color	observed	expected	chi-square
	deep green	18		
Alageena	Color	observed	expected	chi-square (1:3)
	light green	4	4	0.0
	deep green	12	12	0.0
	Total	16	16	0.0
Wild 9	Color	observed	expected	chi-square
	deep green	33		
Gefetanuwa-1	Color	observed	expected	chi-square (1:3)
	deep green	17		
Wild 11	Color	observed	expected	chi-square
	deep green	16		
Wild 10	Color	observed	expected	chi-square
	deep green	16		
Gamogofa 71	Color	observed	expected	chi-square (1:3)
	light green	5	4.25	0.132
	deep green	12	12.75	0.044
	Total	17	17	0.176