Chapter 21

Mapping QTL with Epistatic Effects and QTL-by-Environment Interaction Effects

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Purpose

To map quantitative trait loci (QTL) with additive, epistatic, and QTL-by-environment interaction effects for doubled haploid (DH) or recombinant inbred line (RIL) populations.

Definitions

Genetic Model

If multiple-environment data of DH or RIL populations are used for mapping QTL, the phenotypic value of the jth genetic entry in environment h can be expressed as shown in the genetic model

$$
\begin{aligned}
y_{hj} = {} & \mu + a_1 x_{A_{1j}} + a_2 x_{A_{2j}} + aa x_{AA_j} \\
& + u_{E_{hj}} e_{E_h} + u_{A_1 E_{hj}} e_{A_1 E_h} + u_{A_2 E_{hj}} e_{A_2 E_h} + u_{AAE_{hj}} e_{AAE_h} \\
& + \sum_f u_{M_{fj}} e_{M_f} + \sum_l u_{MM_{lj}} e_{MM_l} + \sum_p u_{ME_{hpj}} e_{ME_{hp}} + \sum_q u_{MME_{hqj}} e_{MME_{hq}} + \varepsilon_{hj}
\end{aligned}
$$

where μ is the population mean; a_1 and a_2 are the additive effects of loci Q_1 and Q_2, respectively; aa is the additive × additive epistatic effect of loci Q_1 and Q_2; $x_{A_{1j}}$, $x_{A_{2j}}$, and x_{AA_j} are coefficients of these genetic main effects; e_{E_h} is the random effect of environment h with coefficient $u_{E_{hj}}$; $e_{A_1 E_h}$ (or $e_{A_2 E_h}$) is the additive × environment interaction effect with coefficient $u_{A_1 E_{hj}}$

(or $u_{A_2E_{hj}}$) for Q_1 (or Q_2); e_{AAE_h} is the epistasis $\times$ environment interaction effect with coefficient $u_{AAE_{hj}}$; e_{M_f} is the marker main effect with coefficient u_{M_f}; e_{MM_l} is the marker $\times$ marker interaction effect with coefficient u_{MM_l}; $e_{ME_{hp}}$ is the marker $\times$ environment interaction effect with coefficient $u_{ME_{hpj}}$; $e_{MME_{hq}}$ is the marker $\times$ marker $\times$ environment interaction effect with coefficient $u_{MME_{qhj}}$; and ε_{hj} is the residual effect.

Mixed Linear Model

The epistatic QTL model can be expressed in matrix form as

$$
\begin{aligned}
y = Xb &+ U_E e_E + U_{A_1E} e_{A_1E} + U_{A_2E} e_{A_2E} + U_{AAE} e_{AAE} \\
&+ U_M e_M + U_{MM} e_{MM} + U_{ME} e_{ME} + U_{MME} e_{MME} + e_\varepsilon \\
= Xb &+ \sum_{u=1}^{9} U_u e_u \\
&\sim N(Xb, V = \sum_{u=1}^{9} \sigma_u^2 U_u R_u U_u^T)
\end{aligned}
$$

where y is the phenotype vector; b is the fixed parameter vector for population mean and QTL effects; X is the known incidence matrix of the fixed parameters; $e_1 = e_E \sim N(0, \sigma_E^2 I)$ is the vector of environment effects; $e_2 = e_{A_1E} \sim N(0, \sigma_{A_1E}^2 I)$ is the vector of A1 $\times$ E interaction effects; $e_3 = e_{A_2E} \sim N(0, \sigma_{A_2E}^2 I)$ is the vector of A2 $\times$ E interaction effects; $e_4 = e_{AAE} \sim N(0, \sigma_{AAE}^2 R_{AAE})$ is the vector of AA $\times$ E interaction effects; $e_5 = e_M \sim N(0, \sigma_M^2 R_M)$ is the vector of marker main effects; $e_6 = e_{MM} \sim N(0, \sigma_{MM}^2 R_{MM})$ is the vector of interaction marker main effects; $e_7 = e_{ME} \sim N(0, \sigma_{ME}^2 R_{ME})$ is the vector of M $\times$ E interaction effects; $e_8 = e_{MME} \sim N(0, \sigma_{MME}^2 R_{MME})$ is the vector of MM $\times$ E interaction effects; $e_9 = e_\varepsilon \sim N(0, \sigma_\varepsilon^2 I)$ is the vector of residual effects; $U_u (u = 1, 2, \ldots, 8)$ is the known incidence matrix of the random effects, and $U_9 = I$.

Analysis Methodology

An approach of mixed-model-based composite interval mapping (MCIM) can be constructed for handling epistatic effects and QTL × environment interaction effects. The likelihood function (L) for the parameters of fixed effects b and variance components $[\sigma_u^2]$ is

$$L(b,V) = (2\pi)^{-\frac{n}{2}} |V|^{-\frac{1}{2}} \exp\left[-\tfrac{1}{2}(y-Xb)^T V^{-1}(y-Xb)\right]$$

with the log of the likelihood function (l)

$$l(b,V) = -\tfrac{n}{2}\ln(2\pi) - \tfrac{1}{2}\ln|V| - \tfrac{1}{2}(y-Xb)^T V^{-1}(y-Xb).$$

For searching QTL, the null hypothesis for genetic parameters (QTL main effects and Q × E interaction effects) can be tested by the likelihood ratio statistic (LR):

$$LR = 2l_1(\hat{b}_1, v_1) - 2l_0(\hat{b}_0, v_0).$$

The maximum likelihood estimates of QTL effects in b can be obtained by

$$\hat{b} = (X^T V^{-1} X)^{-1} X^T V^{-1} y$$

with variance-covariance matrix

$$\text{var}(\hat{b}) = (X^T V^{-1} X)^{-1}.$$

Q × E interaction effects (additive × environment interaction e_{A_iE} and e_{A_jE}, epistasis × environment interaction $e_{AA_{ij}E}$) can be obtained by the best linear unbiased prediction (BLUP) method:

$$\hat{e}_u = \sigma_u^2 U_u^T Q y$$

with variance-covariance matrix

$$\text{var}(\hat{e}_u) = \sigma_u^4 U_u^T Q U_u$$

where $Q = V^{-1} - V^{-1} X (X^T V^{-1} X)^{-1} X^T V^{-1}$.

Originators

Wang, D., Zhu, J., Li, Z.K., and Paterson, A.H. (1999). Mapping QTLs with epistatic effects and QTL × environment interactions by mixed linear model approaches. *Theoretical and Applied Genetics* 99:1255-1264.

Zhu, J. (1998). Mixed model approaches of mapping genes for complex quantitative traits. In Wang, L.Z. and Dai, J.R. (Eds.), *Proceedings of Genetics and Crop Breeding in China* (pp. 19-20). Chinese Agricultural Science and Technology Publication House, Beijing.

Zhu, J. and Weir, B.S. (1998). Mixed model approaches for genetic analysis of quantitative traits. In Chen, L.S., Ruan, S.G., and Zhu, J. (Eds.), *Advanced Topics in Biomathematics: Proceedings of International Conference on Mathematical Biology* (pp. 321-330). World Scientific Publishing Co., Singapore.

Software Available

Wang, D., Zhu, J., Li, Z.K., and Paterson, A.H. (1999). *User Manual for QTLMapper Version 1.0: A Computer Software for Mapping Quantitative Trait Loci (QTLs) with Additive Effects, Epistatic Effects and QTL × Environment Interactions* (program free of charge). Contact Dr. Jun Zhu, Department of Agronomy, Zhejiang University, Hangzhou, China. E-mail: <jzhu@zju.edu.cn>.

EXAMPLE

Data of DH population with ninety-six lines and fifty-four markers on three chromosomes (provided by Drs. N. Huang and P. Wu). Data analysis method is described in detail in the user manual for QTLMapper Version 1.0 (Wang et al., 1999).

Data file (ckge.map) for map information:

```
_Chromosomes 3
_MarkerNumbers 18 15 21
_DistanceUnit cM

*MapBegin*
Marker#    ch1         ch2         ch3
1            0           0           0
2          19.236      12.9949      7.7618
3          16.2488      5.3402     13.2518
4           4.8552     22.2875      6.9239
5           4.8047     27.7327      9.8037
```

6	15.3881	6.3438	2.7929
7	15.5969	29.4517	17.5239
8	15.0048	10.2825	41.7545
9	3.8375	8.9339	37.3036
10	3.2747	12.824	15.8394
11	34.4392	8.4598	18.7639
12	2.5322	5.1683	2.5121
13	23.7979	10.1262	5.0168
14	8.2644	5.2896	28.9405
15	13.3483	13.2089	1.9109
16	33.5319		22.7256
17	2.5622		15.2455
18	9.2129		32.48
19			7.1483
20			9.4924
21			18.718

MapEnd

Data file for marker and trait information:

_Population DH
_Genotypes   96
_Observations 192
_Environments yes
_Replications   no
_TraitNumber 5
_TotalMarker   54
_MarkerCode   P1=1   P2=2   F1=3   F1P1=4   F1P2=5

MarkerBegin

Ind	M1	M2	M3	M4	M5	M6	M7	M8	M9	M10	M11	M12	M13	M14	M15	M16	M17	M18	M19	M20	M21	M22	M23	M24	M25	M26	M27
1	2	1	1	1	1	1	1	1	2	2	2	2	2	2	2	2	1	1	1	2	2	2	2	1	1	2	2
2	1	1	1	1	1	1	1	2	2	2	2	2	2	1	1	1	1	1	2	2	2	2	2	1	1	1
3	1	1	2	2	2	2	2	2	2	2	1	1	1	1	1	1	1	1	2	2	2	1	1	1	1	1	1
4	2	2	2	2	2	2	2	2	2	2	1	.	1	1	1	2	2	2	2	2	2	2	1	1	2	2	2
5	2	2	1	.	1	1	1	2	2	2	2	.	.	2	.	1	1	1	2	2	2	2	.	2	2	2	2
6	1	1	2	2	2	2	2	2	2	2	1	1	.	1	1	2	2	2	2	2	1	1	1	1	1	2	2
7	1	1	2	.	2	2	2	2	2	2	2	2	1	1	1	1	1	1	2	2	2	2	2	1	2	2
8	1	2	2	2	2	2	2	2	2	2	1	1	1	1	1	1	1	1	2	2	2	2	2	2	2	2
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11	2	2	2	.	2	2	2	2	2	1	1	.	1	2	2	2	2	2	2	2	1	1	1	1	1	1
12	1	1	1	1	1	1	1	1	1	1	1	1	2	2	1	1	1	1	2	2	2	2	2	2	1	1
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```
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96  1  1  1  1  1  1  2  2  2  2  1  1  1  1  1  1  1  1  2  2  .  2  2  2  2  1  1
```

M28	M29	M30	M31	M32	M33	M34	M35	M36	M37	M38	M39	M40	M41	M42	M43	M44	M45	M46	M47	M48	M49	M50	M51	M52	M53	M54
2	2	2	2	2	2	2	2	2	2	2	2	2	1	2	1	1	1	1	1	1	1	2	2	.	2	;
1	1	1	1	1	1	2	1	1	1	1	1	2	2	2	1	1	1	1	1	1	1	1	1	1	1	;
1	1	1	1	1	.	1	1	1	1	1	1	2	2	2	.	2	2	2	2	2	2	2	2	2	.	2	;
1	2	2	2	2	1	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	.	2	;
2	.	.	2	.	.	1	.	2	2	.	2	2	.	2	1	2	.	.	2	2	2	.	2	.	.	1	;
1	1	1	1	1	.	2	2	2	2	2	2	1	2	2	2	2	1	1	1	.	1	1	.	1	;
2	2	2	2	2	2	1	1	1	2	2	2	2	1	1	2	1	1	1	1	1	1	.	1	1	.	1	;
2	2	2	1	2	1	1	1	2	2	2	2	2	.	2	2	1	1	1	1	1	2	2	2	2	;
1	1	1	1	1	1	1	1	2	2	2	2	2	2	1	2	2	2	2	1	1	1	1	1	1	;
2	2	2	2	2	2	2	2	2	2	2	2	2	1	1	1	1	1	1	1	1	2	2	2	1	;
1	1	1	1	1	1	1	1	1	1	1	1	1	2	1	1	1	1	1	1	1	1	.	1	;
1	1	1	1	1	1	2	2	2	2	2	2	1	1	1	2	1	1	1	1	1	1	1	1	.	2	;
2	2	2	1	1	1	1	1	2	2	2	2	1	1	1	1	1	2	1	1	1	1	1	1	;
1	1	1	1	1	1	2	2	2	2	2	2	1	1	2	1	1	1	2	2	2	1	1	1	1	;
2	2	2	2	2	2	2	2	2	2	2	2	1	1	.	1	1	1	2	2	2	2	2	.	2	;
2	2	2	2	2	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	.	1	.	2	;
2	2	2	2	2	2	1	1	1	1	1	1	2	2	1	2	2	2	.	1	1	1	1	1	1	;
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2	.	2	.	.	2	.	2	2	.	2	2	.	2	.	1	.	1	1	1	1	1	.	1	;
2	2	2	2	2	2	1	1	1	1	1	1	1	2	1	.	1	1	1	1	1	1	.	1	1	1	;
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2	2	2	2	2	2	2	2	2	2	2	1	1	.	2	2	2	2	2	2	1	1	1	1	;
1	1	1	1	1	1	1	1	1	1	1	2	2	1	.	1	1	1	1	2	2	1	2	2	2	;
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2	2	2	2	2	.	1	1	1	1	.	1	1	2	2	2	2	1	1	1	1	1	.	.	2	;
1	.	1	1	1	1	2	2	2	2	2	1	.	1	1	1	1	2	2	2	2	.	2	.	2	;
1	1	1	2	2	1	1	1	2	2	2	1	1	1	1	1	1	2	2	2	1	1	1	1	;
2	2	2	.	2	.	1	1	1	1	.	1	.	2	1	1	1	1	1	2	2	2	2	.	2	;
1	2	1	1	2	2	2	2	2	2	2	2	1	1	.	1	1	2	2	2	2	2	2	.	2	;
1	.	1	1	1	1	1	1	.	2	2	2	.	1	1	1	1	2	2	2	.	2	2	.	1	;
1	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	1	2	2	2	.	2	;
1	2	2	2	2	2	1	1	1	1	1	1	2	2	2	2	2	2	2	1	1	1	1	.	1	;
2	2	2	2	2	.	2	2	2	2	2	1	2	2	2	2	2	2	2	1	2	2	.	2	;
1	1	1	1	1	1	2	2	2	2	1	1	1	1	1	1	1	.	1	1	1	2	2	.	2	;
1	1	1	1	1	1	2	2	2	2	1	1	1	1	1	1	1	1	1	1	1	2	2	.	2	;

```
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2 2 2 2 2 2 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 2 2 2 ;
2 2 . 1 1 1 2 2 2 2 2 2 1 1 1 1 1 1 1 1 . 1 1 1 . 2 ;
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1 1 1 1 1 1 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 ;
2 2 2 2 2 2 2 2 2 2 2 2 2 1 1 1 1 1 1 1 1 1 1 1 1 1 ;
2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 ;
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2 2 2 2 2 1 1 2 2 2 2 2 1 1 1 1 1 1 1 1 1 2 2 2 2 ;
2 . 2 2 . . 2 2 2 . 2 2 1 1 1 1 2 . 2 2 2 2 2 . 1 ;
2 2 2 2 2 1 1 2 2 2 1 1 1 1 2 2 2 2 2 2 2 2 2 2 2 ;
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2 2 2 2 2 . 1 1 1 1 1 1 1 1 2 2 1 1 1 . 2 2 2 1 1 . 1 ;
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2 2 2 2 2 2 2 2 1 1 1 1 2 1 1 1 1 1 1 1 1 1 1 1 1 ;
1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 2 2 2 2 2 2 2 2 2 2 ;
1 1 1 1 1 1 . 2 2 2 2 2 1 1 1 1 1 1 1 1 1 1 1 . 1 ;
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1 1 1 2 1 2 2 2 2 2 2 2 2 1 1 2 2 2 2 2 2 2 2 2 1 ;
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2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 1 2 2 2 2 2 ;
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2 2 2 2 2 . 2 2 2 2 2 2 2 2 2 2 2 2 1 2 2 1 . 1 ;
2 2 2 2 2 . 2 2 2 2 2 2 2 2 2 . 2 . 1 1 1 1 . 1 ;
2 2 2 2 2 2 1 1 1 1 2 2 2 1 1 1 1 1 . 1 1 1 2 2 . 2 ;
1 1 1 1 1 . 1 . 2 2 2 2 2 2 2 2 . 2 . 1 2 1 1 1 . 1 ;
2 2 2 1 1 1 1 1 1 1 1 1 1 1 1 1 2 2 2 1 1 2 1 . 2 2 2 ;
2 2 2 2 2 2 1 1 1 1 1 1 1 2 2 2 2 2 2 1 2 2 1 . 1 ;
1 1 1 1 1 1 1 2 2 2 2 2 2 2 2 2 2 1 1 . 1 1 1 . 2 ;
```

MarkerEnd

TraitBegin

Env#	Ind#	SH5 ;	Env#	Ind#	SH5 ;	Env#	Ind#	SH5 ;	Env#	Ind#	SH5 ;
1	1	52.5 ;	1	49	77.6 ;	2	1	43.8 ;	2	49	66.7 ;
1	2	62.5 ;	1	50	50.4 ;	2	2	39.5 ;	2	50	50.1 ;
1	3	77.9 ;	1	51	60.0 ;	2	3	57.8 ;	2	51	56.7 ;
1	4	57.2 ;	1	52	68.6 ;	2	4	44.9 ;	2	52	56.4 ;
1	5	51.7 ;	1	53	58.0 ;	2	5	41.9 ;	2	53	53.3 ;
1	6	62.5 ;	1	54	67.2 ;	2	6	44.2 ;	2	54	58.4 ;
1	7	56.0 ;	1	55	65.2 ;	2	7	46.8 ;	2	55	60.1 ;
1	8	62.7 ;	1	56	66.7 ;	2	8	51.4 ;	2	56	57.2 ;
1	9	62.1 ;	1	57	67.1 ;	2	9	46.4 ;	2	57	53.1 ;
1	10	76.2 ;	1	58	59.6 ;	2	10	65.6 ;	2	58	54.9 ;
1	11	69.1 ;	1	59	67.5 ;	2	11	53.0 ;	2	59	56.0 ;
1	12	68.4 ;	1	60	67.7 ;	2	12	58.4 ;	2	60	52.6 ;
1	13	45.4 ;	1	61	60.3 ;	2	13	40.2 ;	2	61	52.0 ;
1	14	68.4 ;	1	62	70.9 ;	2	14	59.1 ;	2	62	57.0 ;
1	15	83.9 ;	1	63	78.8 ;	2	15	67.7 ;	2	63	65.0 ;
1	16	81.5 ;	1	64	70.9 ;	2	16	67.7 ;	2	64	59.0 ;
1	17	74.4 ;	1	65	52.2 ;	2	17	63.7 ;	2	65	46.3 ;
1	18	73.9 ;	1	66	70.7 ;	2	18	68.0 ;	2	66	55.3 ;
1	19	58.7 ;	1	67	66.3 ;	2	19	48.7 ;	2	67	58.4 ;
1	20	64.5 ;	1	68	55.0 ;	2	20	51.8 ;	2	68	48.9 ;
1	21	61.2 ;	1	69	75.3 ;	2	21	49.9 ;	2	69	59.6 ;
1	22	48.5 ;	1	70	75.5 ;	2	22	41.1 ;	2	70	56.8 ;
1	23	48.2 ;	1	71	57.5 ;	2	23	34.1 ;	2	71	43.4 ;
1	24	83.5 ;	1	72	49.7 ;	2	24	71.4 ;	2	72	42.5 ;
1	25	55.2 ;	1	73	75.5 ;	2	25	44.6 ;	2	73	66.5 ;
1	26	49.6 ;	1	74	52.5 ;	2	26	47.0 ;	2	74	40.1 ;
1	27	77.3 ;	1	75	64.6 ;	2	27	62.3 ;	2	75	57.3 ;
1	28	78.5 ;	1	76	57.2 ;	2	28	60.8 ;	2	76	52.8 ;
1	29	71.0 ;	1	77	52.1 ;	2	29	64.1 ;	2	77	43.4 ;
1	30	67.2 ;	1	78	53.9 ;	2	30	62.3 ;	2	78	46.8 ;
1	31	80.9 ;	1	79	72.0 ;	2	31	67.6 ;	2	79	63.1 ;
1	32	88.4 ;	1	80	70.0 ;	2	32	77.3 ;	2	80	57.8 ;
1	33	79.2 ;	1	81	52.3 ;	2	33	66.1 ;	2	81	43.2 ;
1	34	77.1 ;	1	82	55.5 ;	2	34	58.6 ;	2	82	43.3 ;
1	35	72.7 ;	1	83	63.7 ;	2	35	57.9 ;	2	83	48.3 ;
1	36	78.6 ;	1	84	62.1 ;	2	36	60.3 ;	2	84	57.5 ;
1	37	65.1 ;	1	85	61.0 ;	2	37	55.1 ;	2	85	50.2 ;
1	38	48.8 ;	1	86	71.8 ;	2	38	44.3 ;	2	86	59.9 ;
1	39	65.5 ;	1	87	76.6 ;	2	39	47.1 ;	2	87	58.6 ;
1	40	79.3 ;	1	88	55.4 ;	2	40	71.4 ;	2	88	44.1 ;
1	41	81.8 ;	1	89	60.9 ;	2	41	70.1 ;	2	89	43.6 ;
1	42	63.8 ;	1	90	58.9 ;	2	42	57.4 ;	2	90	44.7 ;
1	43	96.6 ;	1	91	44.4 ;	2	43	76.0 ;	2	91	37.0 ;
1	44	67.2 ;	1	92	73.6 ;	2	44	56.7 ;	2	92	56.3 ;
1	45	55.5 ;	1	93	73.8 ;	2	45	46.1 ;	2	93	63.6 ;
1	46	44.2 ;	1	94	82.4 ;	2	46	28.3 ;	2	94	69.8 ;
1	47	80.1 ;	1	95	53.7 ;	2	47	67.7 ;	2	95	41.8 ;
1	48	75.9 ;	1	96	64.2 ;	2	48	66.7 ;	2	96	55.4 ;

TraitEnd

How to use the software:

1. Run QTLMAPPER.EXE to analyze QTL positions and effects. First create two files: one is a map file (ckge.map) and the other is a marker and trait file (ckge.txt). Choose run from submenu and map epistatic QTL.
2. After finishing the general analysis, choose output submenu and screen putative additive-effect QTL or epistatic QTL. The results are presented in Output 1.
3. Run jackknife test in output submenu for detecting significant additive and epistatic effects. The results are presented in Output 2.

Output 1 for Contribution of QTL Effects

```
// Result file created by QTLMapper V 1.0
// Data file name:        D:\QTLSOURCE\ckge.txt
// Marker map file name:  D:\QTLSOURCE\ckge.map
// Environments:          yes
// Replications:          no
// Contents: relative contributions (H^2) for putative main-effect
      QTLs/epistatic QTLs
//     Calculations based on: D:\QTLSOURCE\ckge.jke
//     BGV control method:  A  (control marker main & interaction ef-
      fects)
# Date: 2000-07-04    Time: 14:05:56
```

Trait 1: SH5

Ch-Ini	Int.Namei	Sitei(M)	Ch-Inj	Int.Namej	Sitej(M)	H^2(Ai)	H^2(Aj)	H^2(AAij)	H^2(AEi)	H^2(AEj)	H^2(AAEij)
1-5	M5-M6	0.00	1-17	M17-M18	0.04	0.0000	0.0714	0.0000	0.0000	0.0001	0.0000
1-9	M9-M10	0.00	1-15	M15-M16	0.12	0.0000	0.2532	0.0000	0.0000	0.0001	0.0011
2-6	M24-M25	0.28	3-18	M51-M52	0.06	0.0000	0.0727	0.0000	0.0000	0.0001	0.0000
2-9	M27-M28	0.02	3-16	M49-M50	0.00	0.0625	0.0000	0.0000	0.0000	0.0001	0.0000

General contributions:
  Additive(A): H^2(A)=0.6131;   Epistasis: H^2(AA)=0.0000
  QE Interactions: H^2(AE)=0.0003; H^2(AAE)=0.0011

End

Output 2 for QTL A and AA Effects

```
// Result file created by QTLMapper V 1.0
// Data file name: D:\QTLSOURCE\ckge.txt
// Marker map file name: D:\QTLSOURCE\ckge.map
// Environments:   yes
// Replications:   no
// Contents: Jackknife test results for epistatic QTLs
// Jackknife based on: D:\QTLSOURCE\ckge.fle
// BGV control method: A (control marker main & interaction effects)
// Threshold probability: 0.005000

# Date: 2000-07-04 Time: 13:48:12
```

Trait 1: SH5

Ch-Ini	Int.Namei	Sitei(M)	Ch-Inj	Int.Namej	Sitej(M)	Ai	Probi	Aj	Probj	AAij	Probij
1-5	M5-M6	0.00	1-17	M17-M18	0.04	0.055	0.9410	-4.541	0.0000	1.044	0.1782
1-9	M9-M10	0.00	1-15	M15-M16	0.12	-1.458	0.3977	-8.553	0.0003	-4.077	0.0559
2-6	M24-M25	0.28	3-18	M51-M52	0.06	2.115	0.0270	-4.582	0.0000	-1.209	0.1388
2-9	M27-M28	0.02	3-16	M49-M50	0.00	4.250	0.0000	-0.887	0.2098	-0.175	0.8197

AEi1	Prob	AEi2	Prob	AEj1	Prob	AEj2	Prob	AAEij1	Prob	AAEij2	Prob
-0.122	0.5595	0.122	0.5590	-0.194	0.0532	0.194	0.0534	0.201	0.0558	-0.201	0.0558
0.081	0.7146	-0.080	0.7188	0.144	0.5623	-0.143	0.5645	0.393	0.0001	-0.394	0.0001
0.025	0.8673	-0.026	0.8604	-0.158	0.1465	0.159	0.1452	0.159	0.1237	-0.159	0.1233
0.137	0.2064	-0.137	0.2064	-0.130	0.2267	0.131	0.2254	-0.144	0.1296	0.144	0.1303
End											