

ARAŞTIRMA MAKALESİ


RESEARCH ARTICLE

Utilizing Phenotypic Selection to Enhance Yield and Develop *T. urticae* Resistance in Interspecific Hybrid Tomatoes Derived from *S. habrochaites***Mohammad DAWOOD^{1*}, John SNYDER²****Abstract**

Tomatoes play a significant role in global agriculture, but they face challenges from pests and diseases, including the *T. urticae*. Researchers have been investigating various approaches to undertake this problem and improve tomato yield. One such strategy being explored is interspecific hybridization, which involves breeding two distinct species belonging to the same genus. This study investigated the genetic basis of resistance to spider mites in 13 BC3F7 generation lines (IS) and two F1 hybrid tomato cultivars (T1: Maglia Rosa and T2: Roma 1). The results showed that the IS lines had significantly higher fruit counts plant⁻¹ than the T lines, with the ISD90-89 displaying the highest fruit count. However, the total fruit weight plant⁻¹ was greater in the T lines than in the IS hybrids, with the IS having relatively smaller fruit weight. In terms of 7-*epizingiberene* content, no significant differences were observed within the lines of a particular IS family. However, a significant difference in 7-*epizingiberene* content was obtained between the two IS families, with the IS-F22 family demonstrating higher levels compared to the IS-D90 family. Notably, no 7-*epizingiberene* content was detected in the T and cultivated cultivars. Regarding repellency, the T1 and T2 tomato varieties were found to be susceptible to spider mites, while the genotypes in the D-90 and F-22 families exhibited varying levels of repellency. Additionally, the analysis revealed a significant negative correlation between average plant yield and 7-*epizingiberene* content in the ISs ($r=-0.731$). As the content of 7-*epizingiberene* increased, the yield tended to decrease, suggesting a potential yield penalty associated with its production. On the other hand, there was a positive correlation of 0.743 between fruit weight plant⁻¹ and total weight plant⁻¹, indicating that higher fruit weights were linked to increased total plant weights. Additionally, a positive correlation of 0.431 was obtained between fruit number plant⁻¹ and 7-*epizingiberene* concentration. The results of this study provide valuable insights into the genetic basis of resistance, yield, and 7-*epizingiberene* production in ISs. This knowledge will contribute to the advancement of breeding programs and the development of sustainable pest management strategies in tomato cultivation.

Keywords: Tomato, Interspecific hybrid, 7-*epizingiberene*, *T. urticae*, Yield, Repellency

¹*Sorumlu Yazar/Corresponding Author: Mohammad Dawood, University of Telafer, College of Agriculture, Mosul, Iraq. E-mail: mohammadh.dawood@uotelafer.edu.iq  ORCID: [0009-0000-1691-0701](https://orcid.org/0009-0000-1691-0701)

² John Snyder, University of Kentucky, College of Agriculture Food and Environment, Lexington, Kentucky, USA. E-mail: snyder@email.uky.edu  ORCID: [0009-0006-6015-461X](https://orcid.org/0009-0006-6015-461X)

Atıf/Citation: Dawood, M., Snyder, J. (2025). Utilizing phenotypic selection to enhance yield and develop *T. urticae* resistance in interspecific hybrid tomatoes derived from *S. habrochaites*. *Journal of Tekirdag Agricultural Faculty*, 22(3): 601-611.

©Bu çalışma Tekirdağ Namık Kemal Üniversitesi tarafından Creative Commons Lisansı (<https://creativecommons.org/licenses/by-nc/4.0/>) kapsamında yayınlanmıştır. Tekirdağ 2025

1. Introduction

Tomatoes (*Solanum lycopersicum*) are a globally significant crop, but they are susceptible to various pests and diseases, including the two-spotted spider mite (*Tetranychus urticae*), which can cause substantial damage and yield loss (Weinblum et al., 2021). To address this issue and enhance crop productivity, researchers have been exploring different strategies, such as utilizing interspecific hybridization. Interspecific hybridization involves crossing two different species within the same genus. In the case of tomatoes, *Solanum habrochaites*, specifically the WT-LA2329 accession, is a promising wild species used for interspecific hybridization due to its resistance to pests and diseases. This species is also known to produce a compound called 7-epizingiberene (Figure 1), which has shown potential as a natural defense mechanism against herbivorous insects. 7-epizingiberene is a semi-volatile compound synthesized by plants of *S. habrochaites* and is a major anti-insect chemical found in its leaf trichomes (Antonious and Snyder, 2006; Dawood and Snyder, 2020; Snyder et al., 1993). The presence of 7-epizingiberene in *S. habrochaites* is localized within types IV and VI glandular trichomes (Guo et al. 1993; Antonious and Kochhar 2003; Antonious and Snyder 2006). This naturally occurring compound is synthesized through the isoprenoid pathway using farnesyl pyrophosphate (FPP) as a precursor (Xie et al., 2021). The significance of 7-epizingiberene lies in its association with resistance against arthropods such as spider mites, aphids, and whiteflies when present in the trichomes of tomatoes (Weston and Snyder 1990, Aragão et al. 2000, Maluf et al. 2001, Freitas et al. 2002, Gonçalves et al. 2006, Bleeker et al. 2011). Additionally, 7-epizingiberene has been recognized for its medicinal properties (Bhatt et al. 2010, da Silveira Vasconcelos et al. 2019).

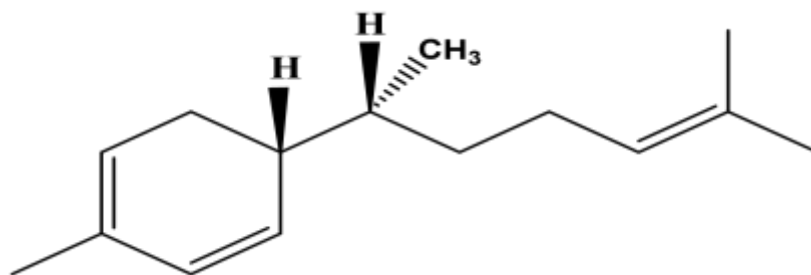


Figure 1. The molecular configuration of 7-epi-zingiberene (C₁₅H₂₄) is depicted, illustrating the presence of two conjugated double bonds within the ring structure.

The two-spotted spider mite, scientifically known as *Tetranychus urticae* Koch, is a significant pest of tomato plants, particularly in dry and hot environments. When *T. urticae* feeds on the leaf surface of the plant, it adversely affects photosynthesis and leaf transpiration. A study by Sances et al. (1979) demonstrated an undesirable correlation between the intensity and duration of mite feeding and the yield of tomato plants. The short lifespan of *T. urticae*, coupled with its high productivity and resistance to various acaricides, has made chemical control of this pest highly challenging (Turhan and Özmen, 2021). As a result, integrated pest management (IPM) techniques, including host plant resistance, have become crucial for *T. urticae* control. Host plant resistance can be mediated by specific chemical components present in the glandular trichomes of the tomato plant (Luczynski et al., 1990).

The inclusion of high levels of 7-epizingiberene from wild tomatoes into cultivated types has gained attention among tomato breeders worldwide. The objective is to improve tomato's resistance to arthropods like spider mites, aphids, and whiteflies, as 7-epizingiberene has been associated with such resistance (Zanin et al., 2021). However, the synthesis of 7-epizingiberene is energy-intensive for the tomato plant due to its oily nature, and this may lead to a negative association between yield and 7-epizingiberene production (Weston and Snyder, 1990). Additionally, interspecific hybrids may experience reduced yield due to genic incompatibilities, known as Bateson-Dobzhansky-Muller interactions (Demuth and Wade, 2005; Lynch and Force, 2000). This research is the first to report on the yields of interspecific hybrid tomatoes with high concentrations of 7-epizingiberene.

Tomato is the second most important vegetable crop, with global production reaching 189 million metric tons from 5.02 million hectares (~12.4 million acres) in 2023 (FAO, 2023). In breeding program, genetic variation from wild tomato relatives has been a valuable resource for enhancing yield, fruit quality, and disease and insect resistance (Rick and Chetelat, 1995). Genetic selection for yield in self-pollinated crops like tomatoes requires careful attention from breeders, as it is a genetically complex trait (de Souza et al., 2012). Understanding the

available genetic diversity is crucial for improving tomato yields, and morphological features have often been used to estimate this diversity (Fufa et al., 2005).

This study aims to evaluate and select interspecific hybrid families derived from *S. habrochaites* for their resistance to *T. urticae*, yield potential, and 7-*epizingiberene* content.

2. Materials and Methods

The experiment was conducted in 2020 at the Horticulture Research Farm in Lexington, Kentucky. The experimental plots were arranged in a randomized complete block design. Each plot consisted of four tomato plants, with a spacing of 0.61 meters (2 feet) between each plant within the row. The rows were set 2.13 meters (7 feet) apart in raised beds, which were equipped with trickle irrigation and covered with black plastic mulch. The study included a total of 13 interspecific hybrid breeding lines (Inbred lines) and two F1 hybrid tomato cultivars, T2 and T1. The genotypes were categorized into three groups, Tomato (T1: Maglia Rosa and T2: Roma 1), D-90 family (ISD90-23, ISD90-68, ISD90-70, ISD90-73, ISD90-83, ISD90-87, ISD90-89, and ISD90-91), and F-22 family (ISF22-13, ISF22-17, ISF22-18, ISF22-19, and ISF22-37). The 7-*epizingiberene* concentration was measured in $\mu\text{g cm}^2$, while the repellency was categorized as HR denotes high resistance, IR denotes intermediate resistance, and S denotes susceptibility to spider mites. These cultivars were evaluated in three blocks, with each block containing the breeding lines and cultivars. The BC3F7 generation lines used in this study were derived through the crossbreeding of two distinct tomato varieties. The first parent was *S. habrochaites* (WT-LA2329), a wild tomato relative known for its natural resistance to spider mites and other arthropods (Savi et al., 2022; Snyder, and Min, 2008). The second parent was Zaofen-2, a determinate variety with pink fruit that was commercially introduced in 1962, known to be susceptible to spider mite infestations. The BC3F7 lines were specifically selected for their high yield and production of zingiberene, a chemical compound found in tomatoes. Among the breeding lines, eight were chosen from the IS-D90 family and five were selected from the IS-F22 family. The experiment timeline is as follows: On April 9th, the seeds were soaked in a 50% sodium hypochlorite solution for 30 minutes. Afterward, they were directly sown into 72-cell flats filled with Fort Light compost-based potting soil from Vermont Compost Co. The transplanting of the seedlings took place on May 10th, when they were moved from the flats to the field. Throughout the cultivation period, standard transplant and field production methods were followed, as outlined in ID-36, available at <https://www2.ca.uky.edu/agcomm/pubs/id/id36/id36.pdf>. The harvest commenced on July 21st, and the tomato plants were harvested weekly for a duration of four weeks. The harvested tomatoes were weighed and counted to assess the yield of each plot.

2.1. Determination of 7-*epizingiberene* in plant leaves

To collect samples, a specific procedure was followed. From each plot, a sample was obtained from the central one-third portion of a leaflet positioned on either the third or fourth leaf of each of the four plants. The sample was carefully placed in a 20 ml vial. Subsequently, 2 ml of a *n*-hexane solution containing 20 μL of *n*-tetradecane as an internal standard was added to the vial. To ensure thorough mixing, the vials underwent vortexing for a duration of 30 seconds. The concentration of 7-*epizingiberene* present in the extract was then determined using gas chromatography, employing the methodology previously outlined in our published study (Dawood and Snyder, 2020). Additionally, the area of the extracted leaflets was determined using image analysis (ImageJ 1.47v, National Institutes of Health, USA). The results were reported as microgram of 7-*epizingiberene* per square centimeter ($\mu\text{g cm}^2$) of leaflet.

2.2. Bridge bioassay

The developed bridge bioassay, following the protocols described by Snyder et al. (2011) and Guo et al. (1993), was employed as a simple and effective method for assessing the repellent properties against two-spotted spider mites (TSSM) in natural products, specifically oleoresins obtained from interspecific hybrids and cultivated F1 hybrids, as well as chromatography-purified compounds. Each concentration of the tested oleoresin or compound was subjected to evaluation with 30 individual mites, resulting in 30 replications for each tested concentration. The evaluation of oleoresins was performed in three separate experiments, while the assessment of purified compounds was conducted twice. Quantification of the compounds in the bridge bioassays was accomplished using GC-FID, following the methodology described in our previous study (Dawood and Snyder, 2020).

2.3. Statistical analysis

The data obtained from this investigation underwent statistical analysis using the Generalized Linear Model (GLM) procedure in SAS version 9.4, a statistical software developed by SAS Institute, Inc., situated in Cary, NC (Der and Everitt, 2015). For comparing the means, either the LSMeans option or Duncan's multiple range test was utilized, depending on the particular analysis requirements. To assess the association between yield and the concentration of 7-epizingiberene as well as the repellency of spider mites in the interspecific hybrids, the Pearson correlation coefficient was computed for these two variables. The effectiveness of spider mite control was assessed using a method outlined by Snyder et al. (2011). The repellency of 7-epizingiberene against spider mites was assessed through chi-squared (X^2) analysis. This approach involved examining the exit ratios of different concentrations of each fraction in a bridge bioassay. To ensure the reliability of the experimental setup, the homogeneity between the two bridges within the arena was evaluated using chi-squared (X^2) test (Snyder et al., 2005).

3. Results and Discussion

The analysis of variance conducted in this study revealed significant variations among different families with respect to yield, number of fruits per plant and average fruit weight. Notably, the number of fruits per plant was significantly higher in interspecific lines when compared to the tomato cultivars, specifically T1 and T2. Among inbred lines, line ISF22-89 exhibited the highest number of fruits, producing 80 fruit plant⁻¹, whereas ISF22-37 had the lowest count of 46 fruit plant⁻¹. T1 yielded 34 fruit plant⁻¹, while T2 produced 45 fruit plant⁻¹. Regarding the total fruit weight, the average was found to be 11.4±0.7 kg plant⁻¹ for the cultivars, whereas the interspecific hybrid lines had an average of 7.6±0.3 kg plant⁻¹. The interspecific hybrids had significantly smaller fruits, weighing around 0.6±0.01 kg fruit⁻¹, compared to the larger fruits produced by the hybrid cultivars, weighing approximately 1.1±0.02 kg fruit⁻¹.

The analysis of variance conducted in this study revealed significant variations among different families with respect to yield, number of fruits per plant, and average fruit weight. Notably, the number of fruits per plant was significantly higher in interspecific lines when compared to the tomato cultivars, specifically T1 and T2. Among the interspecific hybrid lines, line ISF22-89 exhibited the highest number of fruits, producing 80 fruit plant⁻¹, whereas ISF22-37 had the lowest count of 46 fruit plant⁻¹. T1 yielded 34 fruit plant⁻¹, while T2 produced 45 fruit plant⁻¹. Regarding the total fruit weight, the average was found to be 11.4±0.7 kg plant⁻¹ for the cultivars, whereas the interspecific hybrid lines had an average of 7.6±0.3 kg plant⁻¹. The interspecific hybrids had significantly smaller fruits, weighing around 0.6±0.01 kg fruit⁻¹, compared to the larger fruits produced by the hybrid cultivars, weighing approximately 1.1±0.02 kg fruit⁻¹.

In this study, a correlation in Table 1 was utilized to investigate the relationships between various variables, including 7-epizingiberene concentration, fruit weight plant⁻¹, total weight plant⁻¹, and fruit number plant⁻¹. The results revealed important insights into the interplay of these factors on tomato plant development and yield.

Table 1. Correlation analysis of 7-epizingiberene concentration with fruit weight, total weight, and fruit number in tomato plants

Variable	7-epizingiberene ($\mu\text{g cm}^2$)	Fruit weight (g plant ⁻¹)	Total weight (kg plant ⁻¹)
Fruit weight (g plant ⁻¹)	-0.731		
Total weight (kg plant ⁻¹)	-0.671	0.743	
Number of fruits per plant	0.431	-0.731	-0.159

The 7-epizingiberene concentration displayed a negative correlation of -0.731 with fruit weight plant⁻¹, indicating that as the concentration of 7-epizingiberene increased, the fruit weight plant⁻¹ tended to decrease. Similarly, a negative correlation of -0.671 was observed between 7-epizingiberene concentration and total weight plant⁻¹, suggesting that an increase in 7-epizingiberene concentration was associated with a decrease in the total weight of the plant. On the other hand, there was a positive correlation of 0.743 between fruit weight plant⁻¹ and total weight plant⁻¹, indicating that higher fruit weights were linked to increased total plant weights. Additionally, a positive correlation of 0.431 was obtained between fruit number plant⁻¹ and 7-epizingiberene concentration. However, negative correlations were observed between fruit number plant⁻¹ and fruit weight plant⁻¹ (-0.731) as

well as total weight plant⁻¹ (-0.159). This suggests that while higher concentrations of 7-epizingiberene may promote greater fruit production, a higher number of fruits may lead to reduced individual fruit and total plant weights.

3.1. 7-epizingiberene content ($\mu\text{g cm}^2$ of leaf) and repellency

The Table 2 displays the 7-epizingiberene ($\mu\text{g cm}^2$) levels for different genotypes of tomatoes, specifically T1 and T2, and various genotypes of D-90 and F-22 tomato varieties. The range of 7-epizingiberene levels in the samples is from 0 $\mu\text{g cm}^2$ (for T1 and T2) to 49.022 $\mu\text{g cm}^2$ (for ISF22-13). The average level of 7-epizingiberene across all genotypes was calculated by summing the values and dividing by the total number of observations, yielding an average of approximately 28.48 $\mu\text{g cm}^2$. These results suggest that there is variability in the production of 7-epizingiberene among the different genotypes, with the highest levels observed in ISF22-13 of the F-22 variety. The results also presented statistically significant consequences concerning the repellency of different genotypes, as assessed through the chi-square (X^2) test. In the tomato family, genotypes T1 and T2 exhibited similar susceptibility to spider mites, with no notable divergence in their response behavior. Within the D-90 family, several genotypes, including ISD90-23, ISD90-68, ISD90-73, ISD90-83, ISD90-87, and ISD90-91, demonstrated a high level of resistance (HR) to spider mites. Notably, ISD90-23 and ISD90-68 exhibited a statistically significant deviation from the expected exit ratio, further emphasizing their exceptional resistance capabilities. Moving on to the F-22 family, ISF22-13, ISF22-17, ISF22-19, and ISF22-37 exhibited high resistance (HR) to spider mites, as indicated by their significantly lower exit counts. Furthermore, genotype ISF22-18 within the F-22 family exhibited a remarkable level of resistance (HR) to spider mites, with a significant departure from the expected exit ratio.

Table 2. Mite repellency levels and 7-epizingiberene concentration ($\mu\text{g cm}^2$) of T1, T2 inbred lines from D-90 Family (ISD90-23, ISD90-68, ISD90-70, ISD90-73, ISD90-83, ISD90-87, ISD90-89, and ISD90-91), and inbred lines from IS-F22 family (ISF22-13, ISF22-17, ISF22-18, ISF22-19, and ISF22-37)

Family	Genotype	7-epizingiberene ($\mu\text{g cm}^2$)	Repellency	Leaflet wash exit	Control exit	X^2 value
Tomato	T1	0	S	18	15	0.60 ^{ns}
Tomato	T2	0	S	17	13	0.53 ^{ns}
D-90	ISD90-23	25.08	HR	7	23	8.53**
D-90	ISD90-68	32.497	HR	8	22	6.53**
D-90	ISD90-70	28.449	IR	11	19	2.13*
D-90	ISD90-73	30.856	HR	10	20	3.33**
D-90	ISD90-83	18.609	HR	10	20	3.33**
D-90	ISD90-87	31.318	HR	8	22	6.53**
D-90	ISD90-89	20.586	IR	12	18	1.20*
D-90	ISD90-91	20.072	HR	2	28	22.53***
F-22	ISF22-13	49.022	HR	8	22	6.53**
F-22	ISF22-17	43.756	IR	8	22	6.53**
F-22	ISF22-18	41.917	HR	3	27	19.20***
F-22	ISF22-19	22.32	HR	9	21	4.80**
F-22	ISF22-37	19.013	IR	12	18	1.20*

Note: The abbreviations "HR" denoted high resistance, "MR" referred to mid resistance, and "S" indicated susceptibility to spider mites. A notable deviation from the expected 1:1 exit ratio, as determined by X^2 , was represented by significant symbols (*** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$), while the symbol "ns" represented no significance or susceptibility

3.2. Fruit number

In this investigation, a randomized complete block design was employed to assess the fruit number plant⁻¹ across various genotypes. The analysis of variance (ANOVA) consequences provided compelling evidence supporting the influence of genotype on fruit number plant⁻¹ $F(14, 28) = 5.63$, $p < 0.0001$). To further elucidate

the dissimilarities, *Figure 2* was constructed to visually represent the fruit yield plant⁻¹ for each genotype. Remarkably, T1 and T2 genotypes exhibited the most substantial and second-highest fruit numbers plant⁻¹, respectively. Among the D-90 genotypes, ISD90-70 and ISD90-73 demonstrated the highest fruit numbers plant⁻¹. Similarly, within the F-22 genotypes, ISF22-13 and ISF22-17 manifested relatively elevated fruit numbers plant⁻¹.

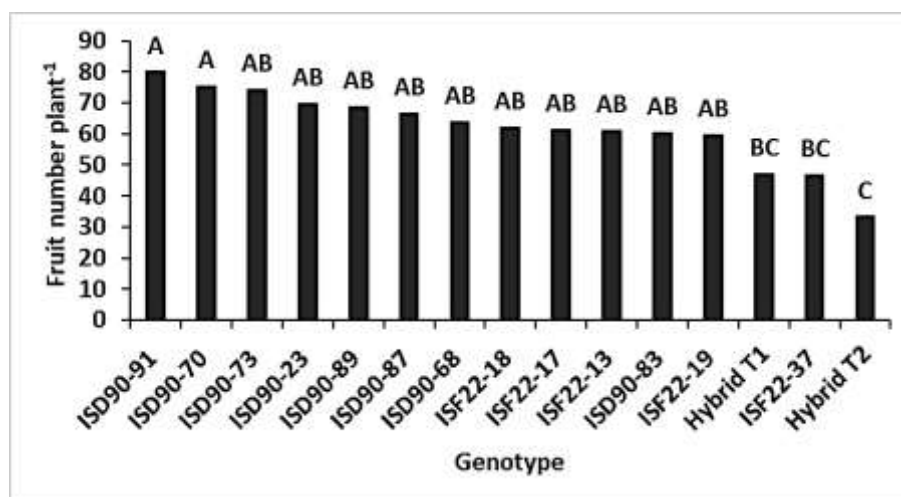


Figure 2. A comparative analysis of fruit number plant⁻¹ in different genotypes: Evaluating the effects of T1, T2, inbred lines from D-90 Family (ISD90-23, ISD90-68, ISD90-70, ISD90-73, ISD90-83, ISD90-87, ISD90-89, and ISD90-91), and inbred lines from IS-F22 family (ISF22-13, ISF22-17, ISF22-18, ISF22-19, and ISF22-37). These Inter-Specific (IS) lines are the result of breeding between *S. habrochaites* (WT-LA2329), a wild tomato relative, and Zaofen-2, a cultivated tomato variety

3.3. Average fruit weight

The statistical analysis conducted indicated a highly significant influence of genotypes on fruit weight ($F = 102.85$, $p < 0.001$), highlighting considerable genetic variation associated with this trait (*Figure 3*). Examining the

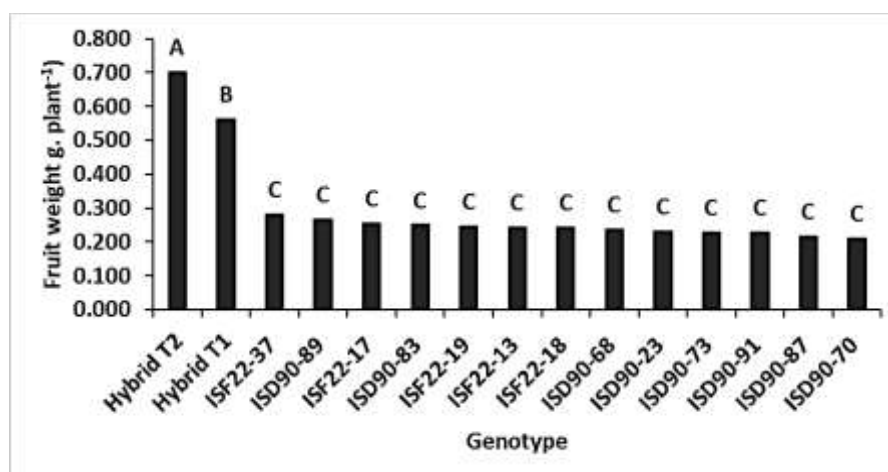


Figure 3. Average weight of fruits (g) of T1, T2, inbred lines from D-90 family (ISD90-23, ISD90-68, ISD90-70, ISD90-73, ISD90-83, ISD90-87, ISD90-89, and ISD90-91), and inbred lines from IS-F22 family (ISF22-13, ISF22-17, ISF22-18, ISF22-19, and ISF22-37). These Interspecific (IS) lines are the result of breeding between *S. habrochaites* (WT-LA2329), a wild tomato relative, and Zaofen-2, a cultivated tomato variety

average fruit weight for each genotype revealed noticeable distinctions among them. Within the tomato genotypes, T1 exhibited an average fruit weight of 0.566 g, while T2 displayed a slightly higher mean of 0.7033 g. In the D-90 family, the genotype ISD90-23 had the lowest mean fruit weight of 0.2333 g, followed by ISD90-68 (0.240 g) and ISD90-70 (0.213 g). Conversely, ISD90-89 exhibited the highest mean fruit weight within this group, measuring 0.270 g. Moving to the F-22 family, ISF22-37 demonstrated the highest mean fruit weight of 0.283 g,

while the remaining genotypes in this family displayed mean fruit weights ranging from 0.246 to 0.256 g. These results provide compelling evidence for substantial genetic variation in fruit weight across different genotypes.

3.4. Total fruit weight

The analysis reveals significant variation in the total fruit weight plant⁻¹ across the different genotypes (Figure 4). For instance, the mean fruit weight for T1 is 12.15 g, while T2 has a slightly lower mean of 10.627 g. Among the D-90 genotypes, ISD90-23 exhibits a mean fruit weight of 7.397 g, whereas ISD90-68, ISD90-70, and ISD90-73 have mean values ranging from 6.867 to 7.713 g. In the F-22 family, ISF22-13, ISF22-17, and ISF22-18 demonstrate mean fruit weights of approximately 6.757 to 7.087 g, whereas ISF22-19 and ISF22-37 have lower means of 6.857 and 6.023 g, respectively.

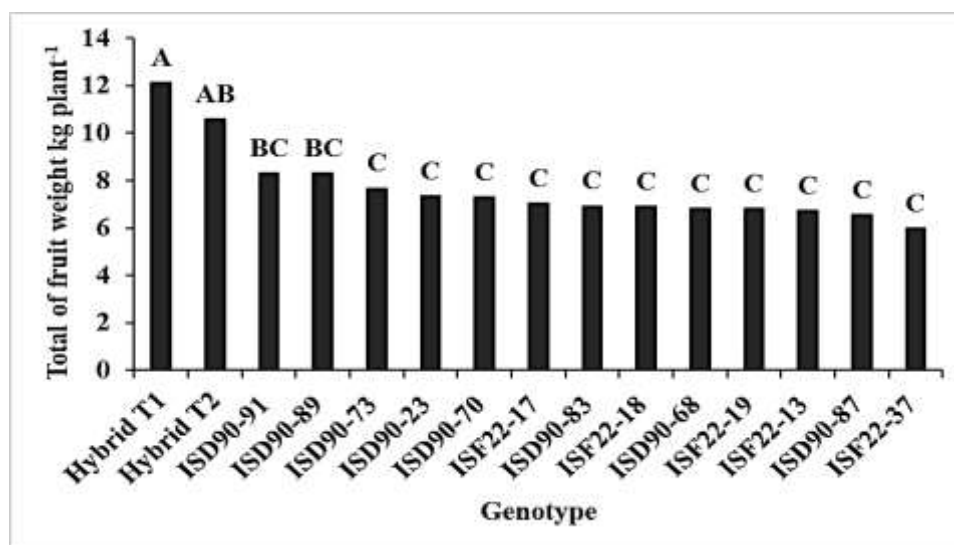


Figure 4. Average of total fruit weight (kg plant⁻¹) of T1, T2, inbred lines from D-90 Family (ISD90-23, ISD90-68, ISD90-70, ISD90-73, ISD90-83, ISD90-87, ISD90-89, and ISD90-91), and inbred lines from IS-F22 family (ISF22-13, ISF22-17, ISF22-18, ISF22-19, and ISF22-37). These inbred lines are the result of breeding between *S. habrochaites* (WT-LA2329), a wild tomato relative, and Zaofen-2, a cultivated tomato variety

The study examined the outcomes and provided empirical evidence to support a negative correlation between the concentration of 7-epizingiberene in interspecific hybrids and the average plant yield. It was observed that higher levels of 7-epizingiberene were associated with a decline in yield, despite the potential benefits of increased concentrations of this compound in terms of pest resistance. These findings enhanced our understanding of the complex relationships between 7-epizingiberene concentration, fruit productivity, and overall plant productivity. Consequently, researchers can now make informed decisions regarding the breeding of tomato plants and optimizing yield.

Regarding the content and repellency of 7-epizingiberene, our findings were agreed with De Oliveira et al. (2020)'s research, emphasizing the significant influence of specific genotypes on spider mite populations due to their heightened resistance mechanisms. These findings were further supported by Snyder et al. (2005), who reported similar susceptibility levels among tomato genotypes. Additionally, the study's outcomes corroborated the work of Zanin et al. (2018), De Oliveira et al. (2018), Santamaria et al. (2020), Panizzon Diniz et al. (2022), and Savi et al. (2022), collectively demonstrating the importance of genotypes in effectively combating spider mite infestations. The experiment revealed variations in 7-epizingiberene levels, resistance to spider mites, and mite exit ratios across different tomato genotypes. Some genotypes showed statistically significant deviations from the expected exit ratio, indicating varying levels of resistance to spider mites. Notably, genotypes with higher concentrations of 7-epizingiberene exhibited increased repellency against pests, as supported by Lucini et al.'s (2015) findings. Further research is necessary to understand the underlying mechanisms and practical applications of these genotypes in pest management strategies, as emphasized by Ulyshen and Shelton (2012).

Furthermore, the study shed light on the significant influence of genotype on fruit yield plant⁻¹. The results highlighted the impact of genotype on variations in fruit production, with implications for breeding prog and strategies aimed at improving crops. These findings aligned with the research conducted by Wang et al. (2019), which further emphasized the presence of genetic traits that positively affect fruit weight, indicating potential avenues for enhancement through breeding prog. Therefore, further investigations are required to unravel the underlying mechanisms responsible for the observed variations in fruit weight. Gaining a comprehensive understanding of the genetic factors and physiological processes associated with fruit development and weight accumulation can facilitate targeted breeding strategies to increase fruit weight in tomato plants, as suggested by Hui et al. (2016) (Cay and Aykaş, 2013).

Regarding the total fruit weight plant⁻¹, the study revealed significant variation among the examined genotypes. Genetic factors influencing fruit development and growth were identified as the primary determinants of these observed differences. These findings were consistent with Mohamed et al. (2012) and Saravanan et al. (2019), both of which emphasized the pivotal role of genotype in determining fruit weight in tomatoes. The study also acknowledged the potential contributions of environmental conditions and cultural practices to the observed variation in fruit weight. Therefore, further investigations are necessary to understand the underlying mechanisms and explore potential strategies for enhancing fruit production.

In summary, the study findings suggest that producing high levels of *7-epizingiberene* may result in a decrease in yield, indicating a potential trade-off associated with its synthesis. However, in this research, interspecific hybrids were successfully developed, exhibiting yields comparable to the recurrent parent while maintaining significant levels of *7-epizingiberene* production. These results offer promising prospects for breeding tomato hybrids with desirable traits, such as high yield and pest resistance, without compromising the production of secondary metabolites like *7-epizingiberene*. Consequently, further research is warranted to uncover the intricacies of *7-epizingiberene* biosynthesis, its impact on yield, and the trade-offs involved. These insights can provide valuable guidance to breeders and researchers in their efforts to develop tomato varieties with enhanced pest resistance and productivity.

4. Conclusions

The findings of the present study have unveiled that interspecific hybrid families exhibited a greater number of fruit plant⁻¹ compared to the tested tomato cultivars. Conversely, the total yield plant⁻¹ was higher in the cultivars than in the interspecific hybrids. Moreover, a negative correlation was observed between the average weight of fruit plant⁻¹ and the content of *7-epizingiberene*, indicating the necessity for further investigation into the true association between *7-epizingiberene* production and yield. These preliminary outcomes offer a promising prospect of developing tomatoes through breeding techniques that combine high yield and adequate *7-epizingiberene* levels in their leaves. The results obtained from the bridge-bioassay test suggest that there are certain unknown neutral substances that exhibit repellent activity in the bioassay, influencing the behavior of spider mites. However, it remains unclear whether these substances specifically contribute to leaflet repellency. Further investigation is required to determine the exact role and impact of these unidentified substances on the repellent properties of the leaflets. This potential achievement could potentially result in enhanced resistance against plant pests and increased overall yield. Further research in this area will undoubtedly shed light on the intricate relationship between *7-epizingiberene* content and yield, providing invaluable insights for future advancements in tomato breeding and agricultural practices.

Acknowledgment

The authors express their gratitude to George F. Antonious, a professor in the Division of Environmental Studies, College of Agriculture, Communities, and the Environment at Kentucky State University, for his valuable support. They also extend their sincere appreciation to Belinda Labadie for her technical assistance in conducting this research.

Ethical Statement

There is no need to obtain permission from the ethics committee for this study.

Conflicts of Interest

The authors declare no conflict of interest.

Authorship Contribution Statement

Concept: Dawood, M.; Snyder, J.; Design: Dawood, M.; Snyder, J.; Data Collection or Processing: Dawood, M.; Statistical Analyses: Dawood, M.; Literature Search: Dawood, M.; Snyder, J.; Writing, Review and Editing: Dawood, M.; Snyder, J.

References

- Antonious, G. F. and Kochhar, T. S. (2003). Zingiberene and curcumen in wild tomato. *Journal of Environmental Science and Health, Part B*, 38(4): 489-500.
- Antonious, G. F. and Snyder, J. C. (2006). Natural products: Repellency and toxicity of wild tomato leaf extracts to the two-spotted spider mite, *Tetranychus urticae* Koch. *Journal of Environmental Science and Health, Part B*, 41(1): 43-55.
- Aragão, C. A., Dantas, B. F. and Benites, F. R. G. (2000). Foliar trichome in tomato with contrasting levels of alelochemical 2-tridecanone. *Scientia Agricola*, 57(4): 813-816.
- Bhatt, A., Naidoo, Y. and Nicholas, A. (2010). The foliar trichomes of *Plectranthus laxiflorus* Benth [Lamiaceae]: An important medicinal plant. *New Zealand Journal of Botany*, 48(2): 55-61.
- Bleeker, P. M., Diergaarde, P. J., Ament, K., Schütz, S., John, B., Dijkink, J., Hiemstra H., de Gelder R., de Both M. T. J., Sabelis, M. W., Haring M. A. and Schuurink R. C. (2011). Tomato-produced 7-epizingiberene and R-curcumen act as repellents to whiteflies. *Phytochemistry*, 72(1): 68-73.
- Çay, A. and Aykaş, E. (2013). Effects of different seedling-bad preparations and cover crop application on yield and post-harvest quality parameters in tomato production. *Journal of Tekirdag Agricultural Faculty*, 10(1): 105-114.
- Da Silveira Vasconcelos, M., Mota, E. F., Gomes-Rochette, N. F., Nunes-Pinheiro, D. C. S., Nabavi, S. M. and de Melo, D. F. (2019). Ginger (*Zingiber officinale* Roscoe). In: Nonvitamin and Nonmineral Nutritional Supplements, Eds: Nabavi S. M. and Silva A. S., Elsevier, London U.K.
- Dawood, M. H. and Snyder, J. C. (2020). The alcohol and epoxy alcohol of zingiberene, produced in trichomes of wild tomato, are more repellent to spider mites than zingiberene. *Frontiers in Plant Science*, 11(35). <https://doi.org/10.3389/fpls.2020.00035>
- De Oliveira J. R. F., de Resende J. T. V., de Lima Filho R. B., Roberto S. R., da Silva P. R., Rech, C. and Nardi, C. (2020) Tomato breeding for sustainable crop systems: High levels of zingiberene providing resistance to multiple arthropods. *Horticulture*, 6(2): 34.
- De Oliveira, J. R. F., de Resende, J. T. V., Maluf, W. R., Lucini, T., de Lima Filho, R. B., de Lima, I. P. and Nardi C. (2018). Trichomes and allelochemicals in tomato genotypes have antagonistic effects upon behavior and biology of *Tetranychus urticae*. *Frontiers in Plant Science*, 9: 1132.
- De Souza, L. M., Melo, P. C. T., Luders, R. R. and Melo, A. M. T. (2012). Correlations between yield and fruit quality characteristics of fresh market tomatoes. *Horticultura Brasileira*, 30(4): 627-631.
- Demuth, J. P. and Wade, M. J. (2005). On the theoretical and empirical framework for studying genetic interactions within and among species. *The American Naturalist*, 165(5): 524-536.
- Der, G. and Everitt B. S. (2015). Essential Statistics Using SAS University Edition, SAS Institute.
- FAO (2023). FAOSTAT: Production Quantities of Tomatoes by Country, 2023. Food and Agriculture Organization of the United Nations. <https://www.fao.org/faostat/en/#data/QCL>
- Freitas, J. A., Maluf, W. R., das Graças Cardoso, M., Gomes, L. A. A., and Bearzotti, E. (2002). Inheritances of foliar zingiberene contents and their relationship to trichome densities and whitefly resistance in tomatoes. *Euphytica*, 127(2): 275-287.
- Fufa, H., Baenziger, P., Beecher, B., Dweikat, I., Graybosch, R.A. and Eskridge, K. M. (2005). Comparison of phenotypic and molecular marker-based classifications of hard red winter wheat cultivars. *Euphytica*, 145: 133-146.
- Gonçalves, L. D., Maluf, W. R., Cardoso, M. D. G., de Resende, J. T. V., de Castro, E. M., Santos, N. M., do Nascimento I. R. and Faria, M. V. (2006). Relação entre zingibereno, tricomas foliares e repelência de tomateiros a *Tetranychus evansi*. *Pesquisa Agrícola Brasileira*, 41(2): 267-273.
- Guo, Z., Weston, P. A. and Snyder, J. C. (1993). Repellency to two-spotted spider mite, *Tetranychus urticae* Koch, as related to leaf surface chemistry of *Lycopersicon hirsutum* accessions. *Journal of Chemical Ecology*, 19(12): 2965-2979.
- Hui, Z., Xiaoxuan, W., Zejun, H. Jianchang, G. Yanmei, G. Yongchen, D. and Hong, H. (2016). Identification of quantitative trait loci for fruit weight, soluble solids content, and plant morphology using an introgression line population of *Solanum pennellii* in a fresh market tomato inbred line. *Horticultural Plant Journal*, 2(1): 26-34.
- Lucini, T., Faria, M. V., Rohde, C., de Resende, J. T. V. and de Oliveira, J. R. F. (2015). Acylsugar and the role of trichomes in tomato genotypes resistance to *Tetranychus urticae*. *Arthropod-Plant Interactions*, 9(1): 45-53.
- Luczynski A, Isman M. B., Raworth D. A. and Chan C. K. (1990). Chemical and morphological factors of resistance against the two spotted spider mite in beach strawberry. *Journal of Economic Entomology*, 83(2): 564-569.
- Lynch, M. and Force, A. G. (2000). The origin of interspecific genomic incompatibility via gene duplication. *The American Naturalist*, 156(6): 590-605.
- Maluf, W. R., Campos, G. A. and das Graças Cardoso, M. (2001). Relationships between trichome types and spider mite (*Tetranychus evansi*) repellence in tomatoes with respect to foliar zingiberene contents. *Euphytica*, 121(1): 73-80.

- Mohamed S. M., Ali E. E. and Mohamed T. Y. (2012). Study of heritability and genetic variability among different plant and fruit characters of tomato (*Solanum lycopersicon* L.). *International Journal of Science and Technology Research*, 1(2): 55-58.
- Panizzon Diniz, F. C., de Resende, J. T. V., de Lima-Filho, R. B., Pilati, L., Gomes, G. C., Roberto, S. R. and da-Silva, P. R. (2022). Development of BC₃F₂ tomato genotypes with arthropod resistance introgressed from *Solanum habrochaites* var. *hirsutum* (PI127826). *Horticulture*, 8(12): 1217.
- Rick, C. M. and Chetelat R. T. (1995). Utilization of related wild species for tomato improvement. *Acta Horticulturae* (412): 21-38. <https://doi.org/10.17660/ActaHortic.1995.412.1>
- Sances, F. V., Wyman J. A. and Ting I. P. (1979). Morphological responses of strawberry leaves to infestations of two spotted spider mite. *Journal of Economic Entomology*, 72(5): 710-713.
- Santamaria, M. E., Arnaiz, A., Rosa-Diaz, I., González-Melendi, P., Romero-Hernandez, G., Ojeda-Martinez, D. A., Garcia, A., Contreras, E., Martinez, M. and Diaz, I. (2020). Plant defenses against *Tetranychus urticae*: Mind the gaps. *Plants*, 9(4): 464.
- Saravanan, K. R., Vishnupriya, V., Prakash, M. and Anandan R. (2019). Variability, heritability and genetic advance in tomato genotypes. *Indian Journal of Agricultural Research*, 53(1): 92-95.
- Savi, P. J., de Moraes, G. J., Carvalho, R. F. and de Andrade, D. J. (2022). Bottom-up effects of breeding tomato genotypes on behavioral responses and performance of *Tetranychus evansi* population. *Journal of Pesticide Science*, 95(3): 1-15.
- Snyder, J. and Min, C. (2008). Insect resistance in *Lycopersicon hirsutum* LA2329-current status. *International Symposium on Vegetable Production, Quality and Process Standardization in Chain: A Worldwide Perspective*, 944, 14-17 October, Beijing, China.
- Snyder, J. C., Antonious G. F. and Thacker, R. (2011). A sensitive bioassay for spider mite (*Tetranychus urticae*) repellency: A double bond makes a difference. *Experimental and Applied Acarology*, 55(3): 215-224.
- Snyder, J. C., Guo, Z., Thacker, R., Goodman, J. P. and Pyrek, J. S. (1993). 2, 3-Dihydrofarnesoic acid, a unique terpene from trichomes of *Lycopersicon hirsutum*, repels spider mites. *Journal of Chemical Ecology*, 19(2): 2981-2997.
- Snyder, J. C., Thacker, R. R., Zhang, X. (2005). Genetic transfer of a two spotted spider mite (Acari: Tetranychidae) repellent in tomato hybrids. *Journal of Economic Entomology*, 98(5): 1710-1716.
- Turhan A. and Özmen N (2021). Effects of chemical and organic fertilizer treatments on yield and quality traits of industrial tomato. *Journal of Tekirdag Agricultural Faculty*, 18 (2): 213-221.
- Ulyshen M. D. and Shelton T. G. (2012). Evidence of cue synergism in termite corpse response behavior. *Naturwissenschaften*, 99(2): 89-93.
- Wang E., Brown H. E., Rebetzke, G. J., Zhao, Z., Zheng, B. and Chapman, S. C. (2019). Improving process-based crop models to better capture genotype×environment×management interactions. *Journal of Experimental Botany*, 70(9): 2389-2401.
- Weinblum, N., Cna'Ani, A., Yaakov, B., Sadeh, A., Avraham, L., Opatovsky, I. and Tzin V. (2021). Tomato cultivars resistant or susceptible to spider mites differ in their biosynthesis and metabolic profile of the monoterpenoid pathway. *Frontiers in Plant Science*, 12: 630155.
- Weston, P. A. and Snyder, J. C. (1990). Thumbtack bioassay: A quick method for measuring plant resistance to two spotted spider mites (Acari: Tetranychidae). *Journal of Economic Entomology*, 83(2), 500-504.
- Xie, Q., Tian, Y., Hu, Z., Zhang, L., Tang, B., Wang, Y., Li, J. and Chen G. (2021). Novel translational and phosphorylation modification regulation mechanisms of tomato (*Solanum lycopersicum*) fruit ripening revealed by integrative proteomics and phosphoproteomics. *International Journal of Molecular Sciences*, 22(21), 11782.
- Zanin, D. S., de Resende, J. T. V., Zeist, A. R., de Lima Filho, R. B., Gabriel, A., Diniz, F. C. P., Perrud, A. C. and Morales, R. G. F. (2021). Selection of F₂BC₁ tomato genotypes for processing containing high levels of zingiberene and resistance to tomato pinworms. *Phytoparasitica*, 49(2): 265-274.
- Zanin, D. S., Resende, J. T. V., Zeist, A. R., Oliveira, J. R.F., Henschel, J. M. and Lima Filho, R. B. (2018). Selection of processing tomato genotypes resistant to two-spotted spider mite. *Horticultura Brasileira*, 36(2): 271-275.