Combining ability of morphological and anatomical traits in carrot (*Daucus carota* L. ssp. *sativus* (Hoffm.))

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Topcross crossing of carrots was carried out at the Lithuanian Institute of Horticulture in 1996 (O. Gaučienė). Seven lines with cytoplasmatic male sterility (CMS) (*N0557, N0563, Š0380b, Š0494, Š0639, G0198$_2$, G0300$_3$*) and the testers *Vitaminnaja 6, NIIOCH 336*, and *No. 01309* were used in the crosses. According to the ratio of general and specific combining ability it is possible to presuppose that for inheritance of the morphological and anatomical traits of carrot roots genes with additive effects were of essential significance, though genes with dominant and epistatic effects were significant as well. The length, weight and smooth surface of roots of CMS lines to a greater scale are controlled by genes with dominant and epistatic effects, though the impact of genes with additive effects is also essential. Genes with additive effects are important for inheritance of root diameter, while genes with dominant and epistatic effects are less significant. Genes with non-additive effects were more significant for inheritance of root phloem diameter than those with additive effects. Genes with additive effects controlled the heritability of root phloem color and root xylem diameter, though genes with non-additive effects were significant as well.

Key words: carrot, combining ability, genes, inheritance, morphological and anatomical traits

INTRODUCTION

In contemporary breeding the main requirements for variety and hybrid creation are as follows: typical root shape, good biochemical composition and long storage durability [2, 11]. Application of heterosis effect is a perspective way in carrot breeding for development of productive varieties and heterotic hybrids [1, 3, 8, 9, 16]. Selection of paternal forms is very important, because only some lines exert a strong heterotic effect. Pairs of this kind are found by determining their combining ability and regularities of trait inheritance [5, 6, 17]. Theoretically and experimentally Sprague and Tatum proved the genetic nature of combining ability [7]. The combining ability of the same form is expressed in two ways: general combining ability (GCA) and specific combining ability (SCA). General combining ability is the heterotic average of all crossing combinations and specific combining ability is deviation from the average in a concrete crossing combination [4].

The topcross scheme is less complex than the dialel design, though it allows establishing the combining ability of paternal forms rather adequately

[20]. O. Masiukova (1979) carried out research on combining ability in the topcross scheme [19]. Some researchers indicate that GCA and SCA values vary depending on environmental conditions [14]. Stable selection of lines with high GCA is possible under changing environmental conditions [14], meanwhile, according to the findings of other researchers, stable GCA values were not always obtained under changing environmental conditions [21]. Thus, the performance of genetic information is closely linked to environmental conditions.

The available collection of carrot varieties and lines had not yet been genetically estimated, therefore for selection of stock for further breeding it was necessary to assess the combining ability of varieties and lines and the heritability of morphological and anatomical traits.

For the first time the combining ability of morphological and anatomical traits of CMS analogues of the Lithuanian carrot varieties *Garduolės 2* and *Šatrija* and *Nanto 04* and the heritability regularities of quantitative characters have been established.

MATERIALS AND METHODS

In 1997–1999, research was carried out in the trial field of the Lithuanian Institute of Horticulture on sod gleyic sandy and light loam, pH 6.1–7.4, containing 185–250 mg/kg of mobile P_2O_5, 105–140 mg/kg of mobile K_2O, 3.0% of humus. On 14–18th of May carrots were seeded on ridges by a manual drill, 70 cm between center points of ridges, in 2 seed lines. The trial was established in 4 randomized replications. The initial trial plot was 7 m^2 and the record 5.6 m^2. In all years of investigation the previous culture was perennial grass.

Meteorological conditions in the years of investigation varied. In 1997 carrot germination was delayed because of moisture deficiency, and in September root quality deteriorated because of a high temperature.

In 1998, during vegetation it was dry and cold. Carrots germinated late and did not have enough time to grow fully.

In 1999, during vegetation the growing conditions were not favorable because of uneven distribution of precipitation. Heavy rains in the last decade of September worsened root quality. A large amount of roots cracked and branched.

During investigation, carrot morphological traits (root length, diameter, weight, smooth root surface, root phloem diameter, root phloem color, root xylem diameter, root xylem color) were assessed [12]. Experimental data on hybrids F_1 were processed by the variance analysis method [15]. General and specific combining ability was established in the CMS lines studied (*N0557, N0563, Š0380b, Š0494, Š0639, G0198$_2$, G0300$_3$*) and in the testers (*Vitaminnaja 6, NIIOCH 336*, *No. 01309*) with the aid of a computer program developed at the Lithuanian Institute of Agriculture [10].

RESULTS AND DISCUSSION

Root length. During investigation, GCA differences in root length were reliable between CMS lines and testers. Reliable differences of SCA were obtained in less favorable years. Roots were of similar length in the progeny of CMS lines *Š0380b, Š0494, Š0639, G0198$_2$, G0300$_3$*. Shorter roots were in the progeny of CMS lines *N0557, N0563*.

The roots were longest in hybrids produced by crossing the CMS lines *Š0494* (GCA effects – 0.14) and *Š0639* (GCA effects – 0.19) with all testers (Table 1). Their GCA was highest. The progeny of CMS line *N0557* (GCA effects –0.25) had the shortest roots. The male crossing component predetermined the root length of the hybrids.

The longest roots were found in hybrids produced in crossings with the male form *Vitaminnaja 6* (GCA effects – 1.62) and the shortest roots – with male form *No 01309* (GCA effects –1.79).

In the testers, GCA variances were higher than SCA variances, indicating that genes with additive effects are very significant for inheritance of this trait (Table 2). In the progeny of most CMS lines, genes with dominant and epistatic effects were more important for root length inheritance.

Table 1. **General combining ability (GCA) effects (g_i) on length, diameter, weight and smooth surface of roots of carrot CMS lines and testers. Babtai, 1997–1999**

Parental forms	GCA effects (g_i) on			
	Root length	Root diameter	Root weight	Root smooth surface
CMS lines:				
N0557	–0.25	0.01	5.78	–0.03
N0563	0.09	–0.10	4.01	0.11
Š0380b	–0.01	–0.04	0.75	–0.04
Š0494	0.14	0.04	2.26	–0.02
Š0639	0.19	0.02	–2.74	0.04
G0198$_2$	–0.04	0.05	0.59	0.08
G0300$_3$	–0.13	0.02	–10.66	–0.15
LSD_{05}	0.25	0.10	4.44	0.07
Testers:				
Vitaminnaja 6	1.62	–0.25	3.61	–0.01
NIIOCH 336	0.17	–0.03	–0.08	–0.06
Nr. 01309	–1.79	0.28	–3.53	0.07
LSD_{05}	0.14	0.06	2.57	0.04

Table 2. **General combining ability (GCA) (g_i) and specific combining ability (SCA) (S_i) variances of root length, diameter, weight and smooth surface of carrot CMS lines and testers. Babtai, 1997–1999**

Parental forms	Root length		Root diameter		Root weight		Root smooth surface	
	$\delta^2_{g_i}$	$\delta^2_{s_i}$	$\delta^2_{g_i}$	$\delta^2_{s_i}$	$\delta^2_{g_i}$	$\delta^2_{s_i}$	$\delta^2_{g_i}$	$\delta^2_{s_i}$
CMS lines:								
N0557	0.05	0.46	–0	0.02	28.52	34.5	–0	0.01
N0563	–0.01	0.01	0.01	–0	11.17	136.01	0.01	0.03
Š0380b	–0.02	–0.03	–0	0	–4.38	41.13	0	0.03
Š0494	0	0.16	–0	–0	0.17	8.87	–0	0.06
Š0639	0.02	0	–0	–0	2.59	–2.2	0	0.03
$G0198_2$	–0,01	0.01	0	–0	–4.59	–7.38	0.01	0.01
$G0300_3$	0	0.02	–0	0.01	108.65	312.96	0.02	0.07
Testers:								
Vitaminnaja 6	2.62	0.12	0.06	0	11.38	97.47	0	0.01
NIIOCH 336	0.02	–0.02	0	–0.01	–1.64	35.58	0	0.05
Nr. 01309	3.20	0.04	0.08	0	10.79	18.54	0.01	0.02

Root diameter. Dispersion analysis of combining ability revealed reliable GCA differences between testers in all years of investigation and in drier years among CMS lines as well. Reliable SCA differences were obtained only in drier years. The mean values of GCA squares of CMS lines and testers were higher 1.5–57.0 times than those of SCA squares, indicating that genes with additive effects are very significant for inheritance of this trait and genes with dominant and epistatic effects are less significant, because only in drier years SCA was reliable.

During investigation, GCA effects in CMS lines were almost equal (Table 1). The biggest diameter was of hybrids produced by crossing different CMS lines with tester *No. 01309*. The progeny of tester *Vitaminnaja 6* had the smallest root diameter and its GCA effects were negative.

Genes with additive effects stipulated genetic control of the investigated trait of the paternal forms *Vitaminnaja 6* and *No. 01309* (Table 2). This means that crossing pairs can be selected according to phenotype in order to produce carrot varieties with a desirable root diameter.

Root weight. Dispersion analysis of combining ability revealed reliable GCA differences between CMS lines and testers in all years except those drier. In drier years GCA of testers did not differ. In those years temperature fluctuations were high, moisture was deficient and carrots germinated later. Differences of SCA among crossing combinations were reliable only in wetter years. The positive value of GCA effects on root weight was only in *N0557* (CMS line) (Table 1).

A comparison of GCA and SCA variances of carrot root weight showed that genes with dominant and epistatic effects were more significant for root weight inheritance. CMS line *Š0639* had higher GCA variances of this trait than SCA. This proves that root weight in the progeny of this line more strongly was predetermined by genes with additive effects (Table 2).

Smooth root surface. In less favorable years, by disperse analysis of combining ability reliable GCA differences of smooth root surface were established. Reliable SCA differences of this trait showed a higher level of reliability. The value of the lines and testers for breeding of carrot varieties with smooth root surface can be determined from GCA effects (Table 1). CMS lines *N0563* and *$G0198_2$* had positive GCA effects in all years. A smooth root surface was best transmitted to progeny by Lithuanian *No. 01309* (tester).

Comparison of GCA and SCA variances for smooth surface of individual CMS lines and varieties (Table 2) indicated that genes with dominant and epistatic effects controlled root surface in most lines and testers.

Root phloem diameter. In optimal years, by disperse analysis of combining ability reliable differences of GCA were established among testers. In wetter years the CMS lines reliably differed according to GCA and SCA effects when environmental conditions were unfavorable for carrot growing. In those years precipitation distribution was uneven during different growth periods, therefore, some of root phloems were bigger and some of them were smaller. Genes with non-additive effects were more significant for inheritance of this trait those with additive effects.

GCA effects show that the progeny of CMS lines were similar in root phloem diameter. Tester

Table 3. **General combining ability (GCA) effects (g_i) on root phloem diameter and color, xylem diameter and color of carrot CMS lines and testers. Babtai, 1997–1999**

Parental forms	Root phloem diameter	Root phloem color	Xylem diameter	Xylem color
CMS lines:				
N0557	–0.01	–0.01	0.02	–0.07
N0563	0.01	–0.13	0.04	–0.06
Š0380b	–0.04	0.06	0.02	0.08
Š0494	0.09	0.25	0.03	0.26
Š0639	–0.03	0.03	–0.02	–0.20
$G0198_2$	–0.05	–0.26	–0.02	0.11
$G0300_3$	0.04	0.04	–0.07	–0.13
LSD_{05}	0.06	0.25	0.05	0.21
Testers:				
Vitaminnaja 6	–0.05	–0.11	0.09	0.04
NIIOCH 336	0.03	0.23	–0.05	0.19
No. 01309	0.02	–0.13	–0.04	–0.23
LSD_{05}	0.04	0.14	0.03	0.12

No. 01309 was most valuable in transmitting of this trait (Table 3). Variety *Vitaminnaja 6* (tester) transmitted the smallest phloem diameter; its values of GCA were negative in all years of investigation.

Root phloem color. In drier years, reliable GCA and SCA differences for the phloem color were established by the dispersion analysis of combining ability. In other years, reliable differences were found either among CMS lines or among testers. This demonstrates that the phloem color is more pronounced in drier weather. The GCA and SCA ratio showed that genes with additive effects controlled the heritability of this trait, though genes with dominant and epistatic effects were significant as well.

Among CMS lines, the brightest phloem was found in line *Š0494* progeny. Among the testers studied, *NIIOCH 336* transmited phloem color best; its values of GCA effects were reliably positive (Table 3).

Root xylem diameter. According to disperse analysis data on combining ability in optimal and drier years, reliable GCA differences of root xylem diameter were obtained among the testers.

Reliable SCA differences were obtained in drier years. The progeny of CMS lines did not differ reliably in root xylem size. The GCA and SCA ratio indicates that genes with additive effects are important for inheritance of this trait, though genes with dominant and epistatic effects exert influence as well.

GCA effects indicate the value of lines and varieties (Table 3). The best line or variety is that which transmits smaller diameter xylem to progeny. In the study years, CMS line $G0198_2$ had negative values of GCA effects. The progeny of No. *01309* had the smallest xylem diameter among the testers.

Root xylem color. Dispersion analysis of the combining ability for root xylem color revealed reliable GCA differences among CMS lines in the optimal years. The testers differed reliably in GCA in all years of investigation. SCA differences of this trait were obtained in less favorable years.

The xylem color of CMS line was brightest in optimal years. The positive values of this trait effects maintained two CMS lines (*Š0380b* and *Š0494*). CMS line *Š0639* had negative values of GCA effects in all years. The tester *NIIOCH 336* had the highest positive values of GCA effects (Table 3).

In optimal years, genes with additive effects were more significant for inheritance of root xylem color in crossing combinations of CMS lines and testers. The contribution of genes with dominant and epistatic effects was very low that year. In unfavorable years genes with dominant and epistatic effects exerted a greater effect on the inheritance of this trait.

According to the findings of other researchers, genes with additive effects were more important for the inheritance of root weight, diameter and length [13, 16, 18]. The same results were obtained in our research as well. In unfavorable years in our trials the expression of morphological and anatomical traits of carrot roots depended, though to a smaller degree but significantly, both on genes with dominant and epistatic effects.

CONCLUSIONS

It has been established that in the group of carrot CMS lines studied, genes with dominant and epistatic effects modify the root xylem diameter. Genes with additive effects do not affect progeny variability for this trait. Root length, weight and smooth surface in this group of CMS lines to a greater scale are controlled by genes with dominant and epistatic effects, though the impact of genes with additive effects is also essential. Genes with additive effects are more important to the heritability of root diameter, because in the CMS lines and testers the mean values of GCA squares were 1.5–57.0 times higher than those of SCA squares. The genetic control system of these traits strongly depends on meteorological conditions during carrot growth.

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Rasa Karklelienė

MORKŲ (*Daucus carota* L. ssp. – *sativus* (Hoffm.)) ŠAKNIAVAISIŲ MORFOLOGINIŲ IR ANATOMINIŲ POŽYMIŲ KOMBINACINĖ GALIA

S a n t r a u k a

1996 m. Lietuvos sodininkystės ir daržininkystės institute atlikti morkų topkroso kryžminimai (O. Gaučienė). Kryžminimui naudotos 7 linijos su citoplazminiu vyrišku sterilumu (CVS): *N0557, N0563, Š0380b, Š0494, Š0639, G0198*$_2$, *G0300*$_3$ ir testeriai: *Vitaminnaja 6, NIIOCH 336, Nr. 01309*. Pagal bendrosios ir specifinės kombinacinių galių santykį galima daryti prielaidą, kad morkų šakniavaisių morfologiniams požymiams paveldėti svarbesni buvo genai su adityviniais efektais, nors reikšmės turėjo ir genai su dominantiniais ir epistaziniais efektais. Šakniavaisio ilgį, vieno šakniavaisio masę ir jo lygų paviršių šioje tirtų CVS linijų grupėje labiau kontroliavo genai su dominantiniais ir epistaziniais efektais, nors genų su adityviniais efektais įtaka taip pat esminė. Šakniavaisio skersmeniui paveldėti buvo svarbūs genai su adityviniais efektais, daug mažiau svarbūs genai su dominantiniais ir epistaziniais efektais. Šakniavaisio floemos skersmeniui paveldėti svarbesni buvo genai su neadityviniais efektais, o mažiau svarbūs – su adityviniais efektais. Šakniavaisio floemos spalvos ir ksilemos skersmens paveldėjimą labiau kontroliavo genai su adityviniais efektais.

Raktažodžiai: genai, kombinacinė galia, morkos, morfologiniai ir anatominiai požymiai, paveldėjimas

Раса Карклялене

КОМБИНАЦИОННАЯ СПОСОБНОСТЬ У МОРФОЛОГИЧЕСКИХ И АНАТОМИЧЕСКИХ ПРИЗНАКОВ КОРНЕПЛОДОВ МОРКОВИ (*Daucus carota* L. ssp. – *sativus* (Hoffm.))

Р е з ю м е

В 1996 г. в Литовском институте садоводства и овощеводства были проведены топкроссные скрещивания моркови (О. Гаучене). Для скрещиваний были использованы 7 линий с цитоплазмической мужской стерильностью: *Н0557, Н0563, Ш03806, Ш0494, Ш0639, Г0198$_2$, Г0300$_3$*, а также 3 тестера: *Витаминная 6, НИИОСХ 336 и № 01309.* По соотношению общей и специфической комбинационных способностей можно делать вывод, что наследование морфологических и анатомических признаков у моркови определяют гены с аддитивными эффектами, но гены с доминантными эффектами также достаточно важны. В группе линий с ЦМС длину, гладкость поверхности корнеплода, а также массу одного корнеплода контролируют гены как с доминантными и эпистатическими, так и с аддитивными эффектами. Диаметры корнеплода, ксилемы и окраска флоемы определяются генами с аддитивными эффектами. Гены с другими эффектами также играют важную роль. Наследование диаметра флоемы корнеплода контролировали гены с неаддитивными эффектами.

Ключевые слова: гены, комбинационная способность, морковь, морфологические и анатомические признаки