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PREDICTING HETEROSIS AND F1 PERFORMANCE IN SPRING RAPESEED (Brassica napus L.): GENETIC DISTANCE BASED ON MOLECULAR OR PHENOTYPIC DATA?

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In rapeseed, there is a constant need for increasing its genetic diversity, particularly through breeding of hybrid varieties in order to produce genotypes with improved seed yield, as well as other important agronomic traits. However, to create commercial hybrids, the knowledge of the genetic diversity of the parents is prerequisite, considering that the hybrid's performance greatly depends on the choice of parental lines. There is a lack of information about using the genetic distance to determine the extent of heterosis in spring rapeseed in Europe. The goals of this research were to determine the genetic variability of rapeseed breeding material for important agricultural traits, to analyse the differences in grouping of the parental genotypes based on their genetic distances determined by morphological traits and molecular markers and to estimate the correlation of the differently established parental genetic distances with hybrid performance, heterosis, general combining ability of both parents and specific combining ability in crosses. This will provide novel information for parental selection in order to develop a better approach for prediction of heterosis in spring rapeseed hybrid breeding program. The field trial included ten spring rapeseed genotypes that were crossed in a half diallel fashion thus making 45 hybrid combinations. Distances between parents were calculated based on data from 14

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analysed phenotypic traits and 64 SSR markers. The obtained results showed that the parental genetic distance based on phenotypic traits was better in predicting heterosis and combining ability in comparison with the distance estimated by SSR analysis. Although the obtained results revealed that the genetic distance based on molecular markers had no correlation with mid-parent and high-parent heterosis, further studies are needed with a larger number and different types of markers to draw the final conclusion.

Keywords: combining ability, heterosis, phenotype analysis, rapeseed, SSR markers.

INTRODUCTION

The growing need for food and bioenergy, as well as the climate change, pose a constant challenge to the plant breeders (XING *et al.*, 2014). Rapeseed (*Brassica napus* L.) is one of the most important oilseed crops worldwide and can be grown as winter or spring type. However, for continuous improvement of seed yield and other agronomic traits, as well as its adaptability to climate change (RAHMAN *et al.*, 2016), high level of genetic diversity is crucial. Genetic variability of *B. napus*, especially in the spring gene pool is narrow (HASAN *et al.*, 2006; QIAN *et al.*, 2006; BUS *et al.*, 2011). As a result, there is a constant need for increasing its genetic diversity, particularly through breeding of hybrid varieties.

The heterosis phenomenon, also known as hybrid vigour, explains the superior performance of the hybrid relative to its parents, considering both yield and adaptability to environmental conditions (FU *et al.*, 2015). Even though it is widely acknowledged in animal and plant breeding, its genetic basis still remains unclear (TAO *et al.*, 2016). Development of hybrids with high level of heterosis for rapeseed improvement is preferred over open-pollinated varieties (AHMAD *et al.*, 2011; AHMAD *et al.*, 2014). However, to create commercial hybrids, the knowledge of the genetic diversity of the parent is prerequisite, considering that the hybrid's performance greatly depends on the choice of parental lines. Moreover, the efficacy of the breeding program can be significantly improved if the best crosses from specific parents' combinations can be predicted before conducting extensive field evaluation (AHMAD *et al.*, 2014; TIAN *et al.*, 2017). Such prediction is possible if there is a significant positive relationship between genetic distance (estimated based on morphological traits or DNA markers) and hybrid performance.

Parental distances based on phenotypic traits in rapeseed can be used to predict heterosis and significant correlations with mid-parent heterosis for seed yield were detected in previous studies (LEFORT-BUSON *et al.*, 1986; ALI *et al.*, 1995). On contrary, no significant correlations with heterosis for seed yield or other evaluated morphological traits were observed in other studies (YU *et al.*, 2005; TIAN *et al.*, 2017). Since it is fast and simple approach, estimation of the phenotypic distance is still considered as useful (YOSEPH *et al.*, 2006). Different DNA-based markers are often applied to exploit the correlation between genetic distance and heterosis, general combining abilities (GCA) and specific combining abilities (SCA) for various traits in rapeseed. Significant correlations between genetic distance and heterosis for different yieldrelated traits were reported (RIAZ *et al.*, 2001; TAN *et al.*, 2007; XING *et al.*, 2014; SANG *et al.*, 2015). On the other hand, in many studies such correlations were not identified (YU *et al.*, 2005; QIAN *et al.*, 2007, 2009; MOHAMMED *et al.*, 2014; LUO *et al.*, 2016; RAHMAN *et al.*, 2016; TIAN *et* *al.*, 2017). Moreover, it was reported that GCA can be used to predict heterosis and yield performance (HUANG *et al.*, 2015; TIAN *et al.*, 2017) and this information can be used to effectively improve rapeseed.

The potential application of genetic distance (based both on morphological traits and molecular markers) is inconclusive and there is a lack of information about using parental genetic distance in determining the extent of heterosis in spring rapeseed in Europe. In order to provide novel information for parental selection and to develop a better approach for predicting heterosis in spring rapeseed hybrid breeding program, the purpose of the present study was to assess the genetic variability of rapeseed breeding material for important agricultural traits, to analyse different grouping of parental genotypes based on their genetic distances determined by morphological traits and molecular markers and to estimate the correlation of both genetic distances, heterosis, GCA of both parents and SCA in crosses.

MATERIAL AND METHODS

Plant material and experimental design

Ten spring rapeseed (*Brassica napus* L.) varieties and advanced breeding lines were used as parents for diallel crossing, without reciprocals, resulting in 45 hybrid combinations (Table 1).

Table 1. Spring rapeseed parental genotypes and hybrid combinations included in the study

No	Genotype	No	Genotype	No	Genotype	No	Genotype
1	Lisora (Germany)	15	Global (Sweden)	29	Lisora x Lisonne	43	Jr-ns-44 x Liaison
2	Lisora x Jr-ns-6	16	Lisora x Ratnik-3	30	Jr-ns-6 x Lisonne	44	Lisonne x Liaison
3	Jr-ns-6 (Serbia)	17	Jr-ns-6 x Ratnik-3	31	Mira x Lisonne	45	Liaison (Germany)
4	Lisora x Mira	18	Mira x Ratnik-3	32	Jr-ns-36 x Lisonne	46	Lisora x Jovana
5	Jr-ns-6 x Mira	19	Jr-ns-36 x Ratnik-3	33	Global x Lisonne	47	Jr-ns-6 x Jovana
6	Mira (Serbia)	20	Global x Ratnik-3	34	Ratnik-3 x Lisonne	48	Mira x Jovana
7	Lisora x Jr-ns-36	21	Ratnik-3 (Serbia)	35	Jr-ns-44 x Lisonne	49	Jr-ns-36 x Jovana
8	Jr-ns-6 x Jr-ns-36	22	Lisora x Jr-ns-44	36	Lisonne (Germany)	50	Global x Jovana
9	Mira x Jr-ns-36	23	Jr-ns-6 x Jr-ns-44	37	Lisora x Liaison	51	Ratnik-3 x Jovana
10	Jr-ns-36 (Serbia)	24	Mira x Jr-ns-44	38	Jr-ns-6 x Liaison	52	Jr-ns-44 x Jovana
11	Lisora x Global	25	Jr-ns-36 x Jr-ns-44	39	Mira x Liaison	53	Lisonne x Jovana
12	Jr-ns-6 x Global	26	Global x Jr-ns-44	40	Jr-ns-36 x Liaison	54	Liaison x Jovana
13	Mira x Global	27	Ratnik-3 x Jr-ns-44	41	Global x Liaison	55	Jovana (Serbia)
14	Jr-ns-36 x Global	28	Jr-ns-44 (Serbia)	42	Ratnik-3 x Liaison		

Both parents and hybrids were grown at experimental field near Skopje, North Macedonia, in randomized complete block design, including two replications with irrigation and two replications in rainfed conditions. The irrigation regime was scheduled according to the long-term average (LTA) daily evapotranspiration for rapeseed in Skopje region. LTA crop evapotranspiration was calculated with FAO software CROPWAT by using crop coefficient (K_c)

and stage length adjusted for local conditions. Each plot was consisted of 3 rows, 2 m long, with 25 cm distance between rows and 5 cm within the row. Standard crop management practices were applied during the growth season. Vegetative parameters, productive parameters and oil content from all experimental units were assessed. Days to flowering (DF), flowering duration (FD), ripening duration (RD) and vegetative growth duration (VG) have been determined on a plot basis. Plant height (PH), number of primary branches per plant (NB), number of pods per plant (NP), pod length (PL), number of seeds per pod (NSP), seed weight per pod (WSP), 1000 seed weight (W1000), seed weight per plant (WSPL) and oil content (O) were examined on 10 randomly selected plants from the middle row of each plot. Oil content was analysed by NMR (nuclear magnetic resonance) method. Oil yield per plant (OY) was estimated on the basis of seed weight per plant and oil content.

Molecular marker analysis for assessing the polymorphism between the parental genotypes was performed with 64 commercial SSR primer combinations, at the Saaten-Union Resistenzlabor GmbH, Germany, using modified method described by STEINER *et al.* (2004).

Data analysis

Analysis of variance (ANOVA) was performed for the hybrid combinations for all analysed traits across two environments. GCA of the parents and SCA of the hybrid combinations as well as their mean squares across both environments for the phenotypic traits were estimated based on the Griffing's method 4 model 1 (fixed model) for diallel crosses (GRIFFING, 1956) using AGD-R set of R programs (RODRIGUEZ *et al.*, 2015). The general sum of combining ability (GSCA) was calculated as the sum of GCAs for two parents of a hybrid, according to HUANG *et al.* (2015). The heterosis effects were calculated as follows:

mid-parent heterosis (MPH)% = (F1 - MP)/MP x 100

high-parent heterosis (HPH) $\% = (F1 - HP)/HP \times 100$,

where: F1 - the hybrid value for the specific trait,

MP = (P1 + P2)/2,

1

where: P1, P2 - performances of the parental genotypes

HP - high parent performance.

The values for all 14 analysed traits were standardized according to the following formula (ROLDAN-RUIZ *et al.*, 2001):

$$y_m = \frac{\left(x_m - \bar{x_m}\right)}{sd_{x_m}}$$

1

where: x_m - value of the trait before standardization (m=1....M, M=14),

 \underline{y}_{m} - standardized value of the trait x_{m} ,

 x_m - mean value of x_m ,

 sd_{x} - standard deviation of x_{m} .

Standardized values of the phenotypic traits were used to compute the Euclidean distance (GDpheno).

For each SSR primer combination, the presence or absence of amplified polymorphic product (fragment) was marked with 1 or 0, respectively. Only polymorphic markers were used for estimation of genetic similarity/distance. The binary matrix was used to estimate the genetic similarity (GS) based on Nei and Li's index of similarity:

 $GS = 2N_{ab}/(N_a + N_b)$

where: N_{ab} - number of fragments shared by samples a and b;

 N_{a} , N_{b} - amplified fragments in samples a and b, respectively (NEI and LI, 1979).

The genetic distance (GDgen) was calculated by subtracting the GS value from 1 (GD = 1 - GS).

The NTSYSpc2.2 software (ROHLF, 2006) was used to calculate both GDgen and GDpheno, to group the genotypes by UPGMA and WARD method respectively, and to perform cluster analysis (SAHN module) to construct the dendrograms.

RESULTS AND DISCUSSION

Analysis of variance showed that the mean squares of both environment (ENV) and the genotypes (ENTRY) were highly significant for all analysed morphological traits in irrigated and non-irrigated conditions (Table 2). Significant variation in all evaluated traits indicated a great potential for rapeseed improvement through hybrid breeding. Partitioning of the entries into components of combining ability indicated that mean squares for SCA were highly significant for all analysed traits in both environments. On the other hand, mean squares for GCA were not significant for NSP, WSP, W1000, DF and FD. For all measured traits, except for WSP, the proportion of GCA effects was larger than SCA effects. The ENVxENTRY and ENVxSCA interactions were significant for PH, WSPL, O, OY, DF, RD and VG, while the ENVxGCA interaction was significant only for oil content (O).

Cluster analysis based on the genetic distances calculated from phenotypic traits (GDpheno) and SSR markers (GDgen) effectively classified the parental genotypes into different groups. Based on GDgen, all genotypes except JR-NS-6 belonged to one group (Fig. 1a). The lowest distance of 0.265 was observed between Mira and Global, while the highest distance was detected between JR-NS-6 and JR-NS-36 (0.842). Considering genetic distance from phenotypic traits, the highest value (0.898) was detected between Lisora and JR-NS-6, and the lowest between Global and Liaison (0.123). The parental lines were grouped in two major clusters (Fig. 1b), the first comprising Global, Liaison and JR-NS-44, and the second cluster all remaining genotypes. Lisora did not belong to any group.

No significant positive correlations were observed between GDgen and MPH, HPH and SCA. The only significant positive relationship was detected between GDgen and GCA of the paternal parent for number of seeds per pod. GDgen was significantly negatively correlated with GCA(m) and GSCA for WSP, W1000 and FD, and with GCA(f) for WSP (Table 3).

Genetic distance calculated from phenotypic traits (Table 4) was significantly positively correlated with MPH and HPH for flowering duration. Negative correlations of MPH with RD, and HPH for OY and RD were observed. No significant relation was detected between GDpheno and SCA and GCA (f). GDpheno was significantly positively correlated with GCA (m) for NB, NP, WSP, WSPL and OY, and with GSCA for NB, NP and WSP. Significant negative correlations with GCA (m) and GSCA for PH, PL, DF, RD and VG were detected. Associations

sources of variation	Df	Hd	NB	NP	PL	NSP	WSP	W1000	WSPL	0	Λ	DF	FD	RD	ŊĠ
ENV	-	1088.096**	3.049**	152.389**	1.623**	73.123**	0.00506**	3.255**	2.918**	18.070**	0.677**	618.914**	453.891**	738.223**	392.891**
REP(ENV)	2	14.197	0.011	3.540	0.014	1.768*	0.00010*	0.030	0.018	0.308	0.004	0.932*	0.964	0.186	1.055
ENTRY	54	724.974**	1.612**	1009.810**	0.784**	25.001**	0.00066**	0.997**	2.516**	22.960**	0.448**	26.189**	5.387**	87.164**	151.907**
GCA	6	2127.066**	3.133*	1855.887*	2.808**	35.383	0.00060	1.540	4.425*	54.230**	0.898*	38.732	7.199	304.962**	468.713**
SCA	45	444.556**	1.307**	840.595**	0.379**	22.925**	0.00067**	0.888**	2.134**	16.706**	0.358**	23.680**	5.025 **	43.605**	88.546**
ENVXENTRY	54	20.633**	0.013	6.010	0.020	0.469	0.00003	0.020	0.076**	0.261**	0.012**	1.247**	1.206	2.778**	1.984**
ENVxGCA	6	20.260	0.013	6.097	0.034	0.829	0.00003	0.012	0.043	0.501*	0.008	1.203	0.888	0.806	2.346
ENVxSCA	45	20.708**	0.013	5.993	0.017	0.398	0.00003	0.021	0.083**	0.213**	0.013**	1.256"	1.269	3.173**	116.1
Residual Error	108	6.827	0.020	4.654	0.020	0.452	0.00003	0.018	0.039	0.115	0.006	0.284	0.862	0.751	0.480

between phenotypic distance and heterosis were also detected by LEFORT-BUSON *et al.* (1986) and ALI *et al.* (1995). However, TIAN *et al.* (2017) identified only non-significant correlations of morphological distance with MPH and HPH. The discrepancies in the obtained results may be due to the differences in the tested genetic material, analysed traits and the environments. The presence of a significant variation in the rapeseed breeding material was confirmed by the results of the combined ANOVA, showing highly significant differences for all 14 measured phenotypic traits in two environments. For all analysed traits, except for weight of seeds per pod (WSP), the mean squares of GCA effects were larger than the SCA effects. This indicates that the additive gene action was more important than the non-additive and that GCA was the main component contributing to the differences among the hybrid combinations. SCA effects were accounted for the differences in WSP. Similar results were reported by TIAN *et al.* (2017), who stated that for 11 analysed traits in rapeseed the additive gene action was more important than on-additive gene action. Obtained results for seed yield and oil content were in line with QIAN *et al.* (2007; 2009).



Figure 1. Dendrograms representing clustering of parental genotypes based on a) parental genetic distance estimated from molecular markers and b) parental genetic distance estimated from phenotypic traits

The phenotypic and molecular genetic distances between the tested parental genotypes were successfully detected. However, the genetic distance was not significantly correlated with mid-parent heterosis, high-parent heterosis and the specific combining ability of the crosses. The only significant positive correlation was observed between GDgen and GCA of the maternal parent for NSP. As such, the molecular markers used in this study cannot be effectively used to predict the combining ability and heterosis in rapeseed. The same conclusion was indicated in previous investigations (SHEN *et al.*, 2002, 2006; YU *et al.*, 2005; QIAN *et al.*, 2007, 2009; MOHAMMED *et al.*, 2014; LUO *et al.*, 2016; TIAN *et al.*, 2017). On the other hand, XING *et al.*

(2014) found that GD was significantly correlated only with HPH for thousand seed weight, and with SCA for seed yield per plant, thousand seed weight, and number of seeds per silique. This suggests that GD, estimated based on molecular markers, can be considered as a valuable genetic parameter for heterosis prediction (FAN *et al.*, 2010; XING *et al.*, 2014), but it should be used together with other parameters. The contradictory results, especially the lack or low level of correlations between the GD and both heterosis and combing ability, may be attributed to the lack of linkage between genes controlling analysed traits and analysed molecular markers (NDHLELA *et al.*, 2015; TIAN *et al.*, 2017). Also, interaction between the studied genotypes and the environment may influence this low correlation level.

T:4-	GDgen					
Traits	MPH	HPH	SCA	GCA(m)	GCA(f)	GSCA
PH	0.20	0.11	0.06	0.22	0.13	0.25
NB	-0.12	-0.12	-0.06	0.02	-0.24	-0.12
NP	-0.08	-0.01	-0.03	-0.02	-0.24	-0.16
PL	0.25	0.13	0.12	0.10	0.22	0.24
NSP	0.08	0.08	0.06	0.31*	-0.09	0.11
WSP	0.11	-0.07	0.09	-0.51**	-0.34*	-0.62**
W1000	-0.09	-0.13	-0.04	-0.65**	-0.22	-0.67**
WSPL	0.13	0.14	0.06	-0.29	-0.08	-0.28
0	0.12	0.02	0.09	0.16	0.03	0.13
OY	0.14	0.13	0.07	-0.23	-0.06	-0.23
DF	0.12	0.07	0.11	0.12	0.01	0.11
FD	-0.21	-0.21	-0.11	-0.58**	0.09	-0.46**
RD	0.06	0.06	0.04	0.18	0.23	0.25
VG	0.04	0.01	0.05	0.10	0.23	0.20

Table 3. Correlations between genetic distance based on molecular markers and mid-parent heterosis (MPH), high-parent heterosis (HPH), specific combining ability (SCA), general combining ability of the male parent (GCA(m)), general combining ability of the female parent (GCA(f)) and the sum of parental general combining ability (GSCA)

* significant at p<0.05

** significant at p<0.01

Parental distance based on phenotypic data better predicted heterosis and combining ability in comparison with the genetic distance based on SSR markers. Similar results were reported by RIDAY *et al.* (2003) in alfalfa, GELETA *et al.* (2004) in pepper and TEKLEWOLD and BECKER (2006) in Ethiopian mustard.

In this study, the phenotypic distance among the parental genotypes was more effective than the genetic distance in predicting heterosis and combining ability in spring rapeseed. However, most of the analysed traits were not significantly associated with neither GCA of the parents, nor with the SCA of the crosses. Although obtained results revealed that the genetic distance based on molecular markers was not in correlation with mid-parent and high-parent heterosis, further studies are needed with a higher number of markers, to draw the final conclusion. The information gained from this investigation can be effectively used for improving rapeseed hybrid breeding.

Table 4. Correlations between parental genetic distance based on phenotypic traits and mid-parent heterosis (MPH), high-parent heterosis (HPH), specific combining ability (SCA), general combining ability of the male parent (GCA(m)), general combining ability of the female parent (GCA(f)) and general combining ability of both parents (GSCA)

Tuoita	GDpheno					
Traits	MPH	HPH	SCA	GCA(m)	GCA(f)	GSCA
PH	0.13	-0.02	0.14	-0.41*	-0.24	-0.45**
NB	0.13	-0.03	0.11	0.61**	-0.15	0.44^{**}
NP	0.10	-0.16	0.13	0.56**	-0.13	0.36^{*}
PL	-0.04	-0.14	0.04	-0.50**	-0.08	-0.39*
NSP	0.09	0.09	0.04	-0.15	-0.01	-0.10
WSP	-0.05	0.11	-0.06	0.39^{*}	0.07	0.34^{*}
W1000	-0.09	-0.16	-0.10	0.28	-0.01	0.22
WSPL	-0.11	-0.29	0.04	0.51**	-0.23	0.23
0	-0.22	-0.22	-0.12	0.16	-0.08	0.04
OY	-0.15	-0.31*	0.02	0.50^{**}	-0.22	0.22
DF	-0.06	-0.13	-0.01	-0.47**	0.00	-0.40^{*}
FD	0.41^{*}	0.34^{*}	0.26	0.25	-0.01	0.22
RD	-0.36*	-0.33*	-0.13	-0.53**	-0.25	-0.48**
VG	-0.23	-0.24	-0.04	-0.55**	-0.23	-0.49**

* significant at p<0.05

** significant at p<0.01

CONCLUSIONS

The significant variation in the rapeseed breeding material used in this study can be successfully utilized in future breeding programs. Cluster analysis based on the genetic distances calculated from morphological traits and molecular markers was effective for classification of the parental genotypes into different groups. Based on GDgen, all genotypes except JR-NS-6 belonged to only one group. Considering the genetic distance from phenotypic traits, the parental lines were grouped in two major clusters and the genotype Lisora did not belong to any cluster. This indicates that the differences between the analysed genotypes were higher when using phenotypic data, than based on molecular markers.

A significant positive correlation was detected between the genetic distance based on molecular markers and GCA of the maternal parent for number of seeds per pod. The genetic distance based on phenotypic traits showed significant positive correlation with mid-parent and high-parent heterosis for flowering duration, GCA of the maternal parent and the sum of parental general combining ability for different traits. The genetic distance based on phenotypic traits better predicted heterosis and combining ability in comparison with the genetic distance based on molecular markers. Such information gives a novel insight into the prediction of heterosis in spring rapeseed which can be effectively utilized for improvement of rapeseed hybrid breeding.

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PREDVIĐANJE HETEROZISA I PERFORMANSE F1 HIBRIDA JARE ULJANE REPICE (*Brassica napus* L.): KORIŠĆENJE GENETIČKE DISTANCE NA OSNOVU MOLEKULARNIH ILI FENOTIPSKIH PODATAKA?

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Izvod

Usled stalne potrebe za povećanjem genetičkog diverziteta uljane repice, oplemenjivanjem hibridnih sorti se teži stvaranju genotipova sa poboljšanim prinosom semena, kao i drugim važnim agronomskim osobinama. Osobenosti hibrida zavise od izbora roditeljskih linija, te je poznavanje genetičkog diverziteta roditelja veoma važno za stvaranje komercijalnih hibrida. Zbog nedovoljno informacija o upotrebi genetičke udaljenosti za određivanje stepena heterozisa jare repice u Evropi, ciljevi ovog rada bili su određivanje genetičke varijabilnosti oplemenjivačkog materijala uljane repice za važne agronomske osobine, analiza razlika u grupisanju roditeljskih genotipova na osnovu genetičke udaljenosti određene morfološkim osobinama i molekularnim markerima. Cilj je bio i utvrđivanje korelacije između genetičke udaljenosti roditelja i performanse hibrida, heterozisa, opštih kombinacionih sposobnosti oba roditelja i posebnih kombinacionih sposobnosti u ukrštanjima. Dobijanje novih informacija za odabir roditelja će omogućiti razvijanje boljeg pristupa za predviđanje heterozisa u programu oplemenjivanja hibrida jare uljane repice. U ogled je uključeno 10 genotipova jare repice koji su ukrštani metodom nepotpunog dialela bez recipročnih ukrštanja uz dobijanje 45 hibridnih kombinacija. Udaljenost između roditelja je određena na osnovu 14 fenotipskih osobina i 64 SSR markera. Genetička udaljenost između roditelja određena na osnovu fenotipskih osobina je bila efikasnija u predviđanju heterozisa i kombinacionih sposobnosti u odnosu na udaljenost određenu SSR markerima. Iako dobijeni rezultati pokazuju da genetička udaljenost bazirana na molekularnim markerima nije u korelaciji sa heterozisom u odnosu na prosečnog, niti boljeg roditelja, potrebna su dodatna istraživanja sa većim brojem i različitim vrstama markera kako bi se potvrdili dobijeni rezultati.

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