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DIALLEL ANALYSIS OF THE KENAF (*HIBISCUS CANNABINUS* L.) RESISTANCE AGAINST ROOT-KNOT NEMATODES

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SUMMARY

The estimation of genetic parameters of the kenaf (*Hibiscus cannabinus* L.) plant resistance against root-knot nematodes (*M. incognita*) using full diallel cross analysis was the aim of this study. Seven *H. cannabinus* parental genotypes, KR-1, KR-4, KR-5, KR-6, KR-15, Kenafindo-2 (Kin-2), and DS-028, as well as their complete diallel F_1 hybrids, were samples used in the study. The experiment commenced by infecting kenaf plants aged 15 days after sowing (DAS) with *M. incognita* nematodes in a population of 40 second-stage juveniles/100 g soil. The resistance variables comprised the number of root-knot nematodes, reproductive factors, the number of second-stage juveniles, the total egg mass, and the average number of eggs per mass. The results showed no significant epistatic interaction between genes in determining *H. cannabinus* resistance against *M. incognita*. Moreover, the effect of the additive genetic variances was greater than the dominance genetic variances. The kenaf resistance against root-knot nematode revealed the primary control of a partially dominant-additive gene. Dominant genes proved more prevalent than recessive genes in the parental genotypes. Both broad- and narrow-sense heritability values emerged as high.

Keywords: Kenaf (*H. cannabinus* L.), root-knot nematodes (*M. incognita*), Hayman's diallel analysis, genetic parameters, additive and dominance genetic variances, heritability

Key findings: The kenaf (*H. cannabinus* L.) resistance against root-knot nematode showed the control of a partially dominant gene. Dominant genes appeared more abundant than recessive ones in the parental genotypes. Both broad- and narrow-sense heritability values were high.

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INTRODUCTION

The root-knot nematode (*Meloidogyne* spp.) is one of the most important plant pathogenic nematodes infecting kenaf (*H. cannabinus* L.) (Parnidi *et al.*, 2021a, 2021b, 2021c; Rafii *et al*., 2023), which causes plants to grow stunted and reduces their yield potential. The *H. cannabinus* yield losses due to root-knot nematode (RKN) infection reached up to 19% (Parnidi *et al*., 2021a, 2021c), and some studies reported yield losses may range from 32% to 67% (Lawrence and Mclean, 1992). RKN infection can reduce the wet weight of kenaf stems up to 3 t/ha. As many as 40 juveniles per 100 grams of soil in the initial population can cause a decrease in kenaf plant yields (Parnidi *et al*., 2021a). In line with previous studies, the damage caused by RKN rises with the number of nematodes infecting root tissues (Shahadati *et al.*, 2017).

Kenaf breeding efforts still pertain to improving the fiber quality, biomass yield, and environmental adaptation (Ali *et al*., 2012; Sudarmadi *et al*., 2018). However, resistance to nematodes has become an issue of increasing attention recently. Research results by Chen *et al*. (2016) found genetic variations in kenaf genotypes against *M. incognita* infection. Additionally, screening programs in India and the United States have identified several kenaf accessions that show moderate to high resistance to RKN (Srivastava *et al*., 2014; Webber *et al.*, 2005). Molecular breeding techniques, such as marker-assisted selection (MAS) and genomic approaches for nematode resistance, have not reached their wide application in kenaf compared with other food crops (Zhang *et al*., 2020).

Based on the kenaf losses due to RKN, plant breeders intend to improve the host plant resistance properties against RKN. Therefore, knowledge of the genetic information associated with kenaf resistance against RKN is essential to develop the resistant cultivars against RKN. This study focused on investigating the genetic behavior of genes associated with *H. cannabinus* resistance against RKN by estimating various genetic parameters (Hayman, 1954; Syukur *et al.*, 2010; Owusu *et al*., 2020).

Diallel cross analysis can be applicable to estimate the diverse genetic parameters. The diallel analysis utilizes a systematic approach, and, from an analytical viewpoint, this analysis utilizes a comprehensive genetic evaluation approach in identifying the best crosses at the early generation for further selection processes. Diallel cross analysis is also beneficial to assess the additive and dominance effects of particular populations, and these effects can help appraise the genetic variance and broad- and narrow-sense heritabilities (Ramya *et al*., 2021; Singh, 2021; Sinare *et al*., 2024).

Basically, diallel cross analysis can pertain to categories of three types a full diallel, a half diallel, and a partial diallel (Kumar *et al*., 2021; Ramya *et al.*, 2021). Likewise, several assumptions require fulfilling to employ a diallel cross analysis. These are a) diploid segregation, b) no difference between reciprocal crosses, c) no interaction between the genes with different alleles, d) no multi-allelism, e) homozygous parents, and f) genes distributed independently among the parental strains used in the diallel crosses (Syukur *et al*., 2010; Kumar *et al*., 2021).

Studies on genetic parameters associated with plant resistance against RKN have previously progressed in past years. Parnidi *et al*. (2021a) reported the gene responsible for kenaf resistance against nematode was monogenic with a dominant gene action. On the other hand, Wubben *et al*. (2020) reported that cotton plant resistance against RKN had the control of two dominant genes. Shahadati *et al.* (2017) studied the tobacco plant's resistance against RKN and found the association of two genes with an additive gene action on the resistance to RKN. The broad and narrow-sense heritability values of RKN were 0.93 and 0.75, respectively. The egg masses were 0.94 cyst per 10 g root and 0.56 cyst per 10 g root, and the number of eggs per egg mass was 0.61 egg per 10 g root and 0.28 egg per 10 g root. Wubben *et al*. (2020) have identified two chromosomal loci associated with cotton plant resistance against RKN, located at chromosomes 11 and 14. QTL 11 and QTL 14 negatively influence the RKN index, as well as nematode egg production.

The F_1 offspring of a cross between *H. cannabinus* (the susceptible parent) and *H. radiatus* (the resistant parent) showed susceptibility to *M. incognita* infection (Setyobudi *et al*., 2002). Novtara *et al*. (2021) stated kenaf resistance to RKN had a simple gene control, with no influence from the environment. They added it has a low to moderate narrow heritability and an additive dominant inheritance pattern for nematode reproduction and the number of eggs per 10 g of roots. Therefore, this study aimed to understand and estimate the genetic parameters associated with *H. cannabinus* plant resistance against RKN *M. incognita* by employing a full diallel cross analysis using seven parental genotypes.

MATERIALS AND METHODS

Study site and breeding materials

This study happened from November 2019 to February 2020 at the Karangploso Experimental Garden and Plant Disease Science Laboratory, Indonesian Sweetener and Fiber Crops Research Institute, which in 2025 became the Indonesian Sweetener and Fiber Crops Engineering and Testing Institute. A semi-field experiment proceeded by using seven parental genotypes, namely, KR1, KR4, KR5, KR6, KR15, Kin2, and DS028, as well as their 42 complete diallel F_1 hybrids. The experiment had a randomized complete block design (RCBD) layout, with three replications. Kenaf planting commenced in polybags with the size of 30 cm × 30 cm and a spacing of 30 cm × 50 cm, with a distance of 100 cm kept between the replications. The planting medium used was sandy soil with a composition of 55% sand, 36% silt, and 17% sterile clay, with its sterilization using 4% formalin solution. The experiment continued by infecting *H. cannabinus* plants aged 15 days after sowing (DAS) with *M. incognita* nematodes at a density of 40 second-stage juveniles per 100 g soil. At the age of 75 days after planting, the dismantling of plants ensued, afterward making observations on several variables of plant resistance against RKN *M. incognita*.

The *H. cannabinus* resistance against RKN *M. incognita* involved categories using several variables, including the number of root-knot nematodes and reproductive factors. A reproductive factor is a comparison between the population of RKN larvae in the soil at the end of the observation and the population of RKN larvae in the initial soil. Other variables are the number of second-stage juveniles, the total egg mass, and the average number of eggs per egg mass. The number of root-knot nematodes, reproductive factors, and the number of second-stage juveniles on roots underwent calculations using the methodology of Shahadati *et al.* (2017) and Parnidi *et al*. (2021a; 2021c). The total egg mass, as calculated, came from a 10-g root sample, immersed first in a floxin B (sigma) solution at a concentration of 0.15 g/l for 15 minutes (Parnidi *et al*., 2021a, 2021b). Ten egg masses obtained from each genotype entailed placement in a 0.5% sodium hypochlorite (1 ml) solution for one minute before shaking well (Parnidi *et al*., 2021a). A total of three samples (50 µl each) succeeded their collection and observation under a light microscope. Furthermore, the calculation of the average number of eggs per egg mass ensued.

Statistical analysis

The obtained data received analysis using the Hayman approach, as well as undergoing an analysis of variance and variance and covariance estimation. Using the data established in the graph, Wr-Vr pursued the variance component estimation and other genetic parameters and the most dominant and recessive parental genotypes (Syukur *et al*., 2010; Kumar *et al.,* 2021*;* Ramya *et al.,* 2021*;* Fernandes *et al.,* 2022). From the data analysis, we obtained the following: a) variations due to additive effects (D); b) the mean of 'Fr' over the arrays (F), and Fr is the covariance of additive and non-additive effects in a single array; c) components of variation due to the dominance effect of the genes (H_1); d) positive and negative gene proportion in the parental genotypes (H_2); e) the dominance effects (as the algebraic sum over all loci in heterozygous phase in all crosses) (h_2); and f) the expected environmental components of variation (E). Other obtained results were g) the mean degree of dominance ($[H_1/D]^{1/2}$); h) the proportion of genes with positive and negative effects in the parental genotypes ($H_2/4H_1$); i) the proportion of dominant and recessive genes in the parental cultivars (Kd/Kr); j) the number of groups of genes that control the character and exhibit dominance (h^2/H_2); k) heritability in broad-sense (h^2_{BS}); and l) heritability in narrow-sense (h^2_{NS}).

RESULTS

The cross between the KR 15 x KR 4 and KR 4 x KR 15 genotypes had relatively lower values for the number of ovules, reproductive factors, and the number of juveniles, egg masses, and eggs per egg mass than other genotypes (Table 1). The number of root-knot nematodes, reproductive factor, the number of second-stage juveniles, the total egg mass, and the average number of eggs per egg mass for KR 15 x KR 4 and KR 4 x KR 15 were 27.83, 2.07, 34.16, 28.75, and 971.35 and 28.80, 2.15, 34.47, 37.39, and 857.70, respectively. The number of root-knot nematodes, reproductive factor, number of second-stage juveniles, total egg mass, and the average number of eggs per egg mass gave the lowest values. The lower the number of root-knot nematodes, reproductive factor, the number of second-stage juveniles, the total egg mass, and the average number of eggs per egg mass, the more resistant it is to root-knot nematodes. According to Setyo-Budi *et al*. (2009), high reproductive factors mean that the genotype is a favorable host for nematode development. The genotype tested showed the average numbers of RKN were 16–35. This means the tested genotype showed the root damage caused by nematode attacks was moderate, implying the level of resistance of the accessions tested was moderate to RKN. Plant resistance to RKN, according to Canto Saenz (1985), is indicative of the combination of the number of root knots seen on the plant roots and reproductive factors. If the number of root knots is less than 16–35 but the reproductive factor is more than 1, the plant is moderately resistant.

Analysis of variance

Estimation of genetic parameters using diallel cross analysis can proceed if significant differences emerge among the genotypes based on the F-test of traits observed (Singh and Chaudhary, 1979). The analysis of variance on the host plant resistance variables against RKN *M. incognita* showed significant differences among the genotypes (Tables 1 and 2). The results about estimation of the genetic parameters using diallel analysis are available in Table 3.

Gene interaction

Gene interaction estimation results from the regression coefficient (b value) of the regression line between Wr (kenaf parental strain variance) and Vr (hybrid variance). If the b value is significantly different from one, then a significant gene interaction existed underlying the traits of interest in the crop plants (Singh and Chaudhary, 1979; Syukur *et al*., 2010; Kumar *et al*., 2021; Ramya *et al.*, 2021; Fernandes *et al*., 2022).

The b regression coefficients (Wr, Vr) were not significantly different from unity on the number of RKN variables (0.93), reproductive factor (0.98), number of second-stage juveniles (0.97), total egg mass (0.98), and average number of eggs per egg mass (0.93) in the kenaf genotypes (Table 3). The results indicated there exists no gene interaction underlying *H. cannabinus* resistance against RKN *M. incognita* based on the evaluated variables related to host plant resistance.

Additive and dominance gene effects

The analysis further revealed no significant additive (D) and dominance (H_1) effects occurred on the number of RKN, number of second-stage juveniles, and the average number of eggs per egg mass. However, considerable additive effects were evident on

Table 1. The number of root-knot nematodes, reproductive factor, the number of second-stage juveniles, the total egg mass (syst), and the average number of eggs per egg mass are variables of kenaf plant resistance to root-knot nematodes.

Genotype	NR	RF	J2	EM	AEEM
KR1XKR4	41.29	5.43	44.62	35.59	1085.38
KR1XKR5	47.93	4.45	51.26	37.39	1172.71
KR1XKR6	56.12	6.11	66.12	43.99	1503.31
KR1XKR15	32.49	7.14	42.49	47.50	969.98
KR1XKIN2	149.78	7.89	76.99	54.88	1544.56
KR1XDS028	65.32	8.46	112.78	52.41	1654.58
KR4XKR1	40.36	6.38	47.02	33.34	983.31
KR4XKR5	34.38	3.79	34.38	39.06	913.84
KR4XKR6	38.29	5.78	38.29	40.67	1180.62
KR4XKR15	28.80	2.15	24.47	37.39	857.70
KR4XKIN2	42.17	6.86	42.17	50.56	1290.63
KR4XDS028	46.80	6.46	46.80	50.73	1327.29
KR5XKR1	45.87	7.13	55.87	40.80	1137.06
KR5XKR4	44.11	2.79	34.78	37.41	1135.28
KR5XKR6	31.31	4.11	36.31	39.02	1423.08
KR5XKR15	24.51	7.03	34.51	42.64	879.53
KR5XKIN2	48.06	5.19	48.06	50.04	922.28
KR5XDS028	70.49	5.09	70.49	45.53	1121.66
KR6XKR1	66.37	7.56	69.71	35.59	1556.06
KR6XKR4	44.13	4.17	44.13	21.79	1306.82
KR6XKR5	42.78	5.38	42.78	29.87	1084.76
KR6XKR15	35.47	7.12	42.13	44.06	785.75
KR6XKIN2	68.33	6.14	68.33	40.84	1372.84
KR6XDS028	47.56	5.48	47.56	47.64	1392.12
KR15XKR1	37.31	8.66	43.98	42.64	1190.35
KR15XKR4	27.83	2.07	24.16	28.75	871.35
KR15XKR5	30.03	6.40	34.37	30.39	885.77
KR15XKR6	43.22	6.57	43.22	33.73	1414.85
KR15XKIN2	37.35	8.50	44.02	42.66	1177.23
KR15XDS028	38.64	5.15	38.64	49.21	1626.89
KIN2XKR1	91.45	8.80	88.12	48.98	1470.96
KIN2XKR4	44.72	6.08	44.72	38.81	1333.33
KIN2XKR5	42.86	6.55	39.53	42.14	1440.94
KIN2XKR6	66.96	6.43	66.96	40.56	1539.60
KIN2XKR15	49.78	7.23	49.78	42.68	1208.79
KIN2XDS028	89.08	6.56	89.08	40.75	1413.28
DS028XKR1	69.11	8.93	122.44	42.66	1677.71
DS028XKR4	49.71	5.42	49.71	32.20	1240.55
DS028XKR5	38.58	5.73	65.24	28.70	1135.28
DS028XKR6	48.86	3.90	48.86	25.42	1414.96
DS028XKR15	39.72	4.99	39.72	40.75	1179.16
DS028XKIN2	47.69	8.15	71.02	49.25	1569.35
KR1	133.42	7.83	110.08	46.00	1632.05
KR4	31.21	2.38	34.87	22.33	908.95
KR5	37.82	3.38	34.49	23.61	1101.40
KR6	53.26	6.76	53.26	36.13	1432.22
KR15	30.88	2.02	34.55	23.28	888.89
KIN2	155.53	7.61	107.53	49.29	1417.28
DS028	47.99	6.76	47.99	33.35	1334.7

Note: NR = the number of root-knot nematodes; RF = reproductive factor; J2 = the number of second-stage juveniles; EM = the total egg mass; and AEEM = the average number of eggs per egg mass.

Table 2. Recapitulation of the analysis of variance based on various variables related to kenaf resistance against RKN *M. incognita*.

Variables	Mean squares	F values
NR	3860.80	5.24**
RF	8.61	4.85**
J2	480.27	4.95**
EM	45.55	4.90**
AEEM	13573.47	6.12**

Note: NR = the number of root-knot nematodes; RF = reproductive factor; J2 = the number of second-stage juveniles; EM = the total egg mass; and AEEM = the average number of eggs per egg mass. ** = statistically significant at a 1% level of significance.

Table 3. Estimation of the genetic parameters for resistance variables of kenaf against RKN *M. incognita* using the diallel cross analysis.

Genetic parameters	Values				
	NR	RF	J2	EM	AEEM
Variance-covariance regression (b) (Wr, Vr)	0.93ns	0.98ns	0.97ns	0.98ns	0.93ns
Additive effect (D)	2582.87ns	7.69**	563.22ns	40.62**	17875.33ns
The mean of F1 (F)	512.15ns	2.40**	306.77ns	12.60**	13261.87ns
Dominance effect (H_1)	946.04ns	0.78ns	93.57ns	3.96ns	6833.14ns
The gene distribution in parental strains (H_2)	785.10ns	0.59ns	55.12ns	2.98ns	4072.17ns
F1 deviation from the average of parental strains (h^2)	119.52ns	0.51ns	11.80ns	2.70ns	5229.51ns
The number of genes controlling the trait of interest (h^2/H_2)	0.15	0.88	0.21	0.91	1.28
Environment (E)	243.23ns	0.59ns	34.26ns	3.15ns	741.37ns
The mean degree of dominance $(H_1/D)^{1/2}$	0.61	0.32	0.41	0.31	0.62
The proportion of genes with positive and negative effects in the parents ($H_2/4H_1$)	0.21	0.19	0.15	0.19	0.15
The proportion of dominant and recessive genes in the parents $(\{4DH_1)^{1/2} +F\}/\{4DH_1)^{1/2}-F\}$ (Kd/Kr)	1.39	2.92	5.03	2.98	4.00
Coefficient correlation ®	0.71	0.94	0.89	0.94	0.81
Estimation of complete dominance and recessive in the parental strains	0.50	0.87	0.79	0.87	0.66
Broad-sense heritability (h^2_{bs}) (%)	88.24	90.00	93.18	89.82	96.04
Narrow-sense heritability (h^2_{ns}) (%)	87.00	89.75	92.99	89.57	95.81

Note: NR = the number of root-knot nematodes; RF = reproductive factor; J2 = the number of second-stage juveniles; EM = the total egg mass; and AEEM = the average number of eggs per egg mass. ** = statistically significant at a 1% level of significance; * = statistically significant at a 5% level of significance; ns = not significant.

the reproductive factor and total egg mass variables (Table 3). The additive effects of the number of RKN, reproductive factor, number of second-stage juveniles, total egg mass, and average number of eggs per egg mass were 2582.87, 7.69, 563.22, 40.62, and 17875.33, respectively. The dominance effects were 946.04, 0.78, 93.57, 3.96, and 6833.14, respectively, for the above traits (Table 3).

Gene distribution in the parental strains

Gene distribution in the parental strains is predictable from the H_2 value. Findings from Kumar *et al.* (2021) and Ramya *et al.* (2021) revealed that if the values of gene distribution in the parental genotypes are nonsignificant, then the inheritance pattern of the variables of interest has an uneven distribution. The presented results showed the H_2 values of all evaluated resistance variables were nonsignificantly different from each other (Table 3), indicating the genes associated with the pattern of inheritance gave an even distribution in the kenaf parental genotypes.

The proportion of positive genes attained estimation from the H_1 value to H_2. If $H_1 < H_2$, then there are more negative genes than positive genes, and vice versa (Syukur *et al*., 2010; Parnidi *et al*., 2021a; Fernandes *et al*., 2022). The genes detected seemingly associated with all the variables mostly belonged to positive genes, as indicated by the values of $H_1 > H_2$ for various traits in kenaf genotypes (Table 3).

Degree of dominance

The magnitude of genetic dominance effects involved the estimation from ratio $H_1/D^{1/2}$. Past studies proposed that a value of $H_1/D^{1/2} > 1$ indicates overdominance, while the value of $H_1/D^{1/2}$ ranging from 0 to 1 signifies a partial dominance (dominant or partially recessive) (Hayman, 1954; Kumar *et al*., 2021; Ramya *et al*., 2021). The $H_1/D^{1/2}$ values of the number of RKN, reproductive factor, number of second-stage juveniles, total egg mass, and average number of eggs per egg mass were 0.61, 0.32, 0.41, 0.31, and 0.62, respectively. Overall, all the variables indicated the values of $D > H_1$ (Table 3).

Number of genes

The number of genes controlling resistance to RKN appeared by the h^2/H_2 ratio. The results suggested that one group of genes was controlling the kenaf resistance against RKN based on the evaluated resistance variables (Table 3).

Dominant and recessive genes ratio

The Kd/Kr value indicates the number of dominant genes in the parental genotypes. If the Kd/Kr value < 1, then there are more recessive genes in the parental strains, and vice versa. In addition, if the Kd/Kr value = 1, then the number of dominant and recessive genes are equal. Based on the proportion of gene values, more dominant genes resulted in the parental genotypes, as the Kd/Kr value was greater than unity (Table 3).

Direction of dominance

The direction and order of parental dominance succeeded in their estimation based on the Wr + Vr values. Sousa and Maluf (2003) stated if the parental position is closer to 0, then more dominant genes belonged with the parental genotypes related to the traits of interest, and vice versa. Based on the number of RKN variables, parental genotype KR 15 contained the highest number of dominant genes for the reproductive factor and total egg mass. Additionally, the genotype KR 5 had the most number of dominant genes based on the average number of eggs per egg mass. However, the parental genotype KR 1 revealed the maximum number of recessive genes based on all the evaluated variables (Figures 1, 2, 3, 4, and 5).

Heritability

The heritability value is a quantitative statement regarding the role of genetic factors, which measures the ability of a particular genotype of a plant population to inherit its traits. Past studies categorized the heritability into three types, i.e., high ($h^2 > 50\%$), moderate ($20\% \leq h^2 \leq 50\%$), and low ($h^2 < 20\%$) (Syukur *et al*., 2010; Kumar *et al*., 2021; Parnidi *et al*., 2021a; Fernandes *et al*., 2022). The analysis using the phenotypic variance and additive genetic variance of all resistance variables against RKN *M. incognita* evaluated engaged the cross-diallel approach. This indicated a high classification for both the broad-sense (h^2_{bs}) and narrow-sense (h^2_{ns}) heritability values (Table 3).

The total phenotypic variations observed for the number of RKN variables (NR), reproductive factor (RF), number of second-stage juveniles (J2), total egg mass (EM), and average number of eggs per egg mass (AEEM) were 88.24%, 90.00%, 93.18%, 89.82%, and 96.04%, respectively. Each variable bore influences from genetic variations (87.00%, 89.75%, 92.99%, 89.57%, and 95.81%, respectively). In this case, the phenotypes sustained influences from an additive gene action with differences in the number of root-knot nematodes = 1.2%, reproductive factor = 0.25%, number of second-stage juveniles = 0.20%, total egg mass = 0.25%, and average number of eggs per egg mass = 0.23%. The results suggested

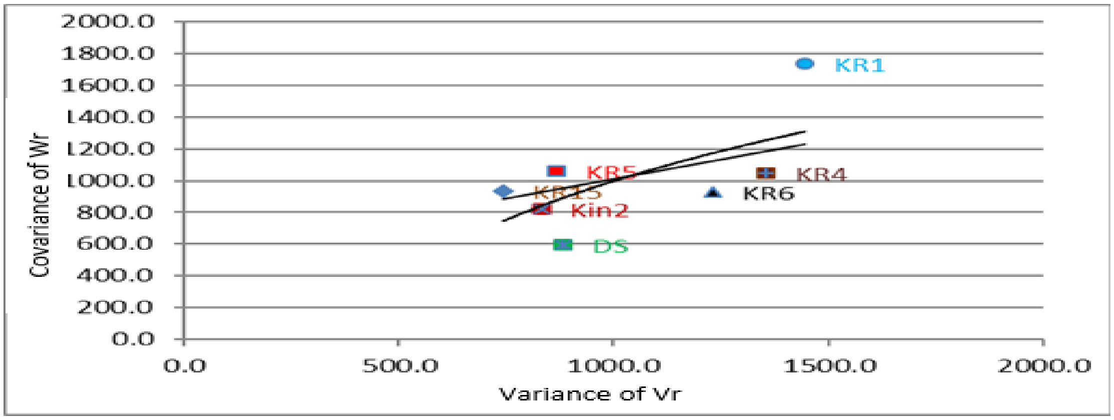

Figure 1. Relationship between Wr and Vr on the number of root-knot nematodes.

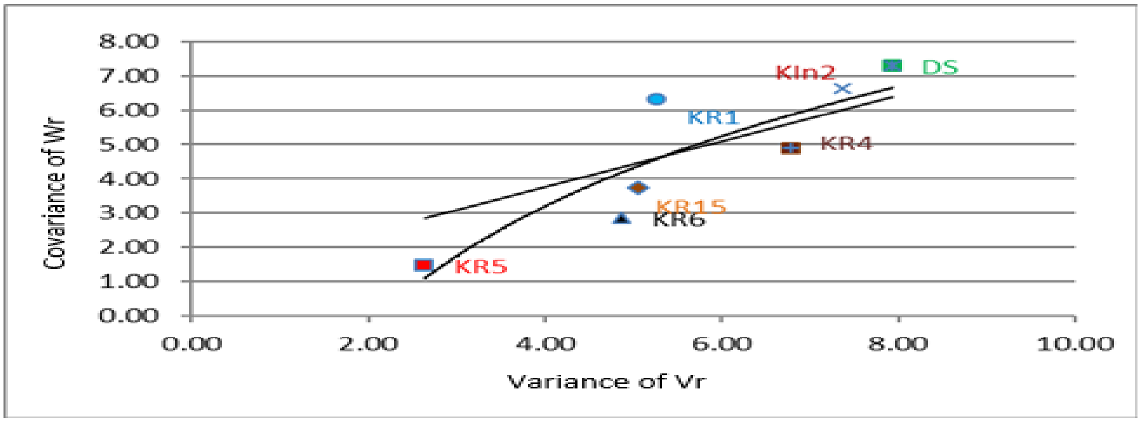

Figure 2. Relationship between Wr and Vr on reproductive factor variables.

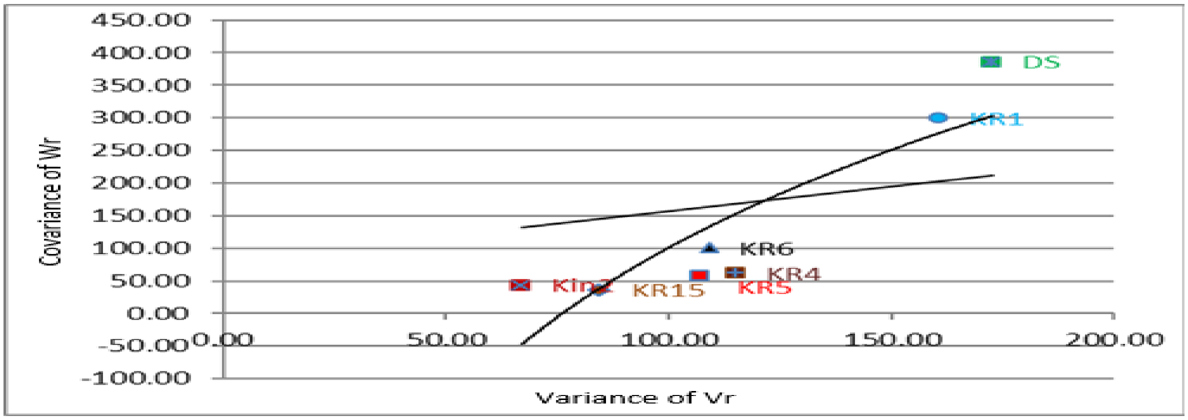

Figure 3. Relationship between Wr and Vr on the variable number of second-stage juveniles per 10 grams of roots.

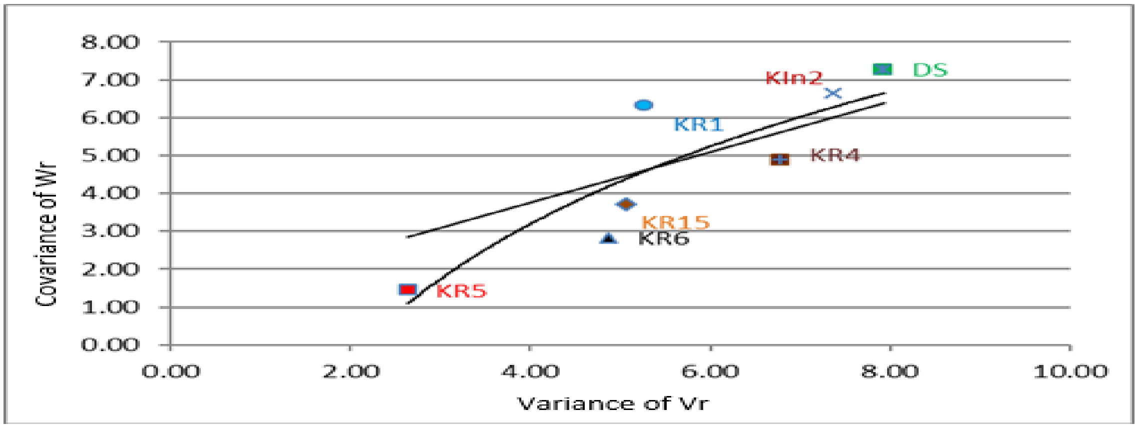

Figure 4. Relationship between Wr and Vr on the variable total egg mass.

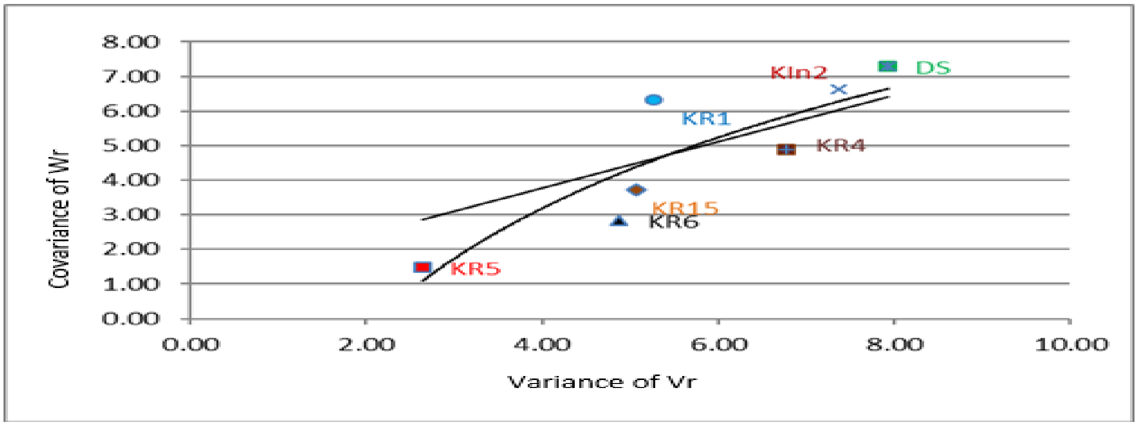

Figure 5. Relationship between Wr and Vr on the variable average number of eggs per egg mass.

the smaller role of non-additive gene action (either dominance or genes' interaction) on *H. cannabinus* resistance against the RKN *M. incognita*. Nevertheless, the highest values of genetic variations from total phenotypic variations indicated that environmental factors (E) have a smaller role on each evaluated variable, specifically the NR = 11.8%, RF = 10%, J2 = 6.1%, EM = 10.2%, and AEEM = 3.9%. These results were in line with the estimation of genetic variance components, which detected that the environmental variance component has no significant effect on the kenaf resistance against RKN (Table 3).

DISCUSSION

Phenotypic variation in crop plants gains basic influences from both genetic variability and the existing environmental factors. Genetic variance that becomes the basis in plant breeding usually has an association with the additive and dominance gene effects and gene interaction (Syukur *et al*., 2010; Shahadati *et al*., 2017; Kumar *et al*., 2021). Additive genetic variance is the main cause for the trait similarities among the parental genotypes and their hybrids' populations. However, the dominance genetic variance is the chief cause for the traits' dissimilarity among the closely related genotypes. These variances, then, become the major basis for heterosis and combining ability in conventional plant breeding.

The degree of dominance $(H_1/D)^{1/2}$ value, ranging from 0 to 1, indicates a partial dominance (dominant or partially recessive). The results indicated the gene controlling some resistance variables was of a partial dominance, with the same also supported by the results of the Vr-Wr graph analysis. The analysis revealed if the D value is less than H_1 (the intercept is positive and the regression line crosses the Wr axis above the basal point), the gene action for the resistance variables is a partial dominance. The average frequencies of positive and negative alleles in the parental strains $(H_2/4H_1)$ were the number of root-knot nematodes = 0.21 (< 0.71), reproductive factor = 0.19 (< 0.94), the number of second-stage juveniles = 0.15 (< 0.89), total egg mass = 0.19 (< 0.94), and average number of eggs per egg mass = 0.15 (< 0.81). It implies an imbalance in the average of allelic frequency at loci containing dominant and recessive genes. In other words, the results signified the proportion of positive and negative genes was an imbalance in the kenaf parental genotypes. The frequency of dominant and recessive genes on the parental strains (Kd/Kr) were the number of root-knot nematodes = 1.39, reproductive factor = 2.92, number of second-stage juveniles = 5.03, total egg mass = 2.98, and average number of eggs per egg mass = 4. It states that more dominant genes exist in the parental strains. These results were analogous to past findings in the cacao tree against the fruit rot disease (Rubiyo *et al*., 2011; Rubiyo and Sudarsono, 2011).

At least one group of genes was without any gene interaction controlling the dominance of a specific character (h^2/H_2), based on the t-test toward the regression coefficient. These results align with previous studies (Wubben *et al*., 2020; Wei *et al*., 2022) regarding tobacco resistance against cyst nematodes and *M. arenaria* (Adamo *et al*., 2021), which sustained control from one partially dominant gene. The tobacco resistance against RKN *M. incognita* race-2 had the control of one partially dominant gene. However, some other studies suggested that plant resistance against nematodes received management from one to four genes (Shahadati *et al*., 2017).

The high influence of genetic variance resulted in the high broad-sense heritability values for all observed variables, as shown in Table 3. This indicates the proportion of additive genetic variance in controlling all the resistance variables was higher than the dominance genetic variance. These results also agreed with previous studies in various crop plants, including cotton (Zhang *et al.*, 2007), tobacco (Shahadati *et al.*, 2017), red clover plant (Call *et al.*, 1997), and sweet potato (Cervantes-flores *et al.*, 2008).

Zhang *et al.* (2007) reported both broad- and narrow-sense heritabilities of cotton plant resistance against *M. incognita* based on the number of RKN were 0.82 and 0.65, respectively. The broad-sense heritability of tobacco plants based on the number of RKN, total egg mass, and average number of eggs per egg mass variables were 0.93, 0.94, and 0.61, respectively (Shahadati *et al*., 2017). However, the values of narrow-sense heritability were 0.75, 0.56, and 0.28 for the variables the number of root-knot nematodes, total egg mass, and average number of eggs per egg mass, respectively. The higher values of narrow-sense heritability indicate a considerable role of additive genes in the traits of interest. The narrow-sense heritability illustrated the proportion of additive genes in determining the genetic diversity in relation to phenotypic diversity (Rahimi and Debnath, 2023; Vasupalli *et al*., 2024).

The success in plant breeding requires large effects from the genetic variability inherited from parental genotypes to the hybrids. The additive genetic component is the only component of genetic diversity that moves on to the offspring. This component can have representatives of the value of narrow-sense heritability through the genetic proportion of the total appearance inherited from parental cultivars to the offspring (Syukur *et al*., 2010; Rahimi and Debnath, 2023; Vasupalli *et al*., 2024). Since *H. cannabinus* is a self-pollinated plant, the selection should be reliant on the additive genetic effects to pool the superior genotypes. However, such a type of selection will be ineffective if the genes controlling the superior genotypes have dominance effects and an interaction between the genes (Cunha *et al*., 2020; Vasupalli *et al*., 2024).

The estimation of the genetic parameters for *H. cannabinus* resistance against RKN *M. incognita* indicated the observed variables had the control of considerable additive gene effects. Its representation was in the form of narrow-sense heritability values as the inherited genetics from parental genotypes to F_1 hybrids. By adopting a fairly strict selection, a successful breeding program may be feasible through selectively pooling superior genotypes. The presented results provide information to researchers that the *H. cannabinus* resistance gene against RKN incurred control from a single gene that was additive in nature, and it is easier to pass on to their offspring. The crosses made among tolerant parental genotypes of the *H. cannabinus* can lead to the development of cultivars tolerant to RKN along with other desirable traits.

Resistance influenced by one gene with additive-dominance and additive-genetic variance was greater than the dominance-genetic variance, with high heritability providing information. Such information states that to obtain varieties resistant to root-knot nematodes, selection can take place from F_2, followed by intensive selection in F_3 and F_4. Selection can proceed by the pedigree selection method or an individual selection by removing susceptible individuals. Selection continues based on the number of knots, reproductive factors, number of second-instar juveniles, number of egg masses, and the average number of eggs on the roots. Since parents have more dominant alleles, selecting the right parents is key to breeding. Parents with high levels of dominant alleles can be valuable candidates for backcrossing to strengthen dominant alleles. Morphologically, selection succeeds by selecting healthy plants with normal growth and no disruptions from nematode infection.

CONCLUSIONS

The results concluded that no gene interaction occurred underlying kenaf resistance against RKN *M. incognita*. The study suggested *H. cannabinus* resistance received control from one gene with a partially dominant additive effect. The value of the additive genetic variance was greater than the dominance genetic variance, with the degree of dominance being partially positive. The number of dominant genes was greater in the parental strains than in F_1 hybrids. The heritability of the kenaf resistance against RKN *M. incognita* emerged as considerably high.

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