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Genetic control of resistance to *Liriomyza sativae* by antixenosis in the melon accession CNPH 94-244[1]

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ABSTRACT - In melon, characterizing germplasm allows identification of genotypes resistant to leafminers; knowing the genetic control of this resistance is indispensable for use in breeding. In this study, the genetic inheritance of resistance to *L. sativae* by antixenosis was investigated in the melon accession CNPH 94-244 (P_R) in crosses with the susceptible hybrids 'Goldex' (P_S) and 'Iracema' ($P_{S'}$), generating two populations. The plants were infested by the insect in screened plant enclosures and in the field. In the enclosures, the number of leaf mines and pupae per plant were evaluated; and in the field, a subjective score was attributed and the number of mines per leaf were counted. The genetic studies were based on the mean values and variances in the different generations (P_R, P_S or $P_{S'}$, F_1, F_2, BC_1, and BC_2), in each population. In the F_1 generation of the CNPH 94-244 × 'Goldex' and CNPH 94-244 × 'Iracema' populations, non-additive allelic interactions were observed in the genetic control of the evaluated traits. The full model explained the inheritance of the variables, with additive effects being the most significant. Narrow-sense heritability was high for mines per plant (in cages) and number of mines (in the field) in the F_2 generation of the CNPH 94-244 × 'Goldex' and CNPH 94-244 × 'Iracema' crosses, respectively. The genetic inheritance of antixenosis resistance to *Liriomyza sativae* in the CNPH 94-244 accession is predominantly additive, being oligogenic for subjective scores and polygenic for mines and pupae per plant in both populations. For the number of mines, inheritance was polygenic in the CNPH 94-244 × 'Goldex' population and oligogenic in the CNPH 94-244 × 'Iracema' population. Therefore, the CNPH 94-244 accession can be used as a resistant parent in breeding programs targeting leafminer resistance in melon.

Keywords: *Cucumis melo*. Leafminer. Heritability. Genes. Germplasm.

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INTRODUCTION

Melon (*Cucumis melo* L.) is one of the most economically significant vegetable crops globally, cultivated in over 100 countries (FAO, 2024). In Brazil, particularly in the Northeast, melon production has a notable socioeconomic impact, driving regional economic growth through job creation, income generation, and foreign exchange earnings (Oliveira *et al*., 2017a). Approximately 40% of Brazilian melon production is exported, with Europe as the primary destination (Brasil, 2024).

The melon prominent position comes with considerable management demands to ensure high-quality fruit production. Among the primary challenges is controlling the leafminer (*Liriomyza sativae*), the major pest affecting melon crops in the Northeast Brazilian (Oliveira *et al*., 2017b). The larval stage of insect causes the most damage, as larvae feed by creating tunnels in the leaves, which reduces leaf area, limits photosynthesis, and can lead to decreased yield and fruit quality, especially in cases of severe infestation (Araujo *et al*., 2007).

Synthetic insecticides remain the dominant method for controlling leafminers in melon fields. However, the frequent use of these chemicals has resulted in the development of resistant leafminer populations (Oliveira *et al*., 2021; Wei *et al*., 2014). Moreover, this reliance on insecticides has triggered outbreaks of new pests and reduced populations of beneficial insects such as natural enemies and pollinators (Devkota *et al*., 2016). Combined with consumer demand for safer food, these issues have driven the search for alternative management strategies, including the use of resistant genotypes. Resistant genotypes are valued for their compatibility with integrated pest management strategies, ease of use, and ability to reduce infestation in susceptible cultivars. These genotypes also contribute to environmental sustainability and farmer health by reducing the need for insecticide applications (Gallo *et al*., 2002).

In plant breeding, identifying resistant genotypes begins with screening those that exhibit lower attack rates (antixenosis), negatively affect insect biology (antibiosis), or show tolerance to damage without suffering yield loss. In melon, efforts to identify resistance sources to leafminers have led to the discovery of genotypes with resistance mechanisms (Celin *et al*., 2017a; Dogimont *et al*., 1999; Ferreira *et al*., 2022; Kennedy *et al*., 1978; Nunes *et al*., 2013; Oliveira *et al*., 2017b; 2022). However, for these genotypes to be utilized in breeding programs, the genetic basis of their resistance must be understood, guiding the introgression of resistance alleles into elite lines (Borém; Miranda; Fritsche-Neto, 2021).

For instance, in the melon accessions PI 282448 and PI 313970, resistance to *Liriomyza* spp. by antixenosis is controlled by recessive and partially dominant genes, respectively (Kennedy *et al*., 1978). Antibiosis in the cultivar Nantais Oblong to *L. trifolli* and in the accession BAGMEL 56-R to *L. sativae* is conferred by single genes with complete dominance, *Lt* (Dogimont *et al*., 1999) and *Ls* (Celin *et al*., 2017b), respectively. These examples show that resistance is controlled by different alleles, as distinct defense mechanisms (morphological, physical, or biochemical) act in various combinations across genotypes.

Thus, when new resistance sources are identified, understanding their genetic control is essential for developing a breeding program aimed at obtaining elite resistant genotypes (Borém; Miranda; Fritsche-Neto, 2021). Generation analysis assists in defining breeding methods and strategies for selecting progeny, allowing for greater genetic gains in developing superior genotypes (Cruz; Carneiro; Regazzi, 2014).

The aim of this study was to elucidate the genetic control of resistance to *L. sativae* by antixenosis in the melon accession CNPH 94-244.

MATERIALS AND METHODS

Initially, the populations for generation analyses were obtained in a greenhouse in Fortaleza, CE, Brazil. These populations were evaluated under artificial and natural infestation. In artificial infestation, the plants were grown in a greenhouse and infested in screened plant enclosures in the plant breeding and genetic resources laboratory in Fortaleza, CE. Evaluations under natural infestation occurred in the Pacajus experimental field, Pacajus, CE. Both facilities belong to Embrapa Agroindústria Tropical, Fortaleza, CE.

Germplasm

The melon accession CNPH 94-244 from the Melon active germplasm bank of Embrapa Hortaliças was used as the parent (P_R) carrying alleles that confer resistance to leafminer by antixenosis (Celin *et al*., 2017a) in crosses with the commercial hybrids Goldex® (P_S) and Iracema® ($P_{S'}$), susceptible to the insect.

The accession CNPH 94-244, a "snow melon" collected in Brazil, has monoicous plants and pyriform, aromatic, and climacteric fruit, with a habit of splitting open, early maturity (20 to 25 days after pollination), yellow, smooth, and thin peel, cream-colored pulp with low sugar content, and small, yellow seeds. The Goldex and Iracema hybrids have vigorous and high-yielding plants. Their fruit is of uniform shape and size with slightly rough peel of yellow-gold color, closed inner cavity, firm pulp,

mean weight of 1.0 kg to 1.5 kg, and soluble solids content of around 12 ºBrix; the beginning of harvest occurs nine weeks after transplanting (Silva; Guimarães; Aragão, 2019).

From separate crosses of CNPH 94-244 × 'Goldex' and CNPH 94-244 × 'Iracema', two populations were structured. First, crosses were made between the pairs of parents to obtain the respective F_1 filial generations. After that, F_1 plants were self-fertilized and backcrossed with the resistant and susceptible parent in a parallel manner, resulting in the F_2 ($F_1 \times F_1$) generations and in the BC_1 ($F_1 \times P_R$) and BC_2 ($F_1 \times P_S$ or $P_{S'}$) backcrosses, respectively.

Planting, growing, and obtaining melon populations

One seed per cell was sown at a depth of 1.0 cm in a 200-cell polyethylene tray filled with a coconut fiber-based powder substrate and Germinaplant® commercial substrate in a 1:1 proportion. The trays remained for two days in total darkness and, after that period, were placed in a greenhouse, where they were watered daily. Ten days after sowing, the seedlings were transplanted to five-liter capacity pots containing a sand and earthworm humus substrate in a 5:1 proportion and kept in a greenhouse. The plants were grown vertically on support stakes and received fertigation according to the nutritional requirements of the crop.

Self-fertilizations and artificial crosses were carried out in the flowering period to obtain the F_1 and F_2, generations and the BC_1 and BC_2 backcrosses, respectively. So as to prevent pollen contamination before pollination, at the end of the afternoon of the previous day, female and male flowers were protected with gelatin capsules. When necessary, hermaphrodite flowers were emasculated, aiming to prevent self-fertilization. After pollination, performed in the morning of the day of anthesis, the flowers were once more protected and duly identified with tags, containing information on the genotypes, types of fertilization, and date of pollination. Fruit was harvested at thirty days after the pollinations, and seeds were extracted one day after harvest.

Genetic control in each population

Aiming to clarify inheritance of resistance to *L. sativae* in each melon population, the parents (P_R and P_S or $P_{S'}$) with the respective generations (F_1 and F_2) and backcrosses (BC_1 and BC_2) obtained were simultaneously infested artificially (in screened plant enclosures) and naturally (in the field) for later evaluation.

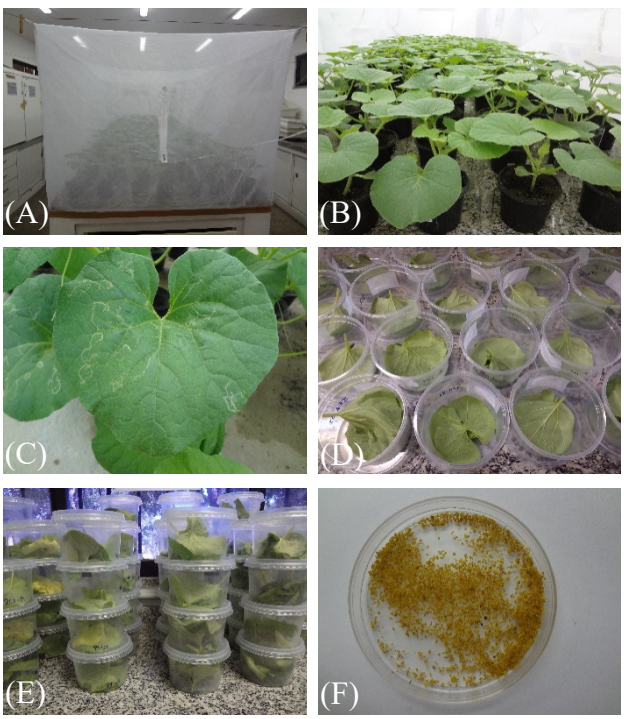
Artificial infestation in plant enclosures

The populations were sown as described above, and the seedlings were transplanted to 0.3-liter capacity polyethylene pots filled with commercial substrate, earthworm humus, and sand in a 1:1:1 proportion. The plants remained in a greenhouse from sowing until the time of infestation and were watered twice a day. The mean temperature recorded during the period of plant growth was 32.8 ºC and mean relative humidity was 42.8%.

A completely randomized design with six treatments (P_R, P_S or $P_{S'}$, F_1, F_2, BC_1, and BC_2, for each population) was used for the trials, and different numbers of plants per generation. Infestation was performed by transporting the plants from the greenhouse to the laboratory when they had three fully expanded true leaves (22 days after sowing), and they were placed in screened plant enclosures (115 × 380 × 90 cm) covered with voile cloth (Figure 1A). After placement of the plants, six leafminer flies (of up to 48 hours of age) per plant were released in the enclosures, which remained closed for 20 hours. These flies were raised on jack bean (*Canavalia ensiformis* L.) in the laboratory. During infestation, the mean temperature was 26.4 ºC and mean relative humidity was 62.6%, under constant lighting.

After infestation, the plants were removed from the enclosure and taken to the greenhouse, where they remained for three more days until evaluation. The number of mines per leaf of each plant was counted and, after that, the total pupae per plant. To obtain the number of pupae, counted at four days after infestation, the leaves with mines were cut off and placed in plastic pots, duly identified, until larval development was complete (Figure 1B-F).

Figure 1 - In cage, infestation of melon germplasm with leafminer: (A) entomological cage; (B) plants under leafminer infestation; (C) leaves with mines; (D) collection of mined leaves; (E) development and acquisition of pupae; and (F) collected pupae



Natural infestation in the field

The seedlings of the two populations, ten days after sowing in trays, were transplanted to the field. A completely randomized experimental design with six treatments (P_R, P_S or $P_{S'}$, F_1, F_2, BC_1, and BC_2) was used and different numbers of plants per generation. The plant spacing adopted was 2.0 meters between rows and 0.4 meters between plants. Plants were irrigated through drip irrigation and fertilized through fertigation. Three weeks after transplanting, the melon vines were guided outward from the plant beds. No insecticide was used for insect control.

The intensity of leafminer attack was evaluated at 41 days after transplanting through attributing subjective scores according to the following scale: 1 - plant without mines in the leaves; 2 - 1% to 25% of leaves with mines; 3 - 26% to 50% of leaves with mines; 4 - 51% to 75% of leaves with mines; and 5 - 76% to 100% of leaves with mines (Figure 2A-E). In addition, the number of mines in three leaves of each adult plant was quantified considering the tenth leaf from the tips of the first three secondary vines of the melon (Figure 2F).

Statistical analyses

In the two melon populations, the genetic studies of resistance to *L. sativae* by antixenosis were based on the means and variances of the parents (P_R and P_S or $P_{S'}$), of the generations (F_1 and F_2), and of the backcrosses (BC_1 and BC_2). The GENES computational program was used in all the statistical procedures (Cruz, 2016).

Figure 2 - Evolution of leafminer infestation levels in melon plants (A → E) and mines in an infested leaf (F) under field conditions

Genetic study of mean values

The study of the genetic parameters was carried out through generation analysis, considering the mean values of the parents (P_R and P_S or $P_{S'}$), of the generations (F_1 and F_2), and of the backcrosses (BC_1 and BC_2) through the following genetic components for η loci (Mather; Jinks, 1974), considering:

$$P_R = m + \alpha + \alpha\alpha \quad (1)$$

$$P_{SorS'} = m - \alpha + \alpha\alpha \quad (2)$$

$$F_1 = m + d + dd \quad (3)$$

$$F_2 = m + \frac{1}{2}d + \frac{1}{4}dd \quad (4)$$

$$BC_1 = m + \frac{1}{2}\alpha + \frac{1}{2}d + \frac{1}{4}\alpha\alpha + \frac{1}{4}\alpha d + \frac{1}{4}dd \quad (5)$$

$$BC_2 = m - \frac{1}{2}\alpha + \frac{1}{2}d + \frac{1}{4}\alpha\alpha - \frac{1}{4}\alpha d + \frac{1}{4}dd \quad (6)$$

where,

m = mean value of all the possible homozygotes of the genes that control the trait;

a = measure of the additive effects of the genes that control the trait;

d = measure of the deviations of dominance of the genes that control the trait;

aa = measure of the additive × additive epistatic interactions between two genes, considering all the genes that control the trait;

ad = measure of the additive × dominance epistatic interactions between two genes, considering all the genes that control the trait;

dd = measure of the dominance × dominance epistatic interactions between two genes, considering all the genes that control the trait.

The *t*-test of significance was applied to the effects at the 1% level of probability. The estimates of parameters were based on mean values of populations from the complete model and calculated through the weighted least squares method (Cruz; Carneiro; Regazzi, 2014), testing the additive × additive (aa), additive × dominance (ad), and dominance × dominance (dd) models.

Genetic study of the variances

From analysis of the variances of the generations, the following components were estimated:

a) Phenotypic variance $\hat{\sigma}^2_{f(F_2)} = \hat{\sigma}^2_{f(F_2)}$ (7)

b) Genotypic variance $\hat{\sigma}^2_{g(F_2)} = \hat{\sigma}^2_{f(F_2)} - \hat{\sigma}^2_{m(F_2)}$ (8)

c) Environmental variance (F_2)

$$\hat{\alpha}^2_{m(F_2)} = \frac{2\hat{\alpha}^2_{F_1} + \hat{\sigma}^2_{P_1} + \hat{\sigma}^2_{P_2}}{4}, \hat{\sigma}^2_{m(BC_1)} = \frac{\hat{\sigma}^2_{F_1} + \hat{\sigma}^2_{P_1}}{2} \text{ and } \hat{\sigma}^2_{m(BC_2)} = \frac{\hat{\sigma}^2_{F_1} + \hat{\sigma}^2_{P_2}}{2} \quad (9)$$

d) Additive variance $\hat{\sigma}^2_{\alpha} = 2\hat{\sigma}^2_{gF_2} - \left[\hat{\sigma}^2_{g(BC_1)} + \hat{\sigma}^2_{g(BC_2)}\right]$ (10)

where:

$$\hat{\sigma}^2_{g(RC_1)} = \hat{\sigma}^2_{f(BC_1)} - \hat{\sigma}^2_{m(RC_1)}, \text{ and } \hat{\sigma}^2_{g(BC_2)} = \hat{\sigma}^2_{f(BC_2)} - \hat{\sigma}^2_{m(BC_2)} \quad (11)$$

e) Variance due to dominance deviations $\hat{\sigma}^2_d = \hat{\alpha}^2_{g(F_2)} - \hat{\sigma}^2_{\alpha}$ (12)

f) Broad-sense heritability $h^2_{\alpha} = \frac{\hat{\sigma}^2_{g(F_2)}}{\hat{\sigma}^2_{f(F_2)}}$ (13)

g) Narrow-sense heritability $h^2_r = \frac{\hat{\sigma}^2_{\alpha}}{\hat{\sigma}^2_{f(F_2)}}$ (14)

h) Average degree of dominance (ADD) $ADD = k = \sqrt{\frac{2\hat{\sigma}^2_d}{\hat{\sigma}^2_{\alpha}}}$ (15)

i) Minimum number of genes involved in determination of the trait (η)

To estimate the number of genes that control the trait, the following presuppositions were considered: the difference between two contrasting homozygotes for a locus is equal to 2a; there are η loci contributing to phenotypic manifestation of the trait; and R is the total amplitude (Burton, 1951):

$$\eta = R^2\left(1 + 0{,}5k^2\right) / 8\hat{\sigma}^2_g \quad (16)$$

where,

R = 2 ηa

a = difference between the homozygotes

k = average degree of dominance $\hat{\sigma}^2_g = \hat{\sigma}^2_{\alpha} + \hat{\sigma}^2_d = 0{,}5\eta\alpha^2 + 0{,}25\eta d^2$ (17)

RESULTS AND DISCUSSION

CNPH 94-244 × 'Goldex'

The parents were contrasting for the number of mines and pupae per plant variables in controlled infestation in the enclosure, and number of mines variable in natural infestation in the field (Table 1). The mean values of the F_1 generation for these same variables were superior to the mean value of the susceptible parent P_S, and the mean values of the F_2 generation were lower in relation to the mean values of F_1 (Table 1).

In the backcross with the resistant parent (BC_1), in controlled infestation, the mean values of number of mines and pupae per plant were in between the values of the parents and lower than the values observed in the F_2 generation. However, for number of mines in natural infestation, the mean value obtained in the BC_1 was similar to the mean values of the susceptible parent (P_S) and of the F_2 generation. For the backcross with the susceptible parent (BC_2), the mean values of number of mines and pupae per plant (enclosure) and number of mines (field) were higher than the mean values of the parents and of the F_2 generation (Table 1). Evaluation of resistance of the population through attribution of the subjective score showed similar mean values among all the generations, including the parents (Table 1).

Based on the estimates of mean and significance of the null hypothesis of the parameters of the complete model (additive-dominance-epistatic) (Table 2), the mean and additive gene effects in the number of mines and pupae per plant variables were significant. For the subjective score, significance was observed in the mean, in dominance deviation, and in the additive × dominance and dominance × dominance epistatic interactions. However, for number of mines, only the additive effects and effects due to dominance were significant.

By non-orthogonal decomposition of the sum of squares of the genetic effects (Table 2), the mean values and the additive effects for number of mines and pupae per plant explained 92.63% and 95.48%, respectively, of the variability contained in the variables studied. The additive × dominance

Table 1 - Number of mines and pupae per plant, subjective score, and number of mines in the melon population obtained from the cross CNPH 94-244 (P_R) × 'Goldex' (P_S), evaluated in a screened enclosure and in the field under infestation of *L. sativae*

Generation†	Enclosure trial			Field trial			
	n	Mines per plant	Pupae per plant	n	Subjective score	n	Number of mines‡
P_R	26	10.04 ± 6.10a	9.38 ± 5.25	10	2.00 ± 0.00	10	7.30 ± 5.33
P_S	24	23.63 ± 7.32	19.71 ± 7.00	10	2.40 ± 0.70	9	24.00 ± 8.17
F_1	19	30.47 ± 7.76	27.26 ± 5.85	20	2.25 ± 0.44	19	34.79 ± 17.16
F_2	158	24.59 ± 13.01	20.92 ± 11.22	109	2.49 ± 0.60	107	24.02 ± 15.84
BC_1	44	17.66 ± 8.40	16.25 ± 8.28	40	2.23 ± 0.42	37	24.54 ± 14.60
BC_2	41	26.95 ± 12.19	23.39 ± 11.03	35	2.91 ± 0.66	26	32.54 ± 15.20

† F_1 - first filial generation ($P_R \times P_S$); F_2 - second filial generation ($F_1 \times F_1$); BC_1 - backcross between P_R and F_1; BC_2 - backcross between P_S and F_1. ‡Number of mines of *L. sativae* obtained in the 10th leaf (from the tip to the base) of three secondary vines. [a]Mean ± standard deviation

and dominance × dominance epistatic effects contributed 30.46% of the variability observed in the subjective score variable. For number of mines, 84.21% of the total variability was explained by the additive and dominance effects.

Fitting the complete model allowed expected mean values to be obtained that correlated with the mean values observed (Table 3). Correlation indicated a magnitude of 0.99 and a coefficient of determination of 0.98 for number of mines and pupae per plant, and 0.98 (r) and 0.96 (R^2) for number of mines. For the subjective score variable, the magnitude (0.66) was moderate and the correlation coefficient (0.44) was weak.

Table 2 - Estimates, variances, significance tests, and non-orthogonal decomposition of the sum of squares of the genetic effects of the complete model, related to resistance to *L. sativae* by antixenosis in the melon population obtained from the cross CNPH 94-244 (P_R) × 'Goldex' (P_S), evaluated in screened enclosures and in the field

Parameter†	Estimate	Variance	t	SS	R^2	Adjusted effect
			Enclosure trial			
			Mines per plant			
m	25.97	38.97	4.16**	17.30	23.68	25.97
a	-6.79	0.92	-7.10**	50.38	68.95	-6.79
d	-10.02	268.15	-0.61^{ns}	0.37	0.51	-10.02
aa	-9.13	38.05	-1.48^{ns}	2.19	3.00	-9.13
ad	-5.00	24.57	-1.01^{ns}	1.02	1.39	-5.00
dd	14.52	117.12	1.34^{ns}	1.80	2.47	14.52
			Pupae per plant			
m	18.94	31.62	3.37**	11.34	23.70	18.94
a	-5.16	0.78	-5.86**	34.34	71.78	-5.16
d	-0.40	222.63	-0.03^{ns}	< 0.01	< 0.01	-0.40
aa	-4.39	30.84	-0.79^{ns}	0.62	1.31	-4.39
ad	-3.96	21.20	-0.86^{ns}	0.74	1.54	-3.96
dd	8.73	95.43	0.89^{ns}	0.80	1.67	8.73
			Field trial			
			Subjective score			
m	1.87	0.13	5.12**	26.19	51.96	1.87
a	-0.20	0.01	-1.81^{ns}	3.27	6.49	-0.20
d	2.10	0.94	2.16*	4.67	9.27	2.10
aa	0.33	0.12	0.96^{ns}	0.92	1.83	0.33
ad	-0.98	0.12	-2.87**	8.23	16.33	-0.98
dd	-1.71	0.41	-2.67**	7.12	14.13	-1.71
			Number of mines‡			
m	-2.43	98.66	-0.24^{ns}	0.06	0.15	-2.43
a	-8.35	2.57	-5.21**	27.18	67.81	-8.35
d	68.59	715.90	2.56*	6.57	16.40	68.59
aa	18.08	96.09	1.84^{ns}	3.40	8.49	18.08
ad	0.70	68.85	0.08^{ns}	0.01	0.02	0.70
dd	-31.36	344.10	-1.69^{ns}	2.86	7.13	-31.36

*and **- significant at 1% and 5% probability, respectively; ns - not significant by the *t*-test. †m - mean; a - additive effect; d - dominance deviation; aa - additive × additive epistasis; ad - additive × dominance epistasis; and dd - dominance × dominance epistasis. ‡Number of mines of *L. sativae* obtained in the 10th leaf (from the tip to the base) of three secondary vines

For the number of mines and pupae per plant and number of mines variables, the phenotypic variances in the F_2 generation were, in large part, due to the genotypic variances. In contrast, for the subjective score, there was predominance of environmental variance over genotypic variance in expression of the phenotype (Table 4). Additive variance was the most important component of genotypic variance for number of mines and pupae per plant and subjective score. However, in number of mines, there was predominance of the dominance effects in relation to the additive effects in constitution of genetic variance (Table 4).

In relation to broad-sense heritability, high values were observed for the variables under analysis, except for the subjective score, which had low heritability. In narrow-sense heritability, the heritability coefficient was high for number of mines per plant, moderate for pupae per plant and subjective score, and low for number of mines (Table 4). The estimated heterosis in the F_1 and the heterobeltiosis of P_R were positive for all the variables analyzed (Table 4).

Based on the variances, the average degrees of dominance for number of mines and pupae per plant and subjective score were less than 1.0. For number of mines, the value of the average degree of dominance was greater than 1.0 (Table 4). In the F_2 generation, the minimum values in the variables analyzed were greater than or equal to the minimum values of the parents, and the maximum values were greater than the values of the parents in the number of mines and pupae per plant and the number of mines variables (Table 4). The genetic inheritance of the variables analyzed in the CNPH 94-244 × 'Goldex' population has a quantitative nature, involving from five genes (subjective score) to thirteen genes (number of mines).

CNPH 94-244 × 'Iracema'

The parents CNPH 94-244 and 'Iracema' were contrasting for all the variables used in evaluation of resistance to *L. sativae*, both under controlled infestation and under natural infestation (Table 5).

The mean values of number of mines and pupae per plant, subjective score, and number of mines in the F_1 generation were higher than the mean point of the parents. The mean values of the F_2 generation and of the BC_2 backcross for all the variables were lower than the mean values of the susceptible parent P_S, whereas in BC_1, the mean values of the variables were nearer the mean values of the resistant parent P_R (Table 5).

Table 3 - Mean values ($\bar{X}$) observed and expected for the generations in the complete model regarding resistance to *L. sativae* by antixenosis in the melon population obtained from the cross CNPH 94-244 (P_R) × 'Goldex' (P_S) evaluated in screened enclosures and in the field

Generation†	*Mines per plant*			*Pupae per plant*		
	$\bar{X}_{observed}$	$\bar{X}_{expected}$	Deviation	$\bar{X}_{observed}$	$\bar{X}_{expected}$	Deviation
	Enclosure trial					
P_R	10.04	9.49	0.55	9.38	8.95	0.43
P_S	23.63	24.18	-0.55	19.71	19.94	-0.23
F_1	30.47	30.04	0.44	27.26	26.73	0.53
F_2	24.59	23.43	1.15	20.92	20.59	0.33
BC_1	17.66	19.76	-2.10	16.25	17.84	-1.59
BC_2	26.95	27.11	-0.16	23.39	23.34	0.06
	r ($\bar{X}_{observed}$, $\bar{X}_{expected}$) = 0.99. R2 = 0.98			r ($\bar{X}_{observed}$, $\bar{X}_{expected}$) = 0.99. R2 = 0.98		
	Subjective score			*Number of mines‡*		
	Field trial					
P_R	2.00	2.00	0.00	7.30	7.52	-0.22
P_S	2.40	2.97	-0.57	24.00	23.85	0.15
F_1	2.25	2.41	-0.16	34.79	35.68	-0.89
F_2	2.49	2.45	0.04	24.02	25.68	-1.66
BC_1	2.23	2.21	0.02	24.54	21.60	2.94
BC_2	2.91	2.69	0.22	32.54	29.76	2.78
	r ($\bar{X}_{observed}$, $\bar{X}_{expected}$) = 0.66. R2 = 0.44			r ($\bar{X}_{observed}$, $\bar{X}_{expected}$) = 0.98. R2 = 0.96		

†F_1 - first filial generation (P_R × P_S); F_2 - second filial generation (F_1 × F_1); BC_1 - backcross between P_R and F_1; BC_2 - backcross between P_S and F_1.
‡Number of mines of *L. sativae* obtained in the 10th leaf (from the tip to the base) of three secondary vines

For the number of mines and pupae per plant and the number of mines variables, the mean values and the additive effects were significant, and the additive × dominance interaction was significant only for the number of pupae per plant (Table 6). Regarding the subjective score, significances were found in the estimated genetic parameters, except for the additive × dominance interaction. By non-orthogonal decomposition of the sum of squares of the genetic effects, considering the complete model, the additive component explained most of the variation observed of the number of mines and pupae per plant and the number of mines variables (Table 6).

The model (m to d) contributed with 94.36% of the variation of the phenotype for the subjective score. The additive × additive and dominance × dominance epistatic effects together contributed 5.45% of the phenotypic variation present in the subjective score variable, while

Table 4 - Estimate of genetic parameters for resistance to *L. sativae* by antixenosis in melon in the F_2 generation of the cross CNPH 94-244 (P_R) × 'Goldex' (P_S) evaluated in screened enclosures and in the field

Parameter†	Enclosure trial		Field trial	
	Mines per plant	Pupae per plant	Subjective score	Number of mines‡
Phenotypic variance	169.31	125.86	0.36	250.79
Environmental variance (F_2)	45.40	38.30	0.24	47.60
Genotypic variance	123.92	87.56	0.12	203.19
Additive variance	119.53	61.56	0.11	57.35
Dominance variance	4.39	26.00	0.01	145.84
Broad-sense heritability (%)	73.19	69.57	32.69	81.02
Narrow-sense heritability (%)	70.60	48.91	31.39	22.87
Heterosis (%)	13.64	12.72	0.05	19.14
Heterobeltiosis – P_R (%)	20.44	17.88	0.25	27.49
ADD§ (variances)	0.27	0.92	0.29	2.26
Maximum value in the parents	38.00	33.00	4.00	39.00
Minimum value in the parents	0.00	2.00	2.00	0.00
Maximum value in F_2	74.00	70.00	4.00	77.00
Minimum value in F_2	2.00	2.00	2.00	0.00
Number of genes	5.42	9.39	4.39	12.92

†P_R - resistant parent and F_2 - second filial generation ($F_1 \times F_1$). ‡Number of mines of *L. sativae* obtained in the 10th leaf (from the tip to the base) of three secondary vines. §ADD - average degree of dominance

Table 5 - Number of mines and pupae per plant, subjective score, and number of mines in the melon population obtained from the cross CNPH 94-244 (P_R) × 'Iracema' (P_S), evaluated in screened enclosures and in the field under infestation of *L. sativae*

Generation†	Enclosure trial			Field trial			
	n	Mines per plant	Pupae per plant	n	Subjective score	n	Number of mines‡
P_R	22	12.05 ± 7.21 a	12.64 ± 5.60	15	3.33 ± 0.72	13	7.85 ± 5.46
P_S	24	54.67 ± 12.79	49.50 ± 18.23	10	4.90 ± 0.32	9	25.78 ± 7.51
F_1	22	34.05 ± 13.70	32.14 ± 13.16	20	4.40 ± 0.82	19	16.74 ± 9.02
F_2	163	31.62 ± 15.70	32.58 ± 15.40	142	4.34 ± 0.76	135	17.58 ± 9.98
BC_1	45	24.00 ± 11.90	28.40 ± 15.19	39	3.62 ± 0.71	37	13.54 ± 7.88
BC_2	45	39.02 ± 15.86	35.84 ± 13.83	40	4.53 ± 0.64	36	19.47 ± 9.42

†F_1 - first filial generation ($P_R \times P_S$); F_2 - second filial generation ($F_1 \times F_1$); BC_1 - backcross between P_R and F_1; BC_2 - backcross between P_S and F_1. ‡Number of mines of *L. sativae* obtained in the 10th leaf (from the tip to the base) of three secondary vines. [a]Mean ± standard deviation

the additive × dominance effect was responsible for 7.96% of the variation observed in pupae per plant (Table 6). The mean values observed correlated with the mean values estimated in high magnitude in relation to the variables studied, with correlations ≥ 0.92 (Table 7).

The genotypic effects acted on the number of pupae por plant and subjective score variables, although the environmental variance had a more pronounced effect on the phenotypic expression of the F_2 generation (Table 8). For the number of mines per plant and number of mines variables, the genotypic variance represented the greatest fraction of the total phenotypic variance. Furthermore, for all the variables, the additive component was that which most contributed to genotypic variance in relation to dominance deviations (Table 8).

Table 6 - Estimates, variances, significance tests, and non-orthogonal decomposition of the sum of squares of the genetic effects of the complete model, related to resistance to *L. sativae* by antixenosis in the melon population obtained from the cross CNPH 94-244 (P_R) × 'Iracema' (P_S), evaluated in screened enclosures and in the field

Parameter†	Estimate	Variance	t	SS	R^2	Adjusted effect
			Enclosure trial			
			Mines per plant			
m	33.79	61.43	4.31**	18.59	8.43	33.79
a	-21.31	2.30	-14.06**	197.73	89.68	-21.31
d	-8.94	440.44	-0.43^{ns}	0.18	0.08	-8.94
aa	-0.43	59.14	-0.06^{ns}	< 0.01	< 0.01	-0.43
ad	12.58	44.13	1.89^{ns}	3.58	1.63	12.58
dd	9.19	207.26	0.64^{ns}	0.41	0.18	9.19
			Pupae per plant			
m	32.91	64.62	4.09**	16.76	14.58	32.91
a	-18.43	3.82	-9.43**	88.97	77.41	-18.43
d	-0.54	473.06	-0.02^{ns}	< 0.01	< 0.01	-0.54
aa	-1.84	60.80	-0.24^{ns}	0.06	0.05	-1.84
ad	21.97	52.80	3.02**	9.15	7.96	21.97
dd	-0.24	220.15	-0.02^{ns}	< 0.01	< 0.01	-0.24
			Field trial			
			Subjective score			
m	5.19	0.17	12.60**	158.85	68.43	5.19
a	-0.78	0.01	-7.39**	54.64	23.54	-0.78
d	-2.61	1.23	-2.35*	5.54	2.39	-2.61
aa	-1.07	0.16	-2.69**	7.25	3.13	-1.07
ad	-0.25	0.14	-0.68^{ns}	0.46	0.20	-0.25
dd	1.82	0.62	2.32*	5.40	2.32	1.82
			Number of mines‡			
m	21.10	30.50	3.82**	14.59	26.55	21.10
a	-8.97	2.14	-6.13**	37.54	68.32	-8.97
d	-9.72	219.86	-0.66^{ns}	0.43	0.78	-9.72
aa	-4.29	28.36	-0.80^{ns}	0.65	1.18	-4.29
ad	6.07	25.13	1.21^{ns}	1.47	2.67	6.07
dd	5.36	103.78	0.53^{ns}	0.28	0.50	5.36

*and **- significant at 1% and 5% probability, respectively; ns - not significant by the *t*-test. †m - mean; a - additive effect; d - dominance deviation; aa - additive × additive epistasis; ad - additive × dominance epistasis; and dd - dominance × dominance epistasis. ‡Number of mines of *L. sativae* obtained in the 10th leaf (from the tip to the base) of three secondary vines

Table 7 - Mean values ($\overline{X}$) observed and expected for the generations in the complete model regarding resistance to *L. sativae* by antixenosis in the melon population obtained from the cross CNPH 94-244 (P_R) × 'Iracema' ($P_{S'}$) evaluated in screened enclosures and in the field

Generation†	Mines per plant			Pupae per plant		
	$\overline{X}_{observed}$	$\overline{X}_{expected}$	Deviation	$\overline{X}_{observed}$	$\overline{X}_{expected}$	Deviation
	Enclosure trial					
P_R	12.05	12.44	-0.39	12.64	13.47	-0.83
$P_{S'}$	54.67	52.07	2.59	49.50	45.15	4.35
F_1	34.05	32.21	1.84	32.14	34.24	-2.11
F_2	31.62	32.23	-0.61	32.58	31.78	0.81
BC_1	24.00	22.32	1.68	28.40	23.86	4.54
BC_2	39.02	42.14	-3.12	35.84	39.70	-3.85
	$r(\overline{X}_{observed}, \overline{X}_{expected}) = 0.99$. $R^2 = 0.98$			$r(\overline{X}_{observed}, \overline{X}_{expected}) = 0.96$. $R^2 = 0.92$		
	Subjective score			Number of mines‡		
	Field trial					
P_R	3.33	3.28	0.06	7.85	8.60	-0.75
$P_{S'}$	4.90	4.91	-0.01	25.78	24.77	1.00
F_1	4.40	4.37	0.03	16.74	17.45	-0.71
F_2	4.34	4.23	0.11	17.58	17.07	0.51
BC_1	3.62	3.82	-0.21	13.54	13.02	0.52
BC_2	4.53	4.64	-0.12	19.47	21.11	-1.64
	$r(\overline{X}_{observed}, \overline{X}_{expected}) = 0.98$. $R^2 = 0.96$			$r(\overline{X}_{observed}, \overline{X}_{expected}) = 0.99$. $R^2 = 0.97$		

†F_1 - first filial generation ($P_R \times P_{S'}$); F_2 - second filial generation ($F_1 \times F_1$); BC_1 - backcross between P_R and F_1; BC_2 - backcross between $P_{S'}$ and F_1. ‡Number of mines of *L. sativae* obtained in the 10th leaf (from the tip to the base) of three secondary vines

The broad-sense and narrow-sense heritability coefficients were moderate for the number of mines per plant, subjective score, and number of mines variables, and low for number of pupae per plant. For all the variables studied, the average degrees of dominance estimated based on the variances were lower than 1.0 (Table 8).

The heterosis in F_1 was positive for number of mines and pupae per plant and subjective score, and negative for number of mines. For heterobeltiosis in relation to the mean of the resistant parent (P_R), the estimated values were positive (Table 8). The minimum values in the F_2 generation for number of mines per plant, subjective score, and number of mines were equal to the minimum values registered in the parents, whereas the minimum value for pupae per plant was higher. The maximum values of F_2 were lower than those of the parents for number of mines and pupae per plant, equal for subjective score, and higher for number of mines (Table 8). The number of genes involved in control of the variables studied in the CNPH 94-244 × 'Iracema' population also ranged from five genes (subjective score and number of mines) to thirteen genes (pupae per plant).

The difference between the mean values of the variables analyzed in the parents indicated that there was adequate genetic variability among the melon genotypes, and that there is the possibility of obtaining superior genotypes for resistance to *L. sativae* by antixenosis through selection. The divergence among the genotypes used in the present study had already been reported by Celin *et al.* (2017a), and this was an essential factor for estimating the genetic parameters in the inheritance studies in both melon populations (Cruz; Carneiro; Regazzi, 2014).

The mean values of number of mines and pupae per plant and the number of mines in the F_1 generation of the cross between the CNPH 94-244 × 'Goldex' parents indicates the existence of heterosis in the sense of greater value of the trait, that is, susceptibility. Reduction in the mean of the F_2 generation in relation to F_1 corroborates this affirmation, since as generations advance, this effect decreases, indicating non-additive interaction. The mean value of the F_1 generation of the CNPH 94-244 × 'Goldex' population by attribution of the subjective score and of the CNPH 94-244 × 'Iracema' population for the number of mines and pupae per plant, subjective score, and number of mines variables showed non-additive allelic interaction, since the phenotypic value of the heterozygote was greater than the mean point of the parents.

Table 8 - Estimate of genetic parameters for resistance to *L. sativae* by antixenosis in melon in the F_2 generation of the cross CNPH 94-244 (P_R) × 'Iracema' (P_S) evaluated in screened enclosures and in the field

Parameter†	Enclosure trial		Field trial	
	Mines per plant	Pupae per plant	Subjective score	Number of mines‡
Phenotypic variance	246.50	237.11	0.58	99.51
Environmental variance (F_2)	107.88	181.87	0.31	43.13
Genotypic variance	138.62	55.24	0.27	56.39
Additive variance	99.93	52.07	0.24	48.23
Dominance variance	38.69	3.18	0.02	8.16
Broad-sense heritability (%)	56.24	23.30	46.22	56.66
Narrow-sense heritability (%)	40.54	21.96	42.11	48.46
Heterosis (%)	0.69	1.07	0.28	-0.08
Heterobeltiosis – P_R (%)	22.00	19.50	1.07	8.89
ADD§ (variances)	0.88	0.35	0.44	0.58
Maximum value in the parents	91.00	96.00	5.00	38.00
Minimum value in the parents	3.00	0.00	2.00	0.00
Maximum value in F_2	78.00	78.00	5.00	43.00
Minimum value in F_2	3.00	6.00	2.00	0.00
Number of genes	7.04	12.45	4.61	4.79

†P_R - resistant parent and F_2 - second filial generation ($F_1 \times F_1$). ‡Number of mines of *L. sativae* obtained in the 10th leaf (from the tip to the base) of three secondary vines. §ADD - average degree of dominance

In the two populations, the additive gene effects by significance of the estimates were the most important in the variability found in all the variables studied, except for the subjective score in the CNPH 94-244 × 'Goldex' population, in which the epistatic effects and the mean value were relevant in genetic control of the variable, showing the importance of use of the complete model in analyses of the generations. The dominance deviations among the genes were less important in genetic control of the variables analyzed, having contributed only to the variability observed in the number of mines in the CNPH 94-244 × 'Goldex' population and subjective score in both populations. However, the negative signal of the dominance deviations of the value attributed to the subjective score in the CNPH 94-244 × 'Iracema' population indicates that dominance acts in the sense of increasing resistance to *L. sativae* by antixenosis in the melon germplasm.

The contribution of each effect by non-orthogonal decomposition showed that the additive gene effect was also the most important regarding the variability available in the number of mines and pupae por plant, subjective score, and number of mines variables in both populations, except for the subjective score in the CNPH 94-244 × 'Goldex' population, in which the mean value and the epistatic effects were those that most contributed to the variability observed in this variable, corroborating what was observed in the mean estimates. Thus, the high magnitude of the additive effect shows the possibility of obtaining homozygote genotypes superior for resistance to *L. sativae* by antixenosis through these crosses, with satisfactory gains in the selection cycles (Cruz; Carneiro; Regazzi, 2014).

The correlation of the means observed with the estimates was high for all the variables analyzed, indicating the fit of the data to the complete model. However, there was low correlation between the means observed and those estimated for subjective score in the CNPH 94-244 × 'Goldex' population. This may be related to the fact of the additive gene effect not having been significant, indicating that it will be difficult to identify homozygote genotypes that are superior for resistance to *L. sativae* by antixenosis in the F_2 generation of the population through this variable.

Environmental variance showed relevance in the number of pupae per plant variable in the CNPH 94-244 × 'Iracema' population and for subjective score in both populations. Thus, the breeder may find difficulty in recognizing the genetic superiority of an individual regarding resistance to *L. sativae*

by antixenosis by estimation of these variables, or to discards desirable genotypes as a result of the environmental effect having hurt their performance. In contrast, in both populations, evaluation of resistance through the number of mines per plant and number of mines variables will allow the breeder to more reliably select superior genotypes because the phenotype in the case of number of mines was mostly due to genotypic variance. The predominance of additive variance over dominance variance in the genotypic component observed in the variables, except for the number of mines in the CNPH 94-244 × 'Goldex' population, corroborates the possibility of obtaining superior genotypes, with greater concentration of alleles for resistance to *L. sativae* by antixenosis through selection (Cruz; Carneiro; Regazzi, 2014).

From the high broad-sense heritability coefficients, it could be inferred that most of the phenotypic variation observed in the number of mines and pupae per plant variables and number of mines in the CNPH 94-244 × 'Goldex' population is due to genetic causes. In the CNPH 94-244 × 'Iracema' population, the estimated broad-sense heritabilities indicated that the environmental causes were those that most contributed to the phenotypic variability observed in the variables analyzed. However, to obtain genotypes that are superior for resistance, narrow-sense heritability is more important by considering only the genetic causes of additive effects that can be inherited by progenies and fixed by selection (Cruz; Carneiro; Regazzi, 2014).

In the CNPH 94-244 × 'Goldex' population, the narrow-sense heritability of greatest coefficient was observed in the number of mines per plant variable, and, in the CNPH 94-244 × 'Iracema' population, in the number of mines. In the other variables, regardless of the population, the estimates of narrow-sense heritability were moderate or low, indicating that most of the phenotypic variability is due to environmental causes. In light of that, it is important to emphasize that heritability is not only the estimate of a trait, but of the population under the environmental conditions to which it was exposed (Ramalho *et al*., 2021). Thus, the genotypes reacted in a different manner in different locations.

The positive heterosis observed in the variables studied indicated that the F_1 generation has worse performance, that is, the plants were more attacked by leafminers, in relation to the mean value of the parents. The superiority of the hybrids for resistance was only observed in the number of mines variable in the CNPH 94-244 × 'Iracema' population. The manifestation of heterosis in the F_1 hybrids is an indication that the parents are contrasting with at least one dominant allele in the loci (Borém; Miranda; Fritsche-Neto, 2021). In a similar way, aiming at plant resistance, negative heterobeltiosis would be more desirable, which would indicate that the F_1 generation was less attacked than the resistant parent, which was not observed in this study.

In the CNPH 94-244 × 'Goldex' population, the magnitude of the average degrees of dominance, estimated based on the variances, indicated the existence of partial dominance interactions between the alleles that control the number of mines and pupae per plant variables, subjective score, and overdominance in control of the number of mines. In relation to the CNPH 94-244 × 'Iracema' population, the values of average degree of dominance suggested the action of partial dominance among the alleles that control the variables studied.

Another aspect of the quantitative traits, when controlled by various genes, is the fact that some of the descendants are found outside of the upper and lower limits of the parents, and they are called transgressive segregants (Hautea *et al*., 1987; Wesp *et al*., 2008). There were no individuals in F_2 with better performance than the resistant parent in either population. However, transgressives occurred for susceptibility to *L. sativae*, observed in the CNPH 94-244 × 'Goldex' population in three of the variables studied, with the exception of subjective score, and in the CNPH 94-244 × 'Iracema' population only in the number of mines variable. Nevertheless, transgressive segregation for susceptibility is not interesting for melon breeding regarding resistance to *L. sativae* since the purpose is selection of individuals with a larger number of alleles for resistance in relation to the best parent.

The estimate of the number of genes in the two populations indicated oligogenic inheritance for the subjective score variable and polygenic for number of mines and pupae per plant. In the number of mines variable, there was contradiction between the populations: it was polygenic (13 genes) when estimated in the CNPH 94-244 × 'Goldex' population and oligogenic (5 genes) in the CNPH 94-244 × 'Iracema' population. Previous studies showed that inheritance of resistance to *Liriomyza* spp. and *L. sativae* was monogenic (Celin *et al*., 2017b; Dogimont *et al*., 1999). However, these are cases of antibiosis resistance.

From the results observed, it can be inferred that the introgression of resistance alleles from the accession CNPH 94-244 will be a time-consuming process. In spite of the predominance of the additive effect, narrow-sense heritability generally has a value from moderate to low. That means that most of the phenotype is due to the environmental effect, which is related to the large number of genes involved in expression of the traits studied, and that makes selection difficult. However, the number of mines per plant variable showed moderate to high narrow-sense heritability and may be the best strategy for selection of superior individuals in segregating generations.

CONCLUSION

Genetic inheritance of resistance to *L. sativae* by antixenosis in the CNPH 94-244 accession has predominance of additive effects: oligogenic for the subjective score variable and polygenic for the number of mines and pupae per plant variables in both populations. By the number of mines variable, it was polygenic in the CNPH 94-244 × 'Goldex' population and oligogenic in the CNPH 94-244 × 'Iracema' population. Therefore, the CNPH 94-244 accession can be used as a resistant progenitor in melon breeding programs aimed at leafminer resistance, with prospects for significant genetic gains in reducing the number of mines and pupae.

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