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Research article

Understanding mode of gene action governing green forage yield and its component traits in pearl millet

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Abstract

Understanding the genetic control of forage yield and related traits can decide breeding strategies for high-biomass cultivars. In this study, generation mean analysis was used to evaluate gene effects and non-allelic interactions for forage yield and its component traits in pearl millet using two experimental crosses developed by using two high-yielding inbreds IP 18168 and IP 22419 and their six generations (P_1, P_2, F_1, BC_1, BC_2 and F_2) were independently evaluated during *Kharif* season 2022. Significant variability and the inadequacy of an additive-dominance model highlighted the role of epistasis, with additive × dominance interactions prominent for forage yield and plant height. Dominance and epistatic effects were also crucial for traits like leaf and internode number, leaf length and leaf width. These findings indicated one or two generations of selfing followed by recurrent selection in advanced generations will be useful in enhancing the frequency of genes with increasing effects on green forage yield. Our findings could be helpful in designing the forage pearl millet breeding programs in India.

Keywords: Epistasis, Forage pearl millet, Gene effects, Generation mean analysis, Green forage yield

Introduction

Crop and livestock are the two main components of the farming system, which influence our agricultural economy and provide sustenance. Pearl millet (*Cenchrus americanus* L.) is an important cereal and forage crop grown in an area of 18 million ha in Africa and 10 million ha in Asia. Pearl millet is a major forage crop of arid and semi-arid regions and is able to produce leafier biomass under limited moisture regimes than forage sorghum and corn. It is becoming a popular summer forage crop in northern and western parts of India (Reddy *et al*., 2013). This crop has the potential to adapt to diverse agro-climatic conditions with good tolerance to abiotic stresses (Vadez *et al*., 2012; Ashok *et al*., 2016). The scarcity of fodder is the major constraint to livestock production in smaller farming communities in arid and semi-arid regions. For instance, presently, the country faces a net shortfall of 35.6% green fodder, 10.5% dry crop leftovers, and 44% concentrate feed ingredients (Singh *et al*., 2022). Improving forage yield and quality is the key to enhancing milk and meat productivity and better growth of the livestock sector. To alleviate the feed shortage in arid and semi-arid regions, the development of superior fodder pearl millet cultivars could be one of the promising solutions. Further, pearl millet has high tillering potential and quick regenerative ability, giving the possibility of multi-cutting, which allows a year-round supply of green/dry forage (Babiker *et al*., 2014; Kumawat *et al*., 2016). Apart from biomass, the nutritional quality of a forage crop depends upon the combination of one or more traits such as crude protein, neutral detergent fiber (NDF), acid detergent fiber (ADF), lignin content and fermentable sugars. On average, fodder pearl millet contains 7 to 10% crude protein, 56 to 64% NDF, 38 to 41% ADF, 33 to 34% cellulose and 18 to 23% hemi cellulose on dry matter basis (Kaushal *et al*., 2024).

Modern plant breeding has continuously concentrated on grain yield improvement rather than forage yield and quality. Large breeding programs were focused on improving grain yield, biofortification, stability and disease resistance in pearl millet (Patil *et al*., 2021). Further, the application of traditional breeding techniques, population improvement programs, advanced breeding techniques and hybrid development are lagging in the

case of forage pearl millet improvement in India. Most of the cultivars released so far in India are purely based on selection from germplasm (Roy *et al*., 2020). The development of open-pollinated varieties (OPVs) was the main purpose of forage pearl millet breeding in India. Understanding genetics and knowledge on gene action is a prerequisite for the improvement of economically important traits (Somraj *et al*., 2018; Puttamadanayaka *et al*., 2020; Raghavendra *et al*., 2021). The choice of the best breeding program for developing superior forage cultivars depends on gene action and their interaction involved in the expression of biomass and its component traits. Generation means analysis (GMA) is used for dissecting gene action controlling quantitative traits by analyzing basic generations based on means and variances using standard statistical models (Kearsey and Jinks, 1968; Mather and Jinks, 2013). These models provide information on the average effects of the genes (additive effects), dominance deviations and epistatic effects, which can assist in quantifying the genotypic value of individuals and, in turn, would contribute to determining the average generation genotypic value (Hayman *et al*., 1958). In this regard, it is valuable that the magnitude of gene action and type of epistasis can result in the designing of breeding strategies (Rajan *et al*., 2018). Limited genetic information is available for enhancing the genotypic traits of forage pearl millet, and only a few studies have yet explored the genetic control of forage yield in pearl millet, including the contributions of additive, dominant and epistatic gene effects. Hence, in the present study, we sought to find information regarding the classical inheritance gene interaction models using six basic generations for green forage yield and its component traits in forage pearl millet.

Materials and Methods

Genetic materials: Genetic material used in the present study comprised six basic generations *viz*., P_1, P_2, F_1, F_2, BC_1 and BC_2, developed from two different sets of diverse pearl millet parental lines. These included two high-forage biomass (IP 18168 and IP 22419) and two low-forage biomass (ICMB 01777 and ICMR 07555) forage pearl millet inbred lines. The following two crosses were developed during *kharif* season 2021: SET-1: ICMB 01777 (P_1) × IP 18168 (P_2) and SET-2: ICMR 07555 (P_1) × IP 22419 (P_2). The F_1 hybrids of both crosses were raised during summer season 2022. The F_1s were selfed to obtain F_2 generations and also backcrossed with their respective parents to obtain BC_1 and BC_2 generations. The seeds from each cross were harvested individually and were used for evaluation in the next season.

Evaluation of six generations: The six basic generations such as P_1, P_2, F_1, F_2, BC_1 and BC_2 generations of two sets of parents were evaluated during *Kharif* 2022 at ICAR-Indian Grassland and Fodder Research Institute, Jhansi. The genetic population consisting of SET-1: 5 plants of each of P_1, P_2 and F_1; 192 F_2; 167 BC_1 and 183 BC_2, SET-2: 5 plants of each of P_1, P_2 and F_1; 156 F_2; 174 BC_1 and 196 BC_2. The non-segregating, homogeneous populations *viz*., P_1, P_2 and F_1 generations of both sets were planted in two separate contiguous blocks in randomized complete block design with two replications, and the segregating, heterogeneous populations *viz*., F_2, BC_1 and BC_2 were planted without any replications. The plants were raised using recommended package of practices. Six basic generations of both SETs were evaluated for plant height (cm), number of leaves, leaf length (cm), leaf width (cm), number of internodes and green forage yield (GFY)/plant (kg) following the pearl millet descriptors (IBPGR and ICRISAT, 1993).

***Data analysis*:** The mean values, standard errors and variance of P_1, P_2, F_1, F_2, BC_1 and BC_2 generations for each character were calculated separately considering each plant data for the generations and subjected to the scaling test and the joint scaling test to estimate the gene effects and interaction components based on six-parameter model (Hayman 1958). The scaling test was performed to detect epistasis and genetic parameters such as m, [d], [h], [i], [j] and [l] where m = constant mean effects, [d] = additive effects, [h] = dominance effects, [i] = additive × additive interaction effects, [j] = additive × dominance interaction effects, [l] = dominance × dominance interaction effects. The significance of the scales and gene effects were tested by using the t-test (Singh and Chaudhary, 1985). The statistical analysis was carried out using the online software OPSTAT (Sheoran *et al*., 1998).

Results and Discussion

Mean performance of six generations: The generation mean analysis was conducted using six basic generations (P_1, P_2, F_1, F_2, BC_1 and BC_2) generated using fodder pearl millet inbred lines to obtain information on the nature of gene action involved for green forage yield and its component traits. The overall mean performance for plant height, number of leaves, leaf length, leaf width, number of internodes and green forage yield were recorded for SET-1 and SET-2 (Table 1). The respective parents involved in SET-1 and SET-2 crosses exhibited significant differences for all the studied characters. The plant height for SET-1 ranged from 113.00 cm for the parental line P_1 to 234.00 cm for the parental line P_2, while in SET-2, the plant height varied from 122.20 cm for the parental line P_1 to 227.00 cm for the parental line P_2. Regarding GFY/plant, in SET-1, the values ranged from 0.28 kg for P_1 (low biomass inbred) to 0.98 kg for P_2 (high biomass inbred), while for SET-2, the parental line P_1 had 0.34 kg GFY/plant

Table 1. Mean performance of green forage yield and its component traits of SET-1 and SET-2 crosses

Cross	Traits	Populations					
		P_1	P_2	F_1	F_2	BC_1	BC_2
		Mean ± SE	Mean ± SE	Mean ± SE	Mean ± SE	Mean ± SE	Mean ± SE
SET-1	PH	113.00 ± 0.94	234.00 ± 0.95	168.00 ± 4.77	185.72 ± 4.94	152.68 ± 5.25	178.34 ± 4.96
	NOL	5.80 ± 0.37	11.00 ± 0.55	6.40 ± 0.51	9.51 ± 0.22	5.71 ± 0.23	8.18 ± 0.22
	LL	59.60 ± 0.51	65.60 ± 0.75	49.00 ± 2.07	59.90 ± 2.98	49.36 ± 1.49	65.22 ± 1.41
	LW	3.60 ± 0.25	3.8± 0.051	3.20 ± 0.10	3.01± 0.14	3.01 ± 0.09	3.98 ± 0.08
	NI	5.40 ± 0.25	6.60 ± 0.40	5.00 ± 0.32	5.72 ± 0.14	4.97 ± 0.15	6.51 ± 0.14
	GFY	0.28 ± 0.01	0.98 ± 0.08	0.65 ± 0.03	0.58 ± 0.02	0.79 ± 0.02	1.05 ± 0.02
SET-2	PH	122.20 ± 0.66	227.00 ± 1.26	185.20 ± 2.69	166.91 ± 7.34	151.10 ± 4.61	185.12 ± 4.55
	NOL	6.00 ± 0.31	9.20 ± 0.37	6.00 ± 0.31	4.82 ± 0.25	5.93 ± 0.18	7.84 ± 0.18
	LL	52.00 ± 0.54	64.00 ± 0.54	46.20 ± 1.46	51.40 ± 2.38	43.75 ± 1.56	58.18 ± 1.53
	LW	2.84 ± 0.05	3.54 ± 0.07	2.62 ± 0.14	2.02 ± 0.08	1.83 ± 0.05	2.42 ± 0.05
	NI	4.60 ± 0.24	7.40 ± 0.40	4.00 ± 0.24	4.99 ± 0.26	5.39 ± 0.16	7.16 ± 0.16
	GFY	0.34 ± 0.01	0.87 ± 0.03	0.45 ± 0.03	0.30 ± 0.02	0.48 ± 0.01	0.64 ± 0.01

SET-1=P_1: ICMB 01777, P_2: IP 18168, F_1: (ICMB 01777 × IP 18168), F_2, BC_1: (F_1 × ICMB 01777), BC_2: (F_1 × IP 18168), SET-2= P_1: ICMR 07555, P_2: IP 22419, F_1: (ICMR 07555× IP 22419), F_2, BC_1: (F_1 × ICMR 07555), BC_2: (F_1 IP 22419), SE: Standard error; PH: Plant height (cm); NOL: Number of leaves; LL: Leaf length (cm); LW: Leaf width (cm); NI: Number of internodes; GFY: green forage yield/plant (kg)

and the parental line P2 had a mean value of 0.87 kg. Further comparison between parents for their mean trait values for other biomass contributing component traits in SET-1 indicated higher trait values in IP 18168 (P_2) than ICMB 01777 (P_1), for number of leaves (P_1: 5.80, P_2:11.00), leaf length (P_1: 59.60 cm, P_2: 65.60 cm), leaf width (P_1: 3.60 cm, P_2: 3.98 cm) and number of internodes (P_1: 5.40, P_2: 6.60). Further in SET-2, IP 22419 (P_2) shown higher mean trait value than ICMR 07555 (P_1) for number of leaves (P_1: 6.00, P_2: 9.20), leaf length (P_1: 52.00 cm, P_2: 64.00 cm), leaf width (P_1: 2.84 cm, P_2: 3.54 cm) and number of internodes (P_1: 4.60, P_2: 7.40). The F_2 mean for GFY was lower than F_1 mean in both the crosses.

Scaling test: The components of means and scaling test results were recorded for SET-1 (ICMB 01777 × IP 18168) and SET-2 crosses (ICMR 07555 × IP 22419; Table 2). The scaling test for plant height revealed that the scales A, B, and D were significant in both SET-1 and SET-2 crosses. All four scaling tests, *i.e.*, A, B, C, and D, exhibited significant deviation from zero for the number of leaves in both SET-1 and SET-2 crosses. Concerning leaf length, the scales A, B, and D were significant in SET-1, while in SET-2, all the scales except D were significant. For leaf width, the scales A, C and D were significant in SET-1, while in SET-2, scales A, B, and C were significant. With regard to the number of internodes in SET-1, all the scales except scale C were significant and SET-2 scales A and B were significant. All the scales were significant for GFY in SET-1 and two scales A and B, were significant in SET-2. The significance of the scaling test indicated that the simple additive-dominance model or simply additive model is not adequate to explain the gene effects of GFY and its component traits in pearl millet. These results indicated the presence of non-allelic interaction controlling these traits. This was in line with earlier reports that indicated the role of non-allelic interaction in governing the expression of forage yield component traits in pearl millet or other crops (Gaoh *et al*., 2020; Vekariya *et al*., 2017; Noori *et al*., 2016; Chaudhari *et al*., 2017).

Gene effects: For plant height and number of leaves partitioning of the generation mean into six different genetic components revealed that all the six genetic components were significant (P< 0.01) and additive × dominant (j) magnitude was higher than that of the other genetic effects assessed in SET-1 (Table 3). The opposite sign observed for the h and l parameters revealed the presence of a duplicate type of epistasis. In SET-2, except for dominant (h) and additive × additive (i) interaction, other genetic components were significant for plant height with higher magnitude was observed for the additive × dominant (j) parameter. Additive, dominance, additive × additive, additive × dominance and dominance × dominance gene actions controlled number of leaves per plant in SET-1 (Table 3). The dominance (h) gene action was non-significant in SET-2. The additive × dominance interaction effect was larger with net negative sign than the additive × additive and dominance × dominance effect in these two sets of crosses.

The dominance × dominance effect for leaf length per plant indicated a significant (p < 0.01) predominant

Table 2. Scaling test for green forage yield and its component traits of SET-1 and SET-2 crosses

Traits	SET-1				SET-2			
	A	B	C	D	A	B	C	D
PH	193.62** ± 11.57	-71.68** ± 11.04	-8.89 ^{NS} ± 21.99	70.41** ± 12.24	168.99** ± 9.81	-49.84** ± 9.51	165.93** ± 29.89	-17.39 ^{NS} ± 16.07
NL	6.98** ± 0.88	-6.17** ± 0.77	-9.46** ± 1.51	5.13** ± 0.55	4.32** ± 0.61	-3.69** ± 0.57	4.89** ± 1.30	-2.13** ± 0.57
LL	54.88** ± 3.72	10.15** ± 3.54	-5.40 ^{NS} ± 12.65	45.21** ± 6.30	48.68** ± 3.50	-16.17** ± 3.43	56.78** ± 10.00	-7.14 ^{NS} ± 5.24
LW	3.72** ± 0.21	-0.17^{NS} ± 0.32	1.48* ± 0.68	1.03** ± 0.32	2.49** ± 0.20	0.60** ± 0.19	3.50** ± 0.47	-0.20 ^{NS} ± 0.19
NI	6.66 ** ± 0.59	-0.62 ^{NS} ± 0.49	2.10* ± 0.97	1.96** ± 0.35	3.20** ± 0.57	-5.13** ± 0.47	-0.77 ^{NS} ± 1.25	-0.58 ^{NS} ± 0.57
GFY	0.52** ± 0.10	-0.46** ± 0.05	-1.18** ± 0.14	0.32** ± 0.05	0.44** ± 0.05	-0.48** ± 0.04	0.07 ^{NS} ± 0.12	-0.05 ^{NS} ± 0.05

*($p < 0.05$); **($p < 0.01$); NS: Non-significant; PH: Plant height (cm); NOL: Number of leaves; LL: Leaf length (cm); LW: Leaf width (cm); NI: Number of internodes; GFY: green forage yield/plant (kg)

effect compared with all other assessed gene and epistatic effects in the SET-1 cross. Additive × dominant epistasis was significant ($p < 0.01$) with a predominant effect in SET-2 cross (Table 3). The cross-wise direct genetic and interaction effects in SET-1 and SET-2 for the leaf width revealed that in SET-1 had duplicate gene interaction with all the gene actions were significant. Among the interaction effects, dominant × dominant was predominant in both the crosses. With regards to the number of internodes, all six parameters were significant in both the crosses apart from dominant and additive × dominant parameters in SET-2. The opposite sign of the parameters h and l revealed the duplicate epistasis in SET-1. Whereas in SET-2, mean (m), additive and additive × dominant parameters were significant, with a predominance of additive × dominant gene interaction (Table 3). For GFY, all six parameters were significant except the dominance × dominance (l) parameter in SET-1. While in SET-2, mean (m), additive (d) and additive × dominant (j) parameters were significant. The additive × dominant (j) parameter was predominant in both crosses, while the dominant (h) effect was predominant over the additive gene effect in SET-1(Table 3).

In both crosses, the additive effects (d) were negative for all the traits because the parent with a lower value was used as P_1 and the parent with a higher value was used as P_2. Therefore, considering the absolute values, the dominance parameters of PH and NL were of higher magnitude than additive parameters, indicating that dominant gene action was predominant over additive gene action for PH and NL in pearl millet. The opposite sign between dominance (d) effects and dominance × dominance effects showed duplicate interaction for PH and NL in SET-1. These findings were in agreement with Gaoh *et al*. (2020) and Bhardwaj *et al*. (2023). Gavali *et al*. (2024) reported the presence of duplicate epistasis and predominance of dominant gene action controlling inheritance plant height in pearl millet. Duplicate epistasis signifies dispersion of alleles at interacting loci and will decrease variation in S_2 or F_2 and subsequent generations, and will delay the pace of progress through selection (Jinks and Jones 1958; Pavan and Gangaprasad, 2022). With respect to leaf length and leaf width, the positive sign and significance of dominance × dominance indicated exploitation of LL and LW is possible through heterosis. According to Gamble (1962), the positive effect of dominance × dominance is desirable. However, the duplicate epistasis in SET-1 cross indicated the selection for higher leaf length and leaf width recombinants in early segregating generations might not be effective.

It was found that all the genetic parameters associated with a number of internodes were significant in SET-1, while in the case of SET-2, the dominant and additive × additive interaction were non-significant. Further, dominance × dominance was predominant with duplicate interaction in SET-1 and additive × dominance interaction was predominant over dominance × dominance interaction in SET-2. Thereby, this confirmed that these interaction effects were cross specific. Green forage yield per plant is amongst the main important character in forage crop improvement. The GFY is controlled by many genes with different effects, making biomass improvement more complex. The significance of the scaling test for both the crosses indicated that the additive-dominance model was not enough to explain the gene effects for GFY per plant in both sets. In the six-parameter model, the additive × dominance effect was predominant in both sets, revealing that these parameters are of primary importance in the inheritance of GFY per plant. Similar findings were reported for grain yield in pearl millet by

Table 3. Estimates of gene effects and types of epistasis for green forage yield and its component traits of SET-1 and SET-2 crosses

Traits	Cross	m	d	h	i	j	l	Epistatic gene action
PH	Set-1	171.72** ± 4.94	-55.65** ± 7.22	-103.83** ± 24.95	-140.83** ± 24.48	-215.31** ± 14.51	172.76** ± 36.31	Duplicate
	Set-2	178.91** ± 7.34	-49.01** ± 6.52	60.38^{NS} ± 32.26	34.78^{NS} ± 32.14	-158.83** ± 13.13	104.36** ± 39.68	-
NL	Set-1	7.76** ± 0.22	-2.47** ± 0.32	-11.77** ± 1.26	-10.27** ± 1.11	-13.15** ± 0.92	11.09** ± 1.99	Duplicate
	Set-2	6.63** ± 0.25	-1.91** ± 0.25	2.16^{NS} ± 1.22	4.26** ± 1.15	-8.02** ± 0.71	-3.62* ± 1.66	-
LL	Set-1	56.61** ± 2.98	-15.86** ± 2.06	-85.53** ± 12.79	-90.43** ± 12.61	-64.73** ± 4.22	115.47** ± 15.10	Duplicate
	Set-2	52.58** ± 2.38	-16.43** ± 2.19	7.47^{NS} ± 10.60	14.27^{NS} ± 10.49	-74.86** ± 4.45	28.22* ± 13.30	-
LW	Set-1	3.43** ± 0.14	-0.97** ± 0.12	-2.44** ± 0.66	-2.06** ± 0.64	-3.90** ± 0.36	5.61** ± 0.84	Duplicate
	Set-2	2.05** ± 0.08	-0.59** ± 0.07	-0.16^{NS} ± 0.42	0.40^{NS} ± 0.39	-1.88** ± 0.18	2.69** ± 0.56	-
NI	Set-1	5.7** ± 0.14	-1.54** ± 0.20	-4.42** ± 0.81	-3.92** ± 0.70	-7.28** ± 0.62	9.96** ± 1.27	Duplicate
	Set-2	5.4** ± 0.26	-1.77** ± 0.23	-1.24^{NS} ± 1.20	1.15^{NS} ± 1.15	-8.34** ± 0.66	-3.08* ± 1.56	-
GFY	Set-1	1.08** ± 0.02	-0.25** ± 0.03	-0.91** ± 0.12	-0.64** ± 0.11	-1.78** ± 0.11	0.10^{NS} ± 0.19	-
	Set-2	0.51** ± 0.02	-0.15** ± 0.02	-0.08^{NS} ± 0.11	0.11^{NS} ± 0.10	0.93** ± 0.05	0.15^{NS} ± 0.14	-

m: Constant mean effects; d: Additive effects; h: Dominance effects; i: Additive × Additive interaction effects; j: Additive × Dominance interaction effects; l: Dominance × Dominance interaction effects; * ($p < 0.05$); ** ($p < 0.01$); NS: Non-significant; PH: Plant height (cm); NOL: Number of leaves; LL: Leaf length (cm); LW: Leaf width (cm); NI: Number of internodes; GFY: Green forage yield/plant (kg)

Gaoh *et al*. (2020), revealing the preponderance of non-additive gene action in the inheritance of grain yield per plant. In SET-1, both additive and dominant gene action were significant and in SET-2, additive gene action was significant; these findings showed that additive genetic effects largely governed the inheritance genes governing the GFY per plant were largely governed by additive genetic effects.

Gene action determined from the six genetic populations of two cross combinations for forage yield and component traits somewhat agreed well that additive, dominance and epistasis of polygenes dominated the inheritance of all studied traits. Though dominant genes with duplicate epistasis-controlled traits such as PH, NL, LL, LW and NI, selection might not be effective in improving genetic gain for these traits as dominance and dominance × dominance gene effects are non-fixable (Maria *et al*., 2012; Shalaby, 2013). Therefore, the selection of desirable lines should be followed in advanced segregating generations or selfing generations by evaluating a large number of families. Inter-mating among the selected segregates followed by one or two generations of selfing will lead to the break of undesirable linkage, decrease additive variance and allow for the accumulation of favorable alleles. The inter-mating in the advanced generation of selfing will expose the dominance variance, allowing the expression of traits for selection and application of recurrent selection for the development of cultivars (Das *et al*., 2020).

Conclusion

Breeding for high-yielding forage pearl millet cultivars is essential to address forage shortages. The joint-scaling test revealed that a simple additive-dominance model inadequately explains green forage yield and related traits, indicating significant epistatic interactions. Notably, additive × dominance interactions for plant height and green forage yield suggest early selection is ineffective; instead, utilizing both additive and dominance effects through one or two selfing cycles

or biparental mating followed by recurrent selection is recommended for developing superior forage genotypes in pearl millet.

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