



RESEARCH ARTICLE

Molecular parental diversity and inter-generation association parameters for yield attributes in the segregating generation of barnyard millet [*Echinochloa frumentacea* (Roxb.) Link] crosses

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ARTICLE HISTORY

Received: 25 August 2024

Accepted: 27 January 2025

Available online

Version 1.0 : 15 April 2025

Version 2.0 : 26 April 2025



Additional information

Peer review: Publisher thanks Sectional Editor and the other anonymous reviewers for their contribution to the peer review of this work.

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Indexing: Plant Science Today, published by Horizon e-Publishing Group, is covered by Scopus, Web of Science, BIOSIS Previews, Clarivate Analytics, NAAS, UGC Care, etc See https://horizonepublishing.com/journals/index.php/PST/indexing_abstracting

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CITE THIS ARTICLE

Monika S, Vanniarajan C, Chandirakala R, Renuka R. Molecular genetic diversity and inter-generation association parameters for yield attributes in the segregating generation of barnyard millet [*Echinochloa frumentacea* (Roxb.) Link] crosses. Plant Science Today. 2025; 12(sp2): 01-07.
<https://doi.org/10.14719/pst.4805>

Abstract

Barnyard millet, recognized for its high nutritional and agronomic value, has garnered significant attention in recent times. However, no short-duration varieties of barnyard millet have been released so far in Tamil Nadu. To address this gap, a study was conducted at the Agricultural College and Research Institute, TNAU, Madurai, Tamil Nadu, India, during the summer of 2020 and 2021. The study aimed to evaluate the diversity among ten barnyard millet parents, varying in duration used in various crosses, employing 30 EST-SSR and SSR markers. Twenty of the thirty primers used demonstrated polymorphism, highlighting molecular diversity. The Polymorphic Information Content (PIC) value extended from 0.18 (BMESR 101 and BMESR 114) to 0.62 (BMESR 120). Two to three alleles per locus were produced by these polymorphic markers. The ten parents were grouped into four clusters, based on Jaccard's coefficient. The parents used for different crosses in the hybridization program were chosen from the distant clusters as confirmed by the parental diversity analysis. The intergeneration heritability parameters, including parent-progeny correlation, regression, and narrow-sense heritability, were analyzed between the F₂ and F₃ generations of crosses involving extra-early parents ACM-15-343 x IEC 82 and Co (Kv) 2 x IEC 107. Regression values for yield attributes were positive and highly significant, confirming the successful inheritance of traits with minimal environmental influence. High narrow-sense heritability estimates for all yield traits indicated the potential for developing early-maturing, high-yielding genotypes. This study highlights the molecular diversity and genetic potential of barnyard millet, paving the way for the development of improved cultivars.

Keywords

F₂; F₃; molecular diversity; parent-progeny regression; PIC; true heritability

Introduction

Barnyard millet is a minor millet grown in Japan, Korea, India, China, Thailand, Vietnam and Nepal (1). Barnyard millet is the fourth most-produced minor millet, providing food and nutritional security to poor people in developing countries. Cultivation of barnyard millet is spread across Uttarakhand in the Himalayan mid-hills and South India covering the Deccan Plateau regions in India (2). It is rich in Fe, Zn and dietary fiber and has a low glycemic index compared to staple foods such as rice, wheat, and maize.

Barnyard millet is rich in polyphenols and carotenoids, which exhibit numerous therapeutic properties, including antioxidant, anticarcinogenic, anti-inflammatory, antimicrobial, and wound-healing effects, as well as benefits for managing biliousness and diseases related to constipation. These attributes make barnyard millet an excellent supplementary and also it can be an alternative crop since it is suitable for adapting to climate uncertainties (3). Despite this significance, the cultivation of barnyard millet remained dormant in the past few decades. Its nutritive and agronomic advantages have increased its demand for cultivation and consumption among the farmers and public at present. Generally, barnyard millet is grown as a rabi crop (4) and its duration remains to be 95-105 days (5). Developing an early maturing barnyard millet cultivar with a high yield would attract farmers, enabling cultivation across all cropping seasons and facilitating its use in mixed or intercropping systems. Existing variability is usually assessed using diversity analysis. Diversity studies based on the morphological characters include the influence of environment which may mislead the information about the exact genetic constitution. Here comes the role of molecular markers which give accurate perception about the pattern of differentiation among the various genotypes and for grouping them into different clusters. Genotypes selected from distant clusters are used as parents in hybridization programs to obtain superior progenies for desirable characters. The study on intergeneration correlation and regression would enlighten an idea for the selection and development of improved genotypes from the segregating generation. It determines the proportion of genetic potential of a character transmitted from one generation to successive generations (6). Narrow sense heritability provides information about the heritable fixable portion of the existing variation which includes additive variance and additive x additive portion of epistatic variance. Literature on parent progeny regression analysis in the segregating population and parental diversity in barnyard millet remains scanty. The present study focuses on the analysis of parental polymorphism using molecular markers, parent proge-

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Parental diversity

Ten genotypes of barnyard millet differing for maturity period utilized in different crosses were used in this experiment. Early maturing genotypes are those that mature within 60-80 days. Late maturing genotypes are those that mature within 90-110 days. Early maturing genotypes included IEc 82 (60 days), IEc 107 (63 days), IEc 108 (64 days), IEc 109 (62 days), IEc 385 (62 days) and IEc 386 (76 days). These lines were obtained from ICRISAT (International Crop Research Institute for Semi-Arid Tropics), Patancheru, Hyderabad, India. Late maturing genotypes were MDU 1 (95-100 days), Co (Kv) 2 (95 days), ACM-15-343 (85-90 days) and ACM-15-353 (90-95 days). These genotypes were obtained from Agricultural College and Research Institute, Madurai, Tamil Nadu, India.

Genomic DNA was extracted from the leaves of ten-day-old seedlings using the CTAB (Cetyl Trimethyl Ammonium Bromide) method (7). The quality of the extracted DNA was assessed using 0.8% agarose electrophoresis. The extracted DNA samples were then amplified using thirty EST-SSR and SSR primers by Polymerase Chain Reaction, of 35 cycles carried out through a thermal cycler. The amplified DNA bands were separated in 3% agarose gel along with Ethidium Bromide in horizontal gel electrophoresis (Fig. 1). The bands formed were scored using binary characters 0 and 1 for the absence and presence of bands, respectively. The scores were used for further surveys. The information obtained using different primers was presented as Polymorphic Information Content (PIC), which was calculated using the formula,

$$PIC = 1 - (\sum p_i^2),$$

where i is the number of alleles, p_i is the frequency of i^{th} allele

The PIC values offer an estimate of the ability of a locus to differentiate genotypes by taking into account

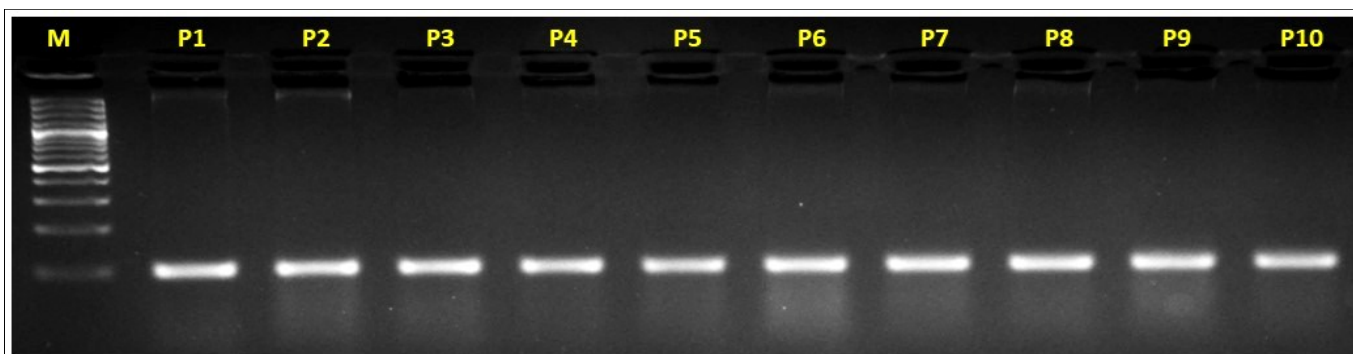


Fig. 1. PCR amplification of the ten parental genotypes using BMESR 109 marker. M - 100 bp Ladder, P1-IEc 82, P2-IEc 107, P3-IEc 108, P4-IEc 109, P5-IEc 385, P6-IEc 386, P7-MDU1, P8-Co(Kv)2, P9-ACM-15-343, P10-ACM-15-353.

ny association parameters, and narrow sense heritability in the early segregating population of extra early barnyard millet parents involved crosses.

Materials and Methods

The present study was conducted at the Department of Plant Breeding and Genetics, Agricultural College and

both the number of alleles at each locus and the relative frequencies of these alleles within the population (8).

A similarity matrix was brought out using the SIMQUAL program of NTSYS pc 2.02i software based on the binary data scores (9). This gives the genetic distance between these parental genotypes. This was further used for forming clusters and represented by a dendrogram

which was constructed based on the Unweighted Pair Group Method with Arithmetic mean (UPGMA) (10). Clusters were separated based on the Jaccard similarity coefficient (11) and it was interpreted that the genotypes present in different clusters are genetically distant and those in the same are identical to each other.

Parent progeny regression

The genetic material used were F_2 and F_3 generation of two crosses of barnyard millet, namely ACM-15-343 x IEC 82 and Co (Kv) 2 x IEC 107, exerted to procure genotypes with early maturity. The parents ACM-15-343 and Co (Kv) 2 are late-maturing cultivars with a duration of 95 days. The IEC lines mature within 60-65 days. 250 plants of F_2 generation were raised during the Summer of 2020. Ten best-performing plants for early maturity and yield were picked from the preceding generation of both the crosses and raised as a family in F_3 during Summer 2021. Observations were recorded for six yield attributes including days to maturity, plant height (cm), number of basal tillers, panicle length (cm), single ear head weight (g), and grain yield per plant (g). Parent progeny regression (b) was computed between F_2 and F_3 generation of two crosses for all the six characters (12):

$$\text{Regression coefficient (b)} = \frac{\text{Co Var (F}_2 \text{ F}_3\text{)}}{\text{Var F}_3}$$

Where, Co Var = Covariance, Var = Variance

Intergeneration correlation between F_2 and F_3 was calculated as reported by (13)

$$\text{Intergeneration correlation (r)} = b \times \frac{\sigma_{F_2}}{\sigma_{F_3}}$$

where, σ_{F_2} - Standard deviation of F_2 , σ_{F_3} - Standard deviation of F_3

Narrow sense heritability was computed to find out the heritable fixable portion of the existing variation such as additive variance and additive x additive component of epistatic variance. It was determined as given in (14)

$$\text{Narrow sense heritability} = \frac{b_{xy}}{2r_{xy}}$$

Where, b_{xy} = regression of F_3 on F_2 , r_{xy} = correlation between F_2 and F_3

Results and Discussion

Parental diversity study

Molecular markers accurately measure the genetic diversity among different genotypes avoiding the impact of the environment. SSR markers are one of the most widely used molecular markers for diversity studies (15). The multiallelic nature of SSR markers and the greater frequency of polymorphism make it easier to establish genotype-to-genotype correlation even with a lesser number of markers (16). EST-SSR markers effectively reveal the diversity present in the genotypes (17). To date, parental diversity studies in barnyard millet using molecular markers seem to be very scarce. In the current study, thirty markers were

utilized for screening ten barnyard millet parental genotypes used in different crosses. Twenty-four out of thirty EST-SSR and SSR markers effectively produced DNA bands and twenty were polymorphic (Table 1). These polymorphic markers can be further used for diversifying the barnyard millet genotypes. The molecular weight of the amplicons ranged from 100 bp (BMESR 109) to 364 bp (PSMP 2201).

The findings from the twenty polymorphic markers show that a sum of 45 alleles was obtained, with an average of 2.25 alleles per locus (Table 2). The range was 2 to 3 alleles per locus. A maximum of three alleles were flaunted by five primers BMESR 120, BMESR 118, BMESR 109, BMESR 112, and BMESR 106. Remaining primers BMESR 102, BMESR 113, BMESR 114, BMESR 115, BMESR 101, BMESR 119, BMESR 104, BMESR 108, BMESR 105, PSMP 2209, PSMP 2205, PSMP 2206, PSMP 2201, PSMP 2203 and RM 240 exhibited a minimum of two alleles per locus. These results were similar to those obtained in barnyard millet (18). The PIC value furnishes the information granted by a marker by considering the number of alleles and the relative frequency of the appeared alleles (19). PIC in the present experiment ranged from 0.18 to 0.62. The highest PIC (0.62) was obtained from BMESR 120 and the lowest (0.18) from BMESR 114 and BMESR 101. An informative marker is one showing a PIC greater than 0.5. Three markers BMESR 120 (0.62), BMESR 112 (0.53), and PSMP 2205 (0.50) were highly polymorphic and thus informative. Other primers such as BMESR 102, BMESR 119, BMESR 115, BMESR 108, PSMP 2209, PSMP 2206, PSMP 2201, PSMP 2203, RM 240 also expressed promising PIC (0.40-0.48). Similar results were noticed in finger millet (20) and barnyard millet (18, 21). Validating these polymorphic markers would provide useful genetic information to save effort and time in breeding program (22). The identified polymorphic markers prove the high transferability for use in makers-assisted breeding.

The genotypes were grouped into different clusters based on the molecular diversity revealed using these markers. Jaccard's similarity coefficient was considered prime for grouping these ten genotypes, which showed the existence of four clusters (Fig. 2) at the similarity coefficient of 0.60. Cluster I and II were solitary, and Cluster III and IV were carrying four genotypes each. IEC 82 and IEC 107 were placed in Cluster I and II respectively. Cluster III had the genotypes, IEC 108, IEC 109, IEC 385, and IEC 386 and Cluster IV had the genotypes, ACM-15-343, ACM-15-353, MDU 1, and Co (Kv)2. Genetically similar genotypes were placed within the same clusters and high diversity will be observed between different and distant clusters. The selection of parents belonging to distant clusters could be used for future hybridization programmes. Genotypes with extra earliness are packed in clusters I, II, and III. Cluster IV had the high yielders. Selection of one of the parents from these clusters for hybridization with high yielding parent from cluster IV can help in widening the genetic base for obtaining promising progenies with extra early maturity coupled with high yield.

Table 1. Sequences and characteristic information on polymorphic markers used in the study

S. No	Marker		Primer Sequences	Annealing temperature (°C)	Amplicon Size (bp)	Reference
1.	BMESSR 120	Forward	GTTACAAGAAGATCGACTTACC	63	125	(28)
		Reverse	TGACACTTTGCCCAATTTAC			
2.	BMESSR 102	Forward	GATGGCCGAGCATATGATAT	52	115	
		Reverse	GGAGCAGGAGAATATGTACG			
3.	BMESSR 118	Forward	TCGAGAACGTACATGAGATA	62	112	
		Reverse	CAGCACATACGAACCTTC			
4.	BMESSR 109	Forward	TTGTCGTATCATCTTCTCTG	57	100	
		Reverse	TTTAGGTCCAAAGCCCAAT			
5.	BMESSR 113	Forward	TGTGCTCCATCAATT CAGA	48.1	144	
		Reverse	GTATACCATAGGCCATCGT			
6.	BMESSR 112	Forward	ACATTTCTTTGTTCTGCCG	63	183	
		Reverse	GATCCTCGATTGTTCCA			
7.	BMESSR 114	Forward	GTACAGGTAGTGAGTGAGTG	60	102	
		Reverse	GAAGAAGAAGACGAGTCCAA			
8.	BMESSR 115	Forward	CCTCATCTGCTCACATTCAT	62	162	
		Reverse	TGGTGCTTGCTGGAGTATA			
9.	BMESSR 101	Forward	GGCAGTCACCATCTATCAG	57	127	
		Reverse	CACTTCCGAACGAACCAT			
10.	BMESSR 119	Forward	CATAAAGGCAGCGTCTCC	65	171	
		Reverse	ATCGGCGATGGATGAGAT			
11.	BMESSR 104	Forward	CGTCGTGTAACCAACCAT	64	141	
		Reverse	ACGCTCCAATGCTGTTAG			
12.	BMESSR 108	Forward	GTATCCATCCACCGTGT	62	120	
		Reverse	GAGGAGACTGCTCATTGG			
13.	BMESSR 106	Forward	TCGGCTTCTTGATCCTCT	63	176	
		Reverse	ACGAGAAAGTGAATGAATGC			
14.	BMESSR 105	Forward	CGCAGATAAAGAGGGAGAT	63	142	
		Reverse	AGTAACTCGGAGCAATGAA			
15.	PSMP 2209	Forward	TTGGACGATTTGGAAGCATAG	52	334	(29)
		Reverse	GAGGAAAAGAGCCATACAGAGAC			
16.	PSMP 2205	Forward	AGGTGCTCACGAGCTGTAAGAG	50	202	
		Reverse	AGCAAGACACTATTTTACCATC			
17.	PSMP 2206	Forward	AGAAGAAGAGGGGTAAGAAGGAG	63	203	
		Reverse	AGCAACATCCGTAGAGGTAGAAG			
18.	PSMP 2201	Forward	CCCGACGTTATGCGTTAAGTT	60	364	
		Reverse	TCCATCCATCCATTAATCCACA			
19.	PSMP 2203	Forward	GAACTTGATGAGTGCCACTAGC	51.8	357	
		Reverse	TTGTGTAGGGAGCAACCTTGAT			
20.	RM 240	Forward	CCTTAATGGGTAGTGTGCAC	58.2	132	(30)
		Reverse	TGTAACCTTCCTTCCATCC			

Parent progeny regression

Parent-offspring association (b) affords an idea on the portion of the genetic information inherited from the parent to the consecutive generation. Intergenerational correlation studies help to determine how much genetic potential of the yield-contributing trait is passed on to future gener-

ations. This helps in choosing better-performing genotypes effectively from the segregating population.

Intergeneration correlation and regression

All six characters manifested significant positive regression values based on the molecular diversity revealed using these markers (Table 3). The regression coefficient values

Table 2. Characteristics of polymorphic markers used in screening ten parental genotypes

S. No	Marker	No. of alleles	Polymorphic Information Content (PIC)	Amplicon size obtained (bp)
1.	BMESSR 120	3	0.62	120-130
2.	BMESSR 102	2	0.48	110, 115
3.	BMESSR 118	3	0.58	112-115
4.	BMESSR 109	3	0.34	100-117
5.	BMESSR 113	2	0.32	144, 150
6.	BMESSR 112	3	0.53	183-188
7.	BMESSR 114	2	0.18	102,105
8.	BMESSR 115	2	0.42	162,165
9.	BMESSR 101	2	0.18	127,130
10.	BMESSR 119	2	0.48	171,175
11.	BMESSR 104	2	0.32	141,145
12.	BMESSR 108	2	0.42	120,123
13.	BMESSR 106	3	0.46	176-180
14.	BMESSR 105	2	0.35	142,144
15.	PSMP 2209	2	0.42	334,337
16.	PSMP 2205	2	0.50	202,205
17.	PSMP 2206	2	0.44	203,205
18.	PSMP 2201	2	0.48	364,366
19.	PSMP 2203	2	0.48	357,360
20.	RM 240	2	0.41	132,135
Average		2.25	0.42	-
Total		45	-	-
Range		2-3	0.18-0.62	100-366

accounted for days to maturity was 1.06, plant height was 0.95, number of basal tillers was 0.86, panicle length was 0.93, single ear head weight was 0.94 and that grain yield per plant was 0.85 in cross I (ACM-15-343 x IEC 82). The b value for days to maturity was drawn as 1.02, for plant height as 0.98, for number of basal tillers, panicle length, single ear head weight, and grain yield per plant as 0.95, 0.91, 0.93, and 0.85 respectively in cross II (Co (Kv) 2 x IEC 107). The intergeneration correlation values were also high, positive, and significant. Intergeneration correlation values were 1.15, 1.05, 0.99, 1.16, 1.30, and 1.09 for days to maturity, plant height, number of tillers, panicle length, panicle weight, and grain yield/ plant respectively in cross I. The traits days to maturity, plant height, the number of tillers, panicle length, weight, and yield/ plant showed r values of 1.13, 1.45, 1.39, 1.09, 1.31, and 1.12 respectively in cross II. When the behaviour of the progeny is highly reliant on its parents, then the selection would be made effective (12). The features noticed in F_2 (parents) for days to maturity, plant height, number of basal tillers, panicle length, single ear head weight, and grain yield per plant had been retained in F_3 (progeny) in both the crosses as registered by the high, significant and positive b and r values. This indicates the successful transfer of the traits from the selected plants to the next generation, which in turn stamps the effectiveness of selection in the preceding generation. This was following the outcome in bread wheat (6, 23) and in rice (24, 25). High (b) values noted for the characters attributing to yield and maturity were good indicators of the high heritability of the genes governing the studied traits. This also stipulated the presence of large genetic effects with less environmental effect and hence, the selection would be heritable and effective (25).

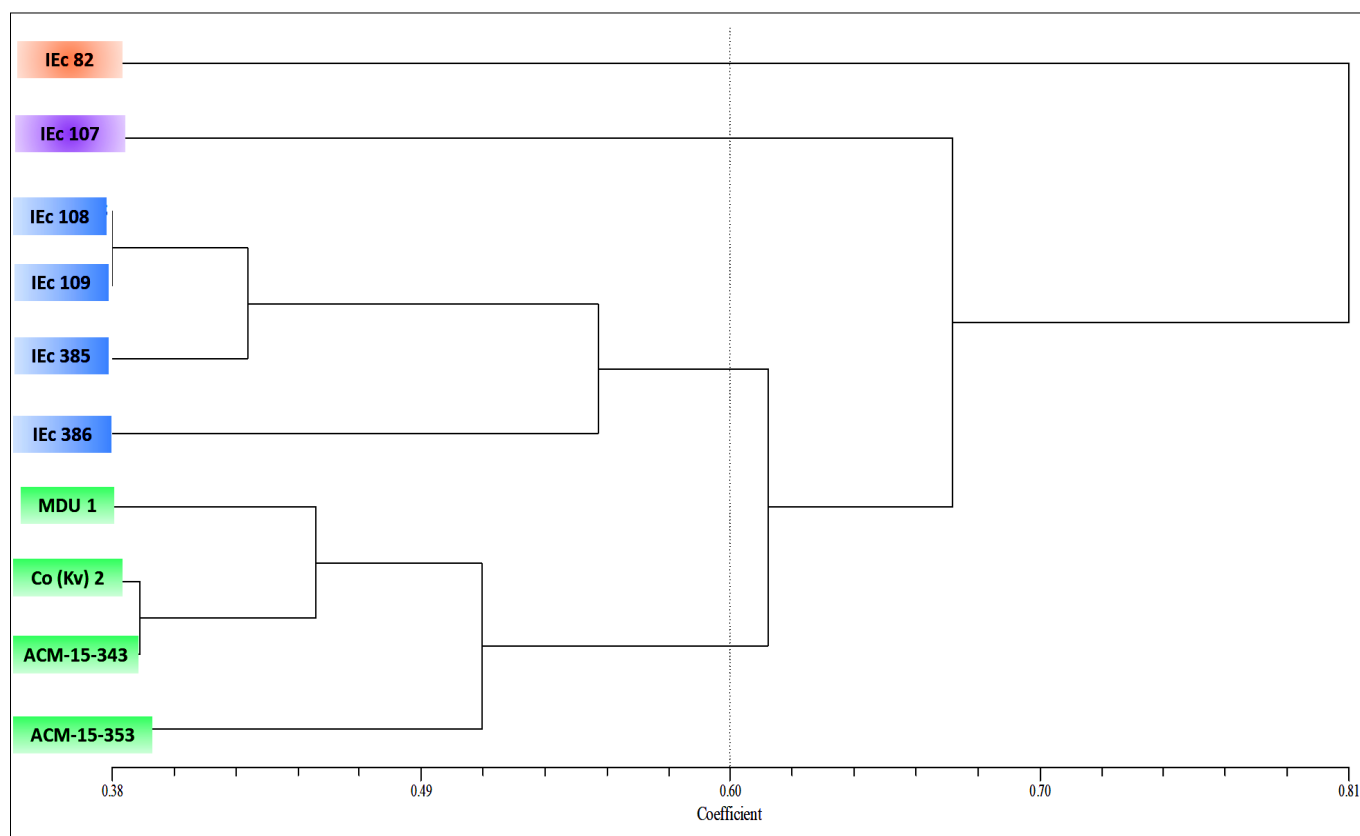
**Fig. 2.** Dendrogram depicting ten parental genotypes based on Jaccard similarity co-efficient.

Table 3. Parent progeny regression between F_2 and F_3 generations of two crosses of barnyard millet

Characters	Cross I: F_2 - F_3			Cross II: F_2 - F_3		
	Intergeneration correlation	Parent progeny regression	Heritability (NS) %	Intergeneration correlation	Parent progeny regression	Heritability (NS) %
Days to maturity	1.15**	1.06**	45	1.13**	1.02**	45
Plant height	1.05**	0.95**	45	1.45**	0.98**	34
Number of tillers	0.99**	0.86**	43	1.39**	0.95**	34
Panicle length	1.16**	0.93**	40	1.09**	0.91**	41
Panicle weight	1.30**	0.94**	36	1.31**	0.93**	35
Grain yield/ plant	1.09**	0.85**	39	1.12**	0.85**	38

Also, effective selection in the early segregating generation for extra early maturity along with improved grain yield is possible. This material can also be used for developing advanced breeding lines such as RILs for grain yield with extra early maturity.

Narrow sense heritability

Narrow sense heritability indicates the fixable portion of the traits carried over to the next generation, which would be useful for successful selection. The highest narrow sense heritability was found for days to maturity and plant height (45%) followed by the number of basal tillers (43%), panicle length (40%), grain yield per plant (39%), and single ear head weight (36%) in cross I. The maximum value was observed for days for maturity (45%), followed by panicle length (41%), grain yield per plant (38%), single ear head weight (35%), plant height, and number of basal tillers (34%) in cross II (Table 3). These results were similar to the results in rice (26). Traits with more than 30% narrow sense heritability show high efficiency for further crop improvement (27). Since all the studied yield attributes had a trend of high true heritability, they provide a scope for selection in F_2 - F_3 generation, which was carried out successfully. Narrow sense heritability is known to be the real heritability, which should be known for the improvement of yield attributes (13). Selection based on these traits will be effective and can be improved for obtaining high yielding, early maturing genotypes.

Conclusion

Summarizing these results, the parents used for the hybridization program had been selected from distant clusters and this helped in obtaining genotypes with early maturity coupled with high yield. Genotypes with early maturity and high yield can be selected for use in further breeding programs to evolve short-duration, high-yielding barnyard millet cultivars. Parent-offspring regression confirmed the successful transmission of genetic potential from the parental generation to the successive generation. Additionally, narrow sense heritability was observed to be high for all traits and was used for further improvement for obtaining early maturing, high-yielding genotypes. Genotypes of F_3 of both crosses produced early maturity with high yield compared to parents and check. Thus, the segregating material is handled according to the method of selection suggested and can be forwarded to F_4 , F_5 , F_6 , and further. The later homozygous generation can be tested

for their stability across different environments. This opens the scope for improving a short-duration, high-yielding cultivar adaptable to diverse conditions, seasons, and cropping systems.

Acknowledgements

The author wishes to acknowledge the Department of Genetics and Plant Breeding, Agricultural College and Research Institute, TNAU, Madurai for providing seed materials, fields and for facilitating laboratory work. Also, the author wishes to acknowledge the Center of Innovation, TNAU, Madurai for providing their instrumentation facility.

Authors' contributions

MS conducted field and lab experiments, collected data, statistical analysis, and manuscript drafting. CV framed out the research work, designed the experiment and edited the manuscript. RC edited the manuscript. RR provided the guidance for molecular work. All authors read and approved the final manuscript.

Compliance with ethical standards

Conflict of interest: Authors do not have any conflict of interests to declare.

Ethical issues: None

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