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Estimation of yield and yield-related genetic parameters in citron watermelon (*Citrullus lanatus* var. *citroides*)

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ABSTRACT

This study aims to improve citron watermelon, an underutilized African crop. Despite its climate resilience and economic importance, the estimation of yield-related genetic parameters remain unexplored. Ten high-yielding accessions were crossed in a bi-parental mating design to develop five hybrids that were evaluated together with their parents in a randomized complete block design, replicated thrice. Traits such as fruit yield, length and weight displayed the greatest potential to respond to selection owing to high heritability (61.64, 73.80% and 59.00%, respectively) and genetic advance (4585.09, 77.32 and 73.27%, respectively). Fruit weight, rind thickness and yield showed significant positive heterosis ($p < .05$) in hybrids 7×8 and 1×2, indicating their potential for heterotic improvement. Hybrids 1×2 and 3×4 were the best cross combinations for elevated Vitamin C levels and rind thickness for both forms of heterosis. Gene number estimates revealed a range from minor to oligogenic control, with fruit weight controlled by 5.81 genes using Wright's estimator. Total soluble solutes had the lowest number of genes in all hybrid combinations coupled with a low genetic advance of 0.44, displaying a low response to selection using this population. This study highlights several traits that have the potential to improve citron watermelon productivity.

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Introduction

Watermelon (*Citrullus lanatus*) is an important cucurbitaceous crop that is globally known for its refreshed summer fruit. China is the epicenter of global production, contributing approximately 60% (around 60 million metric tons), followed by India (3.4 million), Turkey (2.8 million) and Iran (2.8 million) (Anonymous, 2025). Watermelon has several health benefits owing to its high minerals, vitamins and phytochemicals, including antioxidant and cardiovascular support (Bianchi et al., 2018; Jumde et al., 2015).

Regardless of its global significance and advancements in yield and quality, continuous improvement through conventional breeding has been limited owing to the narrowing genetic variation among cultivated varieties to domestication and extensive selection (Kwon et al., 2010; Levi et al., 2017; Singh et al., 2017). These constraints pose challenges to improvement of important agronomic traits such as fruit yield, stress tolerance and disease resistance. To address these challenges, breeders are leveraging the genetic diversity in crop wild relatives such as citron watermelon to improve overall crop performance in both quantitative and qualitative traits. The growing attention in scientific research on citron watermelon is largely driven by the crop's resilience to abiotic and biotic stressors, genetic distinctiveness and underutilized status in breeding programs. Citron watermelon has primarily been cultivated for its seeds and biomass, but it is an underutilized reservoir for cultivated watermelon improvement, particularly for stress tolerance, number of fruits per plant and fruit weight (Katuuramu et al., 2023; Levi et al., 2013).

Studies involving citron watermelon have largely centered on assessing its climatic adaptation, genetic variation and its agronomic and horticultural traits (Mandizvo et al., 2022; Ngwepe et al., 2019). For

example, Levi et al. (2013) evaluated a number of citron genotypes and claimed that there exists a wide genetic diversity and significant combining ability for the fruit yield-related traits. Correspondingly, Katuramu et al. (2023) and Singh et al. (2017) noted significant heterosis and genetic variability in the early-generation hybrid populations' derived from citron watermelon inbred lines. These studies highlight the importance of frequent evaluation of citron watermelon in breeding and cultivar development programs; however, attempts for utilization and estimation of yield-related genetic parameters remain limited.

A detailed understanding of the genetic architecture governing key quantitative traits in citron watermelon and its hybrids remains elusive. More specifically, heritability estimates, genetic advance and gene number for these traits require in-depth exploration to achieve significant gains in citron watermelon breeding. Understanding the extent of the heritable nature of these traits is also critical for genetic improvement. High heritability coupled with high genetic advancement increases the accuracy of predicting the genetic gain of a trait under selection (Poudel et al., 2021). Additionally, the number of genes contributing to variation in a quantitative trait has significant effect on the improvement of watermelons. Estimating of gene numbers controlling a particular trait is critical in modern breeding programs since it informs whether traits are governed by major or minor genes and thus forms the basis of selection (Roka et al., 2024). The easiest and cheapest way to estimate the gene number is to calculate the means and variances of the parents and their hybrids (El-Hashash, 2017). Furthermore, heterosis, or hybrid vigor, which refers to the hybrid developed by crossing two or more distinct dissimilar parents, can be an effective genetic improvement tool in watermelon breeding (Wu et al., 2021).

Therefore, the aim of present study is to estimate the heritability, genetic advance, gene number and heterosis of key yield-related quantitative traits in selected citron watermelon accessions. The goal of this study is to increase the utilization of citron watermelon in breeding programs.

Materials and methods

Site description

The study was conducted at the Lupane State University farm in the Matebeleland North Province of Zimbabwe (18°55.889' S; 27°48.418' E). The area is characterized by a subtropical climate with an annual rainfall ranging from 350 to 500mm and a temperature range of 28–35°C and is dominated by sandy clay loam soils (Mukungurutse et al., 2018).

Field layout and management

Ten high-yielding citron watermelon accessions, sourced from the National Gene Bank, were used in the experiment. The experiment was conducted in two seasons: 2023 and 2024. Bi-parental crosses involving the 10 citron watermelon accessions were performed in the first season (15 September 2023 to mid-January 2024). In the second season (February 1 to mid-May 2024), parents and their hybrids were evaluated. A Randomized Complete Block Design with 15 treatments (10 parents and their five hybrids) and three blocks (slope as blocking factor) was used for the experiment (Table 1). The land was cultivated to a depth of 30cm. Disc harrows and rollers were used to break the clods and produce a fine tilth. Manual planting was performed by placing three seeds per station with an inter-row × in-row spacing of 2 m × 0.9m at a sowing depth of 2cm. No fertilizer application was done during the experiment. Weeds were controlled manually during the experiment, and insect pests, such as aphids and fruit flies, were controlled using Malathion 25WP and Diomethoate 40 EC after scouting. Supplementary irrigation was performed using drip irrigation whenever necessary.

Data collection

Data were collected at the physiological maturity stage. Parameters, including the number of fruits per plant, fruit rind thickness (mm), fruit length (cm), fruit width (cm) and individual fruit weight (kg) were collected from five plants per plot and averaged. Fruit yield (ton/ha) was computed by multiplying the

Table 1. Genetic material used for the estimation of yield genetic parameters, heterosis and yield-related traits in selected citron watermelon (February to May 2024).

Genotype	Pedigree	Generation
1	185	Parent
2	2733	Parent
3	2766	Parent
4	177	Parent
5	179	Parent
6	2767	Parent
7	2660	Parent
8	500	Parent
9	378	Parent
10	60	Parent
11	$P_1 \times P_2$	Hybrid
12	$P_3 \times P_4$	Hybrid
13	$P_5 \times P_6$	Hybrid
14	$P_7 \times P_8$	Hybrid
15	$P_9 \times P_{10}$	Hybrid

P, parent.

weight of each fruit in kilograms by the number of fruits per plant by the plant population of 5555 plants/ha. Using a blender, a kilogram of sliced flesh was turned into juice. The total soluble solids (%) were ascertained using a digital refractometer (ATC-1, Japan) by placing drops of the juice on the prism. The pH of the clear juice was measured using a calibrated handheld pH meter (H198103, India) by immersing its electrode into the liquid. Finally, vitamin C was determined through a redox titration method suggested by Kareem et al. (2010).

Data analyses

The R programming language version 4.4.1 was used for the analysis of variance (ANOVA), while significantly different means were compared using Fisher's Protected Least Significance Difference Test at a 5% level of significance. Before subjecting the data to ANOVA, the assumptions of ANOVA were tested. In cases where the assumptions of ANOVA were not satisfied, the data were transformed, that is, log transformation for count data and arcsine transformation for percentages. Seasonal data were pooled to obtain a more precise estimate after independent analysis to ascertain equal variance of the data means for the evaluation of parents and hybrids.

Heritability

Heritability in the broad sense (H^2), genotypic variance (VG) and Environmental variance (VE) were determined using the method suggested by

$$\text{Genotypic variance (VG)} = \frac{\text{GMS} - \text{EMS}}{R}$$

where;

GMS=Genotype mean squares;

EMS=Error mean square; R = Number of replications.

Environmental variance (VE) = Error mean square (EMS)

Phenotypic variance (VP) = VG+VE

where;

VG=Genotypic variance;

VE=Environmental variance;

$$\text{Broad sense heritability (H}^2\text{)} = \frac{\text{VG}}{\text{VP}} \times 100$$

where;

VG=Genotypic variance;

VP=Phenotypic variance.

Estimation of genetic advance

Genetic advance (GA) was calculated using the method suggested by Ishola Esa et al. (2020).

Table 2. Gene number estimation.

Method	Numerator	Denominator
Weng	$3(P_1 - P_2)^2$	$16Vg$
Wright	$(P_1 - P_2)^2$	$8\sigma_g^2$

P_1 , mean of parent 1; P_2 , mean of parent 2; Vg and σ_g^2 genotypic variance.

$$\text{Genetic advance (GA)} = K(\sigma p)h^2$$

where;

K = selection differential ($K=2.06$ at 5% selection intensity);

σp = phenotypic standard deviation of characteristics; h^2 = broad sense heritability.

Genetic advance as a % of the mean = $\frac{GA}{\bar{x}} \times 100$

where;

GA=Genetic advance;

\bar{x} = Grand mean.

Estimation of gene numbers

Gene numbers were estimated using two estimators: one suggested by Wright (1968) and the other by Weng (1984) (Table 2).

Estimation of heterosis

Mid-parent and better-parent heteroses were determined using the method suggested by Ishola Esa et al. (2020).

$$\text{Mid-parent heterosis} = \frac{F1 - MP}{MP} \times 100$$

$$\text{Heterobeltiosis (better-parent heterosis)} = \frac{F1 - BP}{BP} \times 100$$

where;

F1 = mean performance of the F1;

MP=mean mid-parental value = $(P_1 + P_2)/2$;

P_1 = mean performance of parent 1;

P_2 = mean performance of parent 2;

BP=mean performance of the better parent.

Ethical considerations

This study followed all ethical standards for research, without direct contact with human beings or animals.

Results

Analysis of variance

The mean squares of the genotypes were highly significant for all traits studied. The residual values were lower than the genotypic mean sum of squares, indicating that environmental influence was minimal (Table 3).

Significant differences ($p < .05$) were observed between the genotypes with respect to the number of fruits per plant, fruit length, fruit width, rind thickness, pH and fruit yield (Table 4).

Heritability and genetic advance of quantitative traits of citron watermelon

The analysis revealed substantial genetic diversity in citron watermelon accessions, with traits demonstrating high heritability, genetic advance and genetic variance (Table 5). Traits such as pH, Vitamin C

Table 3. Analysis of variance for genotypes (parents and hybrids) on selected traits of the citron watermelon (February to May 2024).

Source of variation	DF	NFP	IFW	FL	MS FW	RT	VC	TSS	pH	FY
Rep	2	1.27	1.33	2.85	6.34	2.14	0.19	0.52	0.01	1619
Genotype	14	2.28**	5.77**	50.73**	27.56**	17.84**	0.72*	0.41*	0.12**	6816**
Residual	28	0.31	1.09	5.37	6.14	3.07	0.38	0.21	0.03	1171

DF, degrees of freedom; NFP, number of fruits per plant; FL, fruit length (cm); FW, fruit width (cm); IFW, individual fruit weight; RT, rind thickness (mm); VC, vitamin C content; TSS, total soluble solids (%); FY, fruit yield (t/ha).

*Significant at .05 probability; **Significant at .01 probability.

Table 4. Mean performance of genotypes (parents and hybrids) on selected traits of the citron watermelon (February to May 2024).

Trt	GN	NFP	FL (cm)	FW (cm)	RT (mm)	IFW (kg)	TSS	FY (t/ha)	pH	VC
1	Parent	4.67a	45.6b	41.6a	30.53efg	6.876a	2.9	178.174a	6.10a	7.7
2	Parent	2.67ef	32.5d	31.1ef	31.57defgh	3.503efg	3.3	52.067e	5.88abc	5.9
3	Parent	4.00ab	39.3cd	32.3ef	35.63ab	4.989bcde	3.3	111.595bcd	6.02ab	6.2
4	Parent	3.33cd	42.4bcd	40.6ab	30.97efgh	4.001def	3.1	74.576cde	5.83abcd	5.9
5	Parent	4.00ab	40.6cd	36.7bcd	35.47ab	6.088abc	2.8	139.185ab	5.59bcd	6.5
6	Parent	2.67ef	38.8cd	35.9cde	34.37abcd	4.247de	3.5	63.281de	5.88abc	5.6
7	Parent	2.67ef	41.9bcd	35.6cde	35.50ab	4.076de	2.1	63.191de	5.83abcd	6.1
8	Parent	2.33g	36.3cd	34.0def	29.57fg	2.324fg	3.3	30.268e	5.85abcd	6.3
9	Parent	4.67a	50.8a	40.1ab	33.83bcde	6.329ab	3.2	165.282ab	5.56cd	5.9
10	Parent	2.00g	40.9cd	39.4abc	34.27abcd	1.848g	3.3	20.328e	6.00bc	6.6
11	P ₁ × P ₂	4.00ab	40.8cd	38.8ab	35.03abc	5.528abcd	3.4	121.616abc	5.95ab	6.3
12	P ₃ × P ₄	2.33g	39.3cd	38.0abcd	28.93i	3.982def	2.7	51.429e	5.71bcd	6.7
13	P ₅ × P ₆	2.67ef	41.3cd	38.9abc	32.80bcdef	3.882def	3.0	57.904de	5.82abcd	6.4
14	P ₇ × P ₈	2.67ef	39.1cd	38.2abc	32.27cdefg	4.388cde	3.2	64.827cde	5.31d	6.2
15	P ₉ × P ₁₀	3.33cd	43.9bc	38.1abcd	36.87a	3.883def	3.4	74.371cde	5.84abcd	5.9
	GM	3.20	40.9	37.3	33.17	4.396	3.1	84.540	5.816	6.3
	CV%	17.5	5.7	6.6	5.3	23.7	14.6	40.5	9.8	3.1

Trt, treatment; GN, genotype; NFP, number of fruits per plant; FL, fruit length (cm); FW, fruit width (cm); IFW, individual fruit weight; RT, rind thickness (mm); VC, vitamin C content; TSS, total soluble solids (%); FY, fruit yield (t/ha); GM, grand mean; CV%, co-efficient of variation. Values with different letters in a column show significant differences ($p < .05$) as determined by Fisher's protected least significant difference test.

Table 5. Estimation of heritability and genetic advance of quantitative traits of citron watermelon accessions (February to May 2024).

Trait	VE	VG	VP	H ² (%)	GA	GAM
Number of fruits per plant	0.31	0.65	0.97	67.54	1.35	42.17
Fruit length (cm)	5.37	15.12	20.49	73.80	31.15	77.32
Fruit width (cm)	6.14	7.14	13.28	53.79	14.72	39.45
Fruit yield (ton/ha)	1171.00	1881.67	3052.67	61.64	3876.23	4585.09
Rind thickness (mm)	3.07	4.92	7.99	61.60	10.14	30.57
Individual fruit weight (kg)	1.09	1.56	2.65	59.00	3.22	73.27
pH	0.02	0.05	0.07	86.08	0.12	2.13
Total soluble solids (%)	0.03	0.23	0.26	82.84	0.44	14.31
Vitamin C content (mg/100g)	0.04	0.23	0.26	86.08	0.46	7.32

VE, environmental variance; VG, genotypic variance; VP, phenotypic variance; H², broad sense heritability; GA, genetic advance; GAM, genetic advance (as a % of mean).

and total soluble solids (86.08%) showed high broad-sense heritability (Table 5). Similarly, moderate to high heritability was reported for fruit length (73.80%), fruit yield, (61.64%), rind thickness, (61.60%) and individual fruit weight (59.00%). The fruit yield trait had the highest genetic advancement as a percentage of the mean (4585.09%), displaying the maximum potential for improvement through selection. Fruit length and individual fruit weight also exhibited high genetic advancement as a percentage of the mean (77.32% and 73.27%, respectively), indicating that these traits would respond positively to breeding. Lower ranges of genetic advance as a percentage of the mean number of fruits per plant (42.17%) and fruit width (39.45%) were noted, whereas vitamin C content (7.32%) and total soluble solids (14.31%) had a relatively low genetic advance as a percentage of the mean, which indicates that slower improvement is expected from direct selection. In almost all traits, environmental variance (VE) was less than

genotypic variance (VG), indicating that these traits are largely controlled by gene action (Table 5). For example, the number of fruits per plant (VG: 0.65; V_E : 0.31) and fruit length (VG: 15.12; V_E : 5.37) were traits with higher VG, indicating that these traits are highly influenced by the genotype.

Gene number estimation of quantitative traits of citron watermelon accessions

The highest gene numbers using the Wright estimator were for the traits fruit width, individual fruit weight, fruit yield and number of fruits/plant which had 5.81, 4.83, 4.19, 4.10, 3.62 genes respectively, whereas using the Weng estimator, the highest is 3.62 and 2.90 for the trait fruit width (Table 6). The lowest number of genes was 0.01, which was recorded for total soluble solids, rind thickness and fruit length, indicating that these traits were largely controlled by the genotypes and that there was less of an environmental effect. Total soluble solids recorded less than one gene for all traits and all the crosses that were performed. $P_1 \times P_2$ had the highest gene number for all traits, whereas $P_7 \times P_8$ had the lowest for all observed traits.

Heterosis estimation of quantitative traits of citron watermelon

This study analyzed heterosis in citron watermelon for several quantitative traits, including the number of fruits per plant, fruit length, fruit width, rind thickness, individual fruit weight, total soluble solids, fruit yield, pH and vitamin C content (Table 7). Some hybrids, such as 3×4 , expressed considerable negative heterosis ($p < .05$) in the number of fruits per plant, which is indicative of unfavorable gene interactions. In contrast, the 1×2 hybrid produced the highest percentage of mid-parent heterosis (8.99). Fruit length hybrids, such as $P_1 \times P_2$ and $P_9 \times P_{10}$ exhibited significant heterotic values ($p < .05$), which suggests the preponderance of gene effects. However, fruit width indicated significant positive heterosis for hybrids 5×6 and 7×8 , specifically hybrid 7×8 , which had a maximum mid-parent heterosis of 9.77. Rind thickness indicated a significant positive ($p < .05$) mid-parent heterosis and better-parent heterosis in the case of the 1×2 and 9×10 hybrids, indicating that dominance gene action is at play. Individual fruit weight exhibited a significant degree of hybrid vigor in the case of hybrid 7×8 , suggesting that this hybrid can be harnessed to yield large fruits. The hybrids 5×6 and 9×10 , on the other hand, showed significantly negative ($p < .05$) better-parent heterosis, suggesting that genetic control over them is diverse. There was no significant heterosis ($p < .05$) in the total soluble solids in any of the hybrids. Fruit yield displayed a positive significant ($p < .05$) mid-parent heterosis in the 7×8 hybrid, reflecting its yield improvement potential.

Discussion

Heritability and genetic advance of quantitative traits of citron watermelon

The results of this study suggest the potential for citron watermelon genetic improvement using the available set of germplasms. Traits such as fruit yield, fruit length and individual fruit weight have

Table 6. Gene number estimation of quantitative traits of watermelon accessions (February to May 2024).

Trait	Estimator	Parents				
		$P_1 \times P_2$	$P_3 \times P_4$	$P_5 \times P_6$	$P_7 \times P_8$	$P_9 \times P_{10}$
FL	Wright	1.4 ± 0.30	0.07 ± 0.30	1.19 ± 0.30	0.13 ± 0.30	0.03 ± 0.30
	Weng	2.2 ± 0.42	0.12 ± 0.42	0.02 ± 0.42	0.07 ± 0.42	0.01 ± 0.42
FW	Wright	5.81 ± 0.98	0.03 ± 0.98	2.91 ± 0.98	1.16 ± 0.98	2.23 ± 0.98
	Weng	2.90 ± 0.79	3.62 ± 0.79	0.03 ± 0.79	0.13 ± 0.79	0.02 ± 0.79
IFW	Wright	2.74 ± 0.91	0.23 ± 0.91	0.81 ± 0.91	0.01 ± 0.91	4.83 ± 0.91
	Weng	1.34 ± 0.45	0.12 ± 0.45	0.41 ± 0.45	0.01 ± 0.45	2.41 ± 0.45
NFP	Wright	2.31 ± 0.75	0.26 ± 0.75	1.03 ± 0.75	0.06 ± 0.75	4.10 ± 0.75
	Weng	1.15 ± 0.38	0.12 ± 0.38	0.51 ± 0.38	0.03 ± 0.38	2.05 ± 0.38
RT	Wright	0.08 ± 0.54	1.66 ± 0.54	0.09 ± 0.54	2.67 ± 0.54	0.01 ± 0.54
	Weng	0.04 ± 0.27	0.83 ± 0.27	0.05 ± 0.27	1.34 ± 0.27	0.01 ± 0.27
FY	Wright	3.17 ± 0.86	0.27 ± 0.86	0.18 ± 0.86	0.22 ± 0.86	4.19 ± 0.86
	Weng	1.58 ± 0.40	0.14 ± 0.40	0.59 ± 0.40	0.11 ± 0.40	2.09 ± 0.40
TSS	Wright	0.15 ± 0.07	0.03 ± 0.07	0.47 ± 0.07	0.04 ± 0.07	0.01 ± 0.07
	Weng	0.23 ± 0.07	0.06 ± 0.07	0.71 ± 0.07	0.06 ± 0.07	0.01 ± 0.07

NFP, number of fruits/plant; FL, fruit-length (cm); FW, fruit width (cm); RT, rind thickness (mm); FY, fruit yield (t/ha); TSS, total soluble solids (%).

Table 7. Mid-parent and better parent heterosis for studied traits in citron watermelon (February to May 2024).

Hybrids	TRAITS																										
	NFP			FL			FW			RT			IWF			TSS			FY			pH			Vt. C		
	MP	BP	MP	BP	MP	BP	MP	BP	MP	BP	MP	BP	MP	BP	MP	BP	MP	BP	MP	BP	MP	BP	MP	BP			
P ₁ × P ₂	8.99	-14.34	4.48	-10.52*	6.74	-6.73	12.81*	10.95*	6.52	-19.6	9.67	3.03	5.64	-31.74	-0.66	-2.45	-7.35	-18.18*									
P ₃ × P ₄	-36.42*	-41.75*	-3.79	-7.31	4.25	-6.4	-13.12*	-18.8*	-11.41	-20.18	-15.62	-18.18	-44.75*	-53.91*	-3.62	-5.14*	10.74*	8.06*									
P ₅ × P ₆	-19.94	-33.25*	4.03	1.72	7.16*	5.99	-6.07	-7.52	-24.87	-36.23*	-4.76	-14.28	-42.8*	-58.39*	1.48	-1.02	5.78	-1.53									
P ₇ × P ₈	6.80	0.00	0.01	-6.68	9.77*	7.3*	-0.81	-9.09*	37.12*	7.65	18.51	-3.03	38.72*	2.58	-9.07*	-9.23*	0.01	-1.58									
P ₉ × P ₁₀	-0.14	-28.69*	-4.25	-13.58*	-4.15	-4.9	8.28*	7.58*	-5.02	-38.64*	4.61	3.03	-19.86	-55.00*	1.03	-2.66	-5.59	-10.6									

NFP, number of fruits/plants; FL, fruit-length (cm); FW, fruit width (cm); RT, rind thickness (mm); FY, fruit yield (t/ha); TSS, total soluble solids (%); MP, mid-parent heterosis; BP, better-parent heterosis.

*Significant at .05 probability.

shown the greatest additive genetic increase because they have both high heritability and genetic advancement. This implies that breeders can use simple selection techniques, such as pedigree breeding and mass selection, which are based on the phenotypic expression of these traits in individual plants (Tolera et al., 2023). Several studies have reported that some of these traits with high heritability are genetically controlled and are quite useful for selection. For instance, Kumari et al. (2020) and Singh et al. (2017) confirmed that fruit length, width and weight in crosses are highly heritable and have a high genetic advance in cucurbits. Correspondingly, Jamatia et al. (2019) and Nisha et al. (2018) observed high heritability and genetic advance as a percentage of the mean for traits such as average fruit weight and yield per plant, indicating that these traits can be improved through selection. On the other hand, traits such as Vitamin C content and pH, which have highly heritable values but low genetic gain, may be subject to masking nonadditive gene action or epistasis. These findings correspond to those of Wehner et al. (2017) who reported high heritability coupled with low genetic advancement in sweet watermelon. Such traits would require breeding strategies such as hybridization, recurrent selection or marker-assisted selection (MAS) to exploit their full genetic potential.

Gene number estimation of quantitative traits of citron watermelon accessions

There was appreciable variation across the investigated traits for the estimation of gene numbers in citron watermelon accessions. The estimates showed minor, major, and oligogenic inheritance of most traits, suggesting the need to use diverse breeding methods, depending on the trait of interest. Total soluble solutes had the lowest number of genes in all hybrid combinations coupled with a low genetic advance of 0.44 and a low response to selection using this population of citron melons. The difference in the estimation of the number of genes controlling fruit weight between the estimators illustrates the variation in the measurement method accuracy. Methodological concerns or biological nature differences in the examined traits may explain the average discrepancy between Wright's and Weng's estimates for the same traits. Noticeably, such discrepancies have been reported before, for instance, Gusmini and Wehner reported a high variability in gene number estimates for fruit weight in watermelon (0.4 to 26.5 genes).

Gene number estimation is a helpful tool but should be used with caution, especially if the different estimators yield conflicting results. Traits such as total soluble solids, rind thickness and fruit length were found to have less than one gene number, which indicates the likelihood of slow response to selection using the available germplasm; similar findings have been reported by El-Hashash (2017) and Hadi et al. (2019), who also demonstrated that some watermelon quantitative traits were controlled by a few genes or even less than one depending on the estimator employed. This calls for knowledge of both genetic and environmental factors whenever there is a need to make breeding decisions to avoid trait fixation. The results of this study indicate that the design of citron watermelon breeding programs is influenced by the presence of different trait genetic architectures. Selection programs would benefit from targeting monogenic traits to achieve rapid progress. In the polygenic approach to traits that have a high number of genes, environmental conditions must be optimized to promote the expression of the trait of interest.

These findings have implications for future citron watermelon breeding programs. However, when balanced with a few gene traits of slight or no environmental influence, the selection would be equally effective. Certain monogenic traits, such as fruit quality traits, can be easily enhanced using conventional methods compared to more complicated environmental ones. Where more environmentally influenced traits appear to be present, breeders may require more advanced approaches such as MAS and/or genomic selection to achieve genetic improvement against environmental influences. Breeders can use molecular techniques to track the development of these traits to enhance the selection of desirable plants while protecting the plants from the impact of environmental factors. El-Hashash (2017) suggested that some genes for which no marker has been identified might be necessary to understand other genes influencing these traits.

Heterosis estimation of quantitative traits of citron watermelon

Rind thickness, fruit width and fruit weight displayed strong positive significant heterosis in specific hybrids, which could be a result of dominance gene action. Such traits are very important in increasing

fruit quality and commercialization of hybrids, for instance, hybrid 7×8, which demonstrated hybrid vigor (mid-parent). These traits have also been noted to be improved through heterosis in cucurbits, such as cucumbers (Preethi et al., 2019), hence they are promising for further selective breeding programs. The lack of significant heterosis for fruit length and total content of soluble solids suggests that these traits are mainly controlled by additive genetic effects. To obtain genetic gains for these traits, recurrent selection methods should be used. The varied heterosis responses for rind thickness and vitamin C content suggest targeted selection of parents in breeding programs. This effect was similar to that reported by Omran et al. (2012) in sweet watermelons, where the heterotic response of the hybrids was also dependent on the genetic makeup of the parental lines.

Hybrid 7×8 has potential for use in breeding programs targeting high yield and quality because of its significant positive heterosis for fruit width, individual fruit weight and fruit yield. Considering that this hybrid was the most promising, future multi-environment testing can be recommended. On the other hand, hybrids 3×4 and 5×6, which showed negative heterosis for most traits, necessitate careful parental selection to avoid unfavorable gene interactions. Hybrids 3×4 and 5×6, on the other hand, showed significant negative heterosis for most of the traits, an indicator of unfavorable gene interactions, highlighting the need for careful parental selection. Shafike and El-Shoura (2024) studied sweet watermelons and found such trends, indicating that hybrids differed in their capacity to produce high yields. Similarly, Rady et al. (2024) recorded negative heterosis for some crosses using sweet watermelon inbred lines. The negative heterosis displayed by these crosses suggests the influence of incompatible parental alleles and or linkage drag. The results of this study further emphasize the need to identify hybrids that can express significant positive heterosis for certain traits in order to breed superior varieties of citron watermelon. For instance, traits such as fruit width and rind thickness can be used in the development of new hybrids to exploit positive heterotic effects. More emphasis should be placed on the understanding of genotype-by-environment interactions to maximize a given trait expression. Conducting multi-environmental experiments will help determine the extent of heterosis stability over a wider spectrum of environments.

Conclusions and recommendations

The current study illustrates the potential of citron watermelon genetics for advancement by selection, with the assumption of different degrees of heritability, genetic advancement, and environmental effects on the traits. Traits such as fruit yield, fruit length and individual fruit weight have shown the greatest additive genetic increase because they have both high heritability and genetic advancement. The number of genes that govern a particular trait varies depending on the estimator used, and is also different from that of other traits. In addition, several economically important traits, such as total soluble solids, rind thickness and fruit length, had gene numbers of less than one. This suggests less environmental influence on the expression of these traits, which improves their responses to selection. Fruit weight, rind thickness and fruit yield had significant positive heterosis in hybrids 7×8 and 1×2, indicating their potential to improve yield. More emphasis should be placed on the understanding of genotype-by-environment interactions to maximize a given trait expression. The study relied only on phenotypic data, hence, there is a need to incorporate qualitative trait loci mapping and genome-wide association studies for deeper genomic insights.

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Author contributions

CRedit: **Lenon Tembo**: Data curation, Formal analysis, Investigation, Software, Validation, Writing – original draft, Writing – review & editing; **Mcebisi Maphosa**: Conceptualization, Methodology, Resources, Supervision, Writing – original draft, Writing – review & editing.

Mcebisi Maphosa contributed to the research idea, design of the methodology, project administration, resources and supervision. Lenon Tembo was responsible for data curation, formal analysis, investigation, software and

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Data availability statement

The data supporting the findings of this study are available upon request from the corresponding author. The data were not publicly available because of privacy or ethical restrictions.

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