

EFFECT OF CONTINUED BACKCROSSING ON BREEDING POPULATION

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SUMMARY

Continued backcrossing with the desired parental line at successive generations helps the breeders in the task of achieving homozygosity and thereby getting the pure bred lines at a faster rate than by adopting other means like artificial selection. In fact, successive backcrosses with the parental line, if possible, with respect to the desired character over a few generations, advances the progress for attaining homozygosity quicker than in case of selfed or inbred population undergoing complete selection. For the success of quick hybridisation, the breeders should chose frequently backcrossing the parental lines with a view to impregnating multiple characters.

The general expressions for the genotypic frequencies and the genotypic variance components viz, D and H, and the covariances between additive and dominance components for different progeny lines viz, C, being raised after suitable backcrossing are worked out at the n^{th} generation as a special case where the gene frequencies are assumed to be equal (*i.e.* $p=q=0.5$). A comparison with the selfed line under complete elimination of undesired lines is also made. The reduction will obviously be still quicker if on backcrossing at the few initial stages, selfing is practised, thereafter, within such individual line.

1. INTRODUCTION

Continued backcrossing at successive generations help the breeders in achieving homozygosity of the desired lines at a faster rate than even adopting any artificial selection. Complete elimination of certain undesired genotypes is the severest type of selection from the evolutionary point of view which is regarded as a very rapid method of diminishing the undesired gene frequency. In case of inbred lines, when selection acts in one or both directions, the genotypic structure of the population at different generations when either selfing or crossing or both are present in varying proportions has been studied by Sen [6], [7], [9] and [10]. If the breeder seeks

homozygosity, the programme for inbreeding should be within line, while if the breeder is interested for heterozygous lines, his preference will be for selection between distant lines. Backcrossing with the parent with respect to the desired character for a few generations advances the progress of attainment to homozygosity at a faster rate than in case of selfed or inbred population under-going complete selection after elimination of undesired genes at each generation. In fact, under hybridisation programme, the breeders frequently back-cross the pure lines for impregnating desired multiple characters in polygenic cases. Hill [3] also furnished a method for the study of the quantitative inheritances by recurrent back-crossing.

2. FORMULATION

Assuming that there is no linkage, epistasy or differential selection, the frequencies of the different genotypes and the components of genotypic variances under any random mating or non-random mating population may be developed by following the method of Fisher *et al* [1]. and Mather [5].

Let p and q be the gene frequencies and X_n , Y_n and Z_n be the genotypic frequencies for the genotypes AA , Aa and aa respectively. Let, also d and h be the additive and the non-additive increments in the genotypic variance.

Then, the mean at the i th locus in case of non.random mating population is:

$$\mu = (p-q)d_i + 2(Pq-\delta)h_i,$$

where $\delta = (p^2 + \delta)(q^2 + \delta) - (pq - \delta)^2$.

Then, the variance at the i th locus is :

$$v_o = 2(pq + \delta) \{ [d_i - (p-q)\phi h_i]^2 + \phi \{ 1 - \phi(p^2 + q^2 + 2\delta) \} h_i^2 \}$$

In case of random mating population, for monogenic pair,

$$\delta = 0 \quad \text{and} \quad \phi = 1$$

then, $\mu = (p-q)d_i + 2pq h_i$

and

$$V_o = 2pq [d - (p-q)h]^2 + 4p^2q^2h^2.$$

Again, denoting V_a = the additive genetic variance,

and V_d = the component of genetic variance due to dominance,

then, $V_a = 2(pq + \delta) [d_i - (p-q)\phi h_i]^2$

and $V_d = V_o - V_a = 2(pq + \delta)\phi [1 - \phi(p^2 + q^2 + 2\delta)]h_i^2$

which, in case of random mating population, reduces to :

$$V_a = 2pq[d_i - (p-q)h_i]^2, \text{ and}$$

$$V_d = 4p^2q^2h_i^2.$$

3. GENOTYPIC FREQUENCIES AND VARIANCES IN SELFED POPULATION

Again, the genotypic frequencies for the mixed population where reproduction takes place partly by natural crossing (with the proportion, c) and partly by self-fertilisation (with the proportion, $1-c$), at any generation are given as :

$$X_{n+1} = c p_n^2 + (1-c)(x_n + \frac{1}{4} y_n)$$

$$Y_{n+1} = 2c p_n q_n + \frac{1}{2}(1-c)Y_n, \text{ and}$$

$$Z_{n+1} = c p_u^2 + (1-c)(z_n + \frac{1}{4} Y_n).$$

It, then, follows that :

$$p_{n+1} = X_{n+1} + \frac{1}{2} Y_{n+1} = p_n,$$

i.e. in case of the absence of any differential selection, the gene frequencies remain unchanged over generations.

Assuming the covariances (d, h) are negligible, the genetic variance in F_n , for K pairs of genes has been shown by Sen [10] as :

$$\begin{aligned} V(F_n) &= \left(1 - \frac{1}{2^{n-1}}\right) \sum_{i=1}^k d_i^2 \\ &\pm 2 \left[\frac{1-2p}{1+2p} - \frac{(1-2p)^n}{2^{n-1}(1+2p)} \right] \sum_{\substack{i,j=1 \\ (i \neq j)}}^k d_i d_j \\ &+ \left(\frac{1}{2^{n-1}} - \frac{1}{4^{n-1}} \right) \sum_{i=1}^k h_i^2 \\ &\pm 2 \left[\frac{(1-2p+2p^2)^{n-1}}{2^{n-1}} - \frac{1}{4^{n-1}} \right] \sum_{\substack{i,j=1 \\ (i \neq j)}}^k h_i h_j \end{aligned}$$

where p = the recombination fraction which is assumed to be same for all the loci,

when $p = \frac{1}{2}$, *i.e.* linkage is absent

$$V(F_n) = \left(1 - \frac{1}{2^{n-1}}\right) \sum_{i=1}^k d_i^2 + \left(\frac{1}{2^{n-1}} - \frac{1}{4^{n-1}}\right) \sum_{i=1}^k h_i^2$$

Thus, the components (*viz.* *D H*) of genotypic variance can be conveniently worked out.

The variance of mean of F_n -progenies derived as :

$$V(\bar{F}_n) = \left(1 - \frac{1}{2^{n-2}}\right) \sum_{i=1}^k d_i^2 + \left(\frac{1}{2^{n-2}} - \frac{1}{4^{n-1}}\right) \sum_{i=1}^k h_i^2$$

and, the mean variance of F_n progenies is given as :

$$\bar{V}(F_n) = \frac{1}{2^{n-1}} \left(\sum_{i=1}^k d_i^2 + \frac{1}{2} \sum_{i=1}^k h_i^2 \right)$$

If, now, $p=q$ and $c=0$, the distribution of genotypic frequencies and the different components of the genotypic variances for different generations on selfing are, on assumption of absence of selection pressure in either direction, as furnished below :

TABLE I

Population	Genotypic frequency			Mean	Genotypic variances		
	x	y	z	(u)	D	H	C (variances)
P_1 (AA)	1	0	0	d	0	0	0
P_2 (aa)	0	0	1	-d	0	0	0
F_1	0	1	0	h	0	0	0
F_2	1/4	1/2	1/4	(1/2)h	1/2	1/4	0
F_3	3/8	1/4	3/8	(1/4)h	3/4	3/16	0
F_4	7/16	1/8	7/16	(1/8)h	7/8	7/64	0
F_5	15/32	1/16	15/32	(1/16)h	15/16	15/2 ⁵ 6	0
F_6	31/64	1/32	31/64	(1/32)h	31/32	31/1024	0
:	:	:	:	:	:	:	:
F_∞	1/2	0	1/2	0	1	0	0

It is known that the heterozygosity is fixed at the second generation in case of random mating population ($c=1$).

4. GENOTYPIC FREQUENCIES AND VARIANCES UNDER BACKCROSSING

After backcrossing, a number of progeny lines may be raised from the initial parental pure lines at the successive generations. The effect on the frequencies and the components of genotypic frequencies are worked out and presented below :

TABLE 2

Backcross lines	Genotypic frequencies			Genotypic variances		
	<i>x</i>	<i>y</i>	<i>z</i>	<i>D</i>	<i>H</i>	<i>C</i>
$B_1 (=P_1F_1)$	1/2	1/2	0	1/4	1/4	-1/2
$B_2 (=P_2F_1)$	0	1/2	1/2	1/4	1/4	1/2
$B_{11}(=B_1 \times P_1)$	3/4	1/4	0	3/16	3/16	-3/8
$B_{12}(=B_1 \times P_2)$	0	3/4	1/4	3/16	3/16	3/8
$B_{21}(=B_2 \times P_1)$	1/4	3/4	0	3/16	3/16	-3/8
$B_{22}(=B_2 \times P_2)$	0	1/4	3/4	3/16	3/16	3/8
$B_{(11)1}$	7/8	1/8	0	7/64	7/64	-7/32
$B_{(11)2}$	0	7/8	1/8	7/64	7/64	7/32
$B_{(12)1}$	3/8	5/8	0	15/64	15/64	-15/32
$B_{(12)2}$	0	3/8	5/8	15/64	15/64	15/32
$B_{(21)1}$	5/8	3/8	0	15/64	15/64	-15/32
$B_{(21)2}$	0	5/8	3/8	15/64	15/64	15/32
$B_{(22)1}$	1/8	7/8	0	7/64	7/64	-7/32
$B_{(22)2}$	0	1/8	7/8	7/64	7/64	7/32

(N.B. - $B_{(ij)k} = B_i P_j \times P_k$ where $i=1$ or $2, j=1$ or 2 & $k=1$ or 2).

Thus, the continued backcrossing with the desired homozygous parental line reduces the heterozygosity at a faster rate and the undesired line is eliminated completely. The breeder may like to backcross amongst those lines which are closer to the desired parental line with a view to attaining homozygosity quickly and intercross amongst distant lines for retaining heterozygosity.

General Expressions of Genotypic Frequencies and Variances:

The general expressions for the different genotypes at the n th generation when $p=q=\frac{1}{2}$ and $c=1$, after continued backcrossing are as worked out below:

The corresponding expressions at the n th generation for the components of genotypic variances are similarly worked out and presented below:

TABLE 3.1

Sr. No.	Back-crossed population (n th generation)	Genotypic Frequencies		
		x	y	z
1.	$B_{(11\dots 1)1}$	$\frac{2^{n-1}-1}{2^{n-1}}$	$\frac{1}{2^{n-1}}$	0
2.	$B_{(11\dots 1)2}$	0	$\frac{2^{n-1}-1}{2^{n-1}}$	$\frac{1}{2^{n-1}}$
3.	$B_{(12\dots 2)1}$	$\frac{2^{n-2}-1}{2^{n-1}}$	$\frac{2^{n-2}+1}{2^{n-1}}$	0
4.	$B_{(12\dots 2)2}$	0	$\frac{2^{n-2}-1}{2^{n-1}}$	$\frac{2^{n-2}+1}{2^{n-1}}$
5.	$B_{(21\dots 1)1}$	$\frac{2^{n-2}+1}{2^{n-1}}$	$\frac{2^{n-2}-1}{2^{n-1}}$	0
6.	$B_{(21\dots 1)2}$	0	$\frac{2^{n-2}+1}{2^{n-1}}$	$\frac{2^{n-2}-1}{2^{n-1}}$
7.	$B_{(22\dots 2)1}$	$\frac{1}{2^{n-1}}$	$\frac{2^{n-1}-1}{2^{n-1}}$	0
8.	$B_{(22\dots 2)2}$	0	$\frac{1}{2^{n-1}}$	$\frac{2^{n-1}-1}{2^{n-1}}$

(N.B.— $B_{(i, j, \dots, \overline{n-2})_p} = (B_i p_j \dots P_{\overline{n-2}}) P_p$, where each of $(i, j, k, \dots, \overline{n-2}, p) = 1$ or 2; and $\overline{n-2}$ represents the stage of the number of generation after backcrossing).

TABLE 3.2

Sr. No.	Backcross Population (nth generation)	Genotypic Variances		
		D	H	C
1.	$B_{(11 \dots 1)1}$	$\frac{2^{n-1}-1}{2^{2n-2}}$	$\frac{2^{n-1}-1}{2^{2n-2}}$	$\frac{(2^{n-1}-1)}{2^{2n-3}}$
2.	$B_{(11 \dots 1)2}$	$\frac{2^{n-1}-1}{2^{2n-2}}$	$\frac{2^{n-1}-1}{2^{2n-2}}$	$\frac{2^{n-3}-1}{2^{2n-3}}$
3.	$B_{(1^2 \dots 2)1}$	$\left(\frac{2^{n-2}-1}{2^{n-1}}\right) \times \left(1 - \frac{2^{n-2}-1}{2^{n-1}}\right)$	$\left(\frac{2^{n-2}+1}{2^{n-1}}\right) \times \left(1 - \frac{2^{n-2}-1}{2^{n-1}}\right)$	$\left(\frac{2^{2n-4}-1}{2^{2n-3}}\right)$
4.	$B_{(1^2 \dots 2)2}$	$\left(\frac{2^{n-2}+1}{2^{n-1}}\right) \times \left(1 - \frac{2^{n-2}+1}{2^{n-1}}\right)$	$\left(\frac{2^{n-2}-1}{2^{n-1}}\right) \times \left(1 - \frac{2^{n-2}-1}{2^{n-1}}\right)$	$\left(\frac{2^{2n-4}-1}{2^{2n-3}}\right)$
5.	$B_{(2^1 \dots 1)1}$	$\left(\frac{2^{n-2}+1}{2^{n-1}}\right) \times \left(1 - \frac{2^{n-2}+1}{2^{n-1}}\right)$	$\left(\frac{2^{n-2}-1}{2^{n-1}}\right) \times \left(1 - \frac{2^{n-2}-1}{2^{n-1}}\right)$	$\left(\frac{2^{2n-4}-1}{2^{2n-3}}\right)$
6.	$B_{(2^1 \dots 1)2}$	$\left(\frac{2^{n-2}-1}{2^{n-1}}\right) \times \left(1 - \frac{2^{n-2}-1}{2^{n-1}}\right)$	$\left(\frac{2^{n-2}+1}{2^{n-1}}\right) \times \left(1 - \frac{2^{n-2}+1}{2^{n-1}}\right)$	$\left(\frac{2^{2n-4}-1}{2^{2n-3}}\right)$
7.	$B_{(2^2 \dots 2)1}$	$\frac{2^{n-1}-1}{2^{2n-2}}$	$\frac{2^{n-1}-1}{2^{2n-2}}$	$\left(\frac{2^{n-1}-1}{2^{2n-3}}\right)$
8.	$B_{(2^2 \dots 2)2}$	$\frac{2^{n-1}-1}{2^{2n-2}}$	$\frac{2^{n-1}-1}{2^{2n-2}}$	$\left(\frac{2^{n-1}-1}{2^{2n-3}}\right)$

Some of the lines as enumerated may have only academic interests to the breeders. The reduction in the heterozygosity is half in each generation while in the purely selfed lines, the reduction is half of that in the corresponding backcrossed lines, which is the usual expectation.

When the repeated backcrossed lines are raised, two components of the genetic variances viz. the variances of the mean of the families raised and the mean variance of the families are also worked out which will be presented in a subsequent paper in details.

SELFING THE BACK-CROSSED LINES

Sometimes the breeders are interested to self the back-cross lines in order to stabilise the homozygosity, whatever is already achieved by back crossing.

The genotypic frequencies and the components of genotypic variances after selfing the progenies being raised from the initial

backcrossed lines are as worked out below:

TABLE 4

Lines	Genotypic frequencies			Genotypic Variances (components)		
	x	y	z	D	H	C
$B_1(S_1)$	5/8	1/4	1/8	1/2	3/16	(-) 1/4
$B_2(S_1)$	1/8	1/4	1/16	1/2	3/16	1/4
$P_1B_1(S_1)$	13/16	1/8	1/16	5/16	7/64	-3/16
$P_2B_1(S_1)$	3/16	3/8	7/16	9/16	15/64	3/16
$P_1B_2(S_1)$	7/16	3/8	3/16	9/16	15/64	-3/16
$P_2B_2(S_1)$	1/16	1/8	13/16	5/16	7/64	3/16

At the n^{th} generation, there will be $(n-2)$ successive selfing over the initial Backcrossed lines, whose genotypic frequencies are worked out to :

TABLE 5.1

Lines	Genotypic frequency		
	X	Y	Z
$B_1(S_{n-2})$	$\frac{2^{n-1} + 2^{n-2} - 1}{2^n}$	$\frac{1}{2^{n-1}}$	$\frac{2^{n-2} - 1}{2^n}$
$B_2(S_{n-2})$	$\frac{2^{n-2} - 1}{2^n}$	$\frac{1}{2^{n-1}}$	$\frac{2^{n-1} + 2^{n-2} - 1}{2^n}$

Again on the same assumption, the components of genotypic variances at the n^{th} generation work out as :

TABLE 5.2

Lines	Components of genotypic variance		
	D	H	C
$B_1(S_{n-2})$	$\frac{2^{n-1} - 2^{n-3} - 1}{2^{n-1}}$	$\frac{2^{n-1} - 1}{2^{2n-2}}$	$-\frac{1}{2^{n-1}}$
$B_2(S_{n-2})$	$\frac{2^{n-1} - 2^{n-3} - 1}{2^{n-1}}$	$\frac{2^{n-1} - 1}{2^{2n-2}}$	$\frac{1}{2^{n-1}}$

Selving the backcrossed lines reduces the heterozygosity no doubt but the reduction will be quicker if backcrossing one or two stages more with the desired parents, selving is done thereafter on these lines. This eliminates the undesired homozygous lines and also reduces the amount of heterozygosity. Continued back-crossing, in fact, is necessary for the hybridisation work with respect to multiple characteristics of the polygenic cases.

If selection, partial or complete, is present and there is linkage, the situation becomes increasingly interesting. The effect on initially backcrossed line followed thereafter by selving and selection of the desired genotypes have also been studied which will be subsequently presented.

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