

Chapter 10

Developmental Analysis for Quantitative Traits

Jun Zhu

Purpose

To analyze developmental quantitative traits.

Definitions

Genetic Model

For time-dependent traits, the phenotypic data observed at time t ($t = 1, 2, \dots$) have the following mixed linear model:

$$y_{(t)} = Xb_{(t)} + \sum_{u=1}^m U_u e_{u(t)}$$
$$\sim N(Xb_{(t)}, V_{(t)}) = \sum_{u=1}^m \sigma_{u(t)}^2 U_u U_u^T$$

Variance at time t , $\sigma_{u(t)}^2$, can measure genetic variation accumulated from the initial time to time t . Given the observed phenotype vector $y_{(t-1)}$ measured at time $(t-1)$, the conditional random variables of $y_{(t)} | y_{(t-1)}$ at time t have conditional distribution:

$$y_{(t)} | y_{(t-1)} = Xb_{(t|t-1)} + \sum_{u=1}^m U_u e_{u(t|t-1)}$$
$$\sim N(Xb_{(t|t-1)}, V_{(t|t-1)}) = \sum_{u=1}^m \sigma_{u(t|t-1)}^2 U_u U_u^T$$

Since conditional $y_{(t)} | y_{(t-1)}$ is independent of $y_{(t-1)}$, conditional random effects, $e_{(t|t-1)}$, and conditional variance components, $\sigma_{u(t|t-1)}^2$ contain extra variation from time $t-1$ to time t , which is not explainable by the accumulated effects of the initial time to time $t-1$.

Analysis

With observed phenotypic data at time $t-1$ ($y_{(t-1)}$) and time t ($y_{(t)}$), a new random vector $y_{(*)}$ can be obtained using mixed model approaches (Zhu, 1995):

$$y_{(*)} = y_{(t)} - C_{(t-1,t)} V_{(t-1)}^{-1} (y_{(t-1)} - Xb_{(t-1)})$$

The new random vector has variance,

$$\text{var}(y_{(*)}) = V_{(t)} - C_{(t-1,t)} V_{(t-1)}^{-1} C_{(t,t-1)},$$

which is identical to the conditional variance-covariance matrix of $V_{(t|t-1)}$. It can be proved that $y_{(*)}$ is independent of $y_{(t-1)}$.

When the new data ($y_{(*)}$) are used to fit the genetic model,

$$\begin{aligned} y_{(*)} &= Xb_{(*)} + \sum_{u=1}^m \sigma_{u(*)}^2 U_u U_u^T \\ &\sim N(Xb_{(*)}, V_{(*)}) = \sum_{u=1}^m \sigma_{u(*)}^2 U_u U_u^T \end{aligned}$$

unbiased estimation of variances, $\sigma_{u(*)}^2$, can be obtained by REML or MINQUE(1) approaches (Zhu, 1995). Prediction of random effects, $e_{u(*)}$, can be obtained by the linear unbiased prediction (LUP) method (Zhu, 1992; Zhu and Weir, 1996) or the adjusted unbiased prediction (AUP) method (Zhu, 1993; Zhu and Weir, 1996). Since $\sigma_{u(*)}^2$ is equivalent to the conditional variance $\sigma_{u(t|t-1)}^2$, genetic effects $e_{u(*)}$ also have an equivalency to the conditional genetic effects $e_{u(t|t-1)}$.

Originator

Zhu, J. (1992). Mixed model approaches for estimating genetic variances and covariances. *Journal of Biomathematics* 7(1):1-11.

- Zhu, J. (1993). Methods of predicting genotype value and heterosis for offspring of hybrids. *Journal of Biomathematics* 8(1):32-44.
- Zhu, J. (1995). Analysis of conditional effects and variance components in developmental genetics *Genetics* 141(4):1633-1639.
- Zhu, J. and Weir, B.S. (1996). Diallel analysis for sex-linked and maternal effects. *Theoretical and Applied Genetics* 92(1):1-9.

Software Available

- Zhu, J. (1997). GENCOND1.EXE a computer software for calculating conditional phenotypic data. *Analysis Methods for Genetic Models* (pp. 278-285), Agricultural Publication House of China, Beijing (program free of charge). Contact Dr. Jun Zhu, Department of Agronomy, Zhejiang University, Hangzhou, China. E-mail: <jzhu@zju.edu.cn>.

EXAMPLE

Unconditional data (BOL8/4 and BOL8/9) to be analyzed (file: COTBOLM.TXT) (Parent = 4, Year = 2, Blk = 1):

Env	Fem	Male	Cross	BLK	BOL8/4	BOL8/9
1	1	1	0	1	6.46	8.14
1	1	2	1	1	5.77	7.85
1	1	3	1	1	8.64	9.01
1	1	4	1	1	8.33	10.30
1	2	1	1	1	6.70	8.74
1	2	2	0	1	5.65	7.90
1	2	3	1	1	7.94	9.13
1	2	4	1	1	8.47	11.24
1	3	1	1	1	8.72	9.29
1	3	2	1	1	9.32	10.36
1	3	3	0	1	4.98	5.35
1	3	4	1	1	8.90	10.14
1	4	1	1	1	7.58	9.74
1	4	2	1	1	8.74	11.08
1	4	3	1	1	9.34	11.49
1	4	4	0	1	7.02	8.90
2	1	1	0	1	8.06	11.63
2	1	2	1	1	11.36	15.18
2	1	3	1	1	9.31	10.58
2	1	4	1	1	13.30	15.76
2	2	2	0	1	8.09	12.39

2	2	3	1	1	10.87	13.50
2	2	4	1	1	15.60	20.45
2	3	3	0	1	5.05	5.78
2	3	4	1	1	12.76	14.26
2	4	4	0	1	12.29	15.86

Conditional data (BOL8/9|BOL8/4) produced and to be analyzed (Parent = 4, Year = 2, Blk = 1):

Year	Fem	Male	Cross	Blk	BOL8/9 BOL8/4
1	1	1	0	1	9.75974
1	1	2	1	1	10.0186
1	1	3	1	1	8.54954
1	1	4	1	1	9.42577
1	2	1	1	1	9.98357
1	2	2	0	1	10.3079
1	2	3	1	1	9.30607
1	2	4	1	1	10.1621
1	3	1	1	1	8.74997
1	3	2	1	1	9.16348
1	3	3	0	1	8.62587
1	3	4	1	1	8.8201
1	4	1	1	1	9.61174
1	4	2	1	1	9.73354
1	4	3	1	1	9.73246
1	4	4	0	1	8.86123
2	1	1	0	1	14.6502
2	1	2	1	1	14.8385
2	1	3	1	1	12.6994
2	1	4	1	1	12.6991
2	2	2	0	1	14.9987
2	2	3	1	1	13.9182
2	2	4	1	1	14.949
2	3	3	0	1	12.5327
2	3	4	1	1	12.0607
2	4	4	0	1	12.8132

1. Run GENAD.EXE to create mating design matrix files and unconditional data for the additive-dominance (AD) model. Before running these programs, create a data file (e.g., COTBOLM.TXT) for your analysis of unconditional data with five design columns followed by trait columns, which are (1) environment, (2) maternal, (3) paternal, (4) generation, and (5) replication. There is a limitation (<100 traits)

- for the number of trait columns. The data file COTBOLM.TXT contains phenotypic data of two traits (BOL8/4 and BOL8/9).
2. Run the program GENCOND1.EXE for constructing conditional data. The conditional data will have five design columns and will be stored in a file with the name COTBOLM.CON. Afterward, run GENAD.EXE again using the conditional data file COTBOLM.CON to create files for mating design matrix and conditional data by the AD model.
 3. Conditional variances and conditional genetic effects can be obtained by running programs for variance analyses. Standard errors of estimates are calculated by jackknife procedures. If you have multiple blocks for your experiments, you can use GENVAR1R.EXE for jackknifing over blocks. Otherwise, you can use GENVAR1C.EXE or GENCOVIC.EXE for jackknifing over cell means. These two programs will allow you to choose the parental type (inbred or outbred) and the prediction methods (LUP or AUP). You also need to input coefficients (1, 0, or -1) for conducting linear contrasts for genetic effects of parents.
 4. The results will be automatically stored in text files for later use or printing. An example of results is provided in a file named COTBOLM.VAR (output 1) for analysis of conditional variance and conditional genetic effects.
 5. Developmental genetic analysis can also be conducted for other genetic models, such as GENADM.EXE for additive, dominance, and maternal models with $G = A + D + M$; GENADE.EXE for additive, dominance, and epistatic models with $G = A + D + AA$; GENSEX.EXE for additive, dominance, sex-linked, and maternal models with $G = A + D + L + M$; GENDIPLD.EXE for traits of diploid seeds or animals; GENTRIPL.EXE for traits of triploid endosperm.

Output 1 for Conditional Variance Analysis

```
Traits = , 1
Variance components = , 5
Degree of freedom = , 25
File name is cotbolm.VAR
Date and Time for Analysis: Sat Jun 24 19:07:06 2000
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Variance Components Estimated by MINQUE(1) with GENVAR1R.EXE.
Jackknifing Over Block Conducted for Estimating S.E.
Predicting Genetic Effects by Adjusted Unbiased Prediction (AUP)
Method.
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NS = Not significant; S+ = Significant at 0.10 level.

S* = Significant at 0.05 level; S** = Significant at 0.01 level.

Linear Contrast Test:

+<1> +<2> -<3> +<4>

Diallel Analysis of Trait, BOL8/9|BOL8/4, for Public Users.

Var Comp	Estimate	S. E.	P-value	
(1): Additive Var	0.665074	0.120759	5.04e-006	S**
(2): Dominance Var	0.180163	0.0462009	0.00032	S**
(3): Add. * Env. Var	0.193749	0.0588614	0.00148	S**
(4): Dom. * Env. Var	0.331579	0.0779674	0.000129	S**
(5): Residual Var	0.189768	0.0819921	0.0146	S*
(6): Var(Pheno.)	1.56033	0.209525	4.22e-008	S**

Proportion of Var(G)/Var(T)	Estimate	S. E.	P-value	
(1): Additive Var/Vp	0.426239	0.0429252	1.59e-010	S**
(2): Dominance Var/Vp	0.115464	0.0393502	0.00353	S**
(3): Add. * Env. Var/Vp	0.124172	0.0301349	0.000182	S**
(4): Dom. * Env. Var/Vp	0.212505	0.0386894	5.24e-006	S**
(5): Residual Var/Vp	0.12162	0.0341315	0.000753	S**

Heritability	Estimate	S. E.	P-value	
(6): Heritability(N)	0.426239	0.0429252	1.59e-010	S**
(7): Heritability(B)	0.541703	0.0394694	2.53e-011	S**
(8): Heritability(NE)	0.124172	0.0301349	0.000182	S**
(9): Heritability(BE)	0.336677	0.0399954	4.56e-009	S**

Genetic Predictor, S. E., P-value

(1): Random Effect is Additive Effects				
A1,	0.223513,	0.155049,	0.162,	NS
A2,	0.677601,	0.121236,	8.19e-006,	S**
A3,	-0.562930,	0.091853,	2.09e-006,	S**
A4,	-0.338327,	0.119019,	0.00878,	S**
Linear Contrast,	1.95226,	0.371664,	1.94e-005,	S**

(2): Random Effect is Dominance Effects				
D1*1	0.798935	0.436678	0.0793	S+
D2*2	0.018615	0.066023	0.78	NS
D3*3	0.072842	0.101742	0.481	NS
D4*4	-0.412087	0.328823	0.222	NS
D1*2	0.425023	0.229382	0.0757	S+
D1*3	-1.004059	0.598641	0.106	NS
D1*4	-0.661568	0.375175	0.0901	S+
D2*3	-0.076713	0.091950	0.412	NS
D2*4	1.092527	0.629749	0.0951	S+
D3*4	-0.253545	0.321869	0.438	NS

Heterosis <Delta>	-0.563434	0.767809	0.47	NS
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(3): Random Effect is Add. * Env. Effects

AE1 in E1	-0.022308	0.102366	0.829	NS
AE2 in E1	0.036740	0.088970	0.683	NS
AE3 in E1	-0.011993	0.081400	0.884	NS
AE4 in E1	-0.002428	0.153184	0.987	NS
AE1 in E2	0.158196	0.194168	0.423	NS
AE2 in E2	0.357913	0.255052	0.173	NS

AE3 in E2	-0.305599	0.174689	0.0925	S+
AE4 in E2	-0.210610	0.188787	0.275	NS
Linear Contrast	1.58114e-005	1.77345e-005	0.381	NS

(4): Random Effect is Dom. * Env. Effects

DE1 in E1	-0.320161	0.196316	0.115	NS
DE2 in E1	0.368241	0.179784	0.0512	S+
DE3 in E1	-0.184366	0.161795	0.265	NS
DE4 in E1	-0.541939	0.380790	0.167	NS
DE1 in E2	-0.053143	0.150489	0.727	NS
DE2 in E2	-0.057755	0.290609	0.844	NS
DE3 in E2	0.687891	0.349814	0.0604	S+
DE4 in E2	-0.303718	0.189203	0.121	NS
DE1 in E3	-0.340375	0.372988	0.37	NS
DE2 in E3	0.745340	0.610413	0.233	NS
DE3 in E3	0.927552	0.534879	0.0952	S+
DE4 in E3	-0.569171	0.246751	0.0296	S*
DE1 in E4	0.343324	0.197179	0.0939	S+
DE2 in E4	0.301441	0.324563	0.362	NS
DE3 in E4	0.139931	0.334570	0.679	NS
DE4 in E4	-0.560693	0.344209	0.116	NS
DE1 in E5	-1.175256	0.700765	0.106	NS
DE2 in E5	0.311932	0.239635	0.205	NS
DE3 in E5	1.167883	0.778234	0.146	NS
DE4 in E5	-0.887039	0.664529	0.194	NS
Heterosis <Delta>	0	0	1	NS

Fixed Effect <1>, 9.42573

Fixed Effect <2>, 13.616

Time Used (Hour) = 0.000556