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COMBINING ABILITY AND HETEROSIS FOR QUANTITATIVE BLUE MOULD *(Peronospora tabacina Adam)* RESISTANCE IN ORIENTAL TOBACCO

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INTRODUCTION

Blue mould, caused by Peronospora tabacina Adam, is one of the most important fungus diseasea that exist and cause serious damage to tobacco crop. The fungus has been a serious tobacco production problem in Albania since 1960. It is now present in all tobacco-growing regions.

Blue mould is a disease of seedbeds and field and can be exceedingly destructive in both, although, weather conditions largely confine it to being a field problem in Albania. It can be seen that the relatively mild and moist Albanian summer provides an excellent environment for blue mould. Much of the oriental tobacco crop will escape serious field damage in normal season because little rains are expected once the crop is planted out.

Blue mould is difficult to control, particularly when environmental conditions are in its favour. On its control, cultural practices, fungicides and ***resistant cultivars*** are valuable aids to sound farming.

Resistance is graded in variety specifications and needs relating to particular disease and cropping situations. It is known that in most types of tobacco, hybrids have been recommended for temporary situation or for specific uses such as disease resistance.

Genes conditioning qualitative resistance have been intensively used in breeding of tobacco and other plants. This has often resulted in development of virulent isolates (2,3,4,7,11,13).

Quantitative resistance introduced into cultivars with good agronomic performance offer a chance to reduce the selection pressure for virulence and to stabilise the host-pathogen system where level of quantitative resistance remain durable over a long period of time (2,3,4,7,8,9,11,13). This is more difficult than working with qualitative resistance. Thus, for better understanding of the genetic basis of quantitative resistance, *combining abilities* and *heterosis* were estimated and divided into their components by analysing a diallel cross of tobacco, following Gardner and Eberhart (1966).

MATERIALS AND METHODS

The experimental plants material is represented from eight tobacco lines selected as parents with different relative levels of resistance to blue mould *(P. tabacina)*. The genotypes selected as parents lines were Bel 61-9 (resistant), Floria (resistant), Nevrokop and Krumovgrad (susceptible), Hicks-Resistant (resistant), Ft2-5 (resistant) and Basma (susceptible). These eight parental lines were crossed with each other giving a diallel series of crosses (28 crosses), without reciprocal crosses.

The experiment, containing 28 F1 crosses and eight parental lines, was arranged in a randomized block design with four replications. Experiments were conducted for three years at the experimental field of Tobacco Institute of Cerrik. Plants were grown in two rows with 20 plants per plot.

No fungicide effective against blue mould was applied in the seedbeds and in the field. The other cultural and curing practices used were the current ones applied in the area.

Symptoms of natural infestation of disease were observed and evaluated. Ratings were carried out upon first appearance of the pest, and further ratings were calculated at 15 days intervals. The scale of damage ratings was defined according to CORESTA rules defined by P. SCHILTZ (1974). Ratings for upper, middle, and lower leaves were made separately.

DATA ANALYSES

For each experiment, rating corresponding to the maximum of intensity for susceptible genotypes was taken into account in the following synthesis (Table 2, 3, 4 and 5).

The general combining ability (GCA) effects; the specific combining ability (SCA) effects and heterosis were the calculated parameters. The general combining ability (GCA) effects of each line was calculated on the deviation of means of F_1s with this variety ($\breve{y}_j$) from the overall mean of $\mathbf{F_1}$**s** ($\breve{y}_c$) (i.e.) $g_j = (p - 1)/(p-2)(\breve{y}_j - \breve{y}_c)$, where **p** is the number of homozygous lines or parents. These parameters were computed following Gardner and Eberhard (1966) method II and Griffing (1956).

For each combination the specific combining ability (SCA) effect was obtained by calculating the deviation between expected F1 (on the basis of GCA effects only) and observed F1 performance (i.e.) $S_{ij} = y_{ij} - \breve{y}_c - g_i - g_j$; where **yij** is the observed value of the F1 between lines **i** and **j**.

Taking into account the values of the parental lines (y_{jj}) heterosis is calculated and divided into *average heterosis* ($\overline{H}_m = \breve{y}_c - \breve{y}_p$); *variety heterosis* ($h_j = g_j - 1/2(y_{jj} - \breve{y}_p)$ and *specific heterosis* (corresponds to SCA) as proposed by Gardner and Eberhard (1966). $\breve{y}_p$ is the mean of the parents. The difference between y_{jj} and $\breve{y}_p$ is the *variety effect* (v_j) of cultivar **j**. For the analyses of variance, the fixed effects model was applied.

Table 1. Provenience, reaction against blue mould and tobacco varieties crossed in a diallel design.

Табела 1 Потекло, реакција кон болеста пламеница и сорти тутун вкрстени по директен модел

Variety Сорта	Provenience Потекло	Reaction against blue mould Реакција кон пламеница
Bel 61-9	USA	Resistant - отпорна
Floria	Austria	Resistant - отпорна
Nevrokop	Bulgaria	Susceptible - осетлива
Krumovgrad	Bulgaria	Susceptible - осетлива
Samsoun	Turkey	Susceptible - осетлива
Hicks-Resistant	France	Resistant - отпорна
Ft2-5	Greece	Resistant - отпорна
Basma	Greece	Susceptible - осетлива

RESULTS AND DISCUSSION

Compatible host reaction of parents and F1s occurred and leaf symptomes of disease were formed on all genotypes. ANOVA analysis revealed the presence of an important variability in the experimental plant materials. Significant quantitative differences of resistance between all genotypes were found. Mean squares for parents and hybrids were highly significant (at the P_{001} level of the probability) (Table 2). In addition, the contribution of genotypes on total variance is very high (R^2 = 0,9705). The distribution of the values (midparent/ F_1 resistance) around the regression line (with equation **y** = 1.0857x - 1,7927) proved that the observed quantitative resistances are heritable as shown in Figure 1.

The position of the values influenced by *Bel 61-9*, (the values ranged in low on the left of the regression line), proved that dominance for resistance occurred in crosses of this variety, whereas dominance for susceptibility occurred in crosses of Samsoun variety (the values ranged in upper position on the right of regression line).

In other crosses, expected heterosis is less expressed. The regression of F_1 on midparent for all crosses is 0,88721 (Standard error). In our study, significant general combining ability effects (**gj**) were found whereas the specific combining ability effects were significant only in some individual crosses (Table 5).

Significant GCA ($\mathbf{g_j}$) effects and large values of variance ratio of additive and non-additive variances (GCA/SCA) proved that additive genetic variance is more important component in the inheritance of "quantitative resistance " character (Tables 3,4). Our results are similar to those reported by other authors (1,3,4,7,8,11,13) that have in other *host-pathogen* systems found high values for additive gene action and where most gene action among loci was additive (9,11,12,1,2).

Significant of SCA ($\mathbf{S_{ij}}$) effects in some individual crosses proved that in particular crosses the specific heterosis plays an evident role in the inheritance of *"resistance"* character. Marani and Sachs (9), Jinks (8) and Matzinger at al. (10) found high values for additive and dominance variance, and where dominance effects became greater in the adult plant stages (9). Several published results showed that dominance and epistatic effects occurred despite additive effects (1,2,3,4,8,9,10,11).

The data of F_1s and parents were combined to perform Analysis II as proposed by Gardner and Eberhart (1966). Significance of variety heterosis ($\mathbf{h_j}$), variety effects ($\mathbf{v_j}$), GCA effects ($\mathbf{g_j}$) and parents were obtained too, and significant average heterosis was also obtained but its effect was small. Analysis of data for GCA components ($\mathbf{g_j = h_j + 1/2\ v_j}$) show that, significance differences, among eight parental lines for $\mathbf{g_j}$, $\mathbf{h_j}$ and $\mathbf{v_j}$ were found (see Tables 3,4). In Table 4 the relation between the quantitative resistance of varieties ($\mathbf{y_{jj}}$), and variety effects (**vj**), GCA effects ($\mathbf{g_j}$) and variety heterosis ($\mathbf{h_j}$) is given. No significant relation exists between **yjj** and **hj** and significance relation exists between **yjj** and $\mathbf{g_j}$. Our results similar to those reported by Bulmer (1) proved that this correlation might also be negative. This means that if parental value attempts to be higher, the potential value of heterosis attempts to be lower (1,8,9). The ranking of the varieties according to their GCA effects calculated according Gardner and Eberhart (5) and Griffing (6) was similar and, the ranking of hosts according to their pure line performance ($\mathbf{y_{jj}}$) corresponds to that resulting from GCA effects ($\mathbf{g_j}$)(Table 4). Nevertheless, it becomes evident that a great part of the observed variation in GCA ($\mathbf{g_j}$) was conditioned by variety effects ($\mathbf{v_j}$). By using homozygous varieties (i.e. when $\mathbf{d_j}$ = 0) these variety effects (contain additive $\mathbf{a_j}$ gene action) are representing the contribution of homozygous loci to the $\mathbf{j^{th}}$ variety mean (6,8).

Such effects can be used by breeding pure lines and, since differences exist, selection for improved quantitative blue mould resistance may be effective (6,1,8,12).

In our study, the differences between F1 and parent means were significant in a great part of individual crosses. Expressed in percentage of heterosis, the average heterosis for all Bel 61-9 crosses was - 13,7%; for Krumovgrad crosses -0,83% and for Samsoun crosses it was -2,87%; but the observed difference ($\mathbf{\breve{y}_c - \breve{y}_p}$) calculated for all data combined is -0,513.

Fig. 1. The distribution of the values expected and observed
Around the regression line (mid parent/F1 resistance)
Графикон 1 Распоред на очекуваните и набљудуваните вредности по регресиона крива

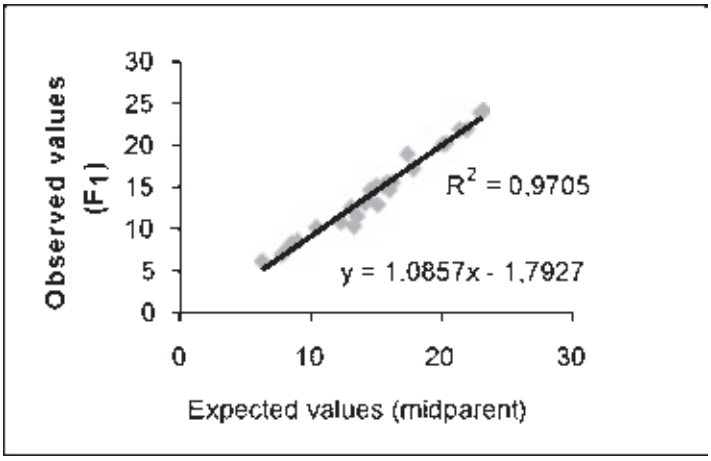

Table 2. Analysis of variance for 8 tobacco varieties and 28 F_1s infected by Blue mould. (*P. tabacina Adam*) (Means of three years)

Табела 2. Анализа на варијансата кај 8 тутунски сорти и 28 F_1 инфицирани од пламеница (средина за 3 години)

Source of variation Извор на варијација	Sum of squares Збир на квадрати	Degrees of freedom Степен на слобода	Mean square Средина на квадратите	F-values F - вредности
Genotypes	**4304,1236**	**35**	**122,9749**	**136,06****
Hybrids	2779,5058	27	103,1302	114,11**
Parents	***1524,6178***	*7*	***217,8025***	***240,98*****
Blocks	**6,7703**	**3**	**2,2567**	**2,4969**
Residual	**94,9036**	**105**	**0,9038 = (Me)**	
Total	**4405,7975**	**143**		

Table 3. Analysis of variance for GCA effects and SCA effects (specific heterosis), average heterosis ($\overline{\mathbf{H}}_\mathbf{m}$), variety heterosis ($\mathbf{h}_\mathbf{j}$) and variety effects ($\mathbf{v}_\mathbf{j}$)

Табела 3. Анализа на варијансата за ОКС и СКС (специфичен хетерозис) просечен хетерозис ($\overline{\mathbf{H}}_\mathbf{m}$), хетерозис на сортата ($\mathbf{h}_\mathbf{j}$) и влијание на сортата ($\mathbf{v}_\mathbf{j}$)

Source of variation Извор на варијација	Sum of squares Збир на квадрати	Degrees of freedom Степен на слобода	Mean square Средина на квадратите	F-values F - вредности
GCA (gj)	1058.2748	7	151.1821	Ms/Mė = 668.95**
SCA (Sij) (specific heterosis)	19,0807	28	0,6815	" " – 3,01**
Average heterosis ((m)	233.9335	1	233.9335	Ms/Me = 247.77**
Variety effects (vj)	***1524,6144***	*7*	***217,8020***	***" " = 240,98*****
Variety heterosis (hj)	20,1051	7	2,8721	" " – 3,18**
Residual	94,9036	105	0,9038	

(Мй = Me/nb; where **nb** → number of blocks = 4)

Table 4. Quantitative Blue mould resistance of eight tobacco varieties ($\mathbf{y}_{ij}$), variety effects ($\mathbf{v}_\mathbf{j}$), variety heterosis ($\mathbf{h}_\mathbf{j}$), means of F_1s according varieties and GCA effects ($\mathbf{g}_\mathbf{j}$)

Табела 4. Отпорност на пламеница кај 8 тутунски сорти ($\mathbf{y}_{ij}$), влијанија на сортата ($\mathbf{v}_\mathbf{j}$), хетерозис на сортата ($\mathbf{h}_\mathbf{j}$), средина на F_j по сорти и ОКС ($\mathbf{g}_\mathbf{j}$)

Nr.	Varieties Сорти	yjj	vj	hj	$\breve{y}_j$	gj`	gj``
1	Bel 61-9	5,50 a	-9,45**	-1,145**	9,40	-5,88**	-5,41**
2	Floria	10,00 c	-4,95**	0,495*	12,74	-2,12**	-2,17**
3	Nevrokop	21,00 e	6,05**	-0,125	16,93	2,90**	2,95**
4	Krumovgrad	21,50 e	6,55**	0,145	17,37	3,42**	3,36**
5	Samsoun	24,62 f	9,67**	0,565*	19,07	5,40**	5,17**
6	Hicks-Resistant	7,12 b	-7,83**	-0,125	10,98	-4,04**	-3,99**
7	Ft2-5	10,87 c	-4,08**	-0,080	12,62	-1,98**	-2,08**
8	Basma	19,00 d	4,05**	0,245	16,39	2,27**	2,17**
	LSD 0,05 LSD 0,01	1,33 1,73	1,30 1,76	0,416 0,566		0,333 0,492	0,333 0,492

Note1: $\mathbf{g}_\mathbf{j}$* is calculated following Gardner & Eberhart (1966), and $\mathbf{g}_\mathbf{j}$** according to Griffing (1956).

2: The variety values ($\mathbf{Y}_{ij}$) followed by the same letter are not significantly different by Duncan's multiple range test (P=5%).

Summarising the data presented and the published results (1,2,3,4,5,7,8,9,12) it becomes evident that the predominance of additive effects is very common in *host-pathogen* systems. Among the fixed set of parents analysed Bel 61-9 and Hick-Resistant are the best for further crosses and for improvement of quantitative blue mould (*P. tabacina*) resistance in tobacco.

Table 5. Values of SCA effects (S_{ij}).
Табела 5. Вредноста на ефектите на СКС

	2	3	4	5	6	7	8
1	0.29	-1.21**	-0.48	-1.09*	1.58**	1.06*	2.08**
2		-0.24	-0.51	1.01*	-0.17	-0.22	2.05**
3			0.99*	1.01*	-0.30	-0.60	2.55**
4				0.74	-0.45	-0.24	2.13**
5					-0.68	-0.60	1.80**
6						0.22	1.99**
7							2.57**

(S_{ij}* significance for $P_{0,05}$ that is =0,88 and S_{ij}** significance for $P_{0,01}$ that is = 1,19).

CONCLUSIONS

From the data presented on teh combining ability and heterosis for quantitative Blue Mould (*Peronospora tabacina Adam*) resinstence in oriental tobacco, the following statements might be drawn:

- Significant general combining ability was found whereas the specific combining ability was significant only in some individual crosses, and variety effects could explain a great part of the general combining ability. Significant variety heterosis was obtained too, and significant average heterosis was also obtained but its effect was small.

- Among those selected for this study, Bel 61-9 and Hicks- Rezistent were the best for further crosses for tobacco resistance against tobacco Blue Mould (*P. tabacina Adam*).

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КОМБИНАЦИСКАТА СПОСОБНОСТ И ХЕТЕРОЗИСОТ ЗА КВАНТИТАТИВНА ОТПОРНОСТ НА *Peronospora tabacina Adam* КАЈ ОРИЕНТАЛСКИОТ ТУТУН

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РЕЗИМЕ

Квантитативната отпорност треба да се внесе во сортите со добри агромномски својства по пат на облагородување на растенијата. За подобро разбирање на генетската основа на квантитативната отпорност, во овој труд ќе го презентираме испитувањето на комбинациските способности и хетерозисот за квантитативна отпорност на пламеницата (*Peronospora tabacina Adam*) кај осум ориенталски тутунски сорти. За таа цел, една полудијалелна крстоска и нејзините родители (Бел 61-9; Флорија, Неврокоп, Крумовград, Самсун, Hicks-Rezistent, Фт2-5 и Басма) се испитувани во четири повторувања по случаен блок систем.

- Симптомите на природна зараза од болеста се набљудувани и проценувани според методологијата на CORESTA, во текот на три години.

- Забележана е сигнификантна општа комбинациска способност, додека специфичната комбинациска способност беш е сигнификантна само кај некои индивидуални крстоски, а голем дел од општата комбинациска способност може да се објасни со влијанијата на вариететот. Исто така, добиен е и сигнификантен хетерозис на вариететот, како и сигнификантен просечен хетерозис, ама неговото влијание е мало.

- Меѓу сортите што се одбрани во ова проучување, Бел 61-9 и Hicks-Rezistent се најдобри за натамошни вкрстувања за отпорност на тутунот против пламеницата.

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