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ANALYSIS OF TRIALLEL CROSS HYBRIDS COMPARED IN BLOCK DESIGN[1]

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Summary. In this paper the analysis of genotypes obtained in triallel crossing system is given. This analysis is presented for data obtained from the experiments laid out in block design. The analysis of variance, estimators of combining abilities as well as statistics for testing of hypotheses concerning those parameters are given.

The triallel crossing system is of interest for breeders dealing with estimation and testing of general combining abilities and specific combining abilities of the first and second order. The considered triallel crossing system due to Arora and Aggarwal (1984) is a system in which $(p-1)$ $(p-2)/2$ two-line hybrids (jk), $2 \leqslant j < k \leqslant p$ obtained from diallel cross of type IV (Griffing 1956) are crossed with p parental lines analysed in this experiment. The crossing is performed in such a way that each line cannot occur two times in crossing, i.e., $1 \leqslant i < j < k \leqslant p$, and $p \geqslant 6$. As a result of this crossing $v = p(p-1)(p-2)/6$ three-line hybrids are obtained.

However, first we have to consider the experimental design which is employed in obtaining the experimental data. We shall consider the analysis conforms to any block design with equal replications of three-line hybrids (treatments) and binary incidence matrix, and particularly to efficiency balanced block design.

ANALYSIS OF VARIANCE FOR BLOCK DESIGN

Before dealing with the combining ability analysis of triallel crosses we have to test the null hypothesis that there are no differences among treatments. This testing is done by the analysis of variance.

The linear model of n observations obtained from an experiment carried out in a block design may be written in the following form

$$\mathbf{y} = \mathbf{1}\mu + \mathbf{D}'\boldsymbol{\beta} + \boldsymbol{\Delta}'\boldsymbol{\tau} + \boldsymbol{\eta}, \tag{1}$$

where $\mathbf{y}$ is the $n \times 1$ observations vector, $\mathbf{1}$ is the vector of ones, $\mathbf{D}'$ is the $n \times b$ design

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matrix for blocks, with a row for each plot and a column for each block, such that an element is 1 if the plot is in the block and is 0 otherwise, $\mathbf{\Delta}'$ is the $n\times v$ design matrix for treatments, with a row for each plot and a column for each treatment, such that an element is 1 if the plot receives the treatment and is 0 otherwise, and μ is the general parameter, $\boldsymbol{\beta}$ is the $b\times 1$ vector of block parameters, $\boldsymbol{\tau}$ is the $v\times 1$ vector of treatment parameters, and where $\boldsymbol{\eta}$ is the $n\times 1$ vector of random errors. Vector $\boldsymbol{\eta}$ has a normal distribution specified by $E(\boldsymbol{\eta})=\mathbf{0}$ and $E(\boldsymbol{\eta}\boldsymbol{\eta}')=\sigma^2\mathbf{I}$ (with $\mathbf{I}$ denoting an identity matrix). The following restrictions are imposed on the parameters of the design: $\mathbf{1}'\boldsymbol{\tau}=\mathbf{k}'\boldsymbol{\beta}=0$, where $\mathbf{k}$ is the $b\times 1$ vector of block sizes.

The analysis of variance for model (1) may well be described, for block design with r replications of treatments, by the matrix

$$\boldsymbol{\Omega}^{-1}=r\mathbf{I}-\mathbf{N}\mathbf{k}^{-\delta}\mathbf{N}'+(r/v)\mathbf{1}\mathbf{1}'$$

where $\mathbf{N}$ is the $v\times b$ incidence matrix and $\mathbf{k}^{-\delta}=\operatorname{diag}[1/k_1, 1/k_2, \ldots, 1/k_b]$.

Writing $\mathbf{Q}=\mathbf{T}-\mathbf{N}\mathbf{k}^{-\delta}\mathbf{B}$, where $\mathbf{B}$ is the $b\times 1$ vector of block totals and $\mathbf{T}$ is the $v\times 1$ vector of treatment totals, the least squares estimate of $\boldsymbol{\tau}$ is $\hat{\boldsymbol{\tau}}=\boldsymbol{\Omega}\mathbf{Q}$. The sum of squares attributable to treatments in the analysis of variance is $T=\mathbf{Q}'\boldsymbol{\Omega}\mathbf{Q}$, while that attributable to errors is $E=(\mathbf{y}'\mathbf{y}-G^2/n)-\mathbf{R}'\mathbf{k}^{-\delta}\mathbf{R}^{s}-\mathbf{Q}'\boldsymbol{\Omega}\mathbf{Q}$, where $\mathbf{R}=\mathbf{B}-(G/n)\mathbf{k}$, $G=\mathbf{1}'\mathbf{B}=\mathbf{1}'\mathbf{T}$.

Now suppose that we want to test the null hypothesis of the equality of all the three-line hybrids effects, H_0: $\boldsymbol{\tau}=\mathbf{0}$. It is known that the appropriate F-statistic for testing H_0 is

$$F=s_T^2/s_E^2,$$

where $s_T^2=T/(v-1)$ and $s_E^2=E/(n-b-v+1)$. If significant F ratio occurs we reject the hypothesis H_0. It means that there are differences between three-line hybrids, which may be investigated further with the combining ability analysis. The effects of combining abilities are the contrasts of treatment parameters. Thus we describe the testing of hypotheses concerning the contrasts.

Let us consider h independent contrasts $\mathbf{c}_1'\boldsymbol{\gamma}$, $\mathbf{c}_2'\boldsymbol{\gamma}$, $\ldots$, $\mathbf{c}_h'\boldsymbol{\gamma}$, where $\mathbf{c}_t'\mathbf{1}=0$, $t=1, 2, \ldots, h$, and $\boldsymbol{\gamma}=\mathbf{1}\mu+\boldsymbol{\tau}$. If we are interested in testing of the hypothesis in the form H_0:$\mathbf{C}'\boldsymbol{\gamma}=\mathbf{0}$, where $\mathbf{C}=[\mathbf{c}_1, \mathbf{c}_2, \ldots, \mathbf{c}_h]$, then the appropriate F-statistic is

$$F=s_K^2/s_E^2, \tag{2}$$

where $s_K^2=K/h$ and

$$K=\mathbf{Q}'\boldsymbol{\Omega}\mathbf{C}(\mathbf{C}'\boldsymbol{\Omega}\mathbf{C})^{-1}\mathbf{C}'\boldsymbol{\Omega}\mathbf{Q}. \tag{3}$$

If, in addition, one is interested in testing a null hypothesis H_0: $\mathbf{c}'\boldsymbol{\gamma}=0$, then the appropriate F-statistic for it is

$$F=(\mathbf{c}'\hat{\boldsymbol{\gamma}})^2/\widehat{\operatorname{Var}}(\mathbf{c}'\hat{\boldsymbol{\gamma}}), \tag{4}$$

where $\widehat{\operatorname{Var}}(\mathbf{c}'\hat{\boldsymbol{\gamma}})=\mathbf{c}'\boldsymbol{\Omega}\mathbf{c}s_E^2$.

Now, as a particular case, let us consider the analysis for efficiency balanced block design with equal treatment replications and binary incidence matrix. A block design is called efficiency balanced if all treatment contrasts $\mathbf{c}'\boldsymbol{\gamma}$ are estimable with exactly the same efficiency factor equal to $\varepsilon=(n-b)/(n-r)$. In this case the matrix $\boldsymbol{\Omega}$ is of the form

$$\boldsymbol{\Omega}=\frac{v-1}{n-b}\left[\mathbf{I}-\frac{b-r}{n(v-1)}\mathbf{1}\mathbf{1}'\right].$$

It should be noted that the balanced incomplete block design and randomized complete block design are particular cases of efficiency balanced block design.

ANALYSIS OF COMBINING ABILITIES

For the considered type of triallel crossing system the number of three-line hybrids (treatments) is $v=p(p-1)(p-2)/6$, where p is the number of parental lines. Let us define the vector of hybrids expected values $\boldsymbol{\gamma}=\mathbf{1}\mu+\boldsymbol{\tau}$ with the elements $\boldsymbol{\gamma}=[\gamma_{123}, \gamma_{124}, \ldots, \gamma_{p-2,p-1,p}]$. The model for the expected values γ_{ijk} is assumed to be

$$\gamma_{ijk}=\mu+g_i+g_j+g_k+s_{ij}+s_{ik}+s_{jk}+t_{ijk},\ 1\leqslant i<j<k\leqslant p,$$

with $\sum_i g_i=0$, $\sum_j s_{ij}=0$ for all $i\neq j$, $s_{ij}=s_{ji}$, $\sum_k t_{ijk}=0$ for all $i,j\neq k$, $i\neq j$, $t_{ijk}=t_{jik}=$ $=t_{ikj}=t_{jki}=t_{kij}=t_{kji}$. Here μ is the general parameter, $g_i(g_j, g_k)$ is the general combining ability effect for the ith (jth, kth) parental line, $s_{ij}(s_{ik}, s_{jk})$ is the first order specific combining ability effect of the ith and jth (ith and kth, jth and kth) lines and t_{ijk} is the second order specific combining ability effect of the ith, jth and kth lines.

As it was mentioned before the effects of combining abilities are the contrasts, which can be defined as follows: $g_i=\mathbf{c}_i'\boldsymbol{\gamma}$, where $\mathbf{c}_i'=[c_{123}^{i}, c_{124}^{i}, \ldots, c_{p-2,p-1,p}^{i}]$ $i=1, 2, \ldots, p$; $s_{ij}=\mathbf{c}_{ij}'\boldsymbol{\gamma}$, where $\mathbf{c}_{ij}'=[c_{123}^{ij}, c_{124}^{ij}, \ldots, c_{p-2,p-1,p}^{ij}]$ $1\leqslant i<j\leqslant p$; $t_{ijk}=\mathbf{c}_{ijk}'\boldsymbol{\gamma}$, where $\mathbf{c}_{ijk}'=[c_{123}^{ijk}, c_{124}^{ijk}, \ldots, c_{p-2,p-1,p}^{ijk}]$ $1\leqslant i<j<k\leqslant p$.

The definition of the (m, n, l) th element of the vector $\mathbf{c}_i$ $1\leqslant m<n<l\leqslant p$ defining g_i effect is as follows (the triple index of elements of $\mathbf{c}_i$ are induced by the triple index of elements of the vector $\boldsymbol{\gamma}$)

$$c_{mnl}^{i}=\frac{2}{p(p-2)(p-3)}\begin{cases}p-3, & i=m \text{ or } i=n \text{ or } i=l\\ -3, & \text{elsewhere.}\end{cases}$$

The definition of the (m, n, l) th element of the vector $\mathbf{c}_{ij}$ defining s_{ij} effect is as follows

$$c_{mnl}^{ij}=\frac{1}{(p-1)(p-2)(p-4)}\begin{cases}(p-3)(p-4), & i=m \text{ and } j=n \text{ or } i=m \text{ and } j=l\\ & \text{or } i=n \text{ and } j=l,\\ -2(p-4), & i=m \text{ or } i=n \text{ or } i=l \text{ or } j=m\\ & \text{or } j=n \text{ or } j=l,\\ 6, & \text{elsewhere.}\end{cases}$$

The definition of the (m, n, l) th element of the vector $\mathbf{c}_{ijk}$ defining t_{ijk} effect is as follows

$$c_{mnl}^{ijk}=\frac{1}{(p-2)(p-3)(p-4)}\begin{cases}(p-3)(p-4)(p-5), & i=m \text{ and } j=n \text{ and } k=l;\\ -(p-4)(p-5), & i=m \text{ and } j=n \text{ or } i=m \text{ and}\\ & j=l \text{ or } i=n \text{ and } j=l \text{ or}\\ & i=m \text{ and } k=n \text{ or } i=m \text{ and}\\ & k=l \text{ or } i=n \text{ and } k=l \text{ or}\\ & j=m \text{ and } k=n \text{ or } j=m \text{ and}\\ & k=l \text{ or } j=n \text{ and } k=l;\\ 2(p-5), & i=m \text{ or } i=n \text{ or } i=l \text{ or}\\ & j=m \text{ or } j=n \text{ or } j=l \text{ or}\\ & k=m \text{ or } k=n \text{ or } k=l;\\ -6 & \text{elsewhere}\end{cases}$$

The estimators of combining abilities we obtain by substituting $\boldsymbol{\gamma}$ by $\hat{\boldsymbol{\gamma}}$, where $\hat{\boldsymbol{\gamma}}=\boldsymbol{\Omega}\mathbf{Q}+(G/n)\mathbf{1}$ and for efficiency balanced block design $\hat{\boldsymbol{\gamma}}=(v-1)\mathbf{Q}/(n-b)+(G/n)\mathbf{1}$.

In the analysis of triallel crosses, after rejecting the null hypothesis H_0: $\boldsymbol{\tau}=\mathbf{0}$, we are interested in testing hypotheses concerning the combining abilities. These hypotheses can be formulated as follows:

1. H_0: $g_1=g_2=\ldots=g_p$,
2. H_0: $s_{12}=s_{13}=\ldots=s_{p-1,p}$,
3. H_0: $t_{123}=t_{124}=\ldots=t_{p-2,p-1,p}$,
4. H_0: $g_i=0$,
5. H_0: $g_i-g_m=0$,
6. H_0: $s_{ij}=0$,
7. H_0: $s_{ij}-s_{im}=0$,
8. H_0: $s_{ij}-s_{mn}=0$,
9. H_0: $t_{ijk}=0$,
10. H_0: $t_{ijk}-t_{ijl}=0$,
11. H_0: $t_{ijk}-t_{inl}=0$,
12. H_0: $t_{ijk}-t_{mnl}=0$.

First, we describe the testing of hypotheses 1—12 for block designs with equal replications and binary incidence matrix.

For testing hypothesis 1 we construct the matrix $\mathbf{C}$ describing the independent contrasts by taking any $p-1$ vectors $\mathbf{c}_i$ defining the general combining abilities g_i, and we use F-statistic given by (2) assuming $h=p-1$.

For testing hypothesis 2 we construct the matrix $\mathbf{C}$ from (3) by taking $p(p-3)/2$ independent vectors $\mathbf{c}_{ij}$. We propose to take all vectors $\mathbf{c}_{ij}$ except these for which $i=p-2$ or $j=p$. In this case we also use F-statistic given by (2), assuming $h=p(p-3)/2$.

The testing of hypothesis 3 proceeds in the same way assuming $h=p(p-1)\times\times(p-5)/6$ with the matrix $\mathbf{C}$ consisting of all vectors $\mathbf{c}_{ijk}$ except these for which $i=p-4$ or $j=p-2$ or $k=p$.

For testing hypotheses 4–12 we use F-statistic given by (4). In the case of any block design the $\widehat{\mathrm{Var}}(\mathbf{c}'\hat{\boldsymbol{\gamma}})$ from (4) cannot be expressed in an explicite form.

Now, we consider the testing of hypotheses 1–12 for experiment carried out in efficiency balanced block design with equal number of treatment replications and with binary incidence matrix. For testing hypotheses 1, 2 and 3, the corresponding F-statistics have the form

— for testing equality of general combining abilities

$$F=\frac{(n-b)(p-2)(p-3)\hat{\mathbf{g}}'\hat{\mathbf{g}}}{2(v-1)(p-1)s_E^2},$$

where $\hat{\mathbf{g}}=[\hat{g}_1, \hat{g}_2, \ldots, \hat{g}_p]'$,

— for the equality of the first order specific combining abilities

$$F=\frac{2(n-b)(p-4)\hat{\mathbf{s}}'\hat{\mathbf{s}}}{(v-1)p(p-3)s_E^2},$$

where $\hat{\mathbf{s}}=[\hat{s}_{12}, \hat{s}_{13}, \ldots, \hat{s}_{p-1,p}]'$,

— for the equality of the second order specific combining abilities

$$F=\frac{6(n-b)\hat{\mathbf{t}}'\hat{\mathbf{t}}}{p(p-1)(p-5)s_E^2},$$

where $\hat{\mathbf{t}}=[\hat{t}_{123}, \hat{t}_{124}, \ldots, \hat{t}_{p-2,p-1,p}]'$.

For testing hypotheses 4–12 the appropriate F-statistics have the form:

— for hypothesis 4

$$F=\frac{p(p-2)(p-3)\hat{g}_i^2}{2(p-1)s_E^2},$$

— for hypothesis 5

$$F=\frac{(p-2)(p-3)(\hat{g}_i-\hat{g}_m)^2}{4s_E^2},$$

— for hypothesis 6

$$F=\frac{(p-1)(p-4)\hat{s}_{ij}^2}{(p-3)s_E^2},$$

— for hypothesis 7

$$F=\frac{(p-2)(p-4)(\hat{s}_{ij}-\hat{s}_{in})^2}{2(p-3)s_E^2},$$

— for hypothesis 8

$$F=\frac{(p-2)(\hat{s}_{ij}-\hat{s}_{mn})^2}{2s_E^2},$$

— for hypothesis 9

$$F=\frac{(p-2)\hat{t}_{ijk}^2}{(p-5)s_E^2},$$

— for hypothesis 10

$$F=\frac{(p-3)(\hat{t}_{ijk}-\hat{t}_{ijl})^2}{2(p-5)s_E^2},$$

— for hypothesis 11

$$F=\frac{(p-3)(p-4)(\hat{t}_{ijk}-\hat{t}_{inl})^2}{2(p-5)s_E^2},$$

— for hypothesis 12

$$F=\frac{(p-3)(p-4)(\hat{t}_{ijk}-\hat{t}_{mnl})^2}{2(p^2-10p+27)s_E^2}.$$

EXAMPLE

To illustrate the theory presented in this paper, let us consider an experiment carried out in partially balanced incomplete block design with $v=20$ hybrids obtained from triallel crossing among $p=6$ lines of maize. The genotypes were allocated in $b=10$ blocks of size $k=8$. Each genotype was replicated $r=4$ times in the experiment. The experimental results taken from Singh and Chaudhary (1979) and adopted to our case are presented in Table 1.

From the analysis of variance significant value $F=21.01$ was obtained, i.e. there are significant differences among genotypes.

The estimates of the combining abilities obtained by formulae given in above section are as follows:

$\hat{g}_1=-2.76$; $\hat{g}_2=-6.68$; $\hat{g}_3=1.49$; $\hat{g}_4=-5.35$; $\hat{g}_5=5.73$; $\hat{g}_6=7.57$;

— the first order specific combining abilities

i \ j	2	3	4	5	6
1	−3.18	2.65	−4.15	−0.90	5.59
2		1.94	7.06	−4.86	−0.97
3			20.14	−2.28	−22.45
4				−16.42	−6.62
5					24.45

— the second order specific combining abilities

ij \ k	3	4	5	6
12	5.54	6.46	−9.93	−2.07
13		−6.40	2.43	−1.56
14			1.90	−1.97
15				5.60
23		−5.60	1.97	−1.90
24			1.56	−2.43
25				6.40
34			2.07	9.93
35				−6.46
45				−5.54

Table 1. Experimental results of maize

Block number	Treatment number	Yield (q/ha)	Treatment number	Yield (q/ha)	Treatment number	Yield (q/ha)	Treatment number	Yield (q/ha)	Treatment number	Yield (q/ha)	Treatment number	Yield (q/ha)	Treatment number	Yield (q/ha)	Treatment number	Yield (q/ha)
1	1	83.62	2	70.36	6	107.38	7	88.26	11	97.46	12	89.70	16	118.60	17	93.16
2	2	90.12	3	66.86	7	70.42	8	69.36	12	82.48	13	72.48	17	99.36	18	83.88
3	3	62.24	4	83.26	8	69.28	9	77.00	13	67.96	14	67.76	18	92.26	19	94.62
4	4	86.14	5	99.04	9	90.96	10	140.82	14	77.62	15	83.02	19	104.66	20	90.46
5	1	99.88	5	92.28	6	84.56	10	135.26	11	106.56	15	80.70	16	128.14	20	96.56
6	1	80.62	3	70.36	6	90.96	8	59.04	11	99.10	13	60.16	16	121.42	18	96.28
7	2	88.52	4	98.42	7	76.36	9	69.12	12	92.58	14	68.28	17	93.32	19	103.36
8	3	59.28	5	94.20	8	65.54	10	136.40	13	66.42	15	88.52	18	97.30	20	88.64
9	1	93.56	4	88.52	6	104.22	9	98.44	11	110.58	14	81.86	16	120.18	19	95.88
10	2	72.36	5	95.98	7	82.78	10	127.72	12	80.30	15	77.16	17	91.44	20	98.72

For testing the hypothesis that there are no differences among general combining ability effects (hypothesis 1) we have obtained $F=17.47>3.41=F_{0.01;\ 5;\ 51}$.

For testing the hypothesis that there are no differences among the first order specific combining ability effects (hypothesis 2) we have obtained $F=29.45>2.79==F_{0.01;\ 9;\ 51}$.

For testing the hypothesis that there are no differences among the second order specific combining ability effects (hypothesis 3) we have obtained $F=8.45>3.41==F_{0.01;\ 5;\ 51}$.

These results indicate highly significant differences for the appropriate combining abilities, so we have provide the testing of significance for individual combining ability effects as well as for some differences between them (hypothesis 4 - 12).

It was stated that the general combining ability effect is significant for lines 2, 4, 5 and 6, and additionally, for example, there is no difference between g_2 and g_4 (H_0: $g_2-g_4=0$ was not rejected).

Among the first order specific combining ability effects significant are: s_{16}, s_{24}, s_{34}, s_{36}, s_{45}, s_{46} and s_{56}. Significant, for example, are also differences $s_{12}-s_{16}$ and $s_{12}-s_{34}$.

The second order specific combining abilities are significant for crosses of the lines: (123), (124), (125), (134), (156), (234), (256), (346), (356), (456). Significant, for example, are also differences $t_{124}-t_{125}$ and $t_{123}-t_{456}$, and not significant is $t_{123}-t_{145}$.

REFERENCES

1. Arora B. S., Aggarval K. R. (1984). Confounded triallel experiments and their applications. Sankhya, 46: 54 - 63.
2. Griffing B. (1956). Concept of general and specific combining ability in relation to diallel crossing system. Australian J. Biol. Sci., 9: 463 - 493.
3. Singh R. K., Chaudhary B. D. (1979). Biometrical Methods in Quantitative Genetic Analysis. Kalyani Publishers, New Delhi.

ANALIZA MIESZAŃCÓW UZYSKANYCH Z KRZYŻOWANIA TRIALLELICZNEGO PORÓWNYWANYCH W UKŁADZIE BLOKOWYM

Streszczenie

W pracy przedstawiano analizę mieszańców otrzymanych z krzyżowania triallelicznego. Uzyskane mieszańce porównywano w doświadczeniu założonym w układzie blokowym. Podana została analiza wariancji, estymatory zdolności kombinacyjnych oraz funkcje testowe dla testowania ich istotności.

АНАЛИЗ ГИБРИДОВ ТРИАЛЛЕЛЬНОГО СКРЕЩИВАНИЯ, СРАВНИВАЕМЫХ ПО СИСТЕМЕ БЛОКОВ

Резюме

В настоящей работе представлен анализ генотипов, полученных в системе триаллельного скрещивания. Этот анализ представлен для данных, полученных из экспериментов, заложенных по системе блоков. Поданы также анализ варианции, эстиматоры комбинационных способностей, а также статистика для проверки гипотез относительно этих параметров.