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RESEARCH ARTICLE

Analysis of yield and its components in black gram through generation mean analysis

Dhamotharan Palanisamy[1], Manivannan Narayana[1*], Ganesan Kalipatty Nalliappan[1], Janaki Ponnusamy[2], Harish Sankarasubramanian[3] & Babu Rajendra Prasad Venugopal[4]

[1]Centre for Plant Breeding and Genetics, Tamil Nadu Agricultural University, Coimbatore 641 003, India

[2]Department of Soil Science and Agricultural Chemistry, Tamil Nadu Agricultural University, Coimbatore 641 003, India

[3]Department of Plant Pathology, Tamil Nadu Agricultural University, Coimbatore 641 003, India

[4]Department of Crop Physiology, Tamil Nadu Agricultural University, Coimbatore 641 003, India

*Email: nm68@tnau.ac.in

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Abstract

Understanding the gene action governing yield and its component traits is crucial for developing an effective breeding strategy. In the present study, generation mean analysis was employed to unravel the genetic architecture of yield and its component traits in three crosses of black gram. The crosses, namely ADT 3 × VBG 17007 (cross 1: C1), ADT 3 × VBG 19010 (cross 2: C2) and VBG 13003 × VBG 17007 (Cross 3: C3), were developed using four parents contrasting in salt tolerance. The analysis of variance revealed significant differences among the five generations-P_1, P_2, F_1, F_2 and F_3-for most of the traits. All studied traits showed significance in either one or both the C and D scales, indicating the inadequacy of the additive-dominance model in explaining the genetic variation. Most traits, except for clusters per plant in Cross 1 (ADT 3 × VBG 17007) and seeds per pod across all crosses, exhibited significant additive genetic components. Furthermore, non-additive components, including dominance, additive × additive and dominance × dominance interactions, were significant for all traits across the three crosses. This suggests the presence of epistasis, emphasizing the need to delay selection to later generations in these crosses for effective genetic improvement.

Keywords

additive-dominance; black gram; component traits; epistasis; generation mean analysis; seed yield

Introduction

Pulses are often referred to as the "poor man's meat" due to their significant dietary value. They have played a crucial role in Indian agriculture, particularly in maintaining soil health by fixing atmospheric nitrogen through symbiotic bacteria in the root nodules (1). However, during the Green Revolution, insufficient attention was given to pulses, leading to low productivity in India (2). The total cultivation area of pulses in India is approximately 4.63 million ha, with a productivity of 987 kg ha^{-1}. In Tamil Nadu, the area under cultivation is 0.41 million hectares, with a productivity of 660 kg ha^{-1} (3). The Indian Council of Medical Research (ICMR) recommends a daily intake of 84g of pulses. However, the per capita availability of pulses in 2021-22 was 53.8g, a decline from 70g in 1959 (4). Pulses are a vital source of protein and the decreasing production and productivity are major contributors to malnutrition, especially with the rapidly growing population. This highlights the urgent need to increase pulse productivity to meet both national and local requirements (5, 6).

Black gram [*Vigna mungo* (L.) Hepper; 2n = 22] is a short-duration, multifunctional and nutritious legume predominantly grown in South and Southeast Asia (7, 8). It serves as an essential protein source for the growing population, provides feed for livestock and contributes to improving soil health and fertility. Believed to have originated in India 3,500 years ago from the wild progenitor *V. mungo var. silvestris*, it later spread to Thailand (9, 10). Black gram is renowned for its nutritional composition, containing 26.2% protein, 1.2% fat, 56.6% carbohydrates and essential minerals such as calcium (185 mg/100g) and iron (8.7 mg/100g), in addition to a substantial calorie content of 350 cal/100g (11, 12). Given its nutritional value, black gram plays a vital role in addressing global nutritional security, particularly in developing countries facing malnutrition challenges. Among legumes, black gram is highly sensitive to salt (13), a factor that exacerbates the situation in the coastal regions of Tamil Nadu, where rice-pulse cropping systems are typically followed (14). Enhancing the productivity of black gram requires a deeper understanding of the genetic basis of traits that influence yield, which will facilitate targeted improvements.

Generally, quantitative traits are influenced by multiple genes interacting in complex ways. A comprehensive understanding of the gene action and genetic variances of these traits is essential for plant breeders aiming to improve them. Knowledge of the genetic architecture of a trait is closely linked to the breeding methods used for improving the breeding population (15). The additive and dominant nature of a trait is directly related to its breeding value and the genetic gain achieved during improvement. Over the last century, several genetic models have been developed to decipher different genetic aspects, such as additive and dominance effects, using various mating designs such as diallel, Line × Tester and North Carolina designs. However, these models often fail to account for epistatic interactions (15), which can lead to overestimation or underestimation of genetic components. To address non-allelic interactions, Hayman in 1958 proposed an assumption-free genetic model using generation mean analysis (GMA). GMA provides insights into the relative importance of average additive gene effects, dominance deviations and effects arising from non-allelic genetic interactions (16). This analysis helps determine the reliable genotypic values of individuals, which is crucial for formulating appropriate breeding strategies. In this context, four salt-tolerance-responsive genotypes were utilized to study the genetics of yield and its component traits using generation mean analysis.

Materials and Methods

Experiment materials

The experiment was conducted at the Centre for Plant Breeding and Genetics, Tamil Nadu Agricultural University, Coimbatore, located at a latitude of 11.012890°N and longitude of 76.936805° W. Three crosses of black gram, namely ADT 3 × VBG 17007 (C1), ADT 3 × VBG 19010 (C2) and VBG 13003 × VBG 17007 (C3), were obtained from two salt-sensitive and two salt-tolerant lines for the seedling stage, i.e., ADT 3, VBG 13003, VBG 17007 and VBG 19010. All four parent materials were sourced from the National Pulses Research Centre, Tamil Nadu Agricultural University, Vamban. F_1 hybrids of the three crosses were selfed to produce F_2 and a portion of the F_1 seeds was used to raise the F_2 generation. Similarly, part of the F_2 seeds were raised to produce seeds for the F_3 generation. Each F_3 family was raised separately and evaluated. Five breeding populations, namely P_1, P_2, F_1, F_2 and F_3, were used in the study. All populations of the three crosses were evaluated from February to April 2024, with a planting spacing of 30 × 10 cm (Fig. 1). The recommended agronomic practices for Tamil Nadu were followed (17).

Observations were recorded for nine quantitative traits on an individual plant basis, including plant height (cm) (PH), number of branches per plant (BPP), number of clusters per plant (CPP), number of pods per cluster (PPC), number of pods per plant (PPP), pod length (cm) (PL), number of seeds per pod (SPP), 100-seed weight (g) (HSW) and seed yield per plant (g) (SYPP). The means and variances of the five generations (P_1, P_2, F_1, F_2 and F_3) were used to evaluate genetic parameters. The details of the plant populations studied are presented in Table 1.

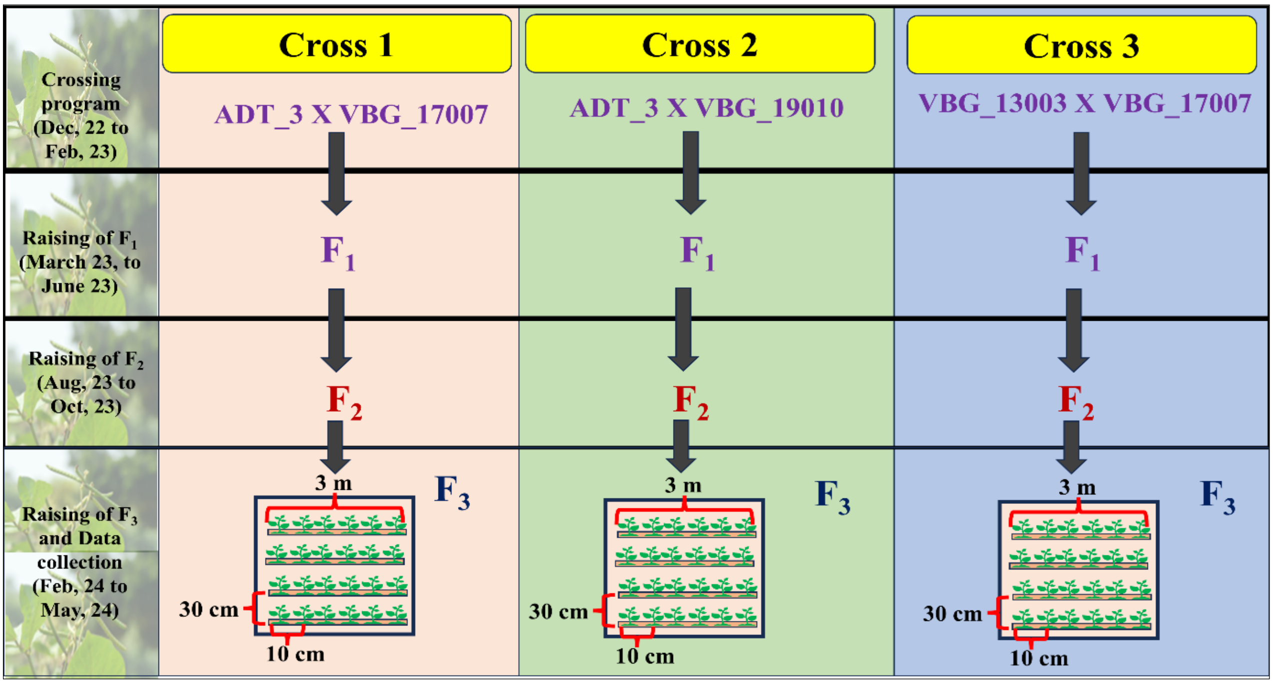

Fig. 1. Schematic workflow of generation mean analysis of three crosses.

Table 1. Total number of plants studied in each generation of three crosses

S No	Generations	C1	C2	C3
1	P_1	10	10	10
2	P_2	10	10	10
3	F_1	10	10	10
4	F_2	106	102	113
5	F_3	396	331	311

Note: C1 - ADT 3 X VBG 17007, C2 - ADT 3 X VBG 19010, C3 - VBG 13003 X VBG 17007

Statistical analysis

A scaling test was used to examine the occurrence of non-allelic interaction components (18, 19). The scales C and D were computed (19) and the significance of any scale indicates the inefficacy of the additive-dominance model.

$$C = 4\bar{F}_2-2\bar{F}_1-\bar{P}_1-\bar{P}_2$$

$$D = 4_3\bar{F}+-2\bar{F}_2-\bar{P}_1-\bar{P}_2$$

Where, $\bar{P}_1$, $\bar{P}_2$, $\bar{F}_1$, $\bar{F}_2$, $\bar{F}_3$ represents the mean values of the respective breeding population for the respective trait. The genetic components for m, d, h, i and l were estimated using TNAUSTAT software (20).

Results and Discussion

Mean comparison

The mean values and standard errors for the various generations of each cross are summarized in Table 2. Table 3 presents the scaling test results and genetic parameters for various yield-related traits. GMA is a promising tool for dissecting the genetic components into fixable and non-fixable effects. It provides valuable insights into the genetic components and mechanisms involved in the expression of yield and other biometric traits, thereby facilitating the identification of suitable breeding strategies (15).

The mean performance of the hybrid and segregating generations of the three crosses showed varying results compared to their parents. In the C1 cross, the F_1 generation exhibited variable performance for six traits, with 100-seed weight (HSW) and plant height (PH) showing better performance than the parents. In the F_2 generation, all traits, except for seeds per pod (SPP) and HSW, underperformed compared to both parents. In the F_3 generation, most traits showed improved performance over the parents, except for pods per cluster (PPC), PH, clusters per plant (CPP) and pods per plant (PPP). The trait PPC exhibited variable performance, while the other three traits showed poor performance.

In the C2 cross, the F_1 generation showed poor performance for most traits, although pod length (PL) and SPP outperformed the parents. In the F_2 generation, all traits, except for PL and HSW, underperformed, with PL and HSW exhibiting intermediate responses. Similar trends were observed in the F_3 generation.

In the C3 cross, the majority of traits in the F_1 generation showed superior performance compared to the parents. However, in both the F_2 and F_3 generations, all traits underperformed relative to the parents. Similar results were observed in earlier studies on black gram (11, 21).

Gene action

The gene effects and scaling tests (C and D) for each cross are summarized in Table 3. The results of the scaling tests were used

Table 2. Mean and standard error for yield and yield contributing traits in various generations of three crosses

Characters	Cross	P_1	P_2	F_1	F_2	F_3
Plant height (cm)	**C1**	48.00 ± 1.81	48.40 ± 1.66	49.90 ± 1.32	41.90 ± 1.27	32.10 ± 0.56
	C2	48.50 ± 3.53	39.80 ± 2.41	34.80 ± 1.34	35.78 ± 1.16	38.47 ± 0.50
	C3	48.60 ± 1.23	49.60 ± 1.18	49.50 ± 1.17	44.01 ± 1.20	29.08 ± 0.56
Branches per plant	**C1**	2.70 ± 0.15	2.90 ± 0.23	2.80 ± 0.13	2.47 ± 0.07	2.95 ± 0.05
	C2	3.80 ± 0.25	3.50 ± 0.22	3.10 ± 0.18	2.88 ± 0.07	2.53 ± 0.05
	C3	2.70 ± 0.15	2.80 ± 0.20	3.10 ± 0.28	2.53 ± 0.08	1.90 ± 0.06
Clusters per plant	**C1**	20.60 ± 1.61	22.60 ± 1.63	21.30 ± 1.15	19.66 ± 0.87	14.50 ± 0.27
	C2	17.40 ± 0.82	19.50 ± 1.21	19.10 ± 1.08	16.41 ± 0.78	15.47 ± 0.38
	C3	22.00 ± 0.93	26.40 ± 1.23	26.00 ± 1.09	17.45 ± 0.68	10.70 ± 0.27
Pods per cluster	**C1**	2.80 ± 0.20	3.60 ± 0.27	3.00 ± 0.21	2.26 ± 0.07	2.97 ± 0.06
	C2	3.20 ± 0.13	3.60 ± 0.16	3.20 ± 0.20	2.08 ± 0.07	3.31 ± 0.25
	C3	3.30 ± 0.26	3.50 ± 0.27	2.70 ± 0.21	2.71 ± 0.09	2.88 ± 0.06
Pods per plant	**C1**	56.40 ± 3.57	58.50 ± 2.20	53.20 ± 2.53	35.09 ± 1.83	30.90 ± 0.86
	C2	42.50 ± 3.80	48.60 ± 3.43	41.70 ± 4.55	22.04 ± 1.61	39.24 ± 1.36
	C3	51.90 ± 3.21	54.50 ± 2.89	55.30 ± 2.03	35.01 ± 1.77	29.51 ± 1.16
Pod length (cm)	**C1**	4.41 ± 0.09	4.26 ± 0.11	4.29 ± 0.08	4.12 ± 0.03	4.76 ± 0.21
	C2	4.31 ± 0.08	4.03 ± 0.08	4.54 ± 0.09	4.12 ± 0.03	4.30 ± 0.02
	C3	4.39 ± 0.09	4.38 ± 0.11	4.4 ± 0.01	4.00 ± 0.03	4.18 ± 0.02
Seeds per pod	**C1**	5.60 ± 0.31	5.30 ± 0.42	5.50 ± 0.31	5.37 ± 0.10	6.21 ± 0.13
	C2	5.50 ± 0.27	5.50 ± 0.37	6.20 ± 0.25	5.19 ± 0.10	5.70 ± 0.05
	C3	2.60 ± 0.16	3.10 ± 0.18	5.00 ± 0.30	5.19 ± 0.09	5.27 ± 0.05
100-seed weight (g)	**C1**	4.34 ± 0.14	3.81 ± 0.19	4.52 ± 0.10	4.01 ± 0.05	6.91 ± 1.72
	C2	4.38 ± 0.24	4.06 ± 0.12	3.97 ± 0.14	4.25 ± 0.08	3.70 ± 0.04
	C3	4.75 ± 0.20	4.11 ± 0.12	4.30 ± 0.14	3.96 ± 0.06	3.85 ± 0.06
Seed yield per plant (g)	**C1**	5.61 ± 0.63	4.90 ± 0.53	5.60 ± 0.22	4.29 ± 0.33	6.79 ± 0.21
	C2	7.54 ± 0.70	7.67 ± 0.71	7.50 ± 0.54	3.79 ± 0.31	7.22 ± 0.28
	C3	6.82 ± 0.95	7.15 ± 0.69	9.81 ± 0.81	3.91 ± 0.28	5.47 ± 0.23

Note: C1 - ADT 3 X VBG 17007, C2 - ADT 3 X VBG 19010, C3 - VBG 13003 X VBG 17007

Table 3. Scaling test and estimates of genetic parameters for various yield and yield contributing traits in black gram

Character	Cross	Scales		Genetic parameters					
		C	D	Main effect (m)	Additive effect (d)	Dominance effect (h)	Additive X Additive (i)	Dominance X Dominance (l)	Type of epistasis
Plant height (cm)	**C1**	-17.5^{**}	-8.71^{**}	35.78^{**}	3.65^{**}	-7.83^{**}	10.18^{**}	11.72^{**}	Duplicate
	C2	-14.76^{**}	-5.97^{**}	35.78^{**}	4.35^{**}	-7.83^{**}	10.22^{**}	11.72^{**}	Duplicate
	C3	-21.16^{**}	-69.91^{**}	44.01^{**}	-0.50^{**}	43.48^{**}	42.08^{**}	-64.99^{**}	Duplicate
Branches per plant	**C1**	-1.31^{ns}	1.24^{**}	2.47^{**}	-0.10^{**}	-1.05^{**}	-1.25^{**}	3.41^{**}	Duplicate
	C2	-1.97^{ns}	-2.93^{**}	2.88^{**}	0.15^{**}	1.07^{**}	1.92^{**}	-1.27^{**}	Duplicate
	C3	-1.58^{ns}	-2.96^{**}	2.53^{**}	-0.05^{**}	2.06^{**}	1.61^{**}	-1.85^{**}	Duplicate
Clusters per plant	**C1**	-8.48^{**}	-6.86^{**}	16.41^{**}	-0.59^{ns}	4.29^{**}	1.98^{*}	2.17^{*}	Complementary
	C2	-9.45^{**}	-7.83^{**}	16.41^{**}	-1.05^{**}	4.29^{**}	1.54^{**}	2.17^{**}	Complementary
	C3	-30.59^{**}	-40.5^{**}	17.45^{**}	-2.20^{**}	23.7^{**}	17.50^{**}	-13.21^{**}	Duplicate
Pods per cluster	**C1**	-3.34^{**}	0.96^{**}	2.26^{**}	-0.40^{**}	-1.40^{**}	-2.00^{**}	5.74^{**}	Duplicate
	C2	-4.89^{**}	2.30^{**}	2.08^{**}	-0.20^{**}	-2.55^{**}	-2.75^{**}	9.58^{**}	Duplicate
	C3	-1.37^{**}	-0.68^{**}	2.71^{**}	-0.10^{**}	-0.48^{**}	0.02^{**}	0.92^{**}	Duplicate
Pods per plant	**C1**	-80.92^{**}	-61.50^{**}	35.09^{**}	-1.05^{*}	23.26^{**}	25.41^{**}	25.90^{**}	Complementary
	C2	-86.34^{**}	21.78^{**}	22.04^{**}	-3.05^{*}	-32.76^{**}	-35.01^{**}	144.16^{**}	Duplicate
	C3	-76.96^{**}	-58.36^{**}	35.01^{**}	-1.30^{*}	28.18^{**}	23.48^{**}	24.81^{**}	Complementary
Pod length (cm)	**C1**	-0.76^{ns}	2.12^{**}	4.12^{**}	0.08^{**}	-1.59^{**}	-1.39^{**}	3.84^{**}	Duplicate
	C2	-0.92^{ns}	0.61^{**}	4.12^{**}	0.14^{**}	-0.19^{**}	-0.28^{**}	2.04^{**}	Duplicate
	C3	6.37^{ns}	-0.08^{**}	4.00^{**}	0.01^{**}	-2.84^{**}	1.12^{**}	-8.60^{**}	Complementary
Seeds per pod	**C1**	-0.43^{**}	3.22^{**}	5.37^{**}	0.15^{ns}	-2.17^{**}	-1.92^{**}	4.87^{**}	Duplicate
	C2	-2.65^{**}	1.44^{**}	5.19^{**}	0.00^{ns}	-0.70^{**}	-1.40^{**}	5.46^{**}	Duplicate
	C3	5.04^{**}	5.00^{**}	5.19^{**}	-0.25^{ns}	-0.34^{**}	-2.99^{**}	-0.06^{**}	Complementary
100-seed weight (g)	**C1**	-1.14^{ns}	11.46^{**}	4.01^{**}	0.27^{**}	-7.38^{**}	-7.30^{**}	16.80^{**}	Duplicate
	C2	0.62^{ns}	-2.14^{**}	4.25^{**}	0.16^{**}	1.28^{**}	1.85^{**}	-3.68^{**}	Duplicate
	C3	-1.6^{ns}	-1.40^{**}	3.96^{**}	0.32^{**}	0.54^{**}	1.31^{**}	0.27^{**}	Complementary
Seed yield per plant (g)	**C1**	-4.58^{**}	8.06^{**}	4.29^{**}	0.36^{**}	-5.79^{**}	-5.42^{**}	16.85^{**}	Duplicate
	C2	-15.04^{**}	6.10^{**}	3.79^{**}	-0.06^{**}	-6.68^{**}	-6.70^{**}	28.20^{**}	Duplicate
	C3	-17.96^{**}	0.11^{**}	3.91^{**}	-0.16^{**}	-0.25^{**}	-3.40^{**}	24.10^{**}	Duplicate

*,** - significant at 1 and 5% probability

Note: C1 - ADT 3 X VBG 17007, C2 - ADT 3 X VBG 19010, C3 - VBG 13003 X VBG 17007

to assess the applicability of the additive-dominance model. All traits in the three crosses showed significance for one or both scales, indicating that the additive-dominance model is insufficient to explain the genetic control of these traits. Epistatic interactions were classified based on the directionality of the h and l parameters, as either complementary gene action (when the direction is the same) or duplicated gene action (when the direction is opposite) (22). In the cross ADT 3 x VBG 17007 (C1), complementary gene action was observed for clusters per plant (CPP) and pods per plant (PPP) (23-25), while all other traits exhibited duplicated epistatic interactions. In the cross ADT 3 x VBG 19010 (C2), complementary gene action was observed for CPP and duplicated epistasis was found for the remaining traits. In the cross VBG 13003 x VBG 17007 (C3), traits such as PPP, pod length (PL), seeds per pod (SPP) and 100-seed weight (HSW) showed complementary epistasis, while the other traits exhibited duplicated epistasis.

For the cross ADT 3 x VBG 17007 (C1), significant additive gene effects were observed for all traits except CPP and SPP. Non-significant additive components were observed for CPP in C1 and for SPP in all three crosses. Non-additive components, such as dominance, additive x additive and dominance x dominance interactions, were significant for all traits across all crosses (26).

The genetic control of traits as dominant or recessive is determined based on the direction of dominance effects (d). A positive direction indicates a dominant nature, while a negative direction suggests a recessive nature (27, 28). Dominant effects were observed for CPP in all crosses (29), while recessive effects were noted for pods per cluster (PPC), PL, SPP and seed yield per plant (SYPP). For various traits, either dominant or recessive gene action was observed across the crosses (26). The signs of gene action reflect the mean performance of the F_1 generation (30). Similarly, the opposite directions of additive and dominance effects indicate genetic divergence between parents, emphasizing the importance of selecting appropriate parents for hybridization (31). Positive and negative signs of additive x additive interactions reveal the association and dispersion of alleles for the concerned trait, respectively (31).

Previous studies have reported a preponderance of dominance gene action for the number of branches in black gram (32) and similar trends of dominant and additive effects for pods per plant (33). Epistatic interactions for the number of pods have also been reported in similar studies (34). In contrast, some studies have suggested an additive-dominance model for seeds per pod and recommended the improvement of this trait through simple plant selection procedures (33).

Conclusion

In conclusion, the present study found that all the traits studied in the three crosses did not conform to the additive-dominance model, indicating the presence of non-allelic interactions. Significant additive components were observed for all traits, except for clusters per plant (CPP) in cross C1 and seeds per pod (SPP) in all crosses. Additionally, all traits exhibited significant non-additive components. Therefore, considering the presence of epistatic interactions, it is recommended that selection be postponed until later generations to achieve homozygosity.

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Authors' Contributions

DP carried out field experiments, data curation, visualization, statistical analysis and manuscript preparation. MN carried out conceptualization, methodology and supervision. BRPV, GKN, JP and HS were involved in conceptualization and manuscript preparation.

Compliance with Ethical Standards

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

Ethical issues: None

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