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Exploring Gene Action Underlying Post-Harvest Water Loss in Fresh Market Peppers

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Abstract: The objective of this study was to evaluate the genetic effects involved in post-harvest water loss of *C. baccatum* fruits and to correlate fruit morphological characteristics. Fruits of eight landraces of *C. baccatum* and their twenty-eight hybrids were evaluated in a randomized, complete block design. Analysis of variance, diallel analysis, phenotypic and genotypic correlation, and path analysis for eight fruit traits were performed. Fruit width, fruit length, dry matter content, and fruit wall thickness were determined by additive gene effects. On the other hand, the non-additive effects played more important role than additive ones, including water loss, cuticle thickness, exocarp thickness, and total soluble solids. The relationship of fruit traits suggested that indirect selection can be carried out from field experiments under different environmental conditions. Overall, genitors 4, 24, 50, and 56 should be selected to form new populations to improve these traits. The Brazilian pepper landraces of *C. baccatum* species are a source of genetic variability for plant breeders, and the new segregating populations emerging through the crossing of pepper lines with reduced water loss should be developed, opening new ways for conventional breeding.

Keywords: shelf life; genetic effects; diallel; narrow-sense heritability

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1. Introduction

Worldwide, only 5 of the 31 species of *Capsicum* are commonly cultivated for commercial purposes [1]. The five domesticated species are *Capsicum annuum*, *Capsicum baccatum*, *Capsicum chinense*, *Capsicum frutescens*, and *Capsicum pubescens* [2]. These species are commercialized as fresh fruits, as raw material for the processing food industry, or as ornamental and medicinal plants [3]. However, peppers grown for fresh market are subjected to water loss once harvested, limiting the fruit shelf life [4,5].

The role of the cuticle in fruit water loss was discussed in recent reviews [4,6–10]. Several studies reported that the fruit cuticle [5,11–14] or exocarp thickness [15] varies among marked cultivars, and this variation likely influences many fruit quality traits, especially water loss rates. The exocarp consists of the cuticle and epidermal cells forming the skin of fruit, which influences the shelf life of ripe fruit. The exocarp tissue was associated with the rate of water loss in tomato fruit [15]. Previous study with *C. chinense* showed the importance of morphophysiological characteristics on shelf life and the benefit of breeding for this trait [16].

C. baccatum and *C. chinense* are the predominant commercial hot pepper species sold in Brazil [17]. The great variability of fruit traits, including color, shape, length, and pungency, between and within these two species remains unknown [2,17,18]. The germplasm bank assembled at the Federal University of Viçosa (Brazil) contains most of the Brazilian cultivated species and is considered one of the most important genetic sources for *Capsicum* collected in the New World [19]. By preserving a large number of local pepper genotypes, it is possible to maintain a large pool of desirable genes that can be used in different pepper selection programs [7,9,14]. Wild plants and/or landraces are important sources that provide information about the diversity of cuticle morphology in pepper fruits. Several germplasm studies have been conducted with peppers to evaluate natural variation of water loss rates and to understand its relationship with cuticle components and properties [20]. Previous analysis of 50 accessions from diverse sources of peppers around the world indicated that water loss is reduced in accessions belonging to *C. baccatum*, particularly those collected in Brazil [11].

Understanding how the cuticle evolves and the role of the major genes involved in cuticle changes during storage is crucial for addressing the role of the cuticle during the post-harvest stage. Despite all efforts made by researchers around the world, genetic studies on post-harvest water loss are still limited in pepper, and more effort is necessary to understand the genetic effects involved on fruit water loss and to allow germplasm screening for accessions with enhanced postharvest characters [3,5,20].

The first step in an effective breeding program is to select the proper parents and, by combining the breeding value of them, to produce superior hybrids. The knowledge of magnitudes of general combining ability (GCA) and specific combining ability (SCA) effects is indicative of the relative importance of additive and non-additive (dominance or epistasis) gene action in the inheritance of a trait, respectively. The crosses presenting desirable specific combining ability along with good general combining ability could be used in breeding programs [18]. Knowledge of the gene action of plant traits is essential for the advance of effective breeding programs [21], alongside studies of hybridization and the heterotic vigor of diallel mating design [22], helping breeders to choose the appropriate improvement method [21,22].

Although several works have been carried out on the cuticle function in water loss with different species and/or genetically divergent genotypes within a species, only a few of them were genetic studies based on multiway crosses. Populations from a biparental cross, such as recombinant inbred lines (RIL), backcross inbred lines (BIL), and near-isogeneic inbred lines (NIL), have been generated to study quantitative traits such as cuticle-associated characteristics under different environmental conditions [12,23]. Conversely, the random intercrossing of multiple founder genotypes produces a multiparent advanced population by diallel cross followed by successive selfing. The resultant populations of a multiparent advanced generation intercross (MAGIC) have multiallelic states of each gene; consequently, a higher genetic and phenotypic variability is achieved as well as higher resolution for QTL mapping compared to biparental populations [24].

Given the significance of water loss in pepper fruit storage, the objective of this study was to evaluate the genetic effects involved in post-harvest water loss of *C. baccatum* fruits and to correlate fruit morphological traits with the shelf water loss.

2. Materials and Methods

2.1. Plant Material

Eight landraces of *C. baccatum*, such as UFV 04, UFV 24, UFV 38, CB 44, CB 46, CB 50, CB 56, and CB 58, from the Federal University of Viçosa—Horticultural Germplasm Bank, were selected according to genetic background and phenotypic diversity (Table 1).

Table 1. Fruit traits for eight parents of *Capsicum baccatum* var *pendulum* used in the diallel cross.

Parents	Color	Cuticle Thickness	Exocarp Thickness	Width	Length	Total Soluble Solids	Dry Matter Content	Wall Thickness
		µm	µm	mm	mm	%	%	mm
UFV—04	red	25	145	53	46	9.6	14	3
UFV—24	red	22	110	32	142	10.2	15	2.3
UFV—38	red	22	65	19	69	8.7	15	1.7
UFV—44	yellow	25	95	15	74	9.4	17	2.3
UFV—46	red	20	90	14	57	9.6	23	1.5
UFV—50	red	25	130	37	44	8.8	18	2.9
UFV—56	red	25	95	10	47	12.9	28	0.9
UFV—58	red	35	105	17	66	10.7	16	1.9
CV (%)		18.1	23.6	59.8	46.8	13.5	24.4	34.3

CV = Coefficient of variation.

2.2. Hybridization and Field Evaluation

The eight landraces were crossed during the winter season, with an average temperature of 16 °C, in a complete diallel at the Garden Field of Federal University of Viçosa, Minas Gerais, Brazil. The F_1 seeds of the 28 hybrids and 8 parents were planted in the field in a randomized, complete block design (r = 3). Experimental plots were comprised of 10 pepper plants with an in-row spacing of 1.0 m and a row spacing of 1.0 m.

In this study, fruits were harvested at maturity with 4 fresh healthy fruits per repetition, totalizing 12 fruits per treatment. The water loss experiment was conducted twice during the summer season at an average temperature of 22 °C. Once significance was not detected within the interaction (genotype × time), the following analyses were performed using the mean of the two experiments. Then, each mean from 24 fruits per treatment was used. The fruits were washed with distilled water, air-dried, and packed in low-density polystyrene (17.5 cm × 20 cm × 0.5 cm) and unpacked kept at 20 ± 1 °C for 9 days. The characteristics of the soil in the 0 –20 cm deep layer was sampled before the experiments were set up, where pH (in water) = 5.3; P = 13.6 mg dm^{-3}; K = 38 mg dm^{-3}; Ca^{2+} = 2.6 cmolc dm^{-3}; Mg^{2+} = 0.7 cmolc dm^{-3}; Al^{3+} = 0.0 cmolc dm^{-3}; H + Al = 2.97 cmolc dm^{-3}; P-rem = 33.6 mg L^{-1}; CTC = 6.37 cmolc dm^{-3}; and V = 53%. The cultural management was carried out according the recommendations for *Capsicum* [25].

2.3. Studied Traits

The water loss of each fruit was measured as the difference of fruit weight before and after storing. In addition, the fruit width, fruit length, total soluble solids, fruit dry matter content, and pericarp thickness was measured in each fruit of all plots following the *Capsicum* descriptors [26]. The cuticle thickness and exocarp thickness were measured using a light microscopy and a 5 mm diameter cork borer, in which longitudinal sections were cut on a manual microtome, and measurements were performed under light microscopy with an ocular-micrometer scale.

2.4. Statistical Analysis

Data were subjected to analysis of variance using the software Genes [27]; when the *F* value was significant, a multiple-means comparison was performed using the Scott–Knott criterion at 0.01 significance.

Genetical analyses were performed using the software Genes [27], in which the diallel analysis was performed to estimate general combining ability (GCA) and specific combining ability (SCA) effects using the procedure described by Griffing [28], Model II, fixed model. The following statistical model was used: $X_{ijk} = u + g_i + g_j + s_{ij} + e_{ijk}$, where X_{ijk} is the observation value for a cross between the parent *i*th and *j*th in the *k*th replication; u is the general population mean; g_i and g_j are the GCA values of the *i*th and *j*th parents, respectively; s_{ij} is the SCA value for the hybrid between the parent *i*th and *j*th; and e_{ijk} is the error. Significant differences among GCA effects and SCA effects were tested using *F* values.

An one-way multivariate analysis of variance model was also fitted to estimate genotypic covariance components using the method of moments. Phenotypic and genotypic correlation matrices were obtained and displayed in a weighted correlation network diagram [29]. To determine the direct and indirect effects of fruit descriptors over the fruit water loss, a path analysis model was fitted. Analyses were carried out with the software R v.4.2.1 [30].

3. Results

3.1. Analysis of Variance

Based on the analysis of variance, there was significant difference among landraces and/or hybrids for all evaluated traits. The general combining ability (GCA) variance was significant for all variables except for exocarp thickness. The specific combining ability (SCA) variance was also significant for all traits except for water loss and fruit dry matter content.

Values of the $\frac{GCA(\hat{\varnothing}_g^2)}{SCA(\hat{\varnothing}_s^2)}$ ratio were higher than one for fruit width, fruit length, dry matter content, and fruit wall thickness, indicating these traits are determined by additive gene effects. These data were validated by the values of narrow-sense heritability. On the other hand, the non-additive effects (dominance and epistasis) played a more important role than the additive ones, including water loss, cuticle thickness, exocarp thickness, and total soluble solids (Table 2).

3.2. Performance of the Evaluated Parents and F1 Hybrids

According to the Scott–Knott test, the highest variability was determined for the exocarp thickness and fruit length (six groups), followed by the fruit width (five groups), total soluble solids and fruit wall thickness (four groups), dry matter content (three groups), and water loss and cuticle thickness (two groups) (Table 3).

The genitors 04, 24, 44, 46, and 56 presented major values of water loss, while the genitors 38, 50, and 58 had lower values of water loss. Among the parents, only 58 presented a high value for cuticle thickness. Regarding exocarp thickness and fruit width, the highest values were presented by genitor 04, followed by genitor 50. Genitor 24 was highlighted for fruit length and total soluble solids (TSS). (Table 3). Higher values of dry matter content were found for genitor 56, while fruit wall thickness were higher for the genotypes 04, 24, and 50.

Among the hybrids combinations, those with higher water loss were 4 × 46, 24 × 46, 24 × 56, 38 × 44, 38 × 46, 44 × 46, 44 × 56, and 46 × 56 and with minor cuticle thickness were 44 × 58, 46 × 58, 50 × 58, and 56 × 58. Regarding TSS and dry mater content, the hybrid 46 × 56 had high values, while for fruit wall thickness, the hybrids 04 × 24, 04 × 38, 04 × 46, 04 × 50, 24 × 50, 44 × 50, 50 × 56, and 50 × 58 were highlighted (Table 3).

3.3. General Combining Ability (GCA)

Parents 46 and 56 had significant positive general combining ability for water loss, according to estimates for the combining ability effects ($\hat{g}_i$). Contrarily, genitors 4 and 58 had a negative general combining ability for water loss. Considering cuticle thickness, parents 4 and 58 had significant positive values of $\hat{g}_i$, and parents 38 and 46 had negative values of $\hat{g}_i$ (Table 4).

Majorly significant positive values of $\hat{g}_i$ for exocarp thickness were measured for parents 4, 46, and 50, while parents 38, 56, and 58 had significant negative values of $\hat{g}_i$ for exocarp thickness (Table 4).

Parents 4 and 50 had significant positive $\hat{g}_i$ effects for fruit width; contrarily, parents 38, 44, 46, 56, and 58 had significant negative $\hat{g}_i$ effects for fruit width (Table 4).

Parents 24 and 38 had significant positive values for fruit length; contrarily, parents 4, 44, 46, 50, and 56 had significant negative values (Table 4).

Significant positive $\hat{g}_i$ values of total soluble solids were measured for parents 24, 46, and 56. All other parents had significant negative values (Table 4).

Considering fruit dry matter content, parents 46 and 56 showed significant positive values, while parents 4, 24, 38, 50, and 58 had negative effects (Table 4).

For fruit wall thickness, only parent 56 presented significant negative $\hat{g}_i$ effects.

Table 2. Analysis of variance (mean squares) and quadratic components of GCA ability ($\hat{\varnothing}_g^2$) and SCA ability ($\hat{\varnothing}_s^2$) for fruit traits of 8 × 8 diallel cross in pepper (*Capsicum baccatum*).

SV	DF	Water Loss	Cuticle Thickness	Exocarp Thickness	Fruit Width	Fruit Length	Total Soluble Solids	Dry Matter Content	Fruit Wall Thickness
		%	µm	µm	mm	mm	%	%	mm
Treatment	35	373.97 **	43.83 **	1,073.92 **	202.83 **	1355.95 **	3.83 **	26.86 **	1.20 **
GCA	7	1222.04 **	85.89 *	1369.19 ^{ns}	769.60 **	5890.07 **	10.04 **	107.65 **	4.97 **
SCA	28	161.95 ^{ns}	33.31 **	1000.10 **	61.13 **	222.43 **	2.35 **	6.67 ^{ns}	0.26 **
Error	36	131.05	12.67	50.35	6.91	55.75	0.32	3.94	0.05
ϕ^2_g		54.55	10.93	3,035.35	38.13	291.71	0.48	5.18	0.24
ϕ^2_s		15.45	48.55	35,862.19	27.11	83.33	1.01	1.34	0.1
ϕ^2_g/ϕ^2_s		3.53	0.22	0.08	1.4	3.5	0.47	3.86	2.4
Mean		37.04	25.55	87.43	21.57	72.59	8.88	17.63	2.14
h^2_b (%)		94.01	71.08	95.31	93.2	95.88	91.73	85.32	95.19
h^2_n (%)		63.26	21.8	21	74.6	81.7	48	71.8	80.27

^{ns}, * and ** = non-significant, significant ($p \leq 0.05$), and significant ($p \leq 0.01$) by F test, respectively. $h^2_{b\ \mathrm{and}}$ h^2_n= broad-sense heritability and narrow-sense heritability, respectively.

Table 3. Means of fruit traits evaluated in 8 parents and 28 hybrids F_1 of pepper (*Capsicum baccatum* var. *pendulum*).

Parents/Hybrids	Water Loss	Cuticle Thickness	Exocarp Thickness	Width	Length	Total Soluble Solids	Dry Matter Content	Wall Thickness
	%	µm	µm	mm	mm	%	%	mm
4	31.47 b[†]	25.00 b	145.00 a	62.15 a	51.10 f	7.50 d	13.70 c	2.80 a
04 × 24	18.64 b	27.50 a	45.00 f	25.80 c	95.25 c	8.65 d	14.45 c	3.15 a
04 × 38	33.31 b	32.50 a	85.00 d	31.70 b	60.75 f	8.50d	14.50 c	2.75 a
04 × 44	17.66 b	35.00 a	105.00 c	19.85 d	61.10 f	9.50 c	15.05 c	2.35 b
04 × 46	45.44 a	25.00 b	100.00 c	20.25 d	55.10 f	7.60 d	17.35 c	2.80 a
04 × 50	36.99 b	30.00 a	115.00 b	33.20 b	52.40 f	7.90 d	16.20 c	3.25 a
04 × 56	31.27 b	30.00 a	60.00 e	13.50 e	59.00 f	10.20 c	20.15 b	1.10 d
04 × 58	14.47 b	30.00 a	65.00 e	25.65 c	84.50 d	8.30 d	14.45 c	2.60 b
24	49.25 a	22.50 b	110.00 c	23.75 d	173.50 a	11.90 b	13.70 c	2.85 a

Table 3. *Cont.*

Parents/Hybrids	Water Loss	Cuticle Thickness	Exocarp Thickness	Width	Length	Total Soluble Solids	Dry Matter Content	Wall Thickness
	%	µm	µm	mm	mm	%	%	mm
24 × 38	22.60 b	30.00 a	90.00 d	19.70 d	128.30 b	7.80 d	12.60 c	1.86 c
24 × 44	32.74 b	27.50 a	70.00 e	20.55 d	107.00 c	10.55 c	15.80 c	2.45 b
24 × 46	58.28 a	30.00 a	70.00 e	21.35 d	88.95 d	8.85 d	16.80 c	2.40 b
24 × 50	25.17 b	23.75 b	120.00 b	32.50 b	105.65 c	9.80 c	14.45 c	3.25 a
24 × 56	57.77 a	30.00 a	95.00 d	12.20 e	70.75 e	11.40 b	23.25 b	1.55 c
24 × 58	25.67 b	20.00 b	75.00 e	21.30 d	99.30 c	7.70 d	16.00 c	2.35 b
38	31.98 b	22.50 b	65.00 e	19.20 d	85.40 d	9.05 c	16.00 c	1.70 c
38 × 44	46.10 a	17.50 b	65.00 e	16.25 e	73.05 e	7.35 d	18.70 c	1.65 c
38 × 46	43.01 a	21.25 b	92.50 d	17.15 d	70.60 e	9.35 c	19.75 b	2.30 b
38 × 50	25.63 b	20.00 b	65.00 e	26.7 c	78.40 e	7.65 d	14.70 c	2.25 b
38 × 56	36.75 b	20.00 b	65.00 e	14.4 e	61.75f	8.70 d	21.00 b	1.00 d
38 × 58	30.23 b	22.50 b	40.00 f	18.35 d	68.85 e	7.50 d	16.0 c	1.65 c
44	45.58 a	25.00 b	95.00 d	14.00 e	56.70 f	7.00 d	18.60 c	1.80 c
44 × 46	41.63 a	20.00 b	82.50 e	13.80 e	60.05 f	9.60 c	21.35 b	1.65 c
44 × 50	35.11 b	22.50 b	102.50 c	30.75 b	56.90 f	7.65 d	15.35 c	3.05 a
44 × 56	44.48 a	22.50 b	85.00 d	13.30 e	64.05 f	9.35 c	22.75 b	1.15 d
44 × 58	26.46 b	32.50 a	90.00 d	15.50 e	84.60 d	8.10 d	17.10 c	1.85 c
46	62.85 a	20.00 b	90.00 d	12.40 e	48.15 f	10.35 c	22.30 b	1.70 c
46 × 50	40.33 a	22.50 b	110.00 c	25.75 c	56.65 f	9.40 c	18.10 c	2.90 b
46 × 56	62.41 a	22.5 b	92.50 d	10.50 e	45.70 f	13.30 a	27.55 a	0.85 d
46 × 58	27.22 b	27.50 a	97.50 d	13.30 e	63.45 f	8.15 d	22.80 b	1.40 c
50	32.35 b	25.00 b	130.00 b	36.05 b	66.65 f	8.20 d	13.65 c	3.10 a
50 × 56	48.52 a	20.00 b	55.00 f	26.10 c	47.05 f	8.35 d	16.00 c	3.20 a
50 × 58	13.75 b	27.50a	75.00 e	31.40 b	54.90 f	8.40 d	15.85 c	3.05 a
56	67.67 a	25.00 b	95.00 d	7.85 e	42.40 f	10.25 c	26.05 a	0.50 d
56 × 58	36.21 b	30.00 a	100.00 c	13.40 e	61.80 f	7.85 d	16.05 c	1.10 d
58	34.71 b	35.00 a	105.00 c	17.00 d	73.5 e	8.20 d	16.70 c	2.00 c

[†] Values followed by different letters within fruit traits (column) indicate significant difference among parents/hybrids according to Scott–Knott's criterion ($p \leq 0.01$).

Table 4. Estimates of general combining effects (g_i) and specific combining effects (S_{ij}) for fruit traits of parents and hybrids, respectively, of an 8 × 8 diallel cross in peppers (*Capsicum baccatum* var. *pendulum*).

	Water Loss	**Cuticle Thickness**	**Exocarp Thickness**	**Width**	**Length**	**Total Soluble Solids**	**Dry Matter Content**	**Wall Thickness**
	%	**μm**	**μm**	**mm**	**mm**	**%**	**%**	**mm**
Parents								
4	−7.26 **	3.00 **	7.81 **	10.01 **	−8.30 **	−0.43 **	−1. 92 **	0.43 ^{ns}
24	0.59 ^{ns}	0.37 ^{ns}	−0.18 ^{ns}	0.67 ^{ns}	38.88 **	0.85 **	−1.80 **	0.33 ^{ns}
38	−3.18 ^{ns}	−2.12 *	−15.43 **	−1.15 *	5.92 **	−0.50 **	−0.95 *	−0.25 ^{ns}
44	0.19 ^{ns}	0.00 ^{ns}	0.31 ^{ns}	−3.61 **	−3.31 *	−0.38 **	0.46 ^{ns}	−0.15 ^{ns}
46	11.05 **	−2.12 *	3.81 **	−4.72 **	−11.65 **	0.70 **	2.96 **	−0.16 ^{ns}
50	−4.32 ^{ns}	−1.62 ^{ns}	11.56 **	8.43 **	−6.81 **	−0.44 **	−2.10 **	0.78 ^{ns}
56	11.93 **	−0.50 ^{ns}	−4.43 **	−7.51 **	−15.84 **	0.97 **	4.01 **	−0.84 *
58	−9.00 **	3.00 **	−3.43 *	−2.12 **	1.11 ^{ns}	−0.76 **	−0.71 ^{ns}	−0.13 ^{ns}
Hybrids								
4 × 24	−11.73 ^{ns}	−1.43 ^{ns}	−50.05 **	−6.45 **	−7.92 ^{ns}	−0.66 **	0.53 ^{ns}	0.23 ^{ns}
4 × 38	6.71 ^{ns}	6.06 **	5.19 ^{ns}	1.26 ^{ns}	−9.45 **	0.54 ^{ns}	−0.27 ^{ns}	0.42 **
4 × 44	−12.30 *	6.44 **	9.44 *	−8.11 **	0.13 ^{ns}	1.43 **	−1.13 ^{ns}	−0.06 ^{ns}
4 × 46	4.61 ^{ns}	−1.43 ^{ns}	0.94 ^{ns}	−6.61 **	2.46 ^{ns}	−1.55 **		0.38 **
4 × 50	11.53 ^{ns}	3.06 ^{ns}	8.19 *	−6.82 **	−5.08 ^{ns}	−0.11 ^{ns}	2.56 *	−0.11 ^{ns}
4 × 56	−10.43 ^{ns}	1.94 ^{ns}	−30.80 **	−10.57 **	10.55 *	0.78 *	0.42 ^{ns}	−0.63 **
4 × 58	−6.30 ^{ns}	−1.55 ^{ns}	−26.80 **	−3.81 *	19.10 **	0.60 ^{ns}	−0.56 ^{ns}	0.15 ^{ns}
24 × 38	−1.86 ^{ns}	6.19 **	18.19 **	−1.39 ^{ns}	10.90 *	−1.44 ^{ns}	−2.29 *	−0.38
24 × 44	−5.09 ^{ns}	1.56	−17.55 **	1.91 ns	−1.16 ^{ns}	1.19 **	−0.50 ^{ns}	0.12 ^{ns}
24 × 46	9.59 ^{ns}	6.19 **	−21.05 **	3.82 *	−10.87 *	−1.59 ^{ns}	−1.99 ^{ns}	0.07 ^{ns}
24 × 50	−8.15 ^{ns}	−0.55 ^{ns}	21.19 **	1.81 ^{ns}	0.97 ^{ns}	0.50 ^{ns}	0.69 ^{ns}	−0.01 ^{ns}
24 × 56	8.19 ^{ns}	4.56 *	12.19 **	−2.54 ^{ns}	−24.89 **	0.69 *	3.40 **	−1.10 ^{ns}
24 × 58	−2.95 ^{ns}	−8.93 **	−8.80 *	1.17 ^{ns}	−13.29 **	−1.29 **	0.87 ^{ns}	−0.002 ^{ns}
38 × 44	12.03 ^{ns}	−3.43 ^{ns}	−7.30 ^{ns}	−0.56 ^{ns}	−2.14 ^{ns}	−0.65 *	1.55 ^{ns}	−0.10 ^{ns}
38 × 46	−1.90 ^{ns}	−0.05 ^{ns}	16.69 **	1.45 ^{ns}	3.74 ^{ns}	0.27 ^{ns}	0.10 ^{ns}	0.56 **
38 × 50	−3.91 ^{ns}	−4.30 *	−18.55 **	−2.13 ^{ns}	6.70 ^{ns}	−0.29 ^{ns}	0.08 ^{ns}	−0.43 **
38 × 56	−9.05 ^{ns}	−2.93 ^{ns}	−2.55 ^{ns}	1.48 ^{ns}	−0.92 ^{ns}	−0.65 *	0.30 ^{ns}	−0.06 ^{ns}
38 × 58	5.37 ^{ns}	−3.93 *	−28.55 *	0.05 ^{ns}	−10.77 *	−0.13 ^{ns}	0.02 ^{ns}	−0.12 ^{ns}
44 × 46	−6.65 ^{ns}	−3.43 ^{ns}	−9.05 *	0.56 ^{ns}	2.43 ^{ns}	0.40 ^{ns}	0.30 ^{ns}	−0.18 ^{ns}

Table 4. *Cont.*

	Water Loss	Cuticle Thickness	Exocarp Thickness	Width	Length	Total Soluble Solids	Dry Matter Content	Wall Thickness
	%	µm	µm	mm	mm	%	%	mm
44 × 50	2.18 ^{ns}	−1.43 ^{ns}	3.19 ^{ns}	4.35 **	−5.57 ^{ns}	−0.41 ^{ns}	−0.67 ^{ns}	0.27 *
44 × 56	−4.69 ^{ns}	−2.55 ^{ns}	1.69 ^{ns}	2.84 ^{ns}	10.61 ^{ns}	−0.11 ^{ns}	0.64 ^{ns}	−0.001 ^{ns}
44 × 58	−1.76 ^{ns}	3.94 *	5.69 ^{ns}	−0.33 ^{ns}	14.21 **	0.36 ^{ns}	−0.29 ^{ns}	−0.006 ^{ns}
46 × 50	−3.44 ^{ns}	0.69 ^{ns}	7.19 ^{ns}	0.46 ^{ns}	2.52 ^{ns}	0.26 ^{ns}	−0.42 ^{ns}	0.13 ns
46 × 56	2.37 ^{ns}	−0.43 ^{nsa}	5.69 ^{ns}	1.15 ^{ns}	0.60 ^{ns}	2.75 **	2.94 *	−0.29 *
46 × 58	−11.98 ^{ns}	1.06 ^{ns}	9.69 *	−1.42 ^{ns}	1.40 ^{ns}	−0.68 *	2.91 *	−0.45 **
50 × 56	3.85 ^{ns}	−3.43 ^{ns}	−39.55 **	3.59 *	−2.89 ^{ns}	1.06 **	−3.57 **	1.11 **
50 × 58	−9.95 ^{ns}	0.56 ^{ns}	−20.55 **	3.51 *	−11.99 **	0.71 *	0.99 ^{ns}	0.25 **
56 × 58	−3.76 ^{ns}	1.94 ^{ns}	20.44 **	1.45 ^{ns}	3.94 ^{ns}	−1.24 **	−4.89 **	−0.07 ^{ns}

^{ns}, * and ** = non-significant, significant ($p \leq 0.05$), and significant ($p \leq 0.01$) by *t*-test, respectively.

3.4. Specific Combining Ability (SCA)

The minimum specific combining ability effect values (negative) for water loss were obtained by the hybrid 4 × 44. This result was enhanced by the SCA analyses, in which the hybrid 4 × 44 had the most reduced water loss (Table 4).

Particularly, the S_{ij} values for cuticle thickness for the hybrids 4 × 8, 4 × 44, 24 × 38, 24 × 46, and 44 × 58 had majorly significant positive values, and the hybrids 24 × 8, 38 × 50, and 38 × 58 had majorly significant negative values (Table 4).

Hybrids 4 × 44, 4 × 50, 24 × 38, 24 × 50, 24 × 56, 38 × 46, 44 × 46, and 46 × 58 presented significant positive values S_{ij} for exocarp thickness (Table 4).

Considering fruit width, hybrids 24 × 46, 44 × 50, 50 × 56, and 50 × 58 were positive, but hybrid 4 × 38 had negatives values of S_{ij} (Table 4).

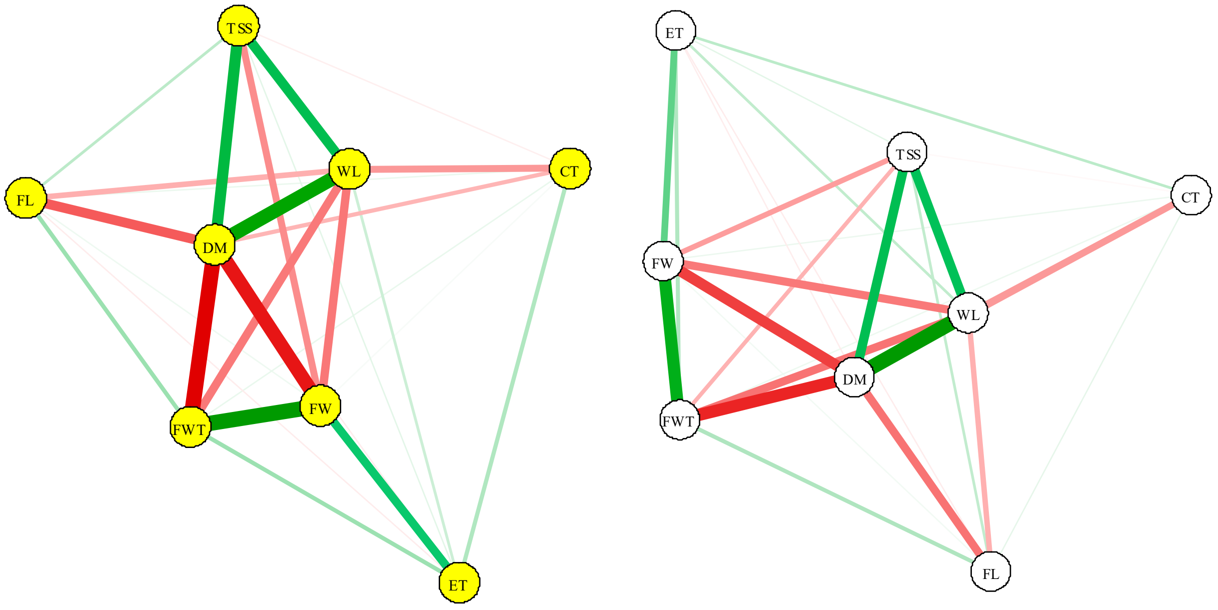
Majorly positive values of S_{ij} for fruit length were found in the hybrids 4 × 56, 4 × 58, 24 × 38, and 44 × 58, while the hybrids 24 × 56, 50 × 58, 24 × 46, and 38 × 58 had negative values.

Regarding TSS, significant values of S_{ij} were measured as positive in the hybrids 4 × 44, 4 × 56, 24 × 44, 24 × 56, 46 × 6, 50 × 56, and 50 × 58 and as negative in 4 × 46, 56 × 58, and 24 × 58 (Table 4).

Considering fruit dry matter content, positive significant S_{ij} values were found for hybrids 4 × 50, 24 × 56, 46 × 56, and 46 × 58. Regarding wall thickness, the hybrids 4 × 38, 4 × 46, 38 × 46, 44 × 50, 50 × 56, and 50 × 58 presented positive significant values (Table 4).

3.5. Interrelationship among Measured Traits

Overall, there was a cluster of phenotypic and genotypic correlations between dry matter content, total soluble solids, wall thickness, fruit width, and water loss (Figure 1; Table 5). The fruit width and fruit wall thickness had strong negative correlations (−0.5 and −0.52) for water loss, respectively. Cuticle thickness and water loss had a moderate negative correlation (−0.38), and dry matter content and water loss had strong positive correlations (0.94).



(**A**) (**B**)

Figure 1. Correlation network for phenotypic (**A**) and genotypic (**B**) for water loss of chili peppers. (CT = cuticle thickness; ET = exocarp thickness; FW = fruit width; FL = fruit length; TSS = total soluble solids; DM = dry matter content; FWT = fruit wall thickness; WL = water loss).

Table 5. Path coefficients of different fruit characters for fruit water loss on pepper.

	CT	**ET**	**FW**	**FL**	**TSS**	**DM**	**FWT**	**Genetic Correlation Coefficient**
CT	−0.56	0.09	−0.03	−0.04	−0.01	0.18	−0.01	−0.38
ET	−0.11	0.47	−0.25	0.04	0.06	0.03	−0.05	0.19
FW	−0.03	0.2	−0.57	−0.02	−0.24	0.34	−0.18	−0.50
FL	−0.04	−0.03	−0.02	−0.51	0.12	0.25	−0.06	−0.29
TSS	0.01	0.04	0.21	−0.09	0.65	−0.29	0.07	0.60
DM	0.21	−0.03	0.4	0.27	0.39	−0.48	0.18	0.94
FWT	−0.03	0.11	−0.44	−0.12	−0.19	0.38	−0.23	−0.52

$R^2 = 0.79$. Residue = 0.46. (CT = cuticle thickness; ET = exocarp thickness; FW = fruit width; FL = fruit length; TSS = total soluble solids; DM = dry matter content; FWT = fruit wall thickness).

The coefficient of determination of the model for the path analysis was high ($R^2 = 0.79$). The highest correlation (0.94) of the WL was with dry matter, with indirect effects of fruit width, fruit length, and TSS; nonetheless, dry matter presented a negative direct effect over WL (Table 5). TSS presented the highest direct effect (0.65) over WL, with indirect effects of dry matter and fruit width. Fruit wall thickness presented a low direct effect over WL, with its correlation (−0.52) being influenced mainly by the indirect effects of fruit width and dry matter. In general, we observed that dry matter and/or fruit width have indirect effects on the correlation of all fruit traits with water loss (Table 5).

4. Discussion

4.1. Analysis of Variance

Genetic diversity among genotypes of different landraces can be used to improve the fruit quality of commercial pepper [12,18,19]. The variation among *C. baccatum* landraces and their hybrids for all evaluated traits in this study is substantiated by the correlations. Furthermore, significant differences were found for water loss (WL), showing a selection of good progenitors for exploring hybrid vigor, which can be efficient and much less expensive in the reduction of fruit post-harvest water loss.

Tropical deforestation is among the most massive and urgent environmental problems facing *Capsicum* germplasm resources [31]. The expansion of agribusiness in many locations around the world, including some states of Brazil, could lead to the extinction of landraces of several endemic chili species, like *C. baccatum.* Furthermore, the indiscriminate expansion of sugar cane, cotton, coffee, and soybean plantations led to the reduction of the Atlantic Forest in Brazil, reducing the genetic pool for the non-domesticated *Capsicum* species before researchers even had the chance to evaluate them [32]. In conclusion, the maintenance of these landraces at the Germplasm Bank of Federal University of Viçosa, associated with studies of diversity and gene action, is essential to preserve this useful genetic material. Additionally, knowledge about native diversity is essential for conserving variability, preventing genetic erosion, and safeguarding food security [33].

The significant additive gene effects in this study, coupled with the high narrow-sense heritability values observed for the evaluated characters, demonstrated that an effective way to reduce water loss and improve fruit width, fruit length, dry matter content, and fruit wall thickness should be achieved through repeated backcrosses and selection of desirable recombinants from segregating populations. The existing variability detected among genotypes associated with additive gene effects allows for gains when selection is practiced in an early generation [18]. On the other hand, to consider cuticle thickness, exocarp thickness, and TSS, the results suggest the possibility of exploring hybrid vigor based on the significant non-additive effects found for these traits.

Other studies corroborate the results found in this work, showing that additive gene effects are predominant for water loss [12], fruit length [34–36], fruit width [35,36], and for fruit wall thickness [37]. On the other hand, some studies have shown that dominant variation is the predominant gene effect for TSS [18,21] in peppers.

The use of divergent parents for water loss was crucial for studying the gene effects since the use of not-divergent genitors did not allow investigation of the inheritance of this trait in a previous study [38].

4.2. Performance of the Evaluated Parents and F1 Hybrids

The cuticle thickness (CT) of evaluated genotypes ranged from 20 to 35 μm and for exocarp thickness (ET) from 40 to 145 μm. These values were superior to the measurements of *C. annuum* genotypes, which reached 8.8 to 21 μm and 20.7 to 116.2 μm for CT and ET, respectively [14]. *C. chinense* species also had thinner ET (10 to 20 μm) compared with the *C. baccatum* landraces evaluated in this study [17].

Regarding wall thickness (WT), the range was similar to results reported for *C. annuum* [14] at around 3 mm but not to *C. chinense* (0.95 to 2.34 mm) [16].

Observing fruit length, that of *C. baccatum* landraces was bigger (42.4 to 173.5 mm) than that of *C. chinense* accessions (28.7 to 45.4 mm) [16] and smaller than that of *C. annuum* (33 to 194.0 mm) [33].

The major value of TSS presented this work was 13.3%, superior to the low PWL-NIL derived from the hybrid of *C. annuum* × *C. chinense* [12].

Thus, the landraces of *C. baccatum* represent a unique material for breeding programs aiming to enhance these traits.

4.3. General Combining Ability (GCA)

In this study, good general combiners showed no better average performance, indicating that the parent should be selected based on estimates of general combining effects (g_i) and not by mean performance. To advance generations in a breeding program based on hybridizations methods, parents with good general combining ability for the target trait must be selected [18,21]. In order to reduce water loss during the selection process, in the successive self-fertilization generations, it is necessary to select a hybrid that has one of the parents with negative g_i estimates, such as parents 4 and 58. These two genitors are also good combiners based on g_i for cuticle thickness. Parents 4 and 50 are good combiners for exocarp thickness and fruit width. The gi values of fruit length of genitors 24 and 38 are the best for enhancing this trait. Parents 24 and 56 were good combiners for TSS. Conversely, parents 46 and 56 were good combiners for dry matter content. Overall, genitors 4, 24, 50, and 56 should be selected to form new populations to improve these traits. On the other hand, a previous study with different varieties of *Capsicum baccatum* indicated only one cultivar, i.e., 'BRS Mari', as a good combiner in a genetic effects study [21].

4.4. Specific Combining Ability (SCA)

Selecting hybrids with good specific combining ability effects (s_{ij}) and at least one parent with ideal estimates of general combining effects for a particular trait is a good strategy for plant breeding [18,21,28]. In this way, we indicate the following selections for water loss (4 × 44), cuticle thickness (4 × 30, 4 × 44, and 44 × 58), exocarp thickness (4 × 44, 4 × 50, 24 × 50, 38 × 46, and 46 × 58), fruit width (44 × 50, 50 × 56, and 50 × 58), fruit length (24 × 38), TSS (4 × 56, 24 × 56, 46 × 56, and 50 × 56), dry matter content (24 × 56, 46 × 56, and 46 × 58), and fruit wall thickness (4 × 38 and 4 × 46).

4.5. Interrelationship among Measured Traits

The similarities among the phenotypic and genotypic correlation matrices are explained by the large values of broad-sense heritability of all fruit traits, indicating that the environmental factors had low effects over both the variability and relationship of fruit traits, suggesting that indirect selection can be carried out from field experiments under different environmental conditions. This kind of similarity was already observed for genotypes of *Capsicum* spp. [39].

Fruit length and exocarp thickness, with low correlation and/or coefficient path values, cannot be used alone to obtain satisfactory genetic gains in WL. On the other hand, it is possible to obtain gains by selecting for those traits along with fruit dry matter and fruit width, respectively, which have indirect effects over WL by the fruit length and exocarp thickness. In *C. chinense*, the exocarp thickness was negatively correlated with water loss [16].

By selecting fruits with higher cuticle thickness and fruit width values and lower TSS values, we are indirectly selecting fruits with lower WL, which may be used as a criterion to help in indirect selection. In agreement with these data, near-isogenic lines with low post-harvest water loss had lower values of TSS [13]. In *C. annuum*, the thickness of the cuticular membrane wedged between subepidermal cells was correlated with water loss [14]. The negative correlation of fruit dimensions (width and length) with post-harvest water loss was reported [40], and here, we demonstrate that there are direct effects. Due to the indirect effects of fruit width, fruit length, and TSS, dry matter should not be used alone for indirect selection of genotypes.

5. Conclusions

Fruit water loss is a major concern for the post-harvest shelf life for pepper destined for fresh market. The multiparent populations developed in this study represent a unique material to use in breeding programs with the goal of extending the shelf life of *Capsicum* fruits. The identification of lines and hybrids with genetically lower total soluble solids and higher cuticle thickness provide genetic variability for improving pepper varieties' shelf life. In addition, the Brazilian pepper landraces of *C. baccatum* species are a source of genetic variability for plant breeders, and the new segregating populations emerging through the crossing of pepper lines with reduced water loss should be developed, opening new ways for conventional breeding. Therefore, the pepper industry and consumers could benefit significantly from newly developed varieties with improved post-harvest qualities.

This study was the first one screening the gene action of post-harvest fruit water loss in Brazilian *C. baccatum* landraces, and it showed low water-loss varieties could be developed from the original landraces held in the UFV germplasm bank. Overall, breeding programs seeking to reduce water loss in the post-harvest management of pepper should indirectly select fruit with a thicker cuticle, larger width, and lower total soluble solids. Contrarily, fruit length and exocarp thickness have no effect on water loss.

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