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Choice of environments in reciprocal recurrent selection programs

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Summary. An alternative method of reciprocal recurrent selection (RRS) in which populations A and B are each evaluated in a different environment is proposed. This method is called dual-environment reciprocal recurrent selection (DERRS). Two genetic models are considered in the theoretical study. A comparison of selection methods shows that genetic gain is larger in DERRS than in RRS for the two models. The difference grows greater as the dominance effects operating in the two environments are more divergent and as the number of selection cycles increases. A greater gain is obtained when the genetic covariances between crosses in the two chosen environments are lower.

Key words: Selection methods – Genetic gain – Genotype × environment interaction – Quantitative genetics – *Zea mays* L.

Introduction

One of the problems that breeders find in selecting the best genotypes is the presence of genotype × environment interaction (Sprague and Federer 1951; Eberhart and Russell 1966; Hill and Baylor 1983). Trying to minimize this type of interaction by increasing locations, years and replications in the selection experiments (Comstock and Moll 1963) requires considerable effort and cost.

A hybrid program to be useful for a wide range of environments, including contrasting environments, would require a special strategy of breeding to reduce the genotype × environment interaction. In the classical reciprocal recurrent selection (RRS) of Comstock et al. (1949), half-sib families from populations A and B are usually both evaluated in the same environment. A method in which progenies from population A are evaluated in one environment and progenies from B are evaluated in another would provide a wider range of genes under selection if different sets of genes were operating in different environments as is indicated, for instance, by larger heterosis between populations of maize from different areas. This method, called dual-environment reciprocal recurrent selection (DERRS), is specially designed for a hybrid program applied in an area where interactions arise from different kinds of environments.

The purpose of this paper is to compare DERRS with RRS and to study how more efficient environments can be chosen.

Genetic models

Model 1

Assume that E is the set of individual environments, e's, for which the breeding program is intended to be useful. Let D_e be the set of genes having marked effects in environment e, from the whole set of genes present in the breeding populations. Also, $D_{e'}$ is the set of genes with marked effects in environment, e'.

The following relations hold:

$$D_e \cap D_{e'} = I_{ee'},$$

$$D_e - I_{ee'} = H_e,$$

$$D_{e'} - I_{ee'} = H_{e'},$$

$$H_e \cup H_{e'} = H_e + H_{e'} = H_{ee'}$$

where, $I_{ee'}$ is the subset of genes common to D_e and

$D_{e'}$. H_e and $H_{e'}$ are mutually exclusive; they are subsets of D_e and $D_{e'}$, respectively.

Model 2

Assume that the set of genes (D) having marked effects is the same for all environments, but the relative effects of genes may change from one environment to another.

General model

A more general model would assume that the common set of genes ($I_{ee'}$) behaves as in model 2, and the uncommon sets (H_e and $H_{e'}$) as in model 1. Therefore, the discussions will be made for models 1 and 2 and can be inferred for the general model.

Methods

Consider a locus M−m, with genotypes MM, Mm and mm, and genotypic values a, d, and −a, respectively.

In the DERRS method, half-sib families from population A are evaluated in one environment, say e, while half-sib families from population B are evaluated in another, say e'. In the RRS method, half-sib families from A and B are both evaluated in the same environment, say e.

Genetic gain after n cycles of selection for DERRS ($\Delta G^{(n)}_{DE}$) and RRS ($\Delta G^{(n)}_{RRS}$) can be derived in the same manner as found in Moreno-González and Grossman (1976).

Model 1

$$\Delta G^{(n)}_{DE} = \sum_{i \in H_e} \Delta p^{(n)}_{Ai}\, \alpha^{(0)}_{Bi} + \sum_{j \in H_{e'}} \Delta p^{(n)}_{Bj}\, \alpha^{(0)}_{Aj} + \sum_{k \in I_{ee'}} (\Delta P^{(n)}_{Ak}\, \alpha^{(0)}_{Bk} + \Delta P^{(n)}_{Bk}\, \alpha^{(0)}_{Ak} - 2\, d_k\, \Delta P^{(n)}_{Ak}\, \Delta P^{(n)}_{Bk}) \quad (1)$$

$$\Delta G^{(n)}_{RRS} = \sum_{x \in D_e} (\Delta p^{(n)}_{Ax}\, \alpha^{(0)}_{Bx} + \Delta p^{(n)}_{Bx}\, \alpha^{(0)}_{Ax} - 2\, d_x\, \Delta p^{(n)}_{Ax}\, \Delta p^{(n)}_{Bx}) \quad (2)$$

where $\sum$ refers to summation over all loci of the subset specified below the $\sum$ symbol. Superscripts (0) and (n) refer to the initial and the n^{th} cycle of selection, respectively. Subscripts i, j, k, and x refer to loci of subsets H_e, $H_{e'}$, $I_{ee'}$, and D_e, respectively. Subscripts A and B refer to populations A and B, respectively. $\Delta p^{(n)}$ is the difference between gene frequencies at the n^{th} and the initial cycle.

$\Delta p^{(n)} = p^{(n)} - p^{(0)}$.

α is the average effect of gene substitutions and can be expressed as

$$\alpha^{(0)}_B = 2\, d\, (\gamma - p^{(0)}_B), \quad (3)$$

where $\gamma = \dfrac{a+d}{2d}$.

In Eq. (1), the first term is the contribution of loci from subset H_e, where favorable gene frequencies increase only in population A but not in B; the second term is the contribution of loci from subset $H_{e'}$, where favorable gene frequencies increase only in B, but not in A; and the third term is the contribution of loci from $I_{ee'}$, where favorable gene frequencies increase in both populations, A and B.

Model 2

Genetic gains can be deduced as for Eqs. (1) and (2), except that loci are summed from the unique set (D) for both methods and that gene effects change from one environment to another.

Comparisons of methods

Model 1

For the comparisons of Eqs. (1) and (2), $\Delta G^{(n)}_{RRS}$ will be considered as the mean of its performance in environments e and e' because although Eq. (2) from the RSS method was written for environment e, but it might be equally written for e'. Also, $\Delta G^{(n)}_{DE}$ will be considered as the mean of two options: (a) when population A was assigned to e and B to e' as in Eq. (1), and (b) when each population was assigned to the reciprocal environment. Therefore, the average difference between the two methods over the two environments will reduce to:

$$\Delta G^{(n)}_{DE} - \Delta G^{(n)}_{RRS} = 1/2 \sum_{z \in H_{ee'}} [\alpha^{(0)}_{Bz} (\Delta p^{(n,D)}_{Az} - \Delta p^{(n,R)}_{Az}) + \alpha^{(0)}_{Az} (\Delta p^{(n,D)}_{Bz} - \Delta p^{(n,R)}_{Bz}) + 2\, d_z\, \Delta p^{(n,R)}_{Az}\, \Delta p^{(n,R)}_{Bz}], \quad (4)$$

where superscripts D and R refer to the DERRS and RRS methods, respectively. Subscript z refers to loci of subset $H_{ee'}$. From Eq. (4), it can be noted that $\Delta G^{(n)}_{DE}$ is larger than $\Delta G^{(n)}_{RRS}$, because

$$\Delta p^{(n,D)}_{Az} > \Delta p^{(n,R)}_{Az} > 0 \quad (5)$$

and

$$\Delta p^{(n,D)}_{Bz} > \Delta p^{(n,R)}_{Bz} > 0\,. \quad (6)$$

To prove Eq. (5), the change in gene frequency between two consecutive cycles of selection (Moreno-González and Grossman 1976) will be:

$$p^{(n)}_{Az} - p^{(n-1)}_{Az} = \frac{i\, d_Z}{\sigma_p}\, p^{(n-1)}_{Az} (1 - p^{(n-1)}_{Az}) (\gamma_z - p^{(n-1)}_{Bz}), \quad (7)$$

where i = selection intensity in standard deviation units, and

σ_P = phenotypic standard deviation of half-sib families.

When gene z ($z \in H_{ee'}$) is selected in population A under the DERRS method, the corresponding gene in population B will not change its frequency, $p^{(n,D)}_{Bz} = p^{(0)}_{Bz}$. By contrast, when gene z is selected in population A, under the RRS method, the corresponding gene in B will increase its frequency. Therefore, $p^{(n,R)}_{Bz} > p^{(n,D)}_{Bz} = p^{(0)}_{Bz}$, and $\gamma_z - p^{(n,R)}_{Bz} < \gamma_z - p^{(n,D)}_{Bz}$.

Applying the last expression to Eq. (7), it can be easily noted that Eq. (5) is true. By the same reasoning, Eq. (6) is also true. Therefore, the genetic gain under the DERRS method is larger than under RRS.

From Eq. (4), it can be derived that the difference in ultimate genetic gain between the two methods will be:

$$\Delta G^{(\infty)}_{DE} - \Delta G^{(\infty)}_{RRS} = \sum_{z \in H_{ee'}} d_z (1 - p^{(0)}_{Az}) (1 - p^{(0)}_{Bz})\,. \quad (8)$$

Model 2

The average difference in genetic gain between DERRS and RRS over the two environments ($\Delta G'^{(n)}_{DE} - \Delta G'^{(n)}_{RRS}$) can be obtained as in model 1:

$$\Delta G'^{(n)}_{DE} - \Delta G'^{(n)}_{RRS} = \sum_{y \in D} d_y (\Delta p^{(n)}_{Aye} - \Delta p^{(n)}_{Aye'}) (\Delta p^{(n)}_{Bye} - \Delta p^{(n)}_{Bye'}) \quad (9)$$

where subscripts e and e' refer to environments e and e', respectively. Subscript y refers to loci of set D, and d_y is the

genotypic value of the heterozygote of the y^{th} locus averaged over the two environments, e and e′.

For the first cycle of selection and taking into account Eq. (7), Eq. (9) will be changed to:

$$\Delta G'_{DE} - \Delta G'_{RRS} = \sum_{y \in D} d_y p_{Ay}(1-p_{Ay}) \cdot p_{By}(1-p_{By})(\gamma_y - p_{Ay})(\gamma_y - p_{By})(s_e d_{ye} - s_{e'} d_{ye'})^2. \quad (10)$$

where $s = \frac{i}{\sigma_p}$ is the selective value for each gene.

It was assumed that $\gamma_{ye} = \gamma_{ye'} = \gamma_y$; that is, the degree of dominance $\frac{d_y}{a_y}$ for each gene remains constant over environments. Equation (10) shows that the genetic gain for the first cycle of selection is larger in the DERRS method than in the RRS. The same can be said for further cycles of selection, because the cumulative genetic gain shows the same trend over cycles. In contrast with model 1, the ultimate genetic gain will be equal for the two methods, because both are operating upon an unique set of loci. However the DERRS will reach the ultimate gain at a greater rate.

Choice of environments

In Eq. (1), which expresses the genetic gain of DERRS after n cycles, α can be substituted by its expression in Eq. (3), $\Delta p_A^{(n)}$ by $f_A(1-p_A^{(0)})$, and $\Delta p_B^{(n)}$ by $f_B(1-p_B^{(0)})$. f_A and f_B represent the fractions of the change in gene frequencies after the n^{th} cycle, relative to the total possible changes $(1-p_A^{(0)})$ and $(1-p_B^{(0)})$, respectively. Eq. (1) can be rewritten as follows

$$\Delta G_{DE}^{(n)} = 2 \sum_{i \in H_e} d_i f_{Ai}(1-p_{Ai})(\gamma_i - p_{Bi}) + 2 \sum_{j \in H_{e'}} d_j f_{Bj}(1-p_{Bj})(\gamma_j - p_{Aj}) + 2 \sum_{k \in I_{ee'}} \left\{ d_k f_{Ak}(1-p_{Ak})(\gamma_k - p_{Bk}) \left(1 - \frac{f_{Bk}(1-p_{Bk})}{2(\gamma_k - p_{Bk})}\right) + d_k f_{Bk}(1-p_{Bk})(\gamma_k - p_{Ak}) \left(1 - \frac{f_{Ak}(1-p_{Ak})}{2(\gamma_k - p_{Ak})}\right)\right\} \quad (11)$$

where superscript (0) of p_A and p_B was omitted to avoid cumbersome notation; f_A and f_B can vary from zero at the initial cycle up to one at the ∞^{th} cycle.

Model 1

Genetic effects in model 1 can be expressed as follows

$$Y_{Are} = g_{Ar.ee'} + t_{Are}$$

$$Y_{Are'} = g_{Ar.ee'} + t_{Are'}.$$

Y_{Are} and $Y_{Are'}$ are the genetic effects of the r^{th} half-sib family from population A, in environments e and e′, respectively. $g_{Ar.ee'}$ is the part of the genetic effect of the r^{th} half-sib family which is common to e and e′. t_{Are} and $t_{Are'}$ are specific genetic effects for environments e and e′, respectively. The restriction of independence among $g_{Ar.ee'}$, t_{Are}, and $t_{Are'}$ is required by the model.

Also, it can be written

$$\sigma^2_{Ae} = C_{Aee'} + R_{Ae},$$

where σ^2_{Ae} is the additive variance of half-sib families from population A in environment e accounted for by Y_{Are} effects from set D_e. $C_{Aee'}$ is the additive genetic covariance of half-sib families between environments e and e′ accounted for by the common genetic effects ($g_{Ar.ee'}$) from subset $I_{ee'}$. R_{Ae} is the residual component of σ^2_{Ae} accounted for by the t_{Are} effects from subset H_e. Likewise, for population B

$$\sigma^2_{Be'} = C_{Bee'} + R_{Be'},$$

where $\sigma^2_{Be'}$, $C_{Bee'}$, and R_{Be} are additive variances accounted for by genetic effects from sets $D_{e'}$, $I_{ee'}$, and $H_{e'}$ in population B, respectively.

The three summation terms (Σ) of Eq. (11) have a similar structure except that each one has to be summed over different number of loci and that the third one is also multiplied by an extra coefficient. Assuming that gene effects and gene frequencies are randomly distributed over the subsets of loci, the number of genes in the subsets can be considered approximately proportional to their respective additive variances. The following approximate formula can be written:

$$\Delta G_{DE}^{(n)} \simeq k \left\{ \bar{f}_A R_{Ae} + \bar{f}_A C_{Aee'} \left(1 - \frac{\bar{f}_B(1-\bar{p}_B)}{2(\bar{\gamma} - \bar{p}_B)}\right) + \bar{f}_B R_{Be'} + \bar{f}_B C_{Bee'} \left(1 - \frac{\bar{f}_A(1-\bar{p}_A)}{2(\bar{\gamma} - \bar{p}_A)}\right)\right\} \quad \text{(approximately)} \quad (12)$$

k is a coefficient of proportionality, and $\bar{f}_A$ and $\bar{f}_B$ refer to the average of f_A and f_B, weighted for each locus in such a way that expression (12) can be obtained. Likewise, $\bar{\gamma}$, $\bar{p}_A$ and $\bar{p}_B$ are weighted averages of γ, p_A, and p_B, respectively. For the first cycle of selection, where $\bar{f}_A$ and $\bar{f}_B$ are very small, Eq. (12) agrees with classical equations of genetic gain. This can be easily seen by letting $k\bar{f}_A = k\bar{f}_B = \frac{i}{\sigma_p}$. Different cases can be studied in Eq. (12).

Case 1. Ultimate genetic gain and complete dominance for all genes. Then,

$$\bar{f}_A = \bar{f}_B = \gamma = 1.$$

Substituting in Eq. (12),

$$\Delta G_{DE}^{(\infty)} \simeq k(R_{Ae} + 1/2\, C_{Aee'} + R_{Be'} + 1/2\, C_{Bee'}) = k(\sigma^2_{Ae} + \sigma^2_{Be'} - 1/2\, C_{Aee'} - 1/2\, C_{Bee'}) \quad \text{(approximately)}. \quad (13)$$

Equation (13) is the ultimate genetic gain for the two environments (e and e′) where populations were selected.

If these populations are to be used over the whole set of environments, then the correlated response over all environments can be deduced in the same manner as in Falconer (1981); that is, multiplying the direct response in Eq. (13) by the corresponding genetic regression coefficients. So, the regression coefficient for subset D_e in population A is $\frac{C_{Ae}}{\sigma^2_{Ae}}$, and for $D_{e'}$ in B is $\frac{C_{Be'}}{\sigma^2_{Be'}}$, where C_{Ae} is the additive covariance between half-sib families in environment e and overall environments for population A. $C_{Be'}$ is the same for environment e′ and population B. Therefore, Eq. (13) will be changed into:

$$\overline{\Delta G}^{(\infty)}_{DE} \simeq k\left[C_{Ae}\left(1-\frac{C_{Aee'}}{2\sigma^2_{Ae}}\right)+C_{Be'}\left(1-\frac{C_{Bee'}}{2\sigma^2_{Be'}}\right)\right], \quad \text{(approximately)} \qquad (14)$$

where $\overline{\Delta G}_{DE}$ is the ultimate genetic gain over environments.

Case 2. General case: average fractions, $\bar{f}_A$ and $\bar{f}_B$, of the total increase in gene frequencies are objectives of the selection program, and an average degree of dominance, $\frac{d}{a}$, is present in the genetic background of populations.

Because p_A and p_B cannot be known, we establish the following relationships:

$$\bar{\beta}_A=\frac{1-\bar{p}_A}{\frac{\bar{a}+\bar{d}}{2\bar{d}}-\bar{p}_A}, \quad \text{and} \quad \bar{\beta}_B=\frac{1-\bar{p}_B}{\frac{\bar{a}+\bar{d}}{2\bar{d}}-\bar{p}_B}. \qquad (15)$$

If complete dominance, $\bar{d}=\bar{a}$, and $\bar{\beta}=1$. If $\bar{d}<\bar{a}$ (incomplete dominance), $\bar{\beta}<1$. Furthermore, if $\bar{p}_A$ and $\bar{p}_B=0.5$, then $\beta=\frac{\bar{d}}{\bar{a}}$; for other values of $\bar{p}_A$ and $\bar{p}_B$, $\bar{\beta}$ will deviate very little from $\frac{\bar{d}}{\bar{a}}$. Then, the average degree of dominance can be taken as a rough estimate of $\bar{\beta}$ for all cases.

By the same reasoning as in Case 1, substituting Eq. (15) in Eq. (12), Eq. (14) will be changed into the general equation:

$$\overline{\Delta G}^{(n)}_{DE} \simeq k\,\bar{f}_A\left(C_{Ae}-\frac{C_{Ae}}{2\sigma^2_{Ae}}\bar{f}_B\bar{\beta}_B C_{Aee'}\right) + k\,\bar{f}_B\left(C_{Be'}-\frac{C_{Be'}}{2\sigma^2_{Be'}}\bar{f}_A\bar{\beta}_A C_{Bee'}\right) \quad \text{(approximately)}. \qquad (16)$$

Best two environments will be those that maximize $\overline{\Delta G}^{(n)}_{DE}$.

Model 2

When population A is selected in environment e and B in e′, the average genetic gain over all environments ($\overline{\Delta G}'_{DE}$) for the first cycle is as follows:

$$\begin{aligned}\overline{\Delta G}'_{DE} = {} & 1/2\, s_e \sum_{y\in D} p_{Ay}(1-p_{Ay})\,\alpha_{Bye}\,\bar{\alpha}_{By} \\ & + 1/2\, s_{e'} \sum_{y\in D} p_{By}(1-p_{By})\,\alpha_{Aye'}\,\bar{\alpha}_{Ay} \\ & - 1/2\, s_e \sum_{y\in D} \bar{d}_y\, p_{Ay}(1-p_{Ay})\,\alpha_{Bye}\,\Delta p_{By} \\ & - 1/2\, s_{e'} \sum_{y\in D} \bar{d}_y\, p_{By}(1-p_{By})\,\alpha_{Aye'}\,\Delta p_{Ay} \end{aligned} \qquad (17)$$

where $\bar{\alpha}$ and $\bar{d}$ refer to the average gene substitution and the heterozygous genotypic value over all environments, respectively. The first term of Eq. (17) is $s_e C_{Ae}$. The second term is $s_{e'} C_{Be'}$. The third term can be expressed as:

$$s_e C_{Aee'}\frac{\overline{\Delta P_B}\,\bar{d}}{\bar{\alpha}_{Be'}} = s_e C_{Aee'}\frac{\bar{f}'_B\bar{\beta}_B\bar{d}}{2\bar{d}_{e'}},$$

where

$$C_{Aee'} = 1/2 \sum_{y\in D} p_{Ay}(1-p_{Ay})\,\alpha_{Bye}\,\alpha_{Bye'};$$

the sign $-$ over letters refers to the weighted average of the corresponding parameters; and $\bar{f}'$ refers to the average fraction of gene frequency change in the first selection cycle. Similar expression can be obtained for the fourth term. Therefore, Eq. (17) can be written as:

$$\overline{\Delta G}'_{DE} = s_e\left(C_{Ae}-\frac{\bar{d}}{2\bar{d}_{e'}}\bar{f}'_B\bar{\beta}_B C_{Aee'}\right) + s_{e'}\left(C_{Be'}-\frac{\bar{d}}{2\bar{d}_e}\bar{f}'_A\bar{\beta}_A C_{Bee'}\right). \qquad (18)$$

The similarity between Eqs. (16) and (18) is obvious.

Discussion

Comparison of the two methods shows that genetic gain was larger in the DERRS than in the RRS for the two models (Eqs. (4) and (10)). In model 1, the difference is as much greater as the heterozygous genotypic values and the number of genes in the uncommon sets are higher. In model 2, the genetic gain difference is larger as the difference between the heterozygous genotypic values in the two environments is greater (Eq. (10)). Therefore, the DERRS method will be better than the RRS. This agrees with observations from experience where heterosis between populations selected in different environments is larger.

The general Eq. (16) for model 1 is an approximate formula and is based on the assumption of random

distribution of gene effects and gene frequencies over the subsets of loci operating in different environments in each population. There are difficulties in assigning values to $\bar{f}_A$ and $\bar{f}_B$. $\bar{\beta}_A$ and $\bar{\beta}_B$ can be approximated by the estimate of the degree of dominance. Expression (16) becomes more precise as it approaches the ultimate genetic gain and complete dominance (Eq. (14)).

The similarity between Eqs. (16) and (18), each obtained from a different model and selection cycle, suggests that the general expression (16) might be used for any genetic situation.

The covariance between environments should be as small as possible to obtain higher gain. The covariance effect on the DERRS method becomes more important as the degree of dominance and the number of selection generations increases. If the breeding program is designed for the very long term and model 1 is assumed, Eq. (14) can be applied. For intermediate term selection programs, Eq. (16) can be used and values around 0.5 could be assigned to $\bar{f}_A$ and $\bar{f}_B$. For short-term selection programs, Eq. (18) would be valid with low values for $\bar{f}_A$ and $\bar{f}_B$. The DERRS method will be more useful when the breeding program is designed for the long term.

The two best environments to be chosen in each situation are those that maximize Eqs. (13, 14, 16 or 18).

From the practical point of view, before starting a reciprocal recurrent program for the long term, it would be useful to estimate the variance–covariance matrices of half-sib families among a sample of environments for populations A and B. Appropriate estimates for each pair of environments should be substituted in Eqs. (14) or (16) to determine the pair with the highest genetic gain.

If selection is to be conducted in two sets of environments, E for population A and E′ for B, these could be formed in the following way: after choosing the first pair of environments as described above, they are eliminated from the variance–covariance matrix, and a second pair is chosen from the remainder and incorporated to the sets. The procedure continues until the increase in genetic gain due to the last incorporated pair does not compensate for the increase in effort and cost.

If combined S_2 and crossbred family selection (Moreno-González and Hallauer 1982) is applied, it would be better to use half-sib (HS) instead of full-sib families. S_2 and HS families from each population should be assigned to each environment.

There has been much controversy about the use of stress or non-stress environments in selection programs. Troyer and Rosenbrook (1983) found that increased densities reduced the number of tests needed to differentiate maize hybrids. Ordas and Stucker (1977) concluded that selection for maize yield should be done at relative high plant densities. The data from Stuber and Moll (1977) seem to dictate the conclusion that hybrid evaluation should be done at several densities. In contrast, Cross and Hammond (1982) did not find significant genotype × plant density interaction, indicating that selection could be carried out at any density. The DERRS method applied to different controlled environments, as irrigated versus not irrigated or high versus low plant density, would likely help to reduce the genotype × environments interaction.

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