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GENE ACTION AND HERITABILITY ESTIMATES IN F₂ POPULATIONS OF FOXTAIL MILLET (*SETARIA ITALICA* L.)

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SUMMARY

From a nutritional and health point of view, Foxtail millet (*Setaria italica* [L.] P. Beauv.) is one of the valuable millets due to its adaptability to adverse environmental conditions and ideal characteristics for functional genomics studies. Despite the increased number of studies on foxtail millet globally, however, presently in Indonesia, it is an underutilized crop species. Through conventional hybridization, combining superior traits has been conducted to produce high-yielding cultivars with early maturity and medium plant stature in foxtail millet. The pertinent study aimed to elucidate the genetic diversity in F₂ populations derived from the cross of Botok-10 × ICERI-5 and approximate the broad-sense heritability and gene actions controlling various traits in foxtail millet. The study's genetic material used 352 F₂ populations from the crossing of two potential parental genotypes of the foxtail millet: Botok-10 and ICERI-5. The results enunciated several individual F₂ populations with medium plant stature and earlier heading time compared with the parental genotypes. These potential F₂ segregants were also higher yielders than the male parent (ICERI-5). Non-additive gene action controlled the inheritance of the three targeted traits, i.e., plant height, heading time, and grain weight per plant in the foxtail millet. The heading time and grain weight per plant traits showed the highest genetic coefficient of variation (GCV) and moderate broad-sense heritability, and the plant height showed moderate GCV and low broad-sense heritability in the foxtail millet. All observed traits, except stem diameter, showed a significant positive correlation with grain weight per plant. The selection differential values indicated that the selected individuals have faster heading time and higher grain weight per plant than the overall F₂ populations.

Keywords: Foxtail millet (*Setaria italica* L.), broad-sense heritability, gene action, kurtosis, skewness, underutilized crops

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Key findings: The promising F₂ segregants derived from the cross, Botok-10 × ICERI-5, met the breeding objectives like medium plant stature, early heading, and high productivity in foxtail millet. All the vital traits were under the control of a non-additive gene action. The heading time and grain weight per plant showed the highest GCV and moderate heritability, and the plant height showed moderate GCV and low heritability.

INTRODUCTION

Foxtail millet (*Setaria italica* [L.] P. Beauv.), a minor cereal grain, acquired significant attention due to its nutritional and health benefits and adaptability to varied climatic conditions (FAO, 2023). Among the minor millets, foxtail millet ranks second in millet production, with an average of six million tons from the Southern parts of Europe and Asia alone (FAO, 2021). This year (2023), it also celebrated the International Year of Millets (FAO, 2023). From the nutritional point of view, foxtail millet comprised a low glycemic index, high content of proteins (11%), minerals (3%), fats (4%), and dietary fibers (17%), and the potential for antioxidants (Goudar *et al.*, 2023). Recently, studies also suggested that foxtail millet is promising as anti-hyperglycemic, anti-cholesterol, and anti-hypertension (Sabuz *et al.*, 2023). Several studies also reported the adaptive nature of foxtail millet to unfavorable environmental conditions and abiotic stresses, such as drought (Xiao *et al.*, 2021) and salinity (Ardie *et al.*, 2015; Akter *et al.*, 2020). Regardless of the colossal importance of this species, foxtail millet still needs to strengthen its crop utilization in Indonesia.

The release of superior foxtail millet varieties has occurred in China and India. Cross-breeding resulted in many foxtail millet varieties in China, including the stress-tolerant and high-yielding 'Jigu32' (Li *et al.*, 2014). Meanwhile, in India, pure-line selection resulted in the high-yielding foxtail millet variety 'GPUF 3' (Nagaraja *et al.*, 2022). Until recently, the release of a superior foxtail millet variety has yet to happen in Indonesia. Cross-breeding of foxtail millet is challenging due to the tiny size of its florets, with a low cross-pollination probability (1.4%–4.0%) (Diao and Jia, 2016). Nugroho *et al.* (2020) successfully induced male sterility in foxtail millet by

immersing the inflorescence in warm water at 48 °C for 3 min, which further led to foxtail millet cross-breeding in Indonesia. Characterization of Indonesian local foxtail millet accessions identified genotypes with desired traits for further breeding programs (Widyawan *et al.*, 2018; Firdaus *et al.*, 2020; Ramlah *et al.*, 2020).

Selection is an essential process in plant breeding programs. The selection's effectiveness depends on influences by the level of genetic variability, heritability value, the number of genes, and the actions of genes controlling the targeted traits (Singh *et al.*, 2023). Given its high genetic variability, selection in the F₂ population is preferable to obtain plant individuals with desirable qualities (Hussain *et al.*, 2021). Selection in the F₂ population of a cross between homozygous parents will be effective if the choice traits are highly heritable, as a high heritability estimate indicates that the plant phenotype is more influenced by genetic factors than the environment (Majhi, 2020). Skewness and kurtosis provide information about the nature of gene action and the number of genes controlling the traits (Roy, 2000), which is necessary to increase the selection efficiency in breeding programs.

Botok-10 is an Indonesian local foxtail millet genotype originating from East Nusa Tenggara, with tall stature, late maturity, and high-productivity features. In contrast, the ICERI-5 genotype was a collection of the Indonesian Cereals Research Institute, with low productivity yet short stature and early harvest facets (Sintia *et al.*, 2023). Moreover, reports stated ICERI-5 showed tolerance to salinity and drought stress (Ardie *et al.*, 2015; Lapuimakuni *et al.*, 2018), while Botok-10 tended to be sensitive to salinity and drought stress by the *SiDREB2*-based SNAP marker (Widyawan *et al.*, 2018). Populations with combined desirable traits derived from the

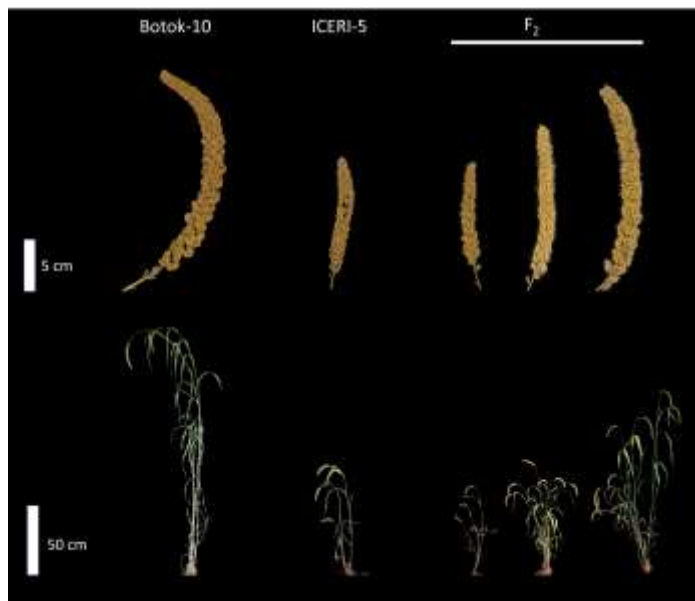


Figure 1. Panicle (upper panel) and plant habitus (below panel) of the foxtail millet parental genotypes (Botok-10 and ICERI-5) and three representatives of F₂ individuals in this study.

crossing of Botok-10 and ICERI-5 genotypes have more probability of generating foxtail millets with high-yielding segregants of the targeted ideotypes. In this study, authors have developed F₂ populations of foxtail millet derived from the crossing of Botok-10 and ICERI-5 genotypes. The presented study sought to elucidate the genetic variability of this F₂ foxtail millet population, estimate the broad-sense heritability, and understand the gene action controlling several traits in foxtail millet.

MATERIALS AND METHODS

Genetic material

Genetic material comprising 352 F₂ populations came from crossing foxtail millet genotypes, i.e., Botok-10 and ICERI-5, and their parental genotypes (Figure 1). Foxtail millet is highly self-pollinated (Zhang *et al.*, 2012); thus, a male-sterile induction proceeded by immersion into 48 °C warm water for three minutes before hybridization (Nugroho *et al.*, 2020). In the F₁ progenies, validating the successful hybridization resulted from *SidREB2*-based

SNAP markers developed by Widyawan *et al.* (2018). The female parent (Botok-10) showed only a 300 bp band for the G allele, the male parent (ICERI-5) showed only the band specific for the A allele, and the F₁ progenies showed both the A and G alleles. Sown seeds from the main panicle of one F₁ plant served as the F₂ population for this study.

Experimental design and procedure

The presented study on foxtail millet ran from February to August 2021 at the Cikabayan Bawah Experimental Station (6°33'24.23"S, 106°43'33.4"E), Department of Agronomy and Horticulture, IPB University, Indonesia. The experimental station has an elevation of 240 m above sea level, with the weather conditions during the research recorded an average temperature of 26.02 °C, relative humidity at 84.78%, and total rainfall of 279.60 mm. Seeds of foxtail millet F₂ populations continued to sow in seedling trays containing compost and manure (1:1, v/v). Seedlings with five to six leaves proceeded to transplant in the field. The conducted experiment had three blocks with a size of 45 m × 10.4 m. Each block consisted of eight plots with a dimension of 45

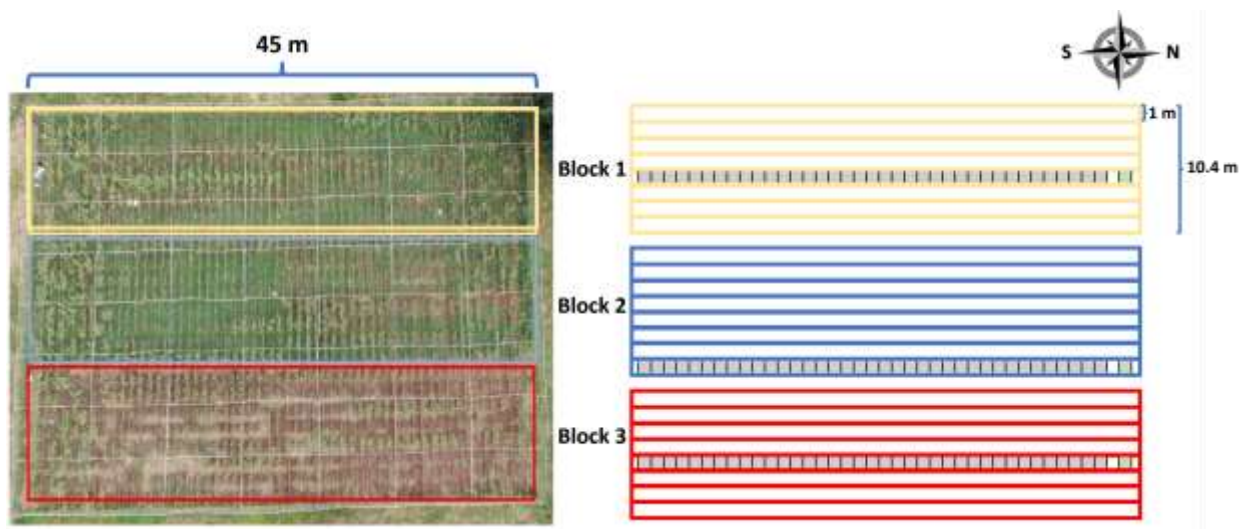


Figure 2. The aerial view of experimental blocks (left) and schematic experimental layout (right). The striped plot in each block showed experimental plots used in this study. Each vertical line in each plot indicates planting rows, consisting of 38 rows of F_2 individuals and two rows of parental genotypes (Botok-10 and ICERI-5) at the right-most rows of each plot.

m × 1 m, and this experiment used only one plot in each block, as shown by a striped area in Figure 2. A plot consisted of 38 planting rows of F_2 individuals and two rows of parental genotypes (Botok-10 and ICERI-5). Each row consisted of eight plants with a crop spacing of 75 cm × 10 cm. Fertilizer applications ensued two weeks after planting (WAP) with a half rate of nitrogen in the form of urea (150 kg ha^{-1}) and the complete rates of phosphorus in the form of SP-36 (150 kg ha^{-1}) and potassium in the form of KCl (75 kg ha^{-1}). The urea's second half rate application (150 kg ha^{-1}) continued at six WAP. A plant net, installed at two WAP, protected the plants from birds and other pests in the field.

Data recorded

The data recorded for foxtail millet parental genotypes and their F_2 populations included the following morphological and yield-related traits: plant height (cm), number of leaves, stem diameter (mm), length and width of flag leaf (cm), the number of productive tillers and panicles per plant, heading time (days after transplanting - DAT), harvesting time (DAT),

panicle weight (g), and grain weight per plant (g).

Data analysis

The recorded data for each trait in foxtail millet parental genotypes and their F_2 populations incurred analysis of means and standard deviation. Adjusted means compilation ensued before further analysis due to high block variations. The adjusted means' calculation used the SAS software, with the standardized adjusted means, their standard deviation, and correlation analysis calculated using Minitab-18. The selection index (SI) formula comprised - plant height - flowering time + ($3 \times$ grain weight per plant) to select 10% of the 352 F_2 individuals. The top 35 individuals with the highest selection index values became the formula to calculate the selection differential. Table 1 shows the summary of equations used to analyze data in this study.

An additive gene action occurs when both the skewness (Z_s) and kurtosis (Z_k) test results are not significantly different with a critical value of $Z_{0.01/2} = -2.58$ or 2.58 and $Z_{0.05/2} = -1.96$ or 1.96 (Hair *et al.*, 1998). The

Table 1. Parameters and equations used to analyze the F₂ populations derived from the cross of Botok-10 and ICERI-5.

Parameters	Equations
Adjusted mean (\hat{y}_{ij})	$y_{ij} - a_j, a_j = \bar{X}_{.j} - \bar{\bar{X}}$
Standardized adjusted mean (X_n)	$\frac{X_{ij} - \bar{X}_i}{Si}$
Standard deviation (σ)	$\sqrt{\frac{\sum_{i=1}^N (x_i - \mu)^2}{N}}$
Standard error of skewness (SE_S)	$\sqrt{\frac{6n(n-1)}{(n-2)(n+1)(n+3)}}$
Standard error of kurtosis (SE_K)	$2(SE_S) \times \sqrt{\frac{n^2-1}{(n-3)(n+5)}}$
Statistics test of skewness (Z_S)	SE/SE_S
Statistics test of kurtosis (Z_K)	SK/SE_K
Phenotypic variance (σ_p^2)	$\sigma^2 F_2$
Environmental variance (σ_e^2)	$\frac{P_1 + P_2}{2}$
Genotypic variance (σ_g^2)	$\sigma_p^2 - \sigma_e^2$
Genotypic coefficient of variation (GCV)	$\frac{\sqrt{\sigma_g^2}}{\bar{x}} \times 100\%$
Broad-sense heritability (h_{bs}^2)	$\frac{\sigma_g^2}{\sigma_p^2} \times 100\%$
Correlation coefficients (r)	$\frac{\sum xy - \frac{\sum x \sum y}{n}}{\sqrt{(\sum x^2 - \frac{(\sum x)^2}{n})(\sum y^2 - \frac{(\sum y)^2}{n})}}$
Differential selection (S)	$\frac{\bar{x}_i - \bar{x}_0}{\bar{x}_i - \bar{x}_0}$

Note: \hat{y}_{ij} = the adjusted mean of the i-th selection in the j-th block; y_{ij} = value of each trait in the i-th selection in the j-th block; a_j = the adjustment factor for the j-th block; $\bar{X}_{.j}$ = mean value of all checks in j-th block; $\bar{\bar{X}}$ = general mean; X_{ij} : means of each genotype, \bar{X}_i : means of the variable, S_i : standard deviation of the variable, P1: parent 1, P2: parent 2, x : each value from the population, μ : mean, N: total of population, \bar{x}_i : mean selected population, \bar{x}_0 : mean population before selection.

genetic coefficient of variation (GCV) has categories of three different intensities, i.e., low (0%–10%), moderate (11%–20%), and high (>21%) (Sivasubramanian and Madhavamenon, 1973). The broad-sense heritability also has three categories, i.e., high (50% \leq h_{bs}^2 < 100%), moderate (20% \leq h_{bs}^2 < 50%), and low (0 \leq h_{bs}^2 < 20%) (Stanfield, 1983).

RESULTS AND DISCUSSION

Analysis results on the means and standard deviation of various quantitative traits recorded in parental genotypes (Botok-10 and ICERI-5) and their F₂ populations in foxtail millet are available in Table 2. On average, the recorded F₂ population means showed higher mean values than the parental genotypes for the

Table 2. Mean and standard deviation of F₂ populations derived from the cross of Botok-10 x ICERI-5 and their parental genotypes.

Traits	Mean value and standard deviation		
	Botok-10	ICERI-5	F ₂
Heading time (DAT)	52.68±4.65	32.94±8.97	30.44±9.92
Plant height (cm)	178.91±17.74	73.03±18.96	61.45±20.46
Number of leaves	18.05±5.99	13.29±6.66	17.01±9.96
Stem diameter (cm)	4.74±0.86	2.41±1.26	1.60±1.28
Flag leaf length (cm)	40.18±7.88	30.07±6.43	29.59±7.61
Flag leaf width (cm)	2.33±0.40	2.02±0.35	1.85±0.43
Days to harvest (DAT)	95.85±2.32	35.81±0.65	85.88±8.81
Total number of tillers	1.65±0.58	3.35±2.00	4.67±2.81
Number of productive tillers	0.64±0.59	2.33±1.97	4.02±2.67
Panicle length (cm)	22.11±4.36	12.73±2.62	11.72±4.83
Panicle weight per plant (g)	11.18±6.20	5.85±4.60	7.77±7.32
Grain weight per plant (g)	9.28±5.38	4.82±4.11	5.77±6.14

Note: DAT= days after transplanting

number of productive tillers and total tiller number. For some traits, namely, the number of leaves, days to harvest, panicle length, panicle weight per plant, and grain weight per plant, the population means were at par with the means of the parental genotypes. However, some traits had lower population means than the parental genotypes, i.e., plant height, stem diameter, flag leaf length and width, and heading time.

The expected promising genotypes of foxtail millet were those with medium plant stature, early heading time, and high productivity. For traits plant height and heading time, the F₂ population means derived from Botok-10 and ICERI-5 appeared lower than the parental genotype means, indicating several individuals in the F₂ populations with shorter plant stature and earlier heading than the parental genotypes. In F₂ populations, the grain weight per plant means was higher than the male parent (ICERI-5), implying that potential segregants existed in the F₂ populations. For all traits, except the flag leaf length, the F₂ populations had a higher standard deviation than the parental genotypes, signifying a considerable genetic variability and scope for further improvement in these traits of foxtail millet.

Analysis of skewness and kurtosis can predict the type of gene action in the F₂ populations (Table 3). Results revealed that the trait flag leaf length has an additive gene

action control, with all the other traits governed by non-additive gene action. Past studies also reported that an additive type of gene action was also evident in managing the flag leaf length, and non-additive gene action controlled the inheritance of plant height, heading time, and early maturity in exotic genotypes of foxtail millet (Prasanna *et al.*, 2013).

Traits inheritance managed by additive gene action indicates their heritability to the offspring (Varona *et al.*, 2018). Such gene action implies the individual phenotype with homozygous genotypes and may differ from those with heterozygous genotypes. It opens the opportunity to perform intensive selection in early segregating generations. Assuming that the selected superior individuals have homozygous dominant genotypes, the expression of the traits would be stable from generation to generation, and no further segregation might occur.

Traits controlled by additive gene action will have a high response to selection as the traits of interest and can be helpful as selection criteria for further improvement (Varona *et al.*, 2018). Previous studies reported that pure line selection and mass selection were beneficial for traits managed by an additive gene action in the foxtail millet (Prasanna *et al.*, 2013), while Meriaty *et al.* (2021) used pedigree selection for such traits in soybean.

Table 3. Skewness, kurtosis, and gene action of various traits in F₂ foxtail millet populations derived from the cross of Botok-10 x ICERI-5.

Traits	S	Z _S	K	Z _K	Gene action
Heading time (DAT)	-4.37	-33.61**	56.29	217.09**	Non-Additive
Plant height (cm)	0.31	2.38*	-0.94	-3.63**	Non-Additive
Number of leaves	0.99	7.62**	1.2	4.63**	Non-Additive
Stem diameter (cm)	0.16	0.77 ^{ns}	-1.24	-4.67**	Non-Additive
Flag leaf length (cm)	-0.18	-1.38 ^{ns}	-0.09	-0.35 ^{ns}	Additive
Flag leaf width (cm)	0.08	0.62 ^{ns}	-0.54	-2.08*	Non-Additive
Days to harvest (DAT)	-1.00	-7.69**	-0.55	-2.12*	Non-Additive
Total number of tillers	1.12	8.61**	1.74	6.71**	Non-Additive
Number of productive tillers	1.14	10.00**	1.8	8.25**	Non-Additive
Panicle length (cm)	0.47	3.62**	1.28	4.94**	Non-Additive
Panicle weight per plant (g)	0.86	6.62**	0.18	0.69 ^{ns}	Non-Additive
Grain weight per plant (g)	0.90	6.92**	0.25	0.96 ^{ns}	Non-Additive

Notes: DAT= day after transplanting, S= skewness, SE_S= standard error of skewness (0.130), Z_S= statistical test of skewness, K= kurtosis, SE_K= standard error of kurtosis (0.259), Z_K= statistical test of kurtosis, **= significant at $P < 0.01$, *= significant at $P < 0.05$, ns= not significant.

Non-additive gene action governed the inheritance of three targeted traits in the foxtail millet breeding program, i.e., plant height, heading time, and grain weight per plant. Such gene action implies the phenotypes of individuals with homozygous dominant genotypes are indistinguishable from those with heterozygous genotypes. When selecting heterozygous individuals, segregation may still occur in subsequent generations (Varona *et al.*, 2018). However, this situation has implications for the selection implementation. Selection in early generations of traits affected by non-additive gene action is non-recommendable because the expression of these traits may not be similar in the next generation (Jambormias *et al.*, 2015). A modified bulk selection application for yield and yield-component traits controlled by non-additive gene action transpired on chili (Yudilastari *et al.*, 2018). Pedigree selection, in combination with marker-assisted selection, may be an alternative for traits controlled by non-additive gene action in foxtail millet. Several developed molecular markers are potentially advantageous in the selection for improvement, including SNAP markers associated with drought tolerance (Widyawan *et al.*, 2018) and SSR markers for yield-related traits in foxtail millet (Liu *et al.*, 2022).

The variance components, genetic coefficient of variation (GCV), and broad-sense heritability in the F₂ populations derived from Botok-10 x ICERI-5 appear in Table 4. The GCV ranged from 8.39% to 66.53% for all the traits. The characteristics, viz., heading time, number of leaves, stem diameter, total number of tillers, number of productive tillers, panicle length, panicle weight per plant, and grain weight per plant had greater GCVs (>20%) and attained a high categorization. The GCV estimates for plant height, flag leaf width, and days to harvest were all moderate (10%–20%). Meanwhile, low estimates (<10%) of GCV were visible for flag leaf length. Past studies authenticated that the higher the genetic coefficient of variation, the broader the opportunity for selection (Benjamin, 2020).

Broad-sense heritability values can help estimate the effects of total genetic parameters on the phenotype. The higher the heritability value, the better the complete genetic factors' effect on plant phenotype (Zhu and Zhou, 2020). The targeted traits of heading time and grain weight per plant showed moderate heritability, while plant height showed low heritability. In contrast, Anuradha and Patro (2020) reported the highest heritability values for days to 50% flowering, plant height, and grain yield in

Table 4. Estimates of variance components, coefficient of variation, and broad-sense heritability for several traits in F₂ foxtail millet populations derived from the cross of Botok-10 x ICERI-5.

Trait	σ^2_p	σ^2_e	σ^2_g	h^2_{bs} (%)	Category	GCV (%)	Category
HT(DAT)	98.45	21.60	47.39	48.14	Moderate	22.61	High
PH (cm)	418.75	314.67	81.72	19.52	Low	14.71	Moderate
NL	99.18	35.88	59.07	59.56	High	45.18	High
SD (cm)	1.64	0.74	0.54	29.13	Moderate	45.48	High
FLL (cm)	57.94	62.15	6.16	10.64	Low	8.39	Low
FLW (cm)	0.18	0.16	0.05	24.64	Moderate	11.50	Moderate
DH (DAT)	77.55	5.36	74.65	96.26	High	10.06	Moderate
TN	7.90	0.33	5.74	72.67	High	61.07	High
NPT	7.14	0.34	5.77	70.40	High	47.83	High
PL (cm)	23.31	18.99	10.40	44.60	Moderate	27.51	High
PWP (g)	53.57	3.00	23.76	44.36	Moderate	62.76	High
GWP (g)	37.67	28.96	14.75	39.15	Moderate	66.53	High

Notes: HT= heading time, PH= plant height, NL= number of leaves, SD= stem diameter, FLL= Flag leaf length, FLW= flag leaf width, DH= days to harvest, TN= total number of tillers, NPT= number of productive tillers, PL= panicle length, PWP= panicle weight per plant, GWP= grain weight per plant.

foxtail millet genotypes. The number of leaves, days to harvest, total number of tillers, and number of productive tillers showed high heritability, but flag leaf length showed low heritability. High heritability was also evident for the number of tillers per plant in a study of foxtail millet genotypes (Brunda *et al.*, 2014). Traits with high heritability have genetic factors managing well versus environmental factors, and traits with low heritability have assumptions of environmental factor influences. Other studies used heritability estimates and coefficients of variation as criteria for choosing secondary selection traits in pearl millet (Pallavi *et al.*, 2020).

Selection based on secondary traits with high heritability may be beneficial if the primary trait has a low heritability. The correlation coefficient estimates often indicate the interrelationships of the attributes (Pandey, 2020); thus, the correlation analysis helped identify secondary traits suitable for indirect or multiple-traits selection. Figure 3 shows the correlation between all characteristics in this study. One of the main objectives of foxtail millet breeding is increasing the grain weight per plant, having considered a crucial measure of production. This trait significantly positively correlated with all observed traits except for stem diameter. A significant positive correlation between plant height and heading time with grain weight per plant was apparent

in this study, similar to the previous reports in foxtail millet (Nirmalakumari and Vetriventhan, 2010; Pallavi *et al.*, 2020). This correlation implies that increased yields will have taller plants and longer heading times. Thus, the positive correlation between plant height and heading time with grain weight per plant is undesirable.

In the present foxtail millet breeding program, defining the ideotypes of the targeted cultivars first comprised high productivity, moderate plant stature, and early heading time. The F₂ populations showed that the heading time and grain weight per plant revealed high GCV and moderate heritability values, while plant height showed moderate GCV and low heritability. Therefore, in that population, the predicted response to selection for heading time and grain weight per plant is possibly higher than that of plant height. Moreover, given the positive correlation between plant height and the heading time with grain weight per plant, our strategy for selection that involves multiple traits with different heritability values is to use a weighted index selection method.

Weighted index selection uses relative weights for traits of interest to meet the breeding objective appropriately (Moeinizade *et al.*, 2020). Considering the importance of yield (grain weight per plant) and the positive correlation between plant height and heading



Figure 3. The correlation coefficient among different agronomic traits in F_2 populations of Botok-10 x ICERI-5 cross, HT= heading time, PH= plant height, NL= number of leaves, SD= stem diameter, FLL= Flag leaf length, FLW= flag leaf width, DH= days to harvest, TN= total number of tillers, NPT= number of productive tillers, PL= panicle length, PWP= panicle weight per plant, GWP= grain weight per plant, **= significant at $P < 0.01$, *= significant at $P < 0.05$, ns= not-significant.

Table 5. Selection differential of F_2 populations derived from Botok-10 x ICERI-5 cross.

Traits	X_0	X_1	S
Heading time (DAT)	30.44	24.79	-5.65
Plant height (cm)	61.45	74.40	12.95
Number of leaves	17.01	27.87	10.86
Stem diameter (cm)	1.60	1.89	0.29
Flag leaf length (cm)	29.59	35.50	5.91
Flag leaf width (cm)	1.85	2.21	0.36
Days to harvest (DAT)	85.88	87.45	1.57
Total number of tillers	4.67	5.81	1.14
Number of productive tillers	4.02	5.76	1.74
Panicle length (cm)	11.72	16.22	4.50
Panicle weight per plant (g)	7.77	21.85	14.08
Grain weight per plant (g)	5.77	18.00	12.23

Notes: DAT= days after transplanting, \bar{x}_1 : mean selected population, \bar{x}_0 : mean population before selection, S: selection differential.

time with grain weight per plant, using the following selection index (SI) formula comprised $SI = - \text{plant height} - \text{flowering time} + (3 \times \text{grain weight per plant})$. A selection intensity of 10% applied to 352 F_2 individuals resulted in 35 plants with the highest selection index and was used to calculate the selection differential values (Table 5). Selection differential is the difference between the mean

characteristics of the individuals chosen to spawn the next generation and the mean traits found in the entire population (Xu, 2022); thus, it serves as the primary quantity in the prediction of response to selection. The selection analysis differential values showed that the individuals selected for the preference have a faster heading time and higher grain weight per plant than the overall F_2 population.

However, the chosen individuals showed taller plant heights than the complete F₂ populations, which is opposite the goals of the foxtail millet breeding program.

CONCLUSIONS

The foxtail millet F₂ populations derived from the Botok-10 × ICERI-5 cross met the early heading time, medium plant stature, and high productivity breeding objectives. The potential segregants in the F₂ populations with shorter plant stature and earlier heading versus the parental genotypes were also distinguishable, including those with higher grain weight per plant than the male parent (ICERI-5). The inheritance in the heading time and grain weight per plant had the non-additive gene action control, with a moderate broad-sense heritability, with the plant height managed by a non-additive gene action with a low broad-sense heritability. A recommendation for a weighted selection index method combined with molecular markers associated with targeted traits is necessary for further improvement in foxtail millet.

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