

Theoretical Basis for Determining the Number of X_2 -Plants Required for Improvement of Quantitative Characters of Self-Pollinating Crops

II. Complement to the Theory and Numerical Computations

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Synopsis. Complements to the previously offered theory were presented and some numerical computations of the components, of which the theoretical equation for the estimation of X_2 -population size consists, were carried out for meeting our various necessities.

Introduction

Theoretical equations for estimating the approximate size of X_2 -population for quantitative character breeding were derived by YONEZAWA *et al.* (1970), from which some general conclusions could be obtained.

To make our theory more solid, some complements to the previously given theory will be mentioned in the present paper. In addition, numerical computations of the components, by the combination of which the number of X_2 -plants can be determined, will be offered for meeting our practical necessities and for deriving some other conclusions of practical significance than those obtained in the previous paper.

Three different types of selection model, say models A, B₁ and B₂, were taken up in the previous paper. The substantial difference among these selection models consists in the point that selection or rejection of X_2 -plants are decided on the basis of their phenotypic deviation from mean of the X_2 -line they belong to, from mean of X_2 -population as a whole and from mean of control line, respectively. Among these models, only model B₂ will be taken up in the present paper, since this type of selection is considered to be most preferable for quantitative character breeding and has been ordinarily adopted in actual breeding programmes.

Notation of Parameters

Symbols adopted in this paper are explained below. Readers should consult the previous paper (YONEZAWA *et al.*, 1970) for details.

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C: Selection intensity, or, critical phenotypic desirability or superiority (over the mean of control line) for artificial selection, standardized by the phenotypic standard deviation denoted by σ_X , which may be equalized, according to the will of breeders, to the phenotypic standard deviation of a control line, say σ_E , that of a X_2 -line, say σ_L , that of a X_2 -subpopulation, say σ_B , or that of the whole X_2 -population, say σ_T .

D: Mean of the phenotypic deviations (standardized by σ_X) of all X_2 -plants from means of their respective control lines.

d: Genotypic desirability or superiority of the mutant to be gained, which is defined by the average phenotypic deviation (standardized by σ_X) of the mutant from mean of its control line.

f: Expected frequency of the mutant to be gained, in other words, probability of desirable mutant being included in X_2 -population.

m: Induced mutation rate per allele.

P: Probability of desirable mutant being obtained or detected under some given selection intensity.

S: Ratio of the number of X_2 -plants belonging to the phenotypic range suitable for artificial selection, to the whole of X_2 -population.

Review

The mathematical procedures through which theoretical equations in the preceding paper (YONEZAWA *et al.*, 1970) have been derived are outlined here for the sake of coherence of the present paper.

Under the circumstance that X_2 -plants of **C** or more (in the unit of σ_X) phenotypic supe-

riority over the mean of respective control line are selected, P is formulated by

$$P \doteq \frac{f}{\sqrt{2\pi} S} \int_{(C-d)\sigma_X/\sigma_{E'}}^{\infty} e^{-t^2/2}; C < d \quad (1)$$

where

$$S = \frac{1}{\sqrt{2\pi}} \int_{(C-D)\sigma_X/\sigma_Y}^{\infty} e^{-t^2/2} dt \quad (2)$$

and $\sigma_{E'}$ stands for the phenotypic standard deviation of desirable mutant in the whole X₂-population, in an X₂-subpopulation or in an X₂-line according as one, some or as many control lines as X₂-lines are planted, respectively. Standard deviation σ_Y in equation (2) equals σ_T, σ_B and σ_L according to these number of control lines planted. These definitions of $\sigma_{E'}$ and σ_Y show that both of them are decreased as the number of control lines is increased, and therefore the values of $\sigma_X/\sigma_{E'}$ and σ_X/σ_Y get larger according to the increase in the number of control lines.

Parameter f in equation (1) is under the control of induced mutation rate and genetic composition of breeding material, and is presented by

$$f \doteq \sum_{i=j}^{L_1} \binom{L_1}{j} \left(\frac{1}{2}m\right)^i \left(1 - \frac{1}{2}m\right)^{L_1-i} \left(1 - \frac{3}{2}m\right)^{L_2} \\ \doteq \binom{L_1}{j} \left(\frac{1}{2}m\right)^j \left(1 - \frac{1}{2}m\right)^{L_1-j} \left(1 - \frac{3}{2}m\right)^{L_2} \quad (3)$$

in the case when breeding materials is originally of undesirable genotype for L_1 independent loci and of desirable genotype for L_2 independent loci and when j or more loci among the L_1 loci are to be improved together, keeping the genetic composition of originally desirable L_2 loci unchanged. Obviously, equation (3) becomes

$$\left(\frac{m}{2}\right)^{L_1} \left(1 - \frac{3m}{2}\right)^{L_2} \doteq \left(\frac{m}{2}\right)^{L_1} \cdot \left(1 - \frac{3L_2m}{2}\right)$$

if all of originally undesirable loci are to be improved, namely, j equals L_1 .

Now, the number of X₂-plants to be grown in quantitative character breeding, say N , is determined in such a way that the probability that no desirable mutant is included in the selected portion of X₂-population should be some small value, say ϵ . In mathematical expression, this means that N should be large enough for the equation

$$(1-P)^n = \epsilon \quad (4)$$

to be satisfied, n standing for the number of X₂-plants to be selected under given selection intensity C .

Immediately from equation (4),

$$n = \log \epsilon / \log (1-P) \quad (5)$$

which gives the minimum number of X₂-plants falling into the range of C or more phenotypic desirability or superiority over the mean of respective control line. Then, noticing the relation $n/N = S$, the total number of X₂-plants could be formulated as

$$N = \log \epsilon / S \cdot \log (1-P) \quad (6)$$

which can be approximated by

$$N \doteq \log \epsilon^{-1} / SP = \sqrt{2\pi} \log \epsilon^{-1} / f \\ \cdot \int_{(C-d)\sigma_X/\sigma_{E'}}^{\infty} e^{-t^2/2} dt \quad (7)$$

if P is sufficiently small as compared with unity. This condition is considered to be fulfilled in most, if not all, cases of quantitative character breeding.

Letting selection intensity C be negative infinity, the number of X₂-plants in qualitative character breeding, where the probability of desirable mutant being obtained is equal to that of the mutant being included, is formulated by

$$N' = \log \epsilon / \log (1-f) \quad (8)$$

which gives the size of X₂-population under one-plant-one-grain method of propagation that was proved by YOSHIDA (1962) to be of greatest efficiency if just the number of X₂-plants, but not that of X₁-plants, is taken into account. As is the case of quantitative characters, equation (8) can be approximated by

$$N' \doteq \log \epsilon^{-1} / f = \log \epsilon^{-1} / \left[\binom{L_1}{j} \left(\frac{m}{2}\right)^j \left\{ 1 - \frac{L_1-j+3L_2}{2} m \right. \right. \\ \left. \left. + \frac{\left\{ \binom{L_1-j}{2} + 3(L_1-j)L_2 + 9 \binom{L_2}{2} \right\}}{4} m^2 - \dots \right\} \right] \quad (9)$$

when f is sufficiently small.

Complements to the Previous Theory

As understood from the above outline, at least as frequent X₂-plants as determined by equation (4) or (5) need to fall into the range

of C or more phenotypic desirability for the success of artificial selection. But, there is no firm security for this requisition to be always satisfied under such size of X_2 -population as given by equation (6) which was directly derived by using the relation $n/N=S$. This is because the relation $n/N=S$ is just an expected one and it is easily expected therefore that, owing to sampling error, the requisition or n would not be attained under the X_2 -population size thus determined. Our previous equation for N will be revised in consideration of this point.

The size of X_2 -population, N , should be so large that the elementary condition represented by equation (4) is safely met. By this principle, N is to be determined in such a way that the equation

$$\sum_{i=n}^N \binom{N}{i} S^i (1-S)^{N-i} = \frac{1}{\sqrt{2\pi}} \int_{(n-NS)/\sqrt{NS(1-S)}}^{\infty} e^{-t^2/2} dt = 1 - \delta \quad (10)$$

is satisfied, where $\delta (>0)$ assumes some small value arbitrarily chosen by breeders, n and S being presented by equation (5) and (2) respectively.

Then, the size of X_2 -population under some predetermined values of n , S and δ can be formulated as

$$N = n/S + \frac{(1-S)A_\delta^2 - A_\delta \sqrt{4(1-S)n + (1-S)^2 A_\delta^2}}{2S} \quad (11)$$

where A_δ means the value that is uniquely determined for given δ through the familiar relation $\frac{1}{\sqrt{2\pi}} \int_{A_\delta}^{\infty} e^{-t^2/2} dt = 1 - \delta$. As understood from the feature of normal distribution, A_δ assumes zero, positive or negative values according as $1 - \delta$ is equal to, smaller or larger than 0.5. Noticing that n is much larger than other parameters, equation (11) could be approximated, with little practical inconvenience, by

$$N \approx \frac{n}{S} - A_\delta \sqrt{\frac{1-S}{S}} \cdot \sqrt{\frac{n}{S}} \quad (12)$$

Further, since P is in general expected not to be large for quantitative characters, equation (12) is expressed by

$$N = K_1 N' + K_2 \sqrt{N'} \quad (13)$$

$$; K_1 = \sqrt{2\pi} \int_{(C-d)\sigma_X/\sigma_E}^{\infty} e^{-t^2/2} dt,$$

$$K_2 = -A_\delta \left\{ K_1 \cdot \frac{1-S}{S} \right\}^{1/2}$$

which is of more handy form to treat.

Now, putting n/S into N of equation (10), it is readily known that the elementary condition for selection which is represented by equation (4) can be attained with probability 0.5 under such X_2 -population size as given by equation (6). Generally speaking, this value 0.5 of $1 - \delta$ is considered to be rather insufficient for practical purposes. It is now understood that X_2 -population size is underestimated by our previous equation, and that our previous conclusion (YONEZAWA *et al.*, 1970) that N is inversely proportional to

$$f \approx \binom{L_1}{j} \left(\frac{m}{2} \right)^j$$

is acceptable only in the limited condition that δ is decided to be 0.5, A_δ being zero.

Equations (12) or (13) may be named generalized equation for the estimation of N , in the sense that our previous equation for N is merely one of special forms of the present equation, corresponding to the case of $A_\delta = 0$. The size of X_2 -population for other selection models such as A and B_1 models could be generalized by the same principle.

Numerical Computations and Conclusions

Equation (13) shows that the number of X_2 -plants can be readily calculated if numerical values of such components as N' , K_1 , A_δ and $\sqrt{\frac{1-S}{S}}$ are given. So, numerical computations of these components corresponding to the various values of more elementary parameters such as induced mutation rate, selection intensity etc. will be presented in this section for the uses of breeders and for deriving some general conclusions of practical significance. The approximate size of X_2 -population in individual cases of mutation breeding is to be estimated by the combination of some probable values of these components through equation (13).

The numerical values of A_δ for arbitrary values of δ may be found in any textbook of statistics (e.g. SNEDECOR's *Statistical Methods*); $A_{.10} \approx -1.28$, $A_{.05} \approx -1.65$, $A_{.01} \approx -2.33$ and so

on.

Numerical computations of N' and $\sqrt{N'}$ for some probable values of L_1, j, L_2 and m are given in Table 1. Those numbers of loci adopted in making Table 1 are considered not to be unreasonable, seeing that most of induced mutations are ascribed to the change of just a single allele and the mean number of changed alleles is about $2m(L_1+L_2)$ per plant. Naturally, the large numbers of the loci such as 500 or 1000 correspond to the cases when the evaluation of X₂-plants is conducted on the basis of some multiple attributes *en masse*. The loci affecting the attributes unrelated to the

evaluation need not to be taken into account at all. Judging from GUSTAFSSON (1947), NISHIMURA *et al.* (1952), SCHOLZ (1957) etc., the induced mutation rates 10^{-4} and 10^{-3} are considered not to be far from reality, even if not exactly the case. The rate 10^{-2} , however, seems rather rare, but not impossible as can be predicted from the proposition of YOSHIDA (1962) that values as high as $p_1=10^{-2}$ may occur in rice, p_1 being approximated by $2m$ in the present terminology. Now, it can be seen from Table 1 and equation (9) that N' and consequently N are greatly affected by induced mutation rate, m , and the number of loci to be improved

Table 1. Numerical computations of the size of X₂-population required for one or more desirable mutants to be included, N' , and its square root, $\sqrt{N'}$

| m^{**} (L_1, j, L_2)*** | $N'(\sqrt{N'}); \epsilon^*=0.05$ | | | m^{**} (L_1, j, L_2)*** | $N'(\sqrt{N'}); \epsilon^*=0.05$ | | |
|----------------------------------|----------------------------------|-------------|--------------|----------------------------------|----------------------------------|--------------|--------------|
| | 10^{-4} | 10^{-3} | 10^{-2} | | 10^{-4} | 10^{-3} | 10^{-2} |
| (1, 1, 0) | 5.99† (2.44)†† | 5.99 (2.44) | 5.99 (2.44) | (4, 3, 1000) | 6.96 (2.63) | 12.7 (3.56) | 22.1 (4.70) |
| (1, 1, 50) | 6.04 (2.45) | 6.22 (2.49) | 12.8 (3.57) | (4, 4, 0) | 47.9 (6.92) | 47.9 (6.92) | 47.9 (6.92) |
| (1, 1, 100) | 6.08 (2.46) | 6.46 (2.54) | 27.2 (5.21) | (4, 4, 50) | 48.3 (6.94) | 49.8 (7.05) | 102. (10.0) |
| (1, 1, 500) | 6.46 (2.54) | 8.72 (2.95) | 1.15 (1.07) | (4, 4, 100) | 48.7 (6.97) | 51.7 (7.19) | 217. (14.7) |
| (1, 1, 1000) | 6.96 (2.63) | 12.7 (3.56) | 21.9 (4.67) | (4, 4, 500) | 51.7 (6.19) | 69.8 (8.35) | 9.17 (3.02) |
| (2, 1, 0) | 2.99 (1.72) | 3.00 (1.73) | 3.01 (1.73) | (4, 4, 1000) | 55.7 (7.46) | 101. (10.0) | 175. (13.2) |
| (2, 1, 50) | 3.02 (1.73) | 3.11 (1.76) | 6.41 (2.53) | (5, 1, 0) | 1.20 (1.09) | 1.20 (1.09) | 1.22 (1.10) |
| (2, 1, 100) | 3.04 (1.74) | 3.23 (1.79) | 13.7 (3.70) | (5, 1, 50) | 1.21 (1.10) | 1.25 (1.11) | 2.60 (1.61) |
| (2, 1, 500) | 3.23 (1.79) | 4.36 (2.08) | .576 (.758) | (5, 1, 100) | 1.22 (1.10) | 1.29 (1.13) | 5.54 (2.35) |
| (2, 1, 1000) | 3.48 (1.86) | 6.35 (2.51) | 11.0 (3.31) | (5, 1, 500) | 1.29 (1.13) | 1.75 (1.32) | .234 (.483) |
| (2, 2, 0) | 12.0 (3.46) | 12.0 (3.46) | 12.9 (3.46) | (5, 1, 1000) | 1.39 (1.17) | 2.54 (1.59) | 4.48 (2.11) |
| (2, 2, 50) | 12.1 (3.47) | 12.4 (3.52) | 25.5 (5.04) | (5, 2, 0) | 1.20 (1.09) | 1.20 (1.09) | 1.21 (1.10) |
| (2, 2, 100) | 12.2 (3.49) | 12.9 (3.59) | 54.3 (7.36) | (5, 2, 50) | 1.21 (1.10) | 1.25 (1.11) | 2.59 (1.60) |
| (2, 2, 500) | 12.9 (3.59) | 17.4 (4.17) | 2.29 (1.51) | (5, 2, 100) | 1.22 (1.10) | 1.29 (1.13) | 5.51 (2.34) |
| (2, 2, 1000) | 13.9 (3.72) | 25.4 (5.03) | 43.9 (6.62) | (5, 2, 500) | 1.29 (1.13) | 1.75 (1.32) | .232 (.481) |
| (3, 1, 0) | 2.00 (1.41) | 2.00 (1.41) | 2.02 (1.42) | (5, 2, 1000) | 1.39 (1.17) | 2.54 (1.59) | 4.46 (2.11) |
| (3, 1, 50) | 2.01 (1.41) | 2.08 (1.44) | 4.29 (2.07) | (5, 3, 0) | 2.40 (1.54) | 2.40 (1.54) | 2.42 (1.55) |
| (3, 1, 100) | 2.03 (1.42) | 2.15 (1.46) | 9.15 (3.02) | (5, 3, 50) | 2.41 (1.54) | 2.49 (1.57) | 5.15 (2.26) |
| (3, 1, 500) | 2.15 (1.46) | 2.91 (1.47) | .386 (.621) | (5, 3, 100) | 2.43 (1.55) | 2.59 (1.60) | 11.0 (3.31) |
| (3, 1, 1000) | 2.32 (1.52) | 4.24 (2.05) | 7.39 (2.71) | (5, 3, 500) | 2.58 (1.60) | 3.49 (1.86) | .463 (.680) |
| (3, 2, 0) | 3.99 (1.99) | 4.00 (2.00) | 4.02 (2.00) | (5, 3, 1000) | 2.78 (1.66) | 5.08 (2.25) | 8.87 (2.97) |
| (3, 2, 50) | 4.02 (2.00) | 4.15 (2.03) | 8.55 (2.92) | (5, 4, 0) | 9.59 (3.09) | 9.59 (3.09) | 9.63 (3.10) |
| (3, 2, 100) | 4.05 (2.01) | 4.31 (2.07) | 18.2 (4.26) | (5, 4, 50) | 9.66 (3.10) | 9.96 (3.15) | 20.5 (4.52) |
| (3, 2, 500) | 4.31 (2.07) | 5.82 (2.41) | .768 (.876) | (5, 4, 100) | 9.73 (3.11) | 10.3 (3.20) | 43.7 (6.61) |
| (3, 2, 1000) | 4.64 (2.15) | 8.47 (2.91) | 14.7 (3.83) | (5, 4, 500) | 10.3 (3.20) | 14.0 (3.74) | 1.84 (1.35) |
| (3, 3, 0) | 24.0 (4.89) | 24.0 (4.89) | 24.0 (4.89) | (5, 4, 1000) | 11.1 (3.33) | 20.1 (4.50) | 35.3 (5.94) |
| (3, 3, 50) | 24.1 (4.90) | 24.9 (4.98) | 51.0 (7.14) | (5, 5, 0) | 95.9 (9.79) | 95.9 (9.79) | 95.9 (9.79) |
| (3, 3, 100) | 24.3 (4.92) | 25.8 (5.07) | 109. (10.4) | (5, 5, 500) | 103. (10.1) | 140. (11.8) | 18.3 (4.27) |
| (3, 3, 500) | 25.8 (5.07) | 34.9 (5.90) | 4.59 (2.14) | (5, 5, 1000) | 111. (10.5) | 203. (14.2) | 351. (18.7) |
| (3, 3, 1000) | 27.8 (5.27) | 50.8 (7.12) | 87.8 (9.37) | (10, 1, 0) | .599 (.773) | .601 (.755) | .627 (.791) |
| (4, 1, 0) | 1.50 (1.22) | 1.50 (1.22) | 1.52 (1.23) | (10, 1, 500) | .645 (.803) | .876 (.935) | .120 (.346) |
| (4, 1, 50) | 1.51 (1.22) | 1.56 (1.24) | 3.24 (1.80) | (10, 1, 1000) | .696 (.984) | 1.27 (1.12) | 2.30 (1.51) |
| (4, 1, 100) | 1.52 (1.23) | 1.62 (1.27) | 6.89 (2.62) | (10, 2, 0) | .266 (.515) | .267 (.516) | .277 (.526) |
| (4, 1, 500) | 1.61 (1.26) | 2.18 (1.47) | .291 (.539) | (10, 2, 500) | .287 (.535) | .389 (.623) | .053 (.230) |
| (4, 1, 1000) | 1.74 (1.31) | 3.18 (1.78) | 5.57 (2.36) | (10, 2, 1000) | .309 (.555) | .566 (.752) | 1.02 (1.00) |
| (4, 2, 0) | 2.00 (1.41) | 2.00 (1.41) | 2.01 (1.41) | (10, 3, 0) | .200 (.447) | .200 (.447) | .207 (.164) |
| (4, 2, 50) | 2.01 (1.41) | 2.08 (1.44) | 4.29 (2.07) | (10, 3, 500) | .215 (.463) | .292 (.540) | .040 (.200) |
| (4, 2, 100) | 2.03 (1.42) | 2.15 (1.46) | 9.14 (3.02) | (10, 3, 1000) | .232 (.481) | .425 (.651) | .758 (.870) |
| (4, 2, 500) | 2.15 (1.46) | 2.91 (1.70) | .386 (.621) | (10, 4, 0) | .228 (.477) | .229 (.478) | .235 (.484) |
| (4, 2, 1000) | 2.32 (1.56) | 4.24 (2.05) | 7.39 (2.77) | (10, 4, 500) | .246 (.495) | .333 (.577) | .045 (.212) |
| (4, 3, 0) | 5.99 (2.44) | 5.99 (2.44) | 6.02 (2.45) | (10, 4, 1000) | .265 (.514) | .485 (.696) | .862 (.928) |
| (4, 3, 50) | 6.04 (2.45) | 6.22 (2.49) | 12.8 (3.57) | (10, 5, 0) | .380 (.616) | .381 (.617) | .390 (.624) |
| (4, 3, 100) | 6.08 (2.46) | 6.46 (2.54) | 27.3 (5.22) | (10, 5, 500) | .410 (.640) | .555 (.744) | .075 (.273) |
| (4, 3, 500) | 6.46 (2.54) | 8.72 (2.95) | 1.15 (1.07) | (10, 5, 1000) | .442 (.664) | .808 (.898) | 1.43 (1.19) |

* The probability that no desirable mutant is included in X₂-population (for qualitative characters breeding) or in the portion selected from X₂-population (for quantitative character breeding).

** Induced mutation rate per allele.

*** Left to right, the number of originally undesirable loci of breeding material, the number of the loci to be improved among those loci and the number of originally desirable loci.

† to be multiplied by 10^{2j+4} , 10^{2j+6} and m^{-j} , under the conditions of $m=10^{-2}$ and $L_2=500$, $m=10^{-2}$ and $L_2=1000$ and others, respectively.

†† to be multiplied by 10^{j+2} , 10^{j+3} and $m^{-j/2}$ under the respective conditions.

together, j . The influence of the number of originally desirable loci, L_2 , on N' seems to be relatively small and could be neglected with sufficient accuracy if m is below 10^{-3} or so.

Numerical computations of K_1 and $\sqrt{\frac{1-S}{S}}$ corresponding to the various values of $-(C-d)\sigma_X/\sigma_{E'}$ and $(C-D)\sigma_X/\sigma_Y$ respectively are diagrammatically shown in Figure 1. The numerical values of $\sqrt{K_1}$ were also given for convenience' sake. Two different aspects can be immediately read from this figure and equation (13) together. Firstly, with given genotypic desirability of the mutant to be obtained and with givev number of control lines planted (indicating that the values of d , $\sigma_X/\sigma_{E'}$ and σ_X/σ_Y are fixed), the size of X_2 -population gets larger as selection intensity $C(<d)$ does. This is because $-(C-d)\sigma_X/\sigma_{E'}$ and $(C-D)\sigma_X/\sigma_Y$ are decreased and increased respectively by the increase of C . Secondly, with some fixed values of C , d and D , the increase $\sigma_X/\sigma_{E'}$ and σ_X/σ_Y due to the increase of the number of control lines or due to the improvement of the environmental uniformity results in the diminution of the number of X_2 -plants. These two points were already mentioned in the previous paper.

Figure 1 may give us the impression that, under constant values of selection intensity and the number of control lines, the size of X_2 -population can be smaller as genotypic desirability of the mutant to be obtained, d , is larger. Of course this is not the case, since d is not independent of the parameters such as L_1 , j and L_2 which have not a little influence on the size of X_2 -population. By our theory, d takes larger values when j is decided to be larger.

Judging from the numerical computations and equations, it is the parameters m and j that have the most delicate influence on the size of X_2 -population. This proposes that developing some new method for rising

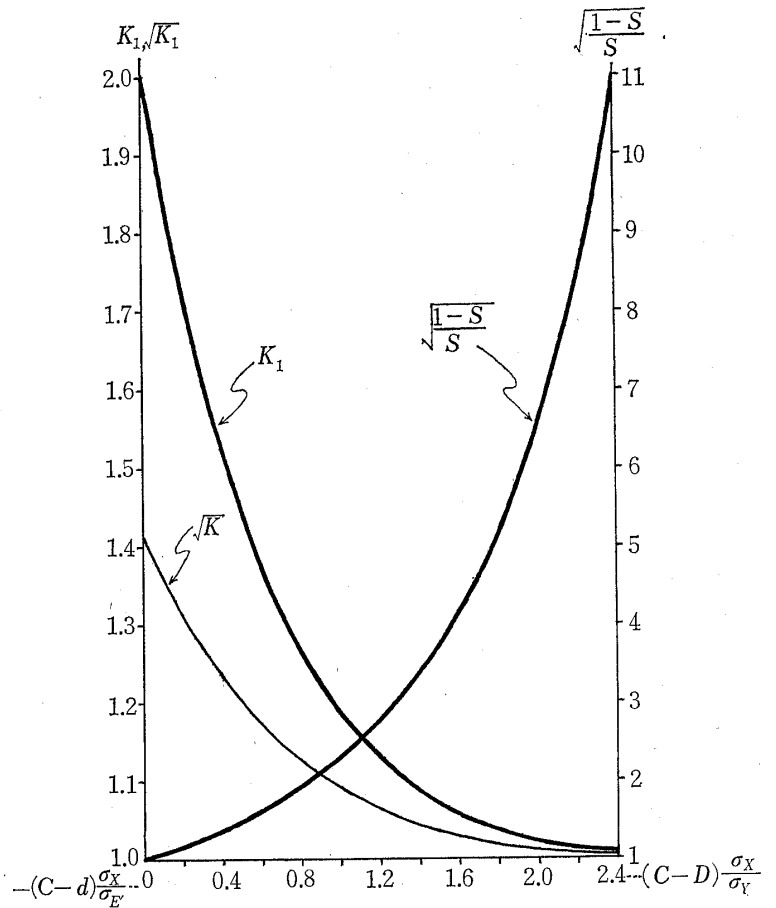


Fig. 1. Diagrammatical presentation of numerical computations of the components constructing the equation (13) made for estimating X_2 -population size in quantitative character breeding.

induced mutation rate of undesirable alleles is of great practical importance. The influence of other parameters such as C , d etc. on X_2 -population size is not so large. Noticing the ratio

$$N/N' = K_1 + K_2/\sqrt{N'} \quad (14)$$

where K_1 is at most 2 and K_2 is considered to be smaller than 25 or something in the ordinary breeding programmes for quantitative characters, the variation of X_2 -population size due to the change of the parameters C , d etc. which need to be introduced only in the case of quantitative characters may be said to be at most three times the size denoted by N' that represents the size of X_2 -population required for one or more desirable mutants to be included, but not necessarily obtained (see equations (8) (9)).

It is considered that the present numerical computations cover the range of our practical necessities. If X_2 -population sizes corre-

sponding to other numerical values of the parameters than those employed in this paper are to be estimated, they should be calculated by the direct use of equation (13) and others. In relation to this, it is noted that population mean of quantitative characters is in most cases not changed by mutagen treatment if mutants with too extremely changed phenotypic appearance to be of practical utility are set aside (OKA *et al.*, 1958, RAWLINGS *et al.*, 1958, MATSUO *et al.*, 1961, KAWAI, 1963 *etc.*). This means that parameter D has just a little, if any, influence on the size of X_2 -population and therefore could be omitted from equation (2). This can be justified also by the numerical computations of the component $\sqrt{\frac{1-S}{S}}$ (see Figure 1), through which D influences rather insensibly on the size of X_2 -population.

Discussion

Equations (9) and (13) shows that X_2 -population size is under strong control of the expected frequency of desirable mutant, f , which in turn is very delicately affected by induced mutation rate per allele, m . Since

$$\frac{df}{dm} \doteq k \cdot \{3(L_1 + L_2)m^2 - 2(L_1 + 3L_2 + 3j)m + 4j\};$$

$$k > 0$$

from equation (3), it can be said that f is maximum and therefore N is minimum at the point

$$m_0 \doteq \{L_1 + 3L_2 + 3j - \sqrt{(L_1 + 3L_2 + 3j)^2 - 12(L_1 + L_2)j}\} / 3(L_1 + L_2)$$

which is expected not to be high in many cases of quantitative character breeding. Within the range of $m > m_0$, the increase in mutation rate does not bring on the progress in the efficiency of mutation breeding, even if induced genetic variability of material population might be increased. This is because the success of selection under some given breeding aim and material depends not on the largeness of genetic variability but mainly on the frequency of desirable mutants to be gained. So, it is under a very large value of m_0 that the increase in mutation rate always results in heightening the practical merit of mutation breeding. The condition for m_0 to be large is that $j (\leq L_1)$ is sufficiently large, L_2 being small, in other words, that breeding ma-

terial is of undersirable genotype for many loci affecting the attributes of breeder's interest.

The foregoing suggests that a higher mutation rate is not necessarily advantageous and optimum mutation rate exists in many cases of quantitative character breeding. By the present theory, the optimum mutation rate is expected to be very small when L_2 is large, or when improving some complex character such as productivity, plant type *etc.* of a cultivated variety is the object of breeding, which has come through the sieve of long-term artificial selection. This can be seen also from the numerical computations in Table 1. Besides chromosomal or cytoplasmic aberrations, too high rate of induced mutation may be one of the main causes of the fact that larger genetic variabilities induced by higher dosages of mutagens seems to be ascribed to the increase of deleterious mutants rather than that of desirable ones (YAMAGATA *et al.*, 1960, TANAKA, 1967 *etc.*).

In the present state of mutation research, optimum mutagen dosage for attaining optimum mutation rate would be by no means easy to appoint in actual breeding programmes. But, it should be stressed at any rate that, even though induction of chromosomal or plasmic aberrations is suppressed by some new method, high mutagen dosages are not always profitable, or should be rather avoided in many cases of actual breeding in which not a few agronomic attributes together are of breeder's interest.

Of course, this does not hold true under the circumstance that mutation spectrum or mutation rate of individual alleles can be freely controlled by the will of breeder. In relation to this problem, the suggestion of JOSHI *et al.* (1967) that mutagen specificities found in qualitatively inherited characters (HAGBERG *et al.*, 1958, EHRENBURG *et al.*, 1961) exist also for the loci affecting quantitative characters would deserve notice and further experimental analyses.

Next, the use of our theoretical equations to practical breeding programmes is briefly discussed. Needless to say, it is just when enough informations on the parameters such as m , L_1 and L_2 are within the use of breeders, that our equations can fully exhibit their

utilities. In the case when knowledges about these parameters are restricted as often happens in quantitative character breeding, breeders cannot but make shift with such rough estimates of X_2 -population size as calculated depending on some probable values of these parameters, which are roughly estimated from the parameters concerning other characters of similar genetic behaviour.

Under the extreme circumstance that no information on the parameters is at hand, let m , L_1 and L_2 be 10^{-3} , unity and zero respectively, and settle the thinkable ranges of σ_X/σ_E' and σ_X/σ_Y . Then, the size of X_2 -population can be given for arbitrary selection intensity and genotypic desirability of the mutant to be gained. Judging from the experiments undertaken hitherto (GUSTAFSSON, 1947, NISHIMURA *et al.*, 1952 *etc.*), the value 10^{-3} of induced mutation rate is considered to be the most commonplace among the three in Table 1. For other parameters, there is no solid ground for securing the adequacy of the above values, except that even such a poor estimate of population size as thus determined would be much better than nothing.

Our equations can be used in other way, *e. g.*, for getting some clue as to the genetic compositions or the genotypic desirability of the mutants that are expected to be safely, namely, with probability $(1-\varepsilon)$ or more, gained under some predetermined size of X_2 -population and selection intensity. This usage of the equations may be most fruitful in the present state of our knowledge and should be adopted in the case when the number of X_2 -plants is fixed and cannot be increased owing to the limitations in breeding area, labour or cost.

Up to here, it has been taken for granted that the yardstick for measuring and expressing the desirability of material plants is ready for our practical uses. Without such a yardstick, those selection models (see Figure 1 of YONEZAWA *et al.*, 1970) premised for formulating the size of X_2 -population cannot be realized, and therefore our equations cannot be directly used for our practical purposes but for getting some general conclusions as given in the previous sections.

The desirability of material plants can be

easily and objectively measured when just a single attribute (either qualitative or quantitative) is concerned with the evaluation of material plants. But, as can be seen from the fact that artificial selections in actual breeding procedures (either in mutation or hybridization breeding) are still being carried out depending mainly on the intuition of skilled breeders, there is no generally-accepted and easily-applicable methodology for expressing the desirability of material plants in the case when some multiple attributes *en masse* are to be taken into account at the same generation. This is one of the most essential problems to be solved in future for the existing gap between field work and theory to be filled.

In showing the present applicability of our equations, it is mentioned that selections should be operated for each agronomic attribute separately rather than simultaneously, in such a way that selections for attributes of the simpler genetic behaviour are operated at the earlier generations after mutagen treatment (YONEZAWA, unpublished). If this granted, the practical utility of our equations would by no means be small. Of course, in such a case, X_2 -population size has to be determined in due consideration of the population sizes required for selections at later generations. Population size at arbitrary generation can be estimated by the equations of this paper without any modifications except changing f in equation (1) by f_t , which means the expected frequency of desirable mutant (concerning the object attribute for artificial selection) at the t th generation, and is formulated by

$$f_t = \binom{L_1}{j} \left(\frac{2^{t-1}-1}{2^{t-1}} m \right)^j \left(1 - \frac{2^{t-1}-1}{2^{t-1}} m \right)^{L_1-j} \left(1 - \frac{2^{t-1}+1}{2^{t-1}} m \right)^{L_2}$$

where of course L_1 and L_2 assume different values according to the object attribute for selection.

Frequency of desirable mutant has to be otherwise formulated than f or f_t if linkages exist among the loci concerned. But, it seems that the influence of linkages on the size of X_2 -population needs not to be made so much of unless the number of undesirable loci of breeding material, L_1 , is large. About this

point, it would be worth noting that mutation breeding is considered to be of greatest utility when just a small portion of the loci of breeding material is to be improved, maintaining the genetic composition of other loci unchanged (TORIYAMA *et al.*, 1962, YONEZAWA *et al.*, 1969). This corresponds to the case of small L_1 .

Summary

Improved equation for estimating the size of X_2 -population was presented in the present paper to make up the insufficiency of the previously offered one, and some numerical computations of the components, from which our improved equation is constructed, were supplied for meeting the practical necessities of breeders. As a result, some other conclusions of practical implication than those previously given could be derived, which is mentioned below.

1) Among the various parameters, by the combination of which X_2 -population size is determined, induced mutation rate per allele, m , and genetic composition of breeding material represented by L_1 , L_2 and j have the most delicate influence on the size of X_2 -population, the latter three symbols standing for the number of originally undesirable loci of breeding material, that of originally desirable loci and that of loci to be improved among the L_1 loci, respectively. The influence of L_2 on X_2 -population size is not so large and may be neglected in many cases unless L_2 is beyond a few hundreds. 2) The influence of other parameters such as selection intensity, genotypic desirability of the mutant to be gained etc. which need to be introduced into the theory only in the case of quantitative characters, is relatively small and the variation of X_2 -population size due to the change in these parameters is expected to be at most three times the value N' that gives the size of X_2 -population required in the case of qualitative characters of the same values of L_1 , L_2 and j . 3) From the improved equation derived in this paper, it is considered that our previous conclusion that X_2 -population size is inversely proportional to $\left(\frac{L_1}{j}\right)\left(\frac{1}{2}m\right)^j$ cannot be generally accepted. 4) It was suggested that opti-

mum mutation rate per allele exists for given breeding material and aim, and moreover this rate is by no means high in many quantitative characters of cultivars. This means that high mutagen dosages would not necessarily be advantageous even if induction of deleterious chromosomal or cytoplasmic aberrations is suppressed by some new method. Besides the induction of chromosomal or extranuclear aberrations, too high mutation rate may partly explain the fact that a larger genetic variability induced by a higher dosage of mutagen is ascribed mainly to the increase of deleterious mutants rather than that of desirable ones.

Applicability of our equations to actual breeding programmes was briefly discussed.

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自殖性作物の量的形質に関する突然変異育種 2 世代目における 栽植個体数推定のための理論的基礎

II. 式の補正および数値計算

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前報で述べた、 X_2 -個体数推定のための理論式を補正し、式を構成する各項の数値計算を行なった。その結果、一般的知見としては次のようなものが得られた。

(1) 関与する種々の母数の中で、 X_2 -個体数に特に強く影響するものは、突然変異率(因子 allele 当りの突然変異率 m で表わす) および育種素材の因子座構成(処理前に劣悪である因子座の数 L_1 , 優良な因子座の数 L_2 , および前者のうちで改良すべきものの数 j で表わす) である。但し、 L_2 の影響は、二、三百以内であれば、多くの場合無視しても大過ないようである(2) 選抜強度とか、変異体の対照区に対する優良度とかのように、量的形質の場合にのみ現われる母数の影響は比較的小さく、これらの母数の変化に起因する X_2 -個体数の変動は、同一因子座構成をもつ質的形質の場合に必要な個体数のたかだか 3 倍であると考えられる。(3) 本報で得た補正式から判断すると、 X_2 -個体数がほぼ $\binom{L_1}{j} \left(\frac{m}{2}\right)^j$ に反比例するとの前報での結論は、一般的には受

け入れられないものようである。(4) m は大きい程望ましいというわけではなく、育種素材の因子座構成によつて決まるところのいわゆる最適突然変異率 m_0 の存在すること、さらに、量的形質の育種の場合には m_0 は決して大きくはないことが示唆された。このことは、仮に実用的価値のない染色体または細胞質の諸変異の誘発を何らかの方法によつて抑えることが出来たとしても、因子突然変異のスペクトルを制御できない限りは、高線量または高濃度処理は必ずしも有益ではないことを示す。染色体または細胞質変異体が増加するというこの他に、因子当りの突然変異率が高過ぎるということも、高線量または高濃度処理による遺伝分散の増加が優良変異体の生起によるものではなく、大部分、劣悪変異体の増加によるものであるという現象の一因として考えられる。

理論式の現時点での実用性ならびに実際場面での用い方などについて簡単に考察した。