Cost Efficiency of Spatial Error Control in Single Plant Selection

Kentaro Yano1), Ryo Ohsawa2) and Katsuei Yonezawa*3)

1) Department of Agronomy, Faculty of Agriculture, Kyoto University, Kitashirakawa, Sakyo, Kyoto 606-8520, Japan
2) Institute of Agriculture and Forestry, University of Tsukuba, 1-1 Tennodai, Tsukuba, Ibaraki 305-8572, Japan
3) Department of Biotechnology, Kyoto Sangyo University, Kamigamo, Motoyama, Kyoto 603-8555, Japan

A criterion for evaluating the practical advantage of spatial error control in single plant selection for lowly heritable traits, by either field preparation for environmental uniformity or statistical adjustment using spatial information from surrounding plants, was defined based on the principle of achieving the greatest success with the same long-term resource investment. The criterion was determined in the context of mass selection under practically possible values of the variables concerned, leading to the prediction that spatial error control will be rewarding only in some plants where the cost for error control is low compared to that for care management to raise the test plants. Error control will be of little use in other plants; improving the precision of selection when the population size is reduced is not rewarding. In cross-fertilizing cereal crops, error control for yield is predicted to be useful when the selection is performed in only a few cycles (generations), but the population size is important when the selection is performed in more cycles to best explore the genetic potential of the target population. In self-fertilizing cereal crops, spatial error control will in no case be cost-efficient. In both cross- and self-fertilizing crops, the population size becomes more important with a higher magnitude of the desired genetic advance.

Key Words: measurement error, single plant selection, spatial error control, yield selection, heritability.

Introduction

The effectiveness of selection depends on the precision with which the genetic potential of individuals or families is assessed. The assessment of the genetic potential for agronomically important quantitative traits is subject to errors of various causes such as environmental heterogeneity in selection field and lack of precision in the process of trait measurement. Non-additive gene effects may also be considered to be an error factor when they prevent the prediction of genetic advance by selection. Various refined concepts and methods for controlling these errors through the use of special field preparation, family data or progeny test have been proposed hitherto on a theoretical basis (Hallauer and Miranda 1988, Bos and Caligari 1995, Kempton and Fox 1997). The use of marker-assisted selection has recently been found to improve the effectiveness of selection for quantitative traits (Knapp 1998, Moreau et al. 1999). Not all the refined methods, however, have been or will be widely adopted in practical breeding projects. Breeders often are reluctant to use a refined precise method because it is resource-consuming. Cost as well as the precision of selection must explicitly be taken into account when deciding the best selection method in practical breeding projects. A theoretical basis for evaluating the cost efficiency of selection methods remains to be developed.

A refined selection method generally requires a high resource investment per plant and population, and therefore limits the number of genotypes and populations (cross combinations) that can be tested under a given total amount of investment. In the long run will reduce the opportunities of obtaining new varieties. In contrast, a large number of populations could be tested if a low-input rough selection method could be used, but none of these populations may give an adequate response to selection. Neither high-input nor rough selection will be efficient. There should be an optimum selection method with an optimum resource input per plant and population to obtain the highest cost efficiency in the long run.

Research on selection methodologies until now has been directed to the development of selection methods for achieving the maximum expected genetic advance in a target population (cross combination). Not all the populations tested have the potential of producing the desired results. In reality, only a small proportion of the populations tested gives successful results. Therefore, high investment per population would not be wise because it limits the number of populations tested and then reduces the chances of success. Similarly, within a cross combination, using a refined costly selection method may not be efficient because it reduces the number of genotypes tested (population size). Therefore, Yonezawa et al. (1999) introduced a new efficiency index, i.e., the ratio of the probability of the desired results being achieved in a target population to the cost expended to that end. A selection strategy or method that maximizes this index will give the largest number of successful results with
the same total amount of investment, although it may not necessarily lead to the highest possible genetic advance in individual populations. It is anticipated that some long unsettled issues relating to the optimization of selection methods could be addressed based on this concept of selection efficiency.

As the first step to facilitate this line of investigations, we determined here the practical advantage of spatial error control in single plant selection, one of the classical, yet unsettled issues, explicitly in terms of genetic and cost variables. The concept of spatial error control was introduced with the start of research on modern selection methodology in the 1940s, and various methods of error control in single plant selection as well as variety trial have been proposed (Fasoulas 1973, Bos 1983, Stam 1984, Kempton 1984, Kempton and Fox 1997). However, extra cost is needed to perform the error control. This disadvantage has to be taken into account properly.

**Theory**

**Precision of Selection**

The precision of selection can be represented by the correlation between the phenotypic scores and the true genotypic values of the selection procedure. In an unreplicated single plant selection, phenotypic score of plant in selection field and year can be expressed as

\[ P_{ijk} = m + G_i + L_j + Y_k + I_{ijk} + E_{ijk}, \]  

where \( m \) is the overall mean; \( G_i \) is the genotypic value of plant \( i \) (defined for the whole target area and years under the breeder’s responsibility, not for the particular field and year used for the selection); \( L_j \) is the environmental effect specific to location \( j \); \( Y_k \) is the environmental effect specific to trial year \( k \); \( I_{ijk} \) is the interaction of genotypes with the environmental conditions specific to location and year, which is further divided into three components, i.e., genotypic \( G \) \times location, \( G \times year \), and \( G \times location \times year \) interaction; and \( E_{ijk} \) is the error independent of genotype, year and location. Effects \( I_{ijk} \) and \( E_{ijk} \) are totally confounded in single plant selection, but need to be separately treated in the following discussion. The correlation of the phenotypic scores \( P_{ijk} \) with the genotypic values \( G_i \), designated as \( \rho_{PG} \), is expressed as

\[ \rho_{PG} = \frac{COV(P, G)}{\sqrt{V_P \cdot V_G}}, \]  

where \( V_P \) is the variance of phenotypic scores; \( V_G \) is the variance of genotypic values; \( V_{P} \) is the variance of genotype \( G \times environment \) interaction \( I_{ijk} \); \( V_I \) is the variance of the error \( E_{ijk} \), and \( COV(P, G) \) is the covariance between \( P_{ijk} \) and \( G_i \) which corresponds to \( V_G \) because the genotypic values are independent from the other effects. \( V_{ET} \) stands for the sum \( V_I + V_E \).

The term \( V_G/(V_G + V_I + V_E) \) in eqn (2) corresponds to the broad-sense heritability, i.e., the precision \( \rho_{PG} \) corresponds to the square root of the broad-sense heritability. Both \( V_I \) and \( V_E \) reduce the precision of assessment of the genotypic value across the target conditions. The error variance \( V_E \) can be divided into three components of different origins, designated as \( V_{E1}, V_{E2}, \) and \( V_{E3} \), which, respectively, are associated with the spatial environmental heterogeneity in the selection field, the developmental instability of the trait concerned (including random, non-spatial micro-environmental heterogeneity between plants), and errors occurring in the process of taking the phenotypic scores. The sum \( V_{E2} + V_{E3} \) is equivalent to the random, non-spatial environmental variance \( \sigma^2_E \) defined by Stam (1984).

The interaction variance \( V_I \), which is caused by the differential response of genotypes to the macro-environmental factors specific to the selection field and year used, cannot be controlled in single plant selection. The error variance \( V_{E1} \) cannot be controlled either. \( V_{E1} \) can be reduced by either field preparation for environmental uniformity or statistical adjustment for the environmental heterogeneity (Kempton and Fox 1997). \( V_{E1} \) can be reduced viz improvement in the measurement procedures or facilities. The components \( V_{E2} \) and \( V_{E3} \) have seldom been treated separately from \( V_{E1} \), but may play an important part in lowly heritable traits such as yield. The total error variance \( V_{ET} = V_I + V_{E1} + V_{E2} + V_{E3} \), which is defined in this paper as the error variance with error-uncontrolled assessment, can be reduced to \( V_{ET}^* \) by controlling the components \( V_{E1} \) and/or \( V_{E2} \).

Then, the precision under an error-controlled assessment designated as \( \rho^*_{PG} \), can be expressed as

\[ \rho^*_{PG} = \frac{1}{\sqrt{1 + V_{ET}^*/V_G}}, \]  

where \( R_E \) stands for the reduction (ratio) in the error variance, i.e., \( V_{ET}^*/V_G \). The term \((1 - \rho_{PG}^*)/\rho_{PG}^* \) in the above equation reaches zero as \( \rho_{PG}^* \) increases toward 1, indicating that error control will not be rewarding unless the precision is low with error-uncontrolled assessment. Selection usually occurs in multiple cycles (generations), and the genotypic variance and heritability \( \rho_{PG}^* \) will decrease with the passage of generations. The genotypic variance \( V_G \) and correlation of eqns (2) and (3) are defined for the initial generation.

**Condition for Efficient Error Control**

The efficiency of selection was evaluated here by the index, \( S/C \), introduced by Yonezawa et al. (1999), where \( S \) is the probability that the desired results are achieved in a target population, and \( C \) is the cost expended to that end. A selection method which gives a larger value of \( S/C \) is more efficient because it offers more opportunities of success under the same total resource investment.

In the case of cross-fertilizing crops, the probability \( S \) is defined as the probability that the population mean is im-
proved to the desired level, while in the case of self-fertilizing crops as the probability that the desired homozygous genotype is obtained. In both cases, \( S \) depends on the precision of the genotypic value assessment as well as some genetic and procedural variables described later. When the selection is operated in \( t \) consecutive generations (years), testing \( N \) plants per generation with a resource expense \( bB \) per plant \((B=\text{expense per plant under error-uncontrolled assessment})\), the cost \( C \) for this selection trial is represented as \( AT + bBNt \), where \( A \) is the annual economic disadvantage due to the loss of time (Yonezawa et al. 1999 for the quantification of \( A \)). The annual expense \( bBN \) in most actual selection trials cannot be freely chosen by the breeder, but is rather fixed to a certain amount \( K \). Under these conditions, the cost \( C \) is represented by \((A+K)t\). Since the term \( A+K \) can be treated as a constant in the present context, the index \( S/t \) under the condition \( bBN = K \) determines the efficiency of selection. It is not necessary to quantify \( B \) in any particular unit and \( B \) can be treated as 1, because only the relative amount of cost \( (b) \) is important in the present discussion.

With an error control of investment \( b \), the assessment precision is improved via relation (3), but the population size \( N \) is reduced from \( K \) to \( K/b \). To alleviate this shortcoming, the error ratio \( R_E \) must be sufficiently small. There should be a critical maximum error ratio, designated as \( \hat{R}_E \); error control is efficient when it has an error ratio smaller than \( \hat{R}_E \). The condition for efficient error control is then expressed as

\[
V_{ET}^r/V_{ET} < \hat{R}_E.
\]

As will be determined later, \( \hat{R}_E \) depends on the investment \( b \) as well as on a number of genetic and procedural variables. It also takes different values depending on whether the target population is cross- or self-fertilizing. The condition (4) can be expressed in terms of reduction in the individual error components as

\[
V_{ET}^r/V_{ET} = \frac{(f_1 + f_2 + f_3 + f_4 + f_5 + f_6) V_{ET}^r}{(1 + f_1 + f_2 + f_3 + f_4 + f_5 + f_6) V_{ET}} = \frac{\sum f_c R_c < \hat{R}_E}{},
\]

where \( f_c \) (\( c = I, E, E, \) and \( \sum f_c = 1 \)) stands for the fraction of error variance component \( c \) in the whole error variance \( V_{ET} \), \( R_c \) being the value under error-controlled relative to error-uncontrolled condition (zero when totally removed and unity when not removed at all).

Not all the error components are controllable. When an error component of a fraction \( f_c \) is reduced to \( r_c \), with the remaining error components unchanged, condition (5) becomes

\[
V_{ET}^r/V_{ET} = \frac{f_c R_c + (1 - f_c) \hat{R}_E}{(1 - f_c) R_c + (1 - R_c) R_c} < \hat{R}_E,
\]

which is written as

\[
f_c > (1 - \hat{R}_E)/(1 - R_c), \quad \text{or} \quad r_c < 1 - (1 - \hat{R}_E)/f_c.
\]

Condition (6) can never be satisfied unless \( f_c > 1 - \hat{R}_E \).

**Numerical computations**

The critical error ratio \( \hat{R}_E \) was obtained here via calculations of the efficiency \( S/t \) under practically possible values of the related variables. The probability of success \( S \) depends on the following variables;

\[\text{V}_G = \text{genotypic variance of the initial generation, which is determined, as mentioned below, by the number and genetic effect of the genes involved.} \]

\[h' = (\rho_{vG}) = \text{broad-sense heritability in the initial generation under error-uncontrolled assessment, which together with } V_G \text{ specifies the value of the error variance } V_{ET} \text{ for error-uncontrolled assessment and } V_{ET}^r(= V_{ET}R_E) \text{ for an error-controlled assessment (cf. eqn (3))}. \]

\(K = \text{resource expense per generation, which, under the quantification of } B = 1, \text{ is equivalent to the population size available with an error-uncontrolled assessment,} \]

\[L = \text{number of loci (or effective factors of Mather and Jinks 1971) involved with the trait to be improved,} \]

\[p = \text{selection rate (fraction selected) per cycle,} \]

\[r_i = \text{minimum desired genetic advance, which is expressed for convenience by the ratio to the maximum genetic advance achievable in the target population tested,} \]

\[R_E = \text{the error variance ratio defined in eqn (3), and} \]

\(t = \text{number of generations of selection.} \)

The probability \( S \) was calculated by Monte Carlo simulations, firstly, assuming mass selection for an allogamous, hermaphroditic (including monoeocious) diploid crop. Selection for an allogamous crop may be operated for both sexes (operated before flowering with the progeny for the next generation being raised via random mating between selected plants), or for the female sex only (operated after flowering). The calculations were made for both cases. \( S \) was obtained as the relative frequency (in a total of 500 to 1000 replicated runs) of the runs that gave a genetic advance as large as or larger than the minimum desired value for \( r_i \). The target population for the selection was initiated as an \( F_2 \) population produced via hybridization between two varieties homozygous for the trait concerned (Yano et al. 2000) for the details of the simulation procedures). Independent inheritance and additive genetic effect without dominance of the \( L \) genes were assumed, with genotypic values 1, and \(-1 \) being assigned to the two homozygotes \( 0 \) to the heterozygote at each locus. In this gene-effect model, the mean and genotypic variance \( (V_G) \) of the initial population were 0 and \( L/2 \), respectively, and the maximum possible genetic advance in this population was \( L \). The error variance \( V_{ET} \) under error-uncontrolled assessment \((b = 1)\) was specified as \( V_G(1 - h'^2)/h'^2 = L(1 - h'^2)/(2h'^2) \) via the relation \( h'^2 = V_G/(V_G + V_{ET}) \), and the error variance under error control, i.e., \( V_{ET}^r \), was given by \( V_{ET}R_E \). The phenotypic score of a plant was represented by the sum of the genotypic value assigned by the above-mentioned gene-effect model and an error effect randomly chosen from a normal distribution \( N(0, V_{ET}) \) for error-uncontrolled assessment and \( N(0, V_{ET}^r) \) for error-controlled assessment.

In the case of selection for traits with a low to moderate heritability, the calculations were made with the following specifications: \( h' = 0.1 \text{ to } 0.5 \), \( K = 200 \text{ to } 5000 \), \( L = 10 \text{ to } 20 \), \( r_i = 0.4 \text{ to } 0.8 \), \( p = 0.05 \), \( R_E = 0.01 \text{ to } 0.9 \), and \( t = 1 \text{ to } 20 \). Four values 1.5, 2, 4 and 8 were assumed to correspond to the relative cost \( b \). The two numbers of loci assumed, i.e., 10
and 20, were considered to be sufficiently large to cover the actual range because the genetic control of agronomically important quantitative traits in artificially generated populations could be explained by the segregation of 10 or fewer loci (Bhatt 1972, Mulitze and Baker 1985, Dingerdissen et al. 1996). When measured in units of the genotypic or phenotypic standard deviation of the initial generation, the values of the three critical genetic advances ($r_g$), 0.4, 0.6 and 0.8, were changed to the values presented in Table 1.

The results of calculations under selection for both sexes (biparental selection) with specifications $h^2 = 0.1$, $K = 500$, $L = 20$, $r_g = 0.6$ and $p = 0.05$ are illustrated in Fig. 1A ~Fig. 1D. Judging from the highest efficiencies ($S/t$) achieved in a sufficiently large number of cycles of selection, an error-controlled assessment for $b = 1.5$ in Fig. 1A is superior to error-uncontrolled assessment ($b = 1$) when the error variance ratio is smaller than about 0.8, i.e., $R_{e}$ for $b = 1.5$ is 0.8 approximately. As seen from figures B to D, the value of $R_{e}$ decreased to about 0.7, 0.4 and 0.2 as $b$ increased from 1.5, 2 through 4 to 8.

Calculations of the selection efficiency for different values of the variables concerned, although omitted for brevity, led to the following trends. Calculations for $h^2 = 0.5$ with the other variables being the same as in Fig. 1 showed that $R_{e}$ is practically the same as for $h^2 = 0.1$, that is, $R_{e}$ is not substantially modified in this range of heritability. It is noted, however, that the magnitude of improvement in the efficiency $S/t$ is not appreciably large when $h^2 (= p^2_{e20})$ is as large as or larger than 0.5, indicating that error control is not effective enough for moderately to highly heritable traits.

With $K = 200$ for $b = 2$ and 4, the $R_{e}$ value decreased to about 0.5 and 0.3, respectively, indicating that error control must be more effective. In other words, a precise yield assessment when the population size is reduced may not be beneficial with a lower availability of resources per generation. With the increase in $K$ from 500 to 2000, on the other hand, the critical error variance ratio $R_{e}$ increased. The increase in $R_{e}$, however, was negligible when $b = 2$, white significant, i.e., increasing from 0.2 to 0.3 approximately, when $b$ was as large as 8. For $K = 5000$, $R_{e}$ increased to 0.8 when $b = 2$, and to 0.4 when $b = 8$. $R_{e}$ was not much influenced by $K$ as far as $b$ was as small as or smaller than 2. Similar magnitude of increase in $R_{e}$ to that with the increase in $K$ was obtained when $L$ decreased from 20 to 10, or $r_L$ decreased from 0.6 to 0.4.

Increase in $r_s$ from 0.6 to 0.8 (under $K = 500$) caused a fairly large reduction in $R_{e}$ as well as the optimum number of selection cycles; $R_{e}$ decreased from 0.7 to 0.6 when $b = 2$, and even to around 0.1 when $b = 8$. It will be difficult to construct an error control device as effective as that to obtain such a small value (0.1) of $R_{e}$. Calculations for $r_s = 0.8$ would practically indicate that the population size and selection cycles rather than the precision of selection are important to achieve a very high genetic advance.

When the selection was operated only for the female sex (uniparental selection) with the other conditions being the same as those defined in Fig. 1, the optimum generation for selection was delayed but the $R_{e}$ value remained almost the same as that with biparental selection (0.7) when $b = 2$ although it increased from 0.2 to 0.3 when $b = 8$. This indicates that error control is slightly more useful in uniparental than biparental selection. Based on the trend obtained in the discussion of optimum mass selection procedures (Yano et al. 2000), dominance was not associated with important modifications; $R_{e}$ did not change substantially unless desirable alleles were either dominant or recessive unidirectionally at the majority of the loci involved.

The above calculations were made under the assumption that expense per year, $bNt$, is fixed to a certain value $K$. Selection procedures may be designed with the total expense per target population, $bNh$, being fixed to a certain value, $K'$. In this case, the efficiency index $S/C$ equals $S/(At + K')$. In a selection trial for developing a new market variety, the term $At$ should be much larger than $K'$ (Yonezawa et al. 1999), and then, the efficiency index becomes $S/(At)$ approximately. The problem now is to obtain $R_{e}$ that maximizes $S/t$ under the condition $bNh = K'$. Calculations for $K' = 4000$ and 8000 with the other variables being specified as in Fig. 1B and Fig. 1D showed that the $R_{e}$ value was almost the same as before, although it increased from 0.2 to 0.3 when $b = 8$ for $K' = 8000$.

In short, the $R_{e}$ value in selection for cross-fertilizing crops falls in a range of 0.2 to 0.8 under practically possible values of the related variables. Calculations for self-fertilizing crops under similar specifications of the related variables as those employed in Fig. 1B and Fig. 1D are presented in

| Table 1. Expression in different units of the minimally desired genetic gain ($r_L$) assumed in the calculation of the selection efficiency |
|---|---|---|---|---|
| In units of | Condition | $L$ | $h^2 (p^2_{e20})$ | 0.4 | 0.6 | 0.8 |
| Genotypic standard deviation of the initial population | 10 | Not specified | 1.799 | 2.683 | 3.578 |
| | 20 | Not specified | 2.530 | 3.795 | 5.060 |
| Phenotypic standard deviation of the initial population | 10 | 0.1 | 0.566 | 0.849 | 1.131 |
| | 0.6 | 1.386 | 2.078 | 2.771 |
| 20 | 0.1 | 0.800 | 1.200 | 3.200 |
| | 0.6 | 1.960 | 2.939 | 3.919 |
Fig. 2A and Fig. 2B, where $S$ indicates the probability that a homozygous genotype as good as or better than $r_L$ is obtained from the target population. Because self-fertilizing plants do not intermate, response to selection is expected to reach a plateau very soon. Harmonizing with this expectation, the figures show that the selection efficiency $S/t$ is maximized in the first two or three generations, and, as a more important point in the present context, the $S$ value is much smaller than that for cross-fertilizing crops mentioned before; it is around 0.4 when $b=2$ and 0.05 when $b=8$.

Fig. 2. Efficiency $S/t$ ($\times 10^{-2}$) for varying values of the error variance ratio $R_e$ in selection for a self-fertilizing crop (calculated for $p_F=0.1$, $K=500$, $L=20$, $r_L=0.6$ and $p=0.05$).

Discussion

The calculations of the efficiency $S/t$ together with the inference by eqn (3) lead to the prediction that error control will be advantageous only for lowly heritable traits such as yield. Usefulness of error control in yield selection is discussed below based on the criterion defined above. Conditions (3) and (6) show that the broad-sense heritability $h^2$ ($p_F$) and fraction $f_c$ of the target error component are the key parameters. Using yield data obtained in the previous experiments, we can estimate, though roughly, the range of
The genotypic value \( G \) and genotype \( \times \) environment interaction \( I_{ij} \) (cf., eqn (1)) are confounded in an unreplicated trial. The broad-sense heritability \( h^2 \) may be markedly overestimated because what is estimated is \((V_G + V_I)/ (V_G + V_I + V_E)\), denoted by \( h^2_c \), and not the heritability in the true sense, \( V_G/(V_G + V_I + V_E) \). Of the two error variance components \( V_I \) and \( V_E \), only the latter can be controlled in single plant selection. The fraction \( V_E/(V_I + V_E) \), denoted by \( f_E \), and the true heritability \( h^2 \) can be expressed, in terms of the raw estimate of heritability \( h^2_r \), as \((1 - h^2_r) \) \((1 + V_I/V_G)/(1 - h^2_r + V_I/V_G)\) and \( h^2_r/(1 + V_I/V_G)\), respectively. As far as the grain yield of cereal or oil crops, either cross-fertilizing or self-fertilizing, is concerned, the raw estimates \( h^2 \) in early segregating generations appear to be in the range of about 0.5 to 0.9 (Zuberi and Ahmed 1973, Ronis et al. 1985, Ashraf 1994). The variance ratio \( V_I/V_G \) can roughly be obtained from the yield experiment data reported previously; \( V_I/V_G \) appears mostly, if not always, to be larger than 1, being even as large as twenty (Sprague and Federer 1951, Hanson and Brim 1962, Robinson 1984). Calculations of \( f_E \) as well as the estimates of the true heritability under conditions of 0.5 to 0.9 for \( h^2_c \) and 1 to 16 for \( V_I/V_G \) are presented in Table 2, indicating that \( h^2 \) and \( f_E \) are in the range of about 0.03 to 0.45 and 10 to 65%, respectively.

Not all the components in \( V_E \) are controllable in an unreplicated trial. It is commonly observed that within-plot (between plants) error variance \( V_w \) for grain yield is larger than that between-plot or block variance \( V_b \), as exemplified in Table 3 for buckwheat (cross-fertilizing) and rice (self-fertilizing). The soil condition within plots in the yield experiments of Table 3 is considered to be highly uniform because the soil and fertilizers were carefully mixed when the experimental plots were prepared. Then, it may be assumed that \( V_w \) is mainly composed of the random non-spatial errors \( V_{E2} \) and \( V_{E3} \) on the other hand, should reflect the spatial environmental heterogeneity in the field, which accounted on the average for less than 20% of the total error variance \( V_E = V_w + V_b \). The controllable spatial error component in single plant selection, \( V_{E1} \), will be even smaller than \( V_b \), because it should reflect the environmental heterogeneity within rather than between blocks (note that a target population for selection does not cover a wide field area unless the size is in the order of \( 10^4 \) or more). Assuming that \( V_{E1} \) accounts for 15%, its fraction \( f_{E1} (= f_E \) in condition (6)) in the total error variance \( V_{ET} \) ranges only from 1.5 (= \( 10 \times 0.15 \) ) to 9.75 (= \( 65 \times 0.15 \) )%. Under these small values of \( f_E \) with the possible range (0.2–0.8 for cross-fertilizing crops and 0.05–0.4 for self-fertilizing crops) of \( R_E \) calculated previously, condition (6) cannot be satisfied. Error control in yield selection, therefore, is not predicted to be advantageous.

Some authors (Mitchell et al. 1982, Fasoulas 1977) have suggested that widely-spaced planting should be used to identify high-yielding genotypes because it relieves the competition between plants. While the non-environment error variance component \( V_{E2} \) may be reduced under widely-spaced planting, \( V_{E1} \) will be rather inflated. No experimental data appear to suggest that the reduction in \( V_{E2} \) is large enough to cancel the disadvantage of spending a wide space per plant. Moreover, a high-yielding genotype under widely-spaced planting does not necessarily give a high yield per unit field area.

A trend more or less different from the abovementioned is recognized when focusing on the selection efficiency that is achieved in the first few, instead of the optimum (to maximize \( S/t \)), generations of selection. In cross-fertilizing crops, an error control even as expensive as \( b = 4 \) or 8 (Fig. 1C and Fig. 1D) gives a significantly higher efficiency than error-uncontrolled assessment (\( b = 1 \)). The calculations of \( S/t \), although not presented here, showed that, as far as the efficiencies in the early two or three generations are concerned, the value of \( R_E \) is close to 1 with any practically possible value of \( b \). In this case, condition (4) becomes almost independent of \( b \), and is approximated as \( V_{ET} > V'_{ET} \), indicating that selection with a high precision is efficient even if expensive. In self-fertilizing crops, on the other hand, a high-input selection is not efficient regardless of whether the selection is operated in only a few or more generations (Fig. 2), indicating that the population size rather than the precision of selection determines the results of selection.

It is inferred that error control with high investment may be advantageous for some plants where a long period of care management is needed to grow the test plants. In these plants, the cost for care management may be much higher than that expended for the genotypic value assessment itself, and then, extra expense for the error control will cause only a slight increase in the relative cost \( b \). When \( b \) is close to 1, condition (4) is approximated as \( V_{ET} > V'_{ET} \), indicating that precision alone determines the efficiency of selection.

The calculations presented in this paper were made assuming that the expense per generation (\( K = bN \) ) or cross

<table>
<thead>
<tr>
<th>( h^2 )</th>
<th>( V_I/V_G )</th>
<th>( V_{E1}/V_{ET} )</th>
<th>( V_{E2}/V_{ET} )</th>
<th>( V_{E3}/V_{ET} )</th>
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<tbody>
<tr>
<td>0.5</td>
<td>0.250/0.667</td>
<td>0.167/0.600</td>
<td>0.100/0.556</td>
<td>0.056/0.529</td>
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<td>0.350/0.462</td>
<td>0.233/0.391</td>
<td>0.140/0.349</td>
<td>0.078/0.325</td>
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<td>0.9</td>
<td>0.450/0.182</td>
<td>0.300/0.143</td>
<td>0.198/0.122</td>
<td>0.100/0.111</td>
</tr>
</tbody>
</table>

1) \( h^2_f \)
The cost efficiency of spatial error control is fixed to a certain value. The calculations gave a clue to determine which of the two variables, population size or the precision of selection, is more important. In some cases, the population size may be predetermined without any explicit limitation on the expense ($b$).

The issue in this situation will be to evaluate the advantage of extra investment $b$ under a fixed value of $N$. This issue also can be addressed using the efficiency index $S / (bB N)$.

### Table 3. Estimates of within-plot and between-block variance components for grain yield (g/plant) of some typical Japanese varieties of buckwheat and rice

<table>
<thead>
<tr>
<th>Variety</th>
<th>Within-plot variance ($V_W$)</th>
<th>Between-block variance ($V_B$)</th>
<th>Fraction of $V_g$: $V_g / (V_g + V_B)$</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Buckwheat</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Kitawase-soba</td>
<td>1.511/2.666</td>
<td>0.379/0.436</td>
<td>0.201/0.141</td>
</tr>
<tr>
<td>Shinano-natsusoba</td>
<td>1.487/2.623</td>
<td>0.352/0.409</td>
<td>0.191/0.135</td>
</tr>
<tr>
<td>Ojiya-zairai 1</td>
<td>1.665/2.937</td>
<td>−0.076/−0.013</td>
<td>0/0</td>
</tr>
<tr>
<td>Shinshu-ohsoba</td>
<td>5.344/9.425</td>
<td>1.144/1.348</td>
<td>0.176/0.125</td>
</tr>
<tr>
<td>Yakoh93FE3</td>
<td>4.242/7.658</td>
<td>0.579/0.745</td>
<td>0.118/0.089</td>
</tr>
<tr>
<td>Yakoh93FE6</td>
<td>6.524/11.506</td>
<td>4.630/4.879</td>
<td>0.415/0.298</td>
</tr>
<tr>
<td>Yakoh93FE8</td>
<td>6.252/11.027</td>
<td>1.900/2.138</td>
<td>0.233/0.162</td>
</tr>
<tr>
<td>Yakoh93FE9</td>
<td>9.997/17.632</td>
<td>−0.964/−0.582</td>
<td>0/0</td>
</tr>
<tr>
<td>Tochigi-zairai</td>
<td>7.502/13.231</td>
<td>1.072/1.358</td>
<td>0.125/0.093</td>
</tr>
<tr>
<td>Hokkai No.3</td>
<td>1.437/2.535</td>
<td>0.357/0.411</td>
<td>0.199/0.140</td>
</tr>
<tr>
<td><strong>Rice</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Nipponbare</td>
<td>18.11</td>
<td>2.04</td>
<td>0.101</td>
</tr>
<tr>
<td>Koshikihari</td>
<td>23.31</td>
<td>3.34</td>
<td>0.125</td>
</tr>
<tr>
<td>Hohenwase</td>
<td>21.42</td>
<td>3.77</td>
<td>0.150</td>
</tr>
<tr>
<td>Todorokiwase</td>
<td>34.08</td>
<td>16.32</td>
<td>0.324</td>
</tr>
<tr>
<td>Kochikaze</td>
<td>77.22</td>
<td>24.26</td>
<td>0.239</td>
</tr>
<tr>
<td>Toyonishiki</td>
<td>34.20</td>
<td>5.22</td>
<td>0.132</td>
</tr>
<tr>
<td>Sasanishiki</td>
<td>26.21</td>
<td>16.76</td>
<td>0.390</td>
</tr>
<tr>
<td>Fujiminori</td>
<td>26.73</td>
<td>4.94</td>
<td>0.156</td>
</tr>
<tr>
<td>Reimei</td>
<td>31.88</td>
<td>0.46</td>
<td>0.014</td>
</tr>
<tr>
<td>Kiyonishiki</td>
<td>61.34</td>
<td>18.09</td>
<td>0.228</td>
</tr>
<tr>
<td>Mutsuminori</td>
<td>23.63</td>
<td>1.27</td>
<td>0.051</td>
</tr>
<tr>
<td>Koshihomare</td>
<td>31.05</td>
<td>27.07</td>
<td>0.466</td>
</tr>
<tr>
<td>Satohikari</td>
<td>19.26</td>
<td>1.04</td>
<td>0.051</td>
</tr>
<tr>
<td>Fuyoh</td>
<td>38.23</td>
<td>4.85</td>
<td>0.113</td>
</tr>
<tr>
<td>Reihoh</td>
<td>39.86</td>
<td>1.39</td>
<td>0.034</td>
</tr>
<tr>
<td>Hohyoku</td>
<td>25.13</td>
<td>5.23</td>
<td>0.172</td>
</tr>
<tr>
<td>Toyotama</td>
<td>27.33</td>
<td>5.71</td>
<td>0.173</td>
</tr>
<tr>
<td><strong>Average</strong></td>
<td>4.606/8.124</td>
<td>1.041/1.172</td>
<td>0.166/0.118</td>
</tr>
</tbody>
</table>

1) The yield data of buckwheat were obtained using three randomized blocks. One hundred fifty plants/variety/block were grown in a plot with a size of 4 m × 1.2 m, and the yield of 20 randomly sampled plants was determined.

2) Because buckwheat is a cross-fertilizing crop, genotypic variance ($V_g$) is confounded in both within-plot ($A$) and between-block ($B$) variances. By the relations $A = V_W + V_{A}$ and $B = A + 20 \cdot (V_B + V_{BA})$, the within-plot error variance $V_W$ and block variance $V_B$ were estimated by $V_W / 20$ and $V_B / 20$, respectively, where $h^2 = (V_g / (V_W + V_B))$ is the broad-sense heritability within plots. The estimates of $V_W$ and $V_B$ were obtained assuming the two values of $h^2$, i.e., 0.45 and 0.03 (see text), presented before and after the slush, respectively.

3) Estimates of $V_B$ with minus sign were regarded as zero.

4) The rice varieties were grown in six randomized blocks prepared in under markedly different cultural conditions (3 seeding dates × 2 fertilizer levels). The yield of twenty plants/variety/block in the central among three 3 m long rows (with a planting density of 0.3 m × 0.15 m/plant) was determined.

The efficiency index $S / (A + bB N)$ is fixed to a certain value. The calculations gave a clue to determine which of the two variables, population size or the precision of selection, is more important. In some cases, the population size may be predetermined without any explicit limitation on the expense ($b$). The issue in this situation will be to evaluate the advantage of extra investment $b$ under a fixed value of $N$. This issue also can be addressed using the efficiency index $S / (A + bB N)$. The index can be approximated to $S / (A + bB N)$ in two extreme cases where the annual expense $bB N$ is sufficiently small or large compared to the economic disadvantage due to the loss of time (years) $A$, respectively. The former case will hold true when a large economic advantage is expected to be gained with the success of selection (and many breeders compete), while the latter case may hold true when the time loss is not important. The efficiency index increased with increasing $b$ in the former case, whereas it decreased in the latter case. Therefore, the optimum expense $b$ depends on the amount of the annual expense $bB N$ relative to the time expenditure $A$. 

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$V_B / 1.041/1.172$
In conclusion, the spatial error control in single plant selection will not be advantageous unless the error variance is reduced to a sufficiently low value ($R_E$) relative to error-uncontrolled assessment. The critical error variance ratio ($R_E$) was calculated to be 0.2 to 0.8 approximately for cross-fertilizing crops and 0.05 to 0.4 for self-fertilizing crops for an extra cost ($b$) less than 8. The calculations based on some experimental data showed that these conditions for $R_E$ are very seldom satisfied in yield selection for cereal crops. The importance of the population size relative to the precision of selection (error control) is more pronounced with a greater magnitude of the genetic advance to be achieved ($r_l$).

Acknowledgements

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Literature Cited