Journal of Plant Physiology and Breeding
ISSN: 2008-5168 2011, 1(1): 63-73

Estimation of Combining Ability and Gene Effects in Forage Maize (*Zea mays* L.) Using Line × Tester Crosses

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Received: 7 June 2010 Accepted: 17 December 2010

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Abstract

Determination of gene effects and combining abilities is a critical stage in maize hybrid breeding. In the present study, 20 S_6 lines as female and three S_6 inbred lines (K18, K19 and K1264/5-1) as tester were crossed and the resulting test cross progenies were evaluated in a randomized complete block design with three replications in 2008. During the growing period, several agronomic characters including forage yield were measured. Effects of lines and testers were significant on all the characters except ASI and days to physiological maturity for lines and ASI for testers. This indicated the importance of additive gene effect in controlling most of the traits under investigation. Inbred lines L5, L14 and L1 were identified as good general combiners for forage yield because they showed significant positive GCA for this trait. L14 was superior compared with L1 and L5 because of significant positive GCA for most of the agronomic characters. These lines, especially L14, have potential additive gene effects to be utilized in the breeding programs. T3 tester showed favorable additive gene effects for forage yield, its components, early maturity and shorter stature. The highest forage yield (79.040 t/ha) with large positive SCA belonged to L5 × T3 combination. L2 × T3 and L15 × T2 crosses were other desirable combinations. Additive genetic variance was substantially higher than dominance genetic variance for all of the traits except days to physiological maturity. This indicated that additive gene effects were more prominent than dominance effects in controlling forage yield and some other agronomic traits in relation to the studied S_6 inbred lines. Therefore, narrow sense heritability estimates closely resembled the broad sense heritability values except for phenological characters. Medium to high narrow sense heritability estimates enable to select for favorable additive gene effects among the studied lines.

Keywords: GCA, Inbred line, Maize, SCA, Testcross, Tester

Introduction

Development of new hybrid varieties in maize requires information about genetic structure of the parental lines and their progenies. This information can be derived from different mating designs such as diallel (Hayman 1954, Jinks 1954, Griffing 1956) and line × tester (Kempthorne 1957) crosses. Venkatesh *et al.* (2001) used line × tester method to evaluate the progeny of 42 test crosses (21 lines and 2 testers) in order to decrease number of lines at the early stage of screening. Line × tester method has been used in various studies (e.g. Hossein and Aziz 1998, Petrovice 1998, Mankir *et al.* 2004, Wali *et al.* 2010, Hefny 2010) to determine general combining ability (GCA) and specific combining ability (SCA) of the lines under study. Petrovice (1998) suggested that combination of lines with significant positive or negative GCA can lead to positive and significant SCA in their test crosses. However, Hossein and Aziz (1998) showed that parents with high GCA for a trait do not give necessarily a high SCA for the same trait. Riboniesa and Efren (2008) classified white inbred lines of maize into two heterotic groups using yield combining ability effects.

Line × tester analysis is also helpful in estimating genetic variance components and types of gene effects (Singh and Chaudhary 1985). Venkatesh *et al.* (2001) using line × tester method found significant differences between lines, testers and line × tester combinations indicating the contribution of both additive and non- additive (dominance) gene actions in controlling grain yield. Hede *et al.* (1999) crossed 23 tropical maize inbred lines with four broad based synthetic testers and evaluated the progenies in six environments. Analysis of variance showed significant GCA and SCA for grain yield. Konak *et al.* (1999) in a 6× 4 line × tester analysis reported that additive gene action was more prominent in controlling plant height and number of kernel rows, however, grain yield, 100 seed weight, ear height, ear length and time to maturity were mainly affected by dominance effects. Petrovice (1998) also obtained the similar results for number of kernel rows, grain yield, 100 seed weight and ear height. Chokan (1999) evaluated the progenies of a line × tester cross in maize at normal and high plant densities. Significant additive genetic variances were observed for kernel number per row and number of kernel rows under high plant density. For other traits, including grain yield, additive and dominance genetic variances were significant in both conditions. Degree of dominance for most traits was in the range of overdominance. Jha and Khera (1992) in a factorial mating system using five testers as female and 16 S_3 lines as male parents in maize under two environments reported significant variation for all the components. For grain yield, SCA and SCA× environment interaction were more important than GCA and its interaction with environment, indicating the role of non-additive gene action in controlling grain yield. Although both additive and dominance type of gene action has been documented in maize, but dominance gene effect was reported more important than the additive type, especially for grain yield.

The objectives of this study were to estimate GCA, SCA and the gene effects for forage yield and related characters in maize using hybrids produced by the line × tester mating system.

Materials and Methods

The experiment was conducted in Khorasan Razavi Agriculture Research and Natural Resources Center, Iran, in 2008 using 60 maize test crosses. A set of 20 S_6 inbred lines as female were crossed with three inbred lines (T1=K18, T2=K19, T3=K1264/5-1) as male parents or testers in three separate fields in 2007. The resulting test crosses were evaluated in 2008 using a randomized complete block design with three replications. Each test cross progeny was planted in a row with 4.5 m length and between-row and within-row spacing of 75 and 16.5 cm, respectively. During the growing season, plant height, ear height, stem diameter, number of leaves above ear, total number of leaves, number of ears per plant were measured randomly on 10 competitive plants in each plot. In addition, days to silking, days to anthesis, anthesis-silking interval (ASI) and days to physiological maturity were reported. Furthermore, all competitive plants from a plot were cut to the ground level at dough stage and after adjusting for moisture level, the forage yield was recorded on the basis of kilograms per hectare of harvested area. The collected data were analyzed by SAS (Version 9.1) program.

GCA and SCA and standard errors of the estimates were determined by the following formula (Singh and Chaudhary 1985):

GCA (Lines) = $Y_{i..}/rt - Y_{...}/rlt$

GCA (Testers) = $Y_{.j.}/rl - Y_{...}/rlt$

SCA= $Y_{ij.}/r - Y_{i..}/rt - Y_{.j.}/rl + Y_{...}/rlt$

SE (GCA for line)= $(Me/rt)^{1/2}$

SE (GCA for tester)= $(Me/rl)^{1/2}$

SE (SCA)= $(Me/r)^{1/2}$

SE ($GCA_i - GCA_{i'}$) line= $(2Me/rt)^{1/2}$

SE ($GCA_j - GCA_{j'}$) tester= $(2Me/rl)^{1/2}$

SE ($SCA_{ij} - SCA_{i'j'}$)= $(2Me/r)^{1/2}$

Where, $Y_{i..}$= Total of the ith line, $Y_{.j.}$= Total of the jth tester, $Y_{...}$= Grand total, r, l and t = number of replications, lines and testers, respectively, SE= Standard error of the estimate and Me= Error mean square

Additive genetic variance (σ^2_A), dominance genetic variance (σ^2_D), narrow sense heritability (h^2_N), broad sense heritability (h^2_B) and average degree of dominance were estimated as below (Singh and Chaudhary 1985):

$\sigma^2_A= (4/1+F)\ \sigma^2_{gca}$

$\sigma^2_D= (2/1+F)^2\ \sigma^2_{sca}$

$h^2_N= \sigma^2_A/\ \sigma^2_P$

$h^2_B= (\sigma^2_A+ \sigma^2_D)/\ \sigma^2_P$

Average degree of dominance= $(2\sigma^2_D/\ \sigma^2_A)^{1/2}$

Where, σ^2_{gca}= Estimate of GCA variance, σ^2_{sca}= Estimate of SCA variance, σ^2_P= Estimate of phenotypic variance (plot mean basis) and F= Inbreeding coefficient, which was considered as unity because both lines and testers were inbred. Lines were considered as random and testers as fixed factors. Therefore, additive genetic variance was only calculated from σ^2_{gca} of the lines.

Results and Discussion

Analysis of variance showed significant differences between test crosses for all ofthe traits except ASI (Table 1). Effects of lines and testers were also significant for all the measured traits except for ASI (both lines and testers) and

for days to physiological maturity (lines) which indicates the existence of genetic variability among lines and testers in terms of general combining ability. However, mean squares for testers were substantially larger than lines for most of the traits under study. Line × tester interaction was only significant for number of leaves above ear, days to silking, days to anthesis and days to physiological maturity suggesting that dominance gene action was also involved in governing these traits.

Table 2 shows the estimates of GCA for lines and testers and their SCA. L5, L14 and L1 Inbred lines showed significant positive GCA for forage yield whereas L1 had significant positive GCA for total number of leaves and number of leaves above ear. L15 also showed significant positive GCA for stem diameter, ear height and days to anthesis and significant negative GCA for ASI. L14 was superior over L1 and L5 having significant positive GCA for most of the agronomic characters including total number of leaves, number of leaves above ear, number of ears per plant, stem diameter, plant height and ear height. Thus, these three inbred lines, especially L14, have potential to be utilized for producing synthetic maize varieties and for other breeding purposes.

Among the testers, T3 showed significant positive GCA for total number of leaves, number of leaves above ear, number of ears per plant, forage yield and significant negative GCA for days to anthesis, days to silking, days to physiological maturity, stem diameter, plant height and ear height (Table 2.). Therefore, this tester had favorable additive genes for forage yield and its components and, also, additive genes for early maturity and shorter stature. T1 and T2 had significant positive GCA for days to anthesis, days to silking and days to physiological maturity indicating that these testers had additive genes for late maturity. On the other hand, for plant height and ear height positive and significant GCA was observed for T2, while negative and significant for T1. The existence of considerable diversity among testers for GCA of different characters justified the use of these genotypes for testing the GCA of S_6 inbred lines under study.

Promising crosses are selected based on *per se* performance, standard heterosis and SCA effects. The highest forage yield (79.040 t/ha) belonged to L5 × T3 combination (Table 3). This combination had also high positive SCA for forage yield. The superiority of L5 × T3 hybrid can be attributed to its higher leaf number, days to physiological maturity and more ears per plant (data not shown). Higher forage yield and SCA for forage yield were also observed in L1 × T2, L2 × T3 and L15 × T2. L15 × T2 had also large positive SCA for number of leaves above ear. Furthermore, negative SCA of days to anthesis and days to silking were observed for L5 × T3, L2 × T3 and L15 × T2, while positive SCA of these characters were determined for L1 × T2. However, none of the SCAs for these combinations were significant. Early and medium-maturing forage maize hybrids are desirable in the area of study in order to decrease the risk of early autumn cold stress. Therefore, for traits such as days to anthesis and silking, negative GCA or SCA are preferred. Thus, on the basis of forage yield and maturity the genotypes L5 × T3, L2 × T3 and L15 × T2 may be regarded as promising hybrids and

should be evaluated further for forage yield and other desirable characters.

Estimates of various genetic parameters are presented in Table 4. Negative estimates of genetic components of variance for some characters were set to zero based on expected mean squares. Negative estimates of genetic components can be derived from unsuitable genetic and statistical model, insufficient sampling of original population, sampling error and improper experimental design (Mather and Jinks1982, Roy 2000). Although dominance genetic variance was present for some characters under study, additive genetic variance was much larger than dominance genetic variance for all of the traits except days to physiological maturity indicating that additive gene effects were more important than dominance effects in controlling forage yield. Therefore, the estimates of narrow sense heritability were very close to those of broad sense except for phenological characters. Narrow sense heritability estimates ranged from 0.17 for days to physiological maturity to 0.84 for plant height. Narrow sense heritability of forage yield was medium (0.51). Medium to high narrow sense heritability estimates suggest the possibility of selecting for additive gene effects among the studied lines.

Except for days to physiological maturity, average degree of dominance was in the range of incomplete dominance. Large over-dominance value (2.14) for days to physiological maturity may be due to the result of correlated gene distributions among parents so that partial dominance appears as over-dominance (Hayman 1954).

Ferret *et al.* (1991) reported that for stover and whole plant dry matter yield (DMY) in two dent maize populations additive gene effect was the most important gene action. Moreno-González *et al*. (2000) in a study using European flint (F) and U.S. corn belt dent (D) populations for forage use, reported non-significant average heterosis for stover DMY. In contrast, all populations had high significant heterosis for ear DMY, and six populations had significant heterosis for whole plant DMY. In addition, overall average heterosis was significant for ear and whole plant DMY. Therefore, they stated that most of the contribution to heterosis of the whole plant DMY was provided by the ear fraction rather than the stover fraction. Similarly, based on the results of Boppenmaier *et al.* (1992), stover fraction of DMY had higher effect on heterosis than the grain in maize hybrids. Moreno-González *et al.* (2000) suggested that dominance gene action for the ear DMY fraction may be present in all F × F, F × D and D × D types of crosses, whereas dominance gene action for the stover DMY fraction may be present in the F × D crosses. Therefore, they concluded that breeding strategies for silage hybrids should use populations from the F × D heterotic pattern.

Both additive and non-additive gene effects for plant height were reported by Konak *et al.* (1999), Lee and Shung (1995) and Menkir *et al.* (2004), leaf number by Jha and Khera (1992), days to silking by Neastares *et al.* (1999) and Mendoza *et al.* (2000) and days to anthesis by Lopes *et al.* (1995) and Menkir *et al*. (2004). Esmaili *et al*. (2005) reproted additive gene effects for plant height, days to anthesis, days to physiological maturity and leaf no. Higher non-additive gene effects was obtained for days to silking by several researchers (Konak *et al.*

1999, Nestares *et al.* 1999, Esmaili *et al.* 2005), although some researchers indicated the contribution of additive gene effects for this character (Rissi and Hallauer 1991, Jha and Khera 1992). Petrovice (1998) indicated the importance of non-additive gene action in governing plant height, while others (Jha and Khera 1992, Konak *et al.* 1999) showed the prominence of additive gene action for the this trait. Furthermore, Hefny (2010) reported the greater role of additive gene effects in controlling days to anthesis. The different results can be due to different experimental materials and environmental conditiona or the use of different methods for estimating genetic parameters (Konak *et al.* 1999).

Acknowledgement

This study was supported by Seed and Plant Improvement Institute (SPII), Karaj, Iran. We thank M. Mohammadi for his help in the field experiments.

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Table 1. Analysis of variance for agronomic traits of maize test crosses

				Mean squares								
Sources of variation	Degrees of freedom	Ear height	Plant height	Stem diameter	Anthesis-silking interval	Days to anthesis	Days to silking	Forage yield	Number of leaves above ear	Number of leaves	Number of ears/plant	Days to Physiological maturity
Replication	2	616.87**	962.62**	14.81**	0.206^{ns}	2.93^{ns}	3.02^{ns}	851.13**	0.138^{ns}	5.36**	0.053*	28.85
Cross	59	261.40**	558.40**	5.51**	0.747^{ns}	18.09**	18.33**	166.96**	0.127**	1.01**	0.025**	62.56**
Line	19	480.22**	838.58**	5.11**	0.974^{ns}	13.05**	12.85**	191.82**	0.691**	1.72**	0.034*	34.48^{ns}
Tester	2	2169.05**	6791.49**	89.17**	0.339^{ns}	308.53**	328.65**	1603.88**	0.681**	8.55**	0.088*	735.8**
Line ×Tester	38	51.59^{ns}	90.26^{ns}	1.31^{ns}	0.655^{ns}	5.32*	4.74*	78.90^{ns}	0.098*	0.27^{ns}	0.017^{ns}	41.17**
Error	118	56.43	71.99^{+}	1.45^{+}	0.578	3.16^{+}	2.98	70.50^{+}	0.061	0.32	0.014	21.88

* , **: Significant at 0.05 and 0.01 probability levels, respectively ns: Non-significant

+: Error mean squares (with 117 degrees of freedom) excluding non-additivity variance

Table 2. Estimates of general combining ability of maize inbred lines and testers

Line	Number of leaves	Number of leaves above ear	Number of ears/plant	Forage yield	Days to silking	Days to anthesis	ASI	Stem diameter	Plant height	Ear height	Days to Physiological maturity
L1	0.70	0.36	0.04	6.36	-0.19	0.12	-0.32	0.60	0.45	-0.22	0.244
L2	0.13	-0.08	0.08	-5.25	0.03	0.01	0.02	0.55	-9.92	-10.86	-0.978
L3	-0.66	-0.31	-0.07	-1.43	-0.64	-0.77	0.13	0.24	-10.95	-11.09	-2.200
L4	-0.33	-0.61	0.07	0.09	-1.31	-1.54	0.24	0.89	-15.93	-1.17	-1.422
L5	0.26	0.04	0.02	10.04	0.92	1.46	-0.54	1.10	3.38	5.79	2.689
L6	-0.64	-0.32	-0.06	-9.45	-2.86	-3.10	0.24	-1.00	-22.36	-13.44	-1.867
L7	-0.24	0.15	-0.06	-2.55	-0.53	-0.77	0.24	-0.01	4.45	-7.67	1.578
L8	0.69	0.21	0.09	2.34	0.47	0.68	-0.21	0.34	6.53	1.23	-0.200
L9	0.32	0.00	-0.05	-0.33	0.92	1.23	-0.32	-0.82	4.45	0.40	0.244
L10	-0.28	-0.12	0.01	-0.30	-0.31	-0.43	0.13	-0.76	-0.89	1.37	0.244
L11	0.53	0.64	0.08	0.72	-0.75	-0.43	-0.32	0.12	1.95	-0.77	-3.867
L12	0.02	-0.01	-0.08	-5.08	-1.97	-1.88	-0.09	-0.61	-11.13	-5.08	-2.533
L13	-0.18	-0.15	-0.03	-2.53	-0.08	-0.10	0.02	-1.14	4.53	5.57	-1.644
L14	0.53	0.26	0.10	7.44	1.03	1.23	-0.21	1.72	19.06	12.69	3.022
L15	-0.08	0.01	0.06	0.21	1.03	1.12	-0.09	0.07	5.84	7.56	1.133
L16	-0.08	0.05	-0.04	-1.02	2.36	1.46	0.91	0.41	0.75	-3.70	3.467
L17	-0.87	-0.38	-0.06	3.80	1.36	0.90	0.46	-0.35	2.60	2.49	2.022
L18	0.10	-0.01	-0.01	-2.73	0.70	0.79	-0.09	-0.53	6.11	7.21	-0.200
L19	-0.10	0.16	-0.09	-3.41	-0.19	0.12	-0.32	-0.72	0.49	-2.26	-0.533
L20	0.15	0.10	0.05	3.15	0.03	-0.10	0.13	-0.09	10.63	11.95	0.800
SE(GCA)	0.189	0.082	0.039	2.799	0.575	0.593	0.253	0.401	2.828	2.504	1.56
SE(GCAi-GCAi')	0.267	0.116	0.056	3.958	0.814	0.838	0.358	0.568	4.000	3.541	2.21
Tester											
T1	-0.05	-0.10	-0.036	-4.44	0.50	0.51	-0.01	0.35	-8.31	-4.23	1.77
T2	-0.35	-0.01	-0.004	-1.24	2.05	1.97	0.08	1.01	11.92	6.88	2.27
T3	0.40	0.11	0.040	5.68	-2.55	-2.48	-0.07	-1.36	-3.69	-2.66	-4.03
SE(GCA)	0.073	0.032	0.015	1.084	0.223	0.229	0.098	0.155	1.095	0.970	0.60
SE(GCAj-GCAj')	0.103	0.045	0.022	1.533	0.315	0.325	0.139	0.220	1.549	1.371	0.85

ASI: Anthesis-silking interval

Table 3. Forage yield and specific combining ability of several characters for line × tester combinations of maize under study

Cross	Forage yield	Specific combining ability				Cross	Forage yield	Specific combining ability			
		Forage yield	Days to silking	Days to anthesis	No. of leaves above ear			Forage yield	Days to silking	Days to anthesis	No. of leaves above ear
L1×T1	51.952	-5.140	-0.722	-0.506	-0.154	L11×T1	50.445	-1.005	-1.500	-1.950	0.035
L1×T2	66.615	6.328	1.061	1.028	-0.046	L11×T2	55.897	1.252	0.617	1.250	0.076
L1×T3	66.019	-1.187	-0.339	-0.522	0.200	L11×T3	61.317	-0.247	0.883	0.700	-0.111
L2×T1	41.954	-3.531	0.389	0.605	0.046	L12×T1	43.154	-2.495	0.056	-0.172	0.113
L2×T2	43.060	-5.621	1.172	1.138	-0.013	L12×T2	55.813	6.968	-0.494	-0.306	0.020
L2×T3	64.752	9.152	-1.561	-1.745	-0.033	L12×T3	51.290	-4.473	0.439	0.478	-0.133
L3×T1	45.981	-3.319	-0.944	-0.283	0.146	L13×T1	53.730	5.530	0.500	1.050	-0.110
L3×T2	53.821	1.325	1.506	0.917	0.087	L13×T2	55.390	3.994	-0.717	-1.083	0.065
L3×T3	61.408	1.994	-0.561	-0.633	-0.233	L13×T3	48.791	-9.524	0.217	0.033	0.045
L4×T1	47.579	-3.159	-1.611	-1.839	-0.221	L14×T1	62.020	3.846	0.056	-0.283	0.179
L4×T2	56.038	2.104	1.172	1.028	0.220	L14×T2	57.463	-3.906	-0.161	0.583	-0.180
L4×T3	61.908	1.055	0.439	0.811	0.000	L14×T3	68.348	0.060	0.106	-0.300	0.000
L5×T1	58.145	-2.625	-0.167	0.161	0.002	L15×T1	48.145	-2.790	1.722	2.161	-0.210
L5×T2	58.433	-5.532	1.283	1.028	-0.057	L15×T2	62.485	8.354	-1.161	-1.306	0.131
L5×T3	79.040	8.156	-1.117	-1.189	0.056	L15×T3	55.486	-5.564	-0.561	-0.856	0.078
L6×T1	40.723	-20.047	0.278	0.050	-0.343	L16×T1	50.876	1.167	0.056	-0.172	0.057
L6×T2	46.820	-17.145	-0.606	-0.750	0.298	L16×T2	54.138	1.233	1.172	0.361	-0.135
L6×T3	49.603	-21.281	0.328	0.700	0.045	L16×T3	57.424	-2.400	-1.228	-0.189	0.078
L7×T1	45.956	-2.227	-1.722	-1.617	0.103	L17×T1	55.821	1.289	0.722	0.383	0.179
L7×T2	48.855	-2.524	0.394	0.250	-0.075	L17×T2	58.371	0.643	-1.161	-0.750	-0.146
L7×T3	63.049	4.751	1.328	1.367	-0.028	L17×T3	62.715	-1.932	0.439	0.367	-0.033
L8×T1	55.243	2.170	0.278	-0.394	0.090	L18×T1	48.457	0.452	-1.278	-1.506	0.013
L8×T2	53.932	-2.337	-0.272	0.472	-0.135	L18×T2	50.340	-0.861	0.172	0.694	-0.046
L8×T3	63.354	0.167	-0.006	-0.078	0.045	L18×T3	58.529	0.409	1.106	0.811	0.034
L9×T1	48.560	-1.838	0.500	1.050	0.268	L19×T1	54.163	6.843	1.611	1.494	0.046
L9×T2	54.715	1.121	0.950	0.917	0.176	L19×T2	42.264	-8.251	-2.272	-2.306	-0.213
L9×T3	61.230	0.717	-1.450	-1.967	-0.444	L19×T3	58.842	1.408	0.661	0.811	0.167
L10×T1	50.246	-0.189	0.389	0.383	-0.143	L20×T1	61.455	7.578	1.389	1.383	-0.098
L10×T2	54.928	1.298	-0.161	-0.417	0.031	L20×T2	49.136	-7.936	-2.494	-2.750	-0.057
L10×T3	59.440	-1.109	-0.228	0.033	0.111	L20×T3	64.349	0.358	1.106	1.367	0.156
SE (mean)	4.848						4.848				
SE (SCA)		4.848	0.997	1.026	0.143			4.848	0.997	1.026	0.143
SE (SCAij – CAi'j')		6.856	1.409	1.451	0.202			6.856	1.409	1.451	0.202

Table 4. Estimates of additive genetic variance, dominance genetic variance, narrow sense heritability, broad sense heritability and average degree of dominance for the maize characters under study

Estimates of parameters	Ear height	Plant height	Stem diameter	Anthesis-silking interval	Days to anthesis	Days to silking	Forage yield	Number of leaves above ear	Number of leaves	Number of ears/plant	Days to Physiological maturity
σ^2_A	94.18	170.35	0.81	0.098	2.20	2.19	26.96	0.14	0.31	0.004	2.8
σ^2_D	0.00	6.09	0.00	0.026	0.72	0.59	2.8	0.012	0.00	0.001	6.43
h^2_N	0.83	0.84	0.63	0.31	0.66	0.58	0.51	0.81	0.74	0.41	0.17
h^2_B	0.83	0.88	0.63	0.39	0.88	0.74	0.55	0.88	0.74	0.52	0.58
Average degree of dominance	-	0.27	-	0.73	0.65	0.73	0.46	0.41	-	0.71	2. 14