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Combining ability of parental forms, inheritance of the trait of lycopene content in fruits of F1 tomato hybrids

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Abstract: Tomatoes contain many vitamins and minerals, and the antioxidant potential is provided by the carotenoid pigment lycopene. The main direction of our research is the improvement of the quality of tomato fruits, the assessment of the general and specific combining ability of five parental forms of tomato, and the establishment of the character of inheritance. Three medium-ripe lines (№492; №494; LK490) and two genotypes (Dark Green, T-3627) with mutant genes for increased lycopene content in fruits ($hp\text{-}2^{dg}$, B^{c}) were selected for diallel crossing (5 x 5). The conducted genetic analysis showed that the content of lycopene in tomato fruits is controlled by an additive-dominant genetic system. The main role in the genetic control of traits is played by the additive effects of genes, which allows selection by phenotype, starting from the second hybrid generation. Inheritance of lycopene content in tomato fruits occurs by the type of incomplete dominance. A high (positive assessment of the effects) of the general combining ability (GCA) according to the content of lycopene in tomato fruits over the three years of research had the Dark Green genotype (0.48-0.54), the LK 490 line (0.26-1.68), genotype T-3627 (0.38-1.09)–for two years.

Key words: tomato, combining ability, lycopene content in fruits, hybrid, breeding

Kombinacijska sposobnost starševskih oblik F1 križancev paradižnika za dedovanje lastnosti vsebnosti likopena vplodovih

Izvleček: Paradižnik vsebuje mnogo vitaminov in mineralov, njegov antioksidacijski potencial daje vsebnost karotenoida likopena. Glavni namen raziskave je bil preučiti možnost izboljšanja kakovosti plodov, oceniti sposobnost splošne in posebne kombinacijske sposobnosti petih starševskih oblik paradižnika in ugotoviti način dedovanja. Tri linije s srednjo zgodnostjo zorenja (№492; №494; LK490) in dva genotipa (Dark Green, T-3627) s spremenjenimi geni za povečanje vsebnosti likopena v plodovih ($hp\text{-}2^{dg}$, B^{c}) so bili izbrani za dialelno križanje (5 x 5). Genetska analiza je pokazala, da je vsebnost likopena v plodovih paradižnika uravnavana z aditivno-dominantnim sistemom dedovanja. Glavno vlogo pri uravnavanja te lastnosti imajo aditivni učinki genov, kar omogoča izbor fenotipov z začetkom v drugi generaciji križancev. Dedovanje vsebnosti likopena v plodovih paradižnika popteka z nepopolno dominanco. Veliko splošno kombinacijsko sposobnost (GCA), ocenjeno po pozitivnih učinkih glede na vsebnost likopena v plodovih je imel v treh letih poskusa genotip Dark Green (0,48-0,54), linija LK 490 (0,26-1,68) in genotip T-3627 (0,38-1,09) sta to izkazala v dveh letih.

Ključne besede: paradižnik, kombinacijska sposobnost, vsebnost likopena v plodovih, križanec, žlahtnenje

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1 INTRODUCTION

Tomato (*Solanum lycopersicum* L.) is one of the most popular fresh vegetables on the world market and occupies a leading position in industrial production (Costa & Heuvelink, 2018; Selvaggi et al., 2021). The health benefits of tomatoes are confirmed by scientific research and human experience. They are the main source of the antioxidant lycopene, which helps in the treatment of many diseases, and also contain easily digestible carbohydrates, pectin substances, rich in vitamins (Poobalan et al., 2019; Madia et al., 2021; Akbari et al., 2022). They have antibacterial and anti-inflammatory effects, regulate the work of the nervous system, they contain a certain amount of phytoncids (Raiola et al., 2014; Sachdeva et al., 2020). Not only this, but they are the main raw material for the cannery industry, as well as active consumption in fresh form for salads and other dishes (Wang et al., 2022; Meng et al., 2022).

Lycopene is a powerful antioxidant and phytonutrient which plays a major role in human life (Arain et al., 2018; Liang et al., 2019; Imran et al., 2020; Li et al., 2021). It has a positive effect on the body's metabolic processes, activates brain activity, normalizes digestive tract activity, improves liver, kidney and genital functions (Sun et al., 2021; Arballo et al., 2021; Abenavoli et al., 2022). According to research, the bioavailability of lycopene in heat-treated tomatoes (tomato pastas, sauces, ketchups) increases compared to fresh tomatoes, which makes it particularly useful for processing (Vitucci et al., 2021; Wu et al., 2022; Tchonkouang et al., 2022).

Currently, there is a worldwide trend towards a healthy diet that is increasing demand for quality products, including tomatoes. The creation of varieties and hybrids with an increased content of lycopene is important to ensuring consumer demand. Our research aims to involve accessions with $hp\text{-}2^{dg}$, B^{c} mutant genes in the breeding process schema, that provides high-value genotypes for future work. The prospects of this direction of research are determined by the successful expansion by scientists of the gene pool of tomato varieties and hybrids with an increased content of lycopene in the fruits.

2 MATERIALS AND METHODS

The basis of our research was the identification of parental forms with high combining ability and carrying out genetic analysis to establish the parameters and character of inheritance of lycopene content in tomato fruits.

The research was carried out in 2017-2019 at the experimental field of the Cherkasy research station of the National Scientific Center «Institute of Agriculture of the National Academy of Agrarian Sciences of Ukraine» (Kholodnyanske) (49^{0} N at 31^{0} 52' E), Ukraine.

The basic material for the study was five parent forms: lines №492, №494, LK490, genotypes Dark Green, T-3627 and twenty F_1 hybrids obtained according to the complete diallel scheme. Experiments were conducted according to the one-factor method of Dospekhov (1985). Analysis of data on lycopene content in fruits was carried out using diallel and genetic analysis (Yates, 1947; Hayman, 1954; Jinks, 1954; Fedin, 1970). Combining ability (general and specific) was determined according to the first scheme of Griffing (1956).

Determination of lycopene content in tomato fruits was carried out according to the simplified method of determination of lycopene by I.K. Murry "Methods of biochemical research of plants" (Ermakov et al., 1952). Tomato fruits for research were selected in the phase of full ripeness. Powdered anhydrous sodium sulfate Na_2SO_4 was used as an adsorbent. Extraction of lycopene from plant material was carried out with a mixture of hexane-acetone (96:4). Indicators were determined on a spectrophotometer using two scales, 451 and 503. Statistical analysis of the results was performed according to the methodology formula in three repetitions (Barrett & Anthony, 2000; Brandt at al., 2003; Anthony & Barrett, 2006; Alda at al., 2009).

3 RESULTS AND DISCUSSION

Over three years of research, significant differences between the options have been established, one can expect unequal content of lycopene in fruits, differences in the combining ability (general or specific) of the studied parental components (Table 1).

It was established that high lycopene content was in LK490 line (4.7-11.0 mg 100 g^{-1}), Dark Green genotype (6.6-10.6) and T-3627 (5.6-8.1 mg 100 g^{-1}). The lowest content in line №492 (1.7-4.0) and №494 (2.1-4.2 mg 100 g^{-1}) (Table 2).

Average indicators of lycopene content in hybrids with the participation of the LK490 line (3.2-8.2 mg 100 g^{-1}), Dark Green genotype (3.5-7.1) and T-3627 (3.4-6.7 mg 100 g^{-1}) exceed the average group indicators for parental components. At the same time, hybrids with the participation of lines №492 and №494 showed lower indicators compared to the average group. The difference between the average indicator of F_1 and the average indicator of the original forms is negative (during the three years of research), that is, the lower expression of the trait dominates.

The conducted analysis of variance of combining ability (Table 3) indicates reliable differences in general

Table 1: Analysis of variance of lycopene content in tomato fruit

Years	Type of scattering	Sum of squares	Degree of freedom	Middle square	F calc.	F тabl.
2017	General	342.7	74			
	Repetitions	0.2	2			
	Options	333.7	24	13.9*	76.4	1.74
	Residual	8.7	48	0.2		
	LSD_{05}			0.7		
2018	General	142.3	74			
	Repetitions	1.1	2			
	Options	124.4	24	5.2*	14.8	1.74
	Residual	16.8	48	0.4		
	LSD_{05}			1.0		
2019	General	169.5	74			
	Repetitions	2.1	2			
	Options	142.7	24	6.0*	11.5	1.74
	Residual	24.7	48	0.5		
	LSD_{05}			1.2		

* Significant at 5 % level

Table 2: Average value of lycopene content in tomato fruits in the parental lines, genotypes, ($^{\bar{x}}P$) and hybrids ($^{\bar{x}}F_1$), mg 100 g^{-1}

Lines, genotypes	Years of research					
	2017		2018		2019	
	P	F1	P	F1	P	F1
№492	4.0	5.5	1.7	2.6	4.0	4.5
№494	4.2	5.6	2.1	2.2	3.3	4.6
LK490	11.0	8.2	4.7	3.2	7.6	6.2
Dark Green	10.6	7.1	6.6	3.5	6.9	6.1
T-3627	8.1	6.2	5.6	3.4	7.4	6.7
$\bar{x}$	7.6	6.5	4.1	3.0	5.9	5.6
LSD05	0.71		0.99		1.20	

and specific combining ability. In addition, a significant reciprocal effect was found in 2017 and 2018.

The genotype Dark Green (0.48-0.54) and the line LK490 (0.26-1.68) had a high (reliable positive assessment of effects) general combining ability (GCA) for lycopene content in fruits over three years of research. Genotype T-3627 had high positive values of GCA for two years of research (0.38-1.09) (Table 4).

Lines №492 and №494 had low (significant negative effect) GCA values–(from minus 1.13 to minus 0.33) and (from minus 1.08 to minus 0.79), respectively, so it is undesirable to use them for creating heterotic hybrids.

As a result of the conducted research, reliable differences in specific combining ability (SCA) were established. To identify lines and genotypes with high or low SCA, the variance for each parental component was calculated for comparison with the overall average value (Table 5).

High reliable values of SCA were observed in two years of research in Dark Green and T-3627 genotypes, and in one year in line LK490.

The variances of the effects of general (δ_{gi}^2) and specific (δ_{Si}^2) combining ability were compared. It was established that in line №494 for three years of research, line №492 for two years of research, genotypes Dark Green, T-3627, line LK490 for one year, the variance of GCA is greater than the variance of SCA, which indicates the superiority of additive effects of genes in the genetic control of the trait "lycopene content in fruits". This makes it possible to recommend selection in the breeding process by phenotype. At the same time, a significant contribution of non-additive effects was revealed, as evidenced by the superiority of SCA variance over GCA in genotypes

Table 3: Analysis of variance of the combining ability of lycopene content in tomato fruits

Years	Type of scattering	Sum of squares	Degrees of freedom	Middle square	F calc.	F tabl.
2017	Hybrids	333.7	24	13.9*	76.4	1.79
	GCA	50.4	4	12.6*	208.0	2.61
	SCA	25.6	10	2.6*	42.3	2.08
	Reciprocals	35.2	10	3.5*	58.0	2.08
	Residual	2.9	48	0.1*		
2018	Hybrids	124.4	24	5.2*	14.7	1.79
	GCA	11.8	4	3.0*	25.3	2.61
	SCA	21.2	10	2.1*	18.1	2.08
	Reciprocals	8.5	10	0.9*	7.3	2.08
	Residual	5.6	48	0.1*		
2019	Hybrids	142.7	24	5.9*	11.8	1.79
	GCA	42.4	4	10.6*	63.2	2.61
	SCA	2.4	10	0.2*	1.4	2.08
	Reciprocals	2.7	10	0.3*	1.6	2.08
	Residual	8.1	48	0.2*		

* Significant at 5 % level

Table 4: Evaluation of effects of general combining ability (GCA) of lycopene content in tomato fruits

Lines,	Years		
genotypes	2017	2018	2019
№492	-1.01*	-0.33*	-1.13*
№494	-0.90*	-0.79*	-1.08*
LK490	1.68*	0,26*	0.60*
Dark Green	0.54*	0,48*	0.52*
T-3627	-0.30*	0.38*	1.09*
LSD05	0.14	0.19	0.23

* Significant at 5 % level

of Dark Green, T-3627, line LK490 over two years of research.

Genetic analysis by Hayman (1954), Jinks (1954) did not reveal an epistatic interaction of genes, the content of lycopene in fruits is determined by an additive-dominant genetic system (Fig. 1-3).

This is confirmed by the high significance of indicators *D* and *H1*, which characterize the variability of lycopene content in tomato fruits (Table 6). The values *H1* and *H2* are unequal, which indicates the presence of alleles that are unevenly distributed among the parental components. The value of *H2/4H1* indicator deviates from the level of 0.25 and is 0.17-0.18, which indicates an unequal number of genes with dominant and recessive alleles in the parental components. The parameter

$\frac{\sqrt{4DH\;1+F}}{\sqrt{4DH\;1-F}}$ ranged from 1.03-2.90, which indicates a more pronounced effect of dominant gene alleles in the studied lines and samples.

The value of parameter *D*, which measures additive variability in the population, was higher compared to values of *H1*, which measures the dominant variability over two years of research. Values *H1* > *H2*, which indicates an unequal ratio of positive and negative effects.

Positive reliable values of *F (F > 0)* indicate a more pronounced influence of dominant alleles in the set of studied lines and samples.

Over two years of research, the average degree of dominance was 0.33-0.82. The regression line crosses the positive part of *Wr* axis, so it is possible to claim incomplete dominance at all loci. In 2018, there was a tendency to dominate, but it is unreliable.

The parameter *h2/H2* is determined in case of a significant difference. Such a difference was observed in 2017 and 2018. This made it possible to calculate the value of this indicator, which is 7.96 and 11.56, respectively.

Table 5: Estimation of variances of general combining ability (GCA) and specific combining ability (SCA) for lines and genotypes of lycopene content in tomato fruits of 2017-2019

Lines, genotypes	Years	№494	LK 490	Dark Green	T-3627	δ_{Si}^2	δ_{gi}^2
№492	2017	0.18	0.68*	-0.23	-0.15	0.10	1.01
	2018	0.04	0.23	-0.45*	0.85*	0.16	0.09
	2019	-0.09	-0.27	-0.02	-0.23	-0.09	1.26
№494	2017		0.39*	-0.34*	0.34*	0.06	0.80
	2018		-0.01	-0.09	-0.63*	0.01	0.60
	2019		-0.11	-0.10	0.45	-0.07	1.15
LK490	2017			-1.10*	-1.06*	0.69*	2.81
	2018			-0.73*	-0.67*	0.17	0.05
	2019			-0.37	-0.10	-0.07	0.34
Dark Green	2017				-1.32*	0.74*	0.28
	2018				-1.38*	0.57*	0.21
	2019				0.22	-0.08	0.25
T-3627	2017					0.71*	0.08
	2018					0.78*	0.12
	2019					-0.05	1.17
Average value	2017					0.46	
	2018					0.34	
	2019					-0.07	

* Significant at 5 % level -Note. δ_{Si}^2 - variance of the effect of specific combining ability; δ_{gi}^2-variance of the effect of general combining ability.

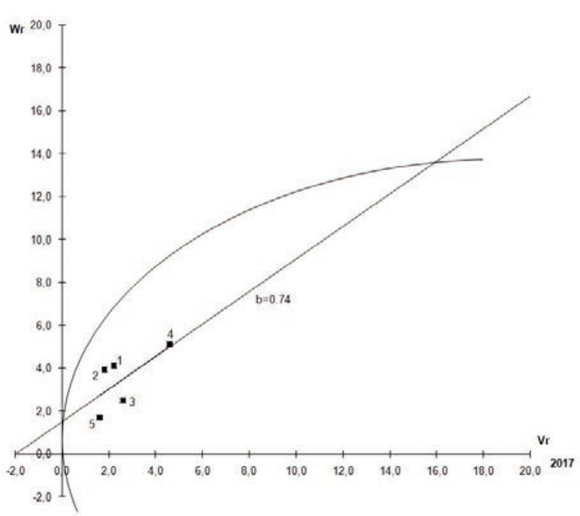

Figure 1: Graph of the dependence of Wr by Vr content of lycopene in tomato fruits, 2017 1-Line №492; 2-Line №494; 3 - Line LK490; 4 - Genotype Dark Green; 5 - Genotype T-3627.

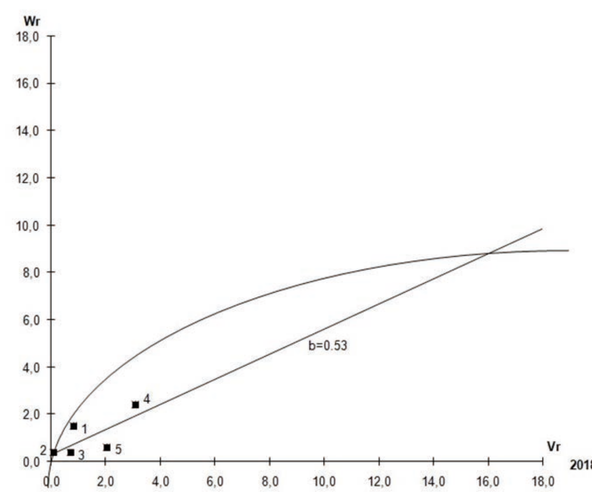

Figure 2: Graph of the dependence of *Wr* by *Vr* content of lycopene in tomato fruits, 2018 1-Line №492; 2-Line №494; 3-Line LK490; 4-Genotype Dark Green; 5-Genotype T-3627.

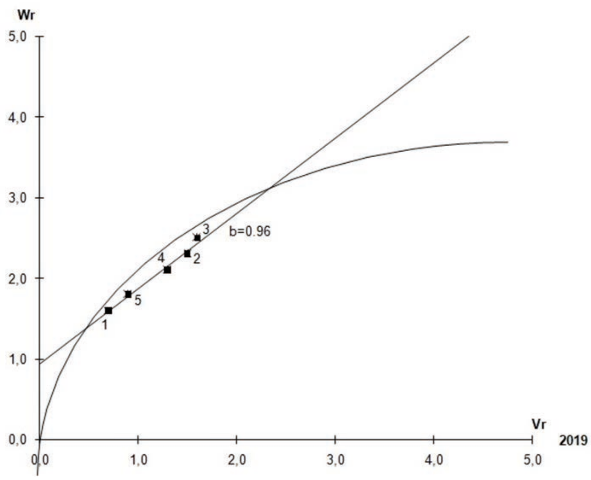

Figure 3: Graph of the dependence of Wr by Vr content of lycopene in tomato fruits, 2019 1 - Line №492; 2-Line №494; 3-Line LK490; 4 - Genotype Dark Green; 5-Genotype T-3627.

That is, the studied parental components differed among themselves from eight to twelve groups of genes, demonstrating the dominance effect.

The highest indicators of the *F* parameter, which reflects the relative contribution of additive and dominant gene action to the phenotypic manifestation of the trait in F_1 hybrids, were obtained in 2017, the lowest in 2019 (Table 7).

Lines №492 and №494, LK490, genotype T-3627 had reliable positive effects in two years of research, in one year – Dark Green genotype. This indicates the dominance of dominant alleles in the indicated lines and samples, one year recessive alleles prevailed.

The correlation coefficient between the average values of lycopene content in tomato fruits of parents ($\bar{x}p$) and the sum *(Wr + Vr)* in 2017 and 2018 was 0.21-0.67 (Table 8). Values of high positive correlation indicate the increasing of the trait by recessive genes. A negative implausible value of the correlation coefficient in 2019 indicates the absence of a dominant direction.

The theoretical values of $W_{dom} + V_{dom}$ and $W_{rec} + V_{rec}$ for lines and genotypes carrying all dominant and recessive alleles were determined on the basis of the correlation coefficient between the average values of parental component traits in parents ($\bar{x}p$) and the sum *(Wr + Vr)*. A line or sample that theoretically had all dominant alleles was characterized by the value $W_{dom} + V_{dom}$ – 6.13 (2017); 2.08 (2018) and 5.85 (2019). The theoretical value of $W_{rec} + V_{rec}$ of the parental component with the largest

Table 6: Genetic parameters of lycopene content in tomato fruits

	Years		
Parameters	2017	2018	2019
D	11.28 ± 0.81	4.57 ± 0.65	4.07 ± 0.03
F	8.73 ± 2.02	4.93 ± 1.63	0.04 ± 0.06
H_1	7.52 ± 2.06	5.58 ± 1.66	0.43 ± 0.06
H_2	5.00 ± 1.98	4.00 ± 1.60	0.14 ± 0.06
h^2	39.70 ± 1.34	46.25 ± 1.08	2.04 ± 0.04
E	0.06 ± 0.33	0.12 ± 0.27	0.17 ± 0.01
H_1/D	0.67	1.22	0.11
$\sqrt{H_1/D}$	0.82	1.11	0.33
$H_2/4H_1$	0.17	0.18	0.08
$\frac{\sqrt{4H\ 1}+F}{\sqrt{4H\ 1}-F}$	2.80	2.90	1.03
h^2/H_2	7.93	11.56	14.14
Conditionally dominant(CD)	6.13	2.08	5.85
Conditionally recessive(CR)	11.65	9.96	5.84

Table 7: Estimation of the direction of dominance (F) by lycopene content in tomato fruits for each parental forms and their hybrids

Lines, genotypes	Years		
	2017	2018	2019
№492	8.19 ± 2.75*	5.08 ± 2.22*	1.93 ± 0.09*
№494	9.35 ± 2.75*	8.78 ± 2.22*	-1.00 ± 0.09*
LK490	10.60 ± 2.75*	7.53 ± 2.22*	-1.69 ± 0.09*
Dark Green	1.33 ± 2.75*	-1.24 ± 2.22*	-0.28 ± 0.09*
T-3627	14.17 ± 2.75*	4.49 ± 2.22*	1.21 ± 0.09*

* Significant at 5 % level

Table 8: The results of correlation and regression analyses of lycopene content in tomato fruits

Indicator	2017	2018	2019
Correlation (r) between Wr and Vr	0.67	0.71	1.00
Regression ($b1$) between Wr and Vr	0.74	0.53	0.96
Correlation (r) between $\bar{x}p$ and Wr and Vr	0.21	0.67	-0.001
Regression ($b2$) between $\bar{x}p$ and Wr and Vr	0.30	0.76	-0.003

number of recessive genes was 11.65 (2017); 9.96 (2018) and 5.84 (2019).

With the help of regression graphs (Fig. 1–3), we obtained more complete information about the manifestation of dominant and recessive effects.

According to the results of the F_1 evaluation, the point with the greatest recessiveness was approached by the Dark Green genotype, which had 75 percent recessive alleles in 2017. Parental components were located in the zone of dominance in 2018 and had 100 % dominant alleles. Line LK490, characterized by the highest lycopene content in fruit, was located closer to the zone with the greatest recessiveness in 2019. The Dark Green genotype point is in the middle of the regression line. The point of line №492 (with low lycopene content in fruits) lies closer to the zone with the greatest dominance.

4 DISCUSSION

The significance of the work is due to the need to solve the important task of expanding the genetic diversity of tomato source material with increased lycopene content in fruits, studying the inheritance of valuable economic traits and determining their breeding value in hybrid generations, to increase the effectiveness of breeding work to create new varieties and hybrids of tomatoes with improved nutritional properties. Highly pigmented forms with *hp-2*^{dg}, *B*^{c} genes are used in the breeding process to create valuable varietal diversity, which contribute to increasing the level of lycopene in fruits.

The work carried out on the study of the character of variability and inheritance in the future makes it possible to effectively forecast breeding work with minimal time expenditure. The created new assortment of tomatoes will expand market opportunities for the consumer and will serve as a basis for further breeding work.

5 CONCLUSIONS

Five parental forms of tomato (*Solanum lycopersicum* L.) to determine the combining ability were studied. Twenty F_1 hybrids obtained according to the full diallel scheme (5 x 5) were used to study the inheritance of the trait “lycopene content in fruits”. Lines №492, №494, LK490 and two collection genotypes with an increased content of lycopene in fruits were used as parental forms in the diallel crossing system according to Hayman (1954) and Jinks (1954): Dark green (*hp-2*^{dg}), T- 3627(*B*^{c}).

An assessment of the general and specific combining ability of five initial forms of tomato evaluated on the trait “lycopene content in fruits”, the character of inheritance of the characteristic was determined. According to the research results, it was established that the lycopene content in fruits is controlled by an additive-dominant genetic system. The trait is inherited by the incomplete dominance. The direction of dominance changes – from the dominance of genes that reduce the manifestation of the trait to its absence.

Over the three years of research, the LK 490 line (0.26-1.68) and the Dark Green genotype (0.48-0.54) had a high (reliably positive assessment of effects) GCA, over two years – the T-3627 genotype (0.38-1.09). They can be recommended for creating heterotic hybrids and varieties.

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