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OBM Genetics

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Research Article

Inheritance Studies of Root-Knot Nematode (*Meloidogyne* Species) Resistance in Tomato (*Solanum Lycopersicum* L.)

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Academic Editor: Prashant Kaushik

Special Issue: Vegetable Breeding and Genetics

OBM Genetics
2025, volume 9, issue 1
doi:10.21926/obm.genet.2501286

Received: August 22, 2024
Accepted: February 12, 2025
Published: February 28, 2025

Abstract

Plant-parasitic nematodes threaten tomato cultivation in Ghana, particularly the root-knot nematodes, causing substantial economic yield losses. However, these yield losses can be prevented through resistant varieties. This study aims to determine the type of gene action, heritability, heterosis and inbreeding depression for root-knot nematode resistance in tomato. A cross between CSIR/CRI-P005 (P_1), an adapted variety with good yield but susceptible to root-knot nematode and VFNT (P_2), which is resistant to root-knot nematode but low-yielding were used to generate six tomato populations. Average fruit weight, yield, root gall index, and reproduction factor were evaluated using a randomized complete block design with three replications. The six tomato populations (P_1, P_2, F_1, F_2, $BC_{1.1}$, and $BC_{1.2}$) were subjected to generation mean analysis. The means of all the populations differed widely for all traits studied. The joint scaling test revealed significant mean, additive, and dominance gene effects

for all traits. Still, the additive-dominance model alone was inadequate in explaining the genetic actions of the studied traits. Using the six-parameter model, epistatic, additive, and dominance gene actions were significant for most traits. Average fruit weight, reproduction factor, and root gall index were found to duplicate dominant or recessive epistasis, while fruit yield per plant showed complementary epistasis. Better parent heterosis was observed for root gall index. Broad sense heritability estimations were high for yield per plant (90.94%), root gall index (92.82%), average fruit weight (78.69%), and reproduction factor (84.71%). Narrow sense heritability estimates were high for reproduction factor (76.59%) and root gall index (71.73%), moderate for yield per plant (32.32%), and low for average fruit weight (0%). High levels of inbreeding depression were detected for average fruit weight (-34.61%), yield per plant (-31.04%), reproduction factor (41.54%), and root gall index (-125.33%). This research suggests that traits with fixed genetic effects can be enhanced through pedigree breeding, whereas traits with non-fixed genetic effects are suitable for heterosis breeding.

Keywords
Disease resistance; dominance; epistasis; gene; heritability; root-knot nematode

1. Introduction

In Ghana, tomato is a vital vegetable crop contributing to the country's agricultural sector and economic development. This crop is crucial in local consumption, food security, and export. It is considered a protective food due to its unique nutritional value, providing essential nutrients like lycopene, beta-carotene, flavonoids, and vitamin C. Moreover, this crop has gained significant popularity particularly in recent years due to the discovery of lycopene's antioxidative properties and anti-cancer effects. As a result, tomato production and consumption continue to rise [1].

However, the average yield of less than 10 metric tons is significantly low compared to the potential yields of 20 to 40 metric tons [2-5]. Various abiotic and biotic factors, including fungal, viral, bacterial, and nematode infections, unfavorable weather conditions, and high post-harvest losses, can be attributed to low tomato productivity. Currently, the significant focuses of breeding programs are disease resistance and fruit quality. Root-knot nematode species, particularly *M. incognita*, *M*. *arenaria*, *M*. *javanica,* and *M. hapla*, are essential and cause significant crop damage. In Ghana, root-knot nematode infections are a substantial problem in tomato production [6], causing damage that impacts both yield quantity and quality. Root-knot nematodes infected tomato plants exhibited abnormal root system development, marked by the formation of characteristic roots. These knots disrupt water and nutrient uptake, hinder the translocation of minerals, and interfere with photosynthesis [3].

Root-knot nematodes are difficult to control because they reside in the soil and are not easily visible to farmers. They are usually detected only when their population has spread extensively and yield has significantly decreased. These pests are significant pathogens affecting tomato production in Ghana, severely limiting fruit yields [7]. Although physical and chemical approaches have been used to control soil nematodes, they are not always effective and can pose environmental pollution and health risks [8]. Hence, using root-knot nematode-resistant tomato cultivars is a more effective

and environmentally friendly approach to managing these soil nematodes [9]. Understanding gene action is crucial for selecting and breeding procedures in tomato improvement [10]. Inheritance pattern and generation mean analysis studies provide essential information for planning tomato breeding programs [11]. Generation means analysis, involving different populations (P_1, P_2, F_1, F_2, $BC_{1.1}$, and $BC_{1.2}$), estimates genetic variance components [7] that detect epistasis, additive variance, dominance variance, heterosis components, etc. This technique detects epistasis, additive variance, dominance variance, heterosis components, and other statistics. This study investigates the type of gene conferring resistance to root-knot nematode in tomato plants.

2. Materials and Methods

2.1 Population Development and Evaluation

The experiment was conducted in pots at the Council for Scientific and Industrial Research (CSIR) - Crops Research Institute (CRI)'s Kwadaso station, which is located in Ghana (latitude 6°40'35.6" N and longitude 1°40'04.6" W) during three seasons from 2019 to 2020.

In the first experiment (2019), two parental lines, CRI-P005 (P_1) and VFNT (P_2), were crossed to obtain an F_1 seed. CRI-P005 is an adapted variety with a good yield (20 t/ha) and large fruit size but is susceptible to root-knot nematodes. VFNT is resistant to root-knot nematode but has low yield (10 t/ha). F_1 individuals were obtained by planting the F_1 seed in the second experiment (2020); the F_1 individuals were selfed and backcrossed to the two parents to produce F_2, $BC_{1.2}$ ($F_1 \times P_2$), and $BC_{1.1}$ ($F_1 \times P_1$) generations, respectively.

A third experiment (2020) was conducted for the six tomato populations (P_1, P_2, F_1, F_2, $BC_{1.1}$, and $BC_{1.2}$) in pots. A randomized complete block design with three replications was used, where 330 plastic buckets filled with sterilized soil were arranged in the open field, which varied as follows: 30 each for the P_1, P_2, and F_1 generations; 120 for the F_2 generations; and 60 each for $BC_{1.1}$ and $BC_{1.2}$ generations. Data were collected on 10 non-segregated plants (P_1, P_2, and F_1), 20 plants each of $BC_{1.1}$ and $BC_{1.2}$, and 40 individual F_2 plants from each replicate. Data collected included average fruit weight, yield, root gall index, and reproduction factor according to Barker and Koenning's method [12].

Ten tomato fruits at the red and final stage were harvested from each plant and weighed individually, and the mean was computed as the average fruit weight. The weight of fruits per plant was taken as cumulative. The total sum of matured fruits per plant was calculated as yield per plant. The test plants were harvested eight weeks after inoculation and the roots of the harvested tomato genotypes were each washed separately and dabbed dry with tissue paper. Galling was scored after 10 weeks of transplanting on a scale of 0-10 according to Bridge and Page [1], where 0 = No galls on roots, 1 = Few small galls challenging to find, 2 = Small galls only but visible. Primary roots clean, 3 = Some larger galls visible. Primary roots clean, 4 = Larger galls predominate, but primary roots clean, 5 = 50% infested. Galling on parts of primary roots. Reduced root system, 6 = Galling on primary roots, 7 = Majority of primary roots galled, 8 = All primary roots galled. Few clean roots visible, 9 = All roots severely galled. Plant usually dying and 10 = All roots severely galled—no root system. The plant is generally dead.

Reproduction Factor (RF) was calculated according to the modified quantitative scheme of Oostenbrink's [13]. **RF = (Pf/Pi)** where; Pf = Final population and Pi = initial population. Final population was obtained by adding the number of eggs and J2 juveniles in roots and soil after

harvesting while the initial population was the inoculum level used. **RF = 1**: The nematode population has remained the same which usually indicates a neutral interaction with the host plant; **RF > 1**: Indicates reproduction, meaning the plant is susceptible to the nematode, and **RF < 1:** Indicates suppression of nematode reproduction, meaning the plant might be resistant or less susceptible to nematode [14].

2.2 Preparation of Nematode Culture

Nematode eggs were extracted from *Meloidogyne* spp. Infested tomato roots were collected from a screen house at Crops Research Institute using the Hussey and Barker method [15]. The infested roots were washed under running tap water and cut into pieces with a sharp knife on a chopping board. The cut roots were then macerated with a kitchen blender. About 100 ml of de-ionized water was added to the macerated roots in a jar. The jar was covered tightly and shaken vigorously. The suspension was poured into a 105 µm sieve mounted over a 45 µm sieve. Egg masses flowed through the 105 µm sieve and collected by a 45 µm sieve below. The egg masses were then scooped into the extraction tray with a plastic spoon. The process was repeated several times to obtain sufficient egg masses. The eggs were later incubated using the extraction tray method [16]. The process involved spreading the egg masses on a 2-ply tissue paper nested in a small plastic basket. The plastic basket was placed in a shallow plastic tray on a level bench. About 100 ml of de-ionized water was gently added by the side of each tray, and the set-up was left for 48 h. The water level was topped up in case it was reduced through evaporation. After 48 h, the second stage nematode suspension in the plastic tray/was shaken gently and poured into a beaker for counting. The collected juveniles were used for inoculating two-week-old tomato seedlings established in pots (Figure 1).

Figure 1 Tomato seedlings in the open field awaiting inoculation.

2.3 Inoculation of Inoculum

The inoculum consisted of a suspension of second-stage juveniles, and inoculation was done two weeks after transplanting tomato seedings to the open field. Each of the six randomized treatments was inoculated with the suspension of one thousand second-stage juveniles and was replicated

three times. The inoculum suspension was dispensed with a pipette in a circular form in a shallow hole 0.5 cm away from the base of each tomato seedling. All the population was watered immediately after inoculation to preserve the inoculum and subsequently as and when watering was needed to prevent damping off.

2.4 Data Analysis

The collected data were analyzed with Analysis of Variance (ANOVA) using the GenStat 12th edition statistical package. The Least Significant Difference (LSD) test was used to separate the treatment means at a 5% level.

Generation mean analysis was used to estimate the inheritance of root-knot nematode resistance in tomatoes, which employed an additive-dominance model parameter following a Joint Scaling test [17]. This involved subjecting generation means to a weighted least squares regression. However, the additive dominance model was insufficient to explain the inheritance of the traits, so the goodness of fit of the six-parameter model was tested [18].

Broad sense heritability for the trait of interest was estimated using Allard's methodology [19]. Narrow sense heritability was computed according to Halloran *et al.*'s method [20]. The percentage increase or decrease of F_1 over the mid-parent and better parent was used to calculate the possible heterotic effect, following Morgan *et al.*'s methodology [21]. Inbreeding depression was estimated by calculating the percentage increase or decrease of the F_2 population over F_1 hybrids [22].

3. Results

For all parameters measured, significant differences were observed between genotypes (Table 1).

Table 1 Analysis of Variance in Fruit Yield and Root-Knot Nematode Resistance in Tomato Populations.

Source	df	Average fruit Weight	Fruit yield per plant	Root gall Index	Reproduction factor
Rep	2	420.48	0.10	5.40*	0.82*
Genotype	5	931.29**	0.47**	229.45**	35.45**
Error	322	1.32	0.05	0.43	0.15
CV	2	10.20	8.90	7.00	10.00

* = Significant at p = 5%; ** = Significant at p = 1% probability levels.

Figure 2, Figure 3, Figure 4, and Figure 5 analysis of six tomato genotypes revealed significant variations in four key traits. Notably, the $BC_{1.1}$ generation exhibited a substantially higher average fruit weight (24.00 g) than the P_2 generation (11.13 g). Furthermore, the yield per plant differed significantly between P_1 (0.36 Kg) and P_2 (0.14 Kg) genotypes. As illustrated in Figure 6 on root gall formation across plant generations, the root gall index exhibited a broad range of values, varying from 0.97 in P_2 to 8.10 in P_1. Additionally, the reproduction factor was highest in P_1 (2.93) and lowest in P_2 (0.29), highlighting the distinct responses of these genotypes to nematode infection.

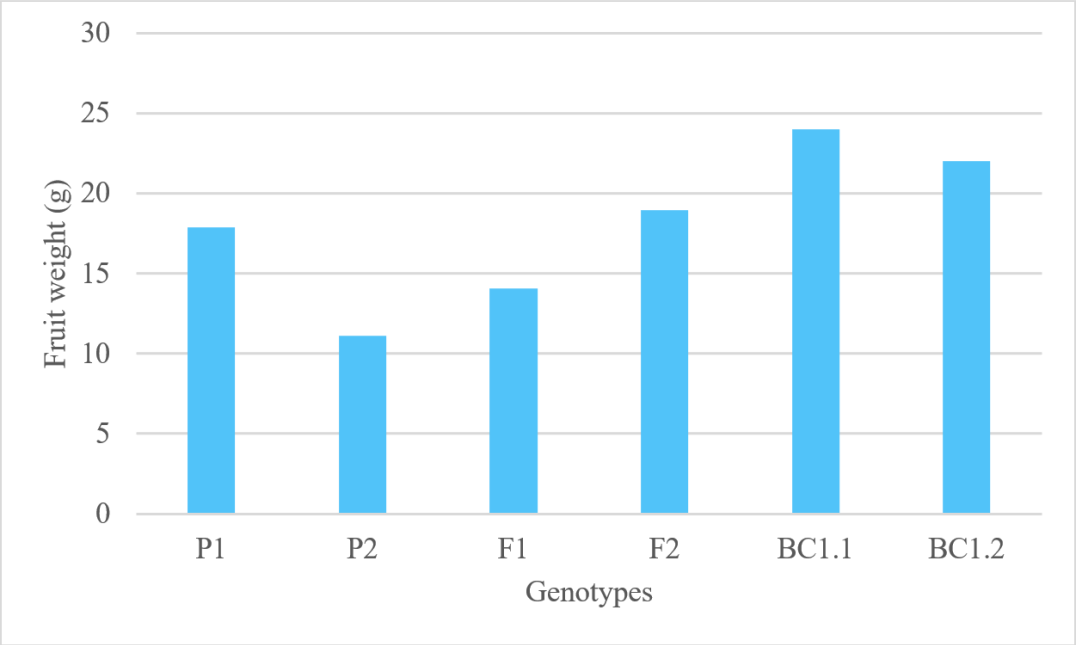

Figure 2 Average fruit weight (g) for six tomato genotypes.

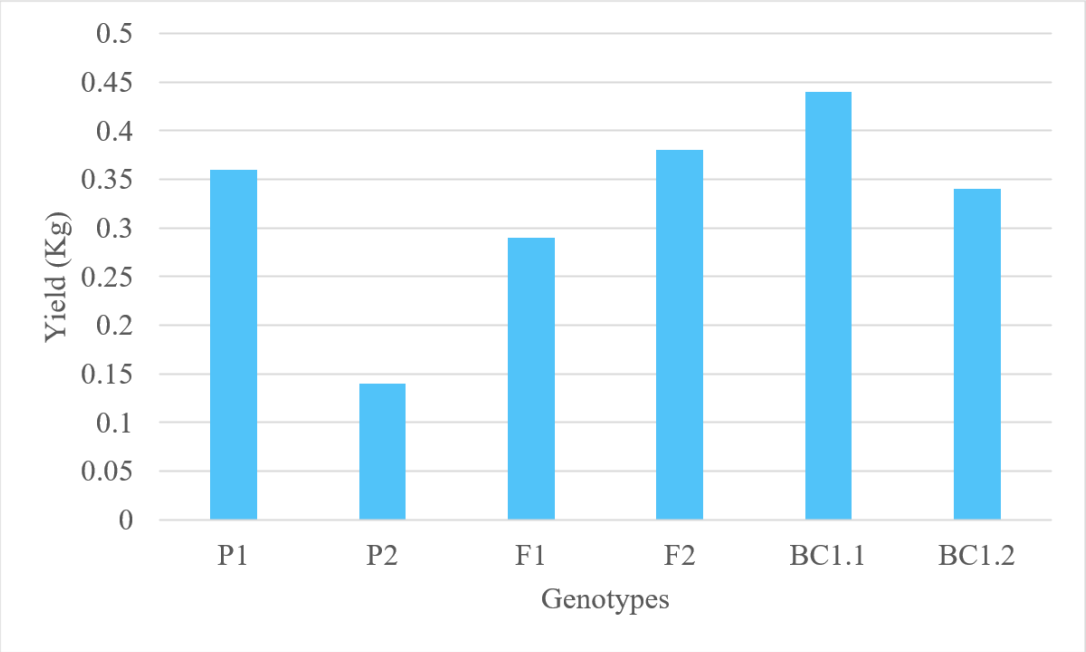

Figure 3 Yield per plant (Kg) performance for six tomato genotypes.

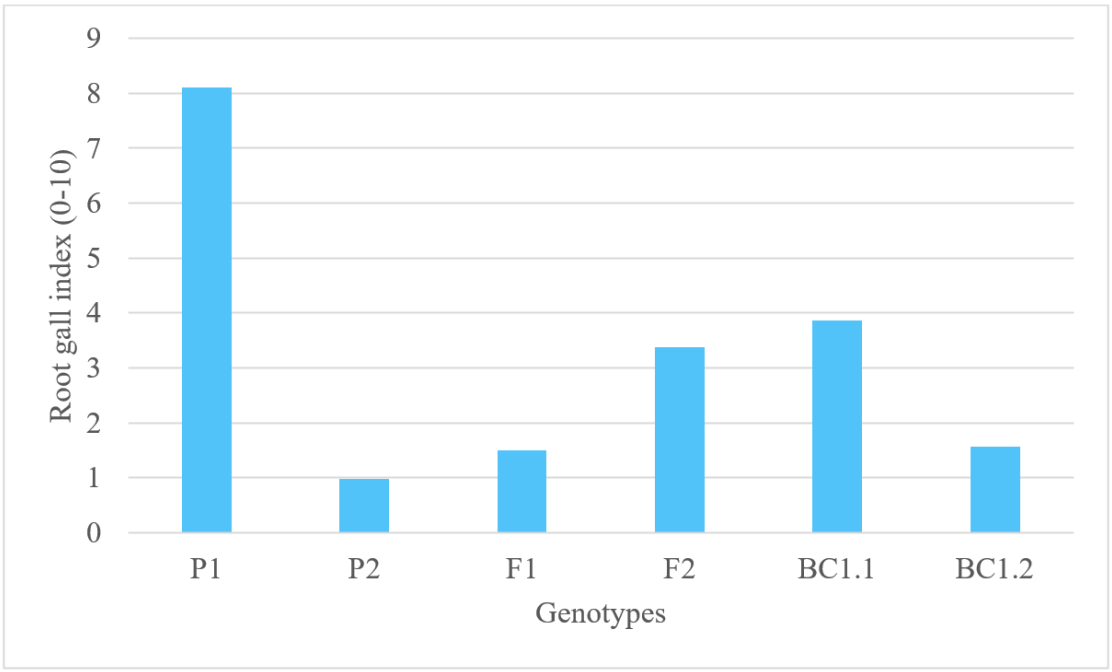

Figure 4 Root galling severity (0-10 scale) across six tomato genotypes.

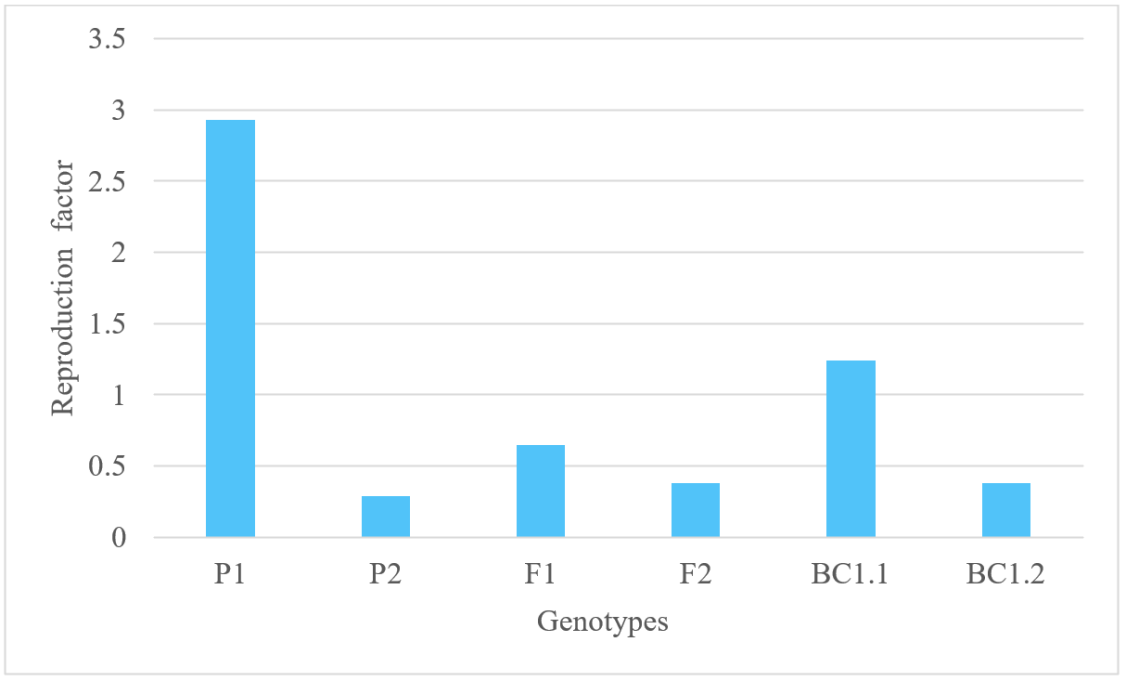

Figure 5 Reproductive performance of root-knot nematodes on six tomato genotypes.

Figure 6 Root gall formation of some of the plant's generations.

Data in Table 2 indicates that at least one of the three scaling tests (A, B and C) was significant for all characters studied. The study reviewed that, scale A was highly significant for average fruit weight (16.07), yield per plant (0.22) and reproduction factor (1.10) while scale B was highly significant for average fruit weight (18.80). Factor C was highly significant for yield per plant (0.44), average fruit weight (18.63) and reproduction factor (1.77). Root gall index (1.87) and yield per plant (0.09) were significant for scaling tests A and B respectively. The χ^2 values for all traits were significant, indicating that the joint scaling tests alone were insufficient to explain the mode of inheritance for all the measured traits.

Table 2 Scaling Tests A, B and C for Fruit Yield and Root-Knot-Nematode Resistance in Tomato.

Parameter	Average fruit weight (g)	Yield (kg/plant)	Root gall Index	Reproduction factor
A	16.07 ± 2.54***	0.22 ± 0.05***	-1.87 ± 0.74*	-1.10 ± 0.27***
B	18.80 ± 1.54***	0.09 ± 0.03**	0.67± 0.36 ns	0.04 ± 0.15 ns
C	18.63 ± 2.82***	0.44 ± 0.06***	1.47 ± 1.01 ns	-1.77 ± 0.39***
χ^2	63.23***	36.25***	4.33*	39.30***

* = Significant at p = 5%; ** = Significant at p = 1%; *** = Significant at p = 0.1% probability levels; ns = not significant.

Using the six-parameter model, all traits were positive and significant for additive gene effects except average fruit weight (Table 3). Dominance gene effects were positive and highly significant for average fruit weight and reproduction factor, but harmful and significant for root gall index. However, the additive × additive gene effect was positive and highly significant for average fruit weight, negative and significant for yield per plant, but positive and highly significant for the reproduction factor. Additive × dominance gene interaction was negative and significant for the

reproduction factor. Average fruit weight was negative but highly significant for dominance × dominance gene interaction. Apart from yield per plant detected as complementary epistasis, all the other traits showed duplicate dominant or recessive epistasis.

Table 3 Using Six-Parameter Model to Estimate Gene Effects of Five Quantitative Characters of Tomato.

Parameter	Average fruit weight (g)	Yield (Kg/plant)	Root gall index	Reproduction factor
m	15.89 ± 2.14**	0.48 ± 0.05**	4.53 ± 0.15***	0.62 ± 0.02***
[d]	3.32 ± 0.26	0.11 ± 0.01*	3.56 ± 0.21*	1.43 ± 0.02**
[h]	63.28 ± 1.64***	-0.20 ± 0.05 ns	-3.03 ± 0.22**	0.98 ± 0.23*
[i]	14.48 ± 0.24***	-0.23 ± 0.05*	-0.26 ± 0.94 ns	0.87 ± 0.03***
[j]	-12.66 ± 21.17 ns	0.09 ± 0.08 ns	-1.62 ± 1.40 ns	-1.05 ± 0.10**
[l]	-49.21 ± 1.70***	-0.07 ± 0.23 ns	0.66 ± 4.88 ns	-1.10 ± 2.31 ns
Epistasis	Duplicate dominant	Complementary	Duplicate dominant	Duplicate recessive

* = Significant at p = 5%; ** = Significant at p = 1%; *** = Significant at p = 0.1% probability levels; ns = not significant; m = mean; d = additive; h = dominance; i = additive × additive; j = additive × dominance; l = dominance × dominance.

High broad sense heritability estimates of 78.68%, 90.94%, 92.82% and 84.71% were recorded for yield per plant, average fruit weight, root gall index and reproduction factor respectively (Table 4). Narrow sense heritability was high for root gall index (71.73%) and reproduction factor (76.59%), moderate for yield per plant (32.32%) and low for average fruit weight. Heterobeltiosis ranged from -19.44% to 124.14% while relative heterosis was from -2.97% to 16.00%. All estimated mid-parent heterosis were negative (2.97%, 56.52% and 66.92%) for average fruit weight, reproduction factor and root gall index respectively except for yield per plant (16.00%). For the better parent heterosis, two of the estimates (yield per plant, 19.44% and average fruit weight, 21.27%) were negative while root gall index (54.64%) and reproduction factor (124.14%) were positive. Inbreeding depression estimates ranged from -31.04% for yield per plant to 41.54% for reproduction factor. All the traits studied for inbreeding depression were negative except the reproduction factor.

Table 4 Estimating Heritability, Heterosis, and Inbreeding Depression for Fruit Yield and Root-Knot-Nematode Resistance in Six Tomato Populations.

Trait	h^2_b (%)	h^2_n (%)	MPH (%)	BPH (%)	ID (%)
Average fruit weight (g)	78.69	0	-2.97	-21.27	-34.61
Yield (Kg/plant)	90.94	32.32	16.00	-19.44	-31.04
Root gall index	92.82	71.73	-66.92	54.64	-125.33
Reproduction factor	84.71	76.59	-56.52	124.14	41.54

h^2_b = Broad sense heritability; h^2_n = Narrow sense heritability; MPH = Mid-parent heterosis; BPH = Better parent heterosis; ID = Inbreeding depression.

4. Discussion

The analysis of variance revealed significant differences among the various generations, indicating a substantial amount of genetic variability for all the traits studied. Genetic variability in

yield and quality of fruit for different populations of tomatoes has been reported by other authors [23, 24]. The presence of significant differences that existed between the traits studied required using generation means to determine the genetic action for their inheritance.

The results revealed that the means of F_1 values fall within the parental limits in the yield per plant and average fruit weight, representing incomplete dominance. These findings supported the observation made by Chauhan *et al.* [25]. The F_2 means for average fruit weight and yield per plant, respectively, exceeded their F_1 hybrid means, which may be due to the high number of fruits in the F_2 plants and transgressive segregation. However, the F_2 mean performance showed overdominance for average fruit weight and yield per plant since they showed higher readings than the better parent. Over-dominance effects regulate the inheritance of the number of branches per plant, yield per plant, and average fruit weight [25-27].

Generally, in most traits the means of $BC_{1.1}$ and $BC_{1.2}$ were higher than those of the F_2 population [1, 28]. Both $BC_{1.1}$ and $BC_{1.2}$ for average fruit weight and yield per plant respectively performed better than their better parents which may be due to over dominance gene effect.

Root-knot nematode parasitism triggered varying treatment responses, leading to differing levels of root gall formation. Susceptible genotypes developed excessive root galls, whereas resistant genotypes showed insignificant or no galls [29]. The gall score rating by Bridge and Page [1] revealed that the mean of the F_1 population was closely aligned with that of P_2, indicating the dominance of the resistant gene over the susceptible P_1. This finding is consistent with reports by Akhtar and Hazra [30] and Khalil and El-Shennawy [31], who also observed similar responses in their studies.

Reproduction factor analysis revealed that P_2 was resistant and P_1 was susceptible to root-knot nematode. Furthermore, the study showed that individual plants in the following generations F_1, F_2, $BC_{1.1}$, and $BC_{1.2}$ were resistant to root-knot nematode. Kamran *et al.* [32] observed that reproduction and root galls were uninhibited on tolerant and susceptible cultivars but inhibited on resistant cultivars. Nematode resistance is estimated based on the reproduction factor and the number of galls formed on the root system. As a result, plants with reduced reproduction rates and gall numbers are selected as resistant genotypes for breeding nematode resistance [33].

In the inheritance of different traits, the study of the gene action type is revealed using scaling tests A, B, and C to determine the adequacy of the additive-dominance model. However, results from the scaling tests A, B, and C showed deviation from zero, indicating that the simple additive-dominance model alone was inadequate in explaining the expression of root-knot nematode disease resistance in tomatoes, suggesting the existence of epistasis.

Thus, the gene effects were analyzed using the six-parameter model (joint scaling tests). Most traits showed significance for additive, dominant, and epistatic gene effects, representing that both additive and non-additive effects were important for the genetic analysis of studied characteristics [34].

Positive or negative expression of additive × additive interaction showed association and dispersion of alleles in parents, respectively. Therefore, the negative significant value of additive × additive interaction for yield per plant in this study showed alleles dispersion in the parents, while positive significant values for average fruit weight and reproduction factor also imply the association of alleles in the parents. A considerable negative interaction of additive × dominance for reproduction factor suggests an interaction between increasing and decreasing alleles, thus providing evidence of dispersion of genes in the parents. The negative significance of dominance × dominance interaction for average fruit weight shows unidirectional dominance. Therefore,

heterosis breeding can improve average fruit weight trait since it expresses dominance × dominance of gene interaction. Alsadon *et al.* [35] illustrated that non-additive gene effects contributed to the basic genetic mechanism of inheriting tomato quantitative characters.

Most traits examined revealed opposite signs of dominance and dominance × dominance effects, thus indicating the duplicate dominant or recessive type of epistasis [24, 36]. Duplicate dominant epistasis was recorded for average fruit weight, root gall index, and reproduction factor, while complimentary epistasis was recorded for yield per plant. Duplicate dominant epistasis observed in this trait suggests the possibility of obtaining transgressive segregants in later generations. As a result, scientists can develop more effective breeding strategies to improve trait performance and sustainability. However, complementary gene interaction can be exploited effectively by selection to enhance the characteristics that reveal the interactions between genes, helping breeders understand how genes work together to shape these traits to improve agricultural productivity. Heterosis breeding may be helpful to for traits that exhibited duplicate dominant epistasis along with pronounced dominance gene effects. In contrast, the traits that showed pronounced additive gene effects and complimentary epistasis suggested the possibility of fixing the particular traits through selection methods [37].

Heritability estimates are a better indicator of the genetic proportion of variation in any population used for predicting the progress from selection [38]. Besides, heritability values are regarded as low (0-30%), moderate (31-60%), and high (above 60%) [23]. Moreover, to reveal all the possible genetic contributions in a population's phenotypic variance, broad-sense heritability is ideal [39]. Heritability in broad-sense with high values showed for the traits studied signifies the minimum effect of the environment influencing the expression of the characteristics making the selection based on phenotypic performance reliable. As revealed by Chaukhe *et al.* [40], a particular plant trait with high heritability can effectively be selected phenotypically. In addition, the high broad-sense heritability estimates reported in this present study for yield per plant and average fruit weight did not translate into high narrow-sense heritability. This suggests the predominance of non-additive gene effects for those traits, possibly due to significant epistatic effects. Paudel *et al.* [41] and Panthee *et al*. [42] reported that low narrow sense heritability was caused by low additive and high dominance gene effects. Heritability in the narrow sense was high for root gall index and reproduction factor which therefore suggests that selection can be effective in early generations. According to Bernardo [43] the best estimate of breeding value indicator is high narrow sense heritability since it represents the portion of phenotypic variation due to additive effects.

Inbreeding depression was positive for the reproduction factor, which was anticipated, as the manifestation of heterosis in the F_1 generation was followed by a decline in performance in F_2 due to an increase in homozygosity. Average fruit weight, yield per plant and root gall index with negative inbreeding depression may be attributed to transgressive segregation in their F_2 generations [44]. The high value of inbreeding depression in average fruit weight, yield per plant, root gall index and reproduction factor were expected since these traits showed high heterosis values. The high level of heterosis and inbreeding depression for these traits was evidence of the importance of dominance gene effects since dominance significantly contributes to heterosis. Therefore, hybrid breeding can be used efficiently to improve these traits. Traits with positive heterosis exhibited the prominence of hybrid vigor. On the other hand, negative heterosis indicates dominance was in the same line of lower values as the parents. Positive heterosis over mid-parent in tomato traits has been reported by many investigators [14, 24, 45-47]. Heterosis over better

parents agreed with the discoveries of Alsadon *et al.* [35], Avdikos *et al.* [48], and Shalaby [49]. High heterosis is well-known to result from the effects of non-additive genes [50].

5. Conclusion

Significantly, there were differences in the traits under study regarding their additive, dominant, and epistatic gene effects. Also, duplicate epistasis was observed for average fruit weight, reproduction factor, and root gall index, while complementary epistasis was recorded for fruit yield. Fixable and non-fixable gene effects showed by these traits can be improved through pedigree selection methods and heterosis breeding.

Author Contributions

Matilda Frimpong contributed to the original draft of the manuscript. Michael Kwabena Osei and Maxwell Darko Asante were responsible for conceptualization, as well as writing, reviewing, and editing. Kingsley Osei and Ruth Naa Ashiokai Prempeh participated in reviewing and editing the manuscript. Joseph Gyau, Isaac Newton Boakye-Mensah and Bismark Abugri critically revised the manuscript.

Competing Interests

The authors have declared that no competing interests exist.

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