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A method of line development using doubled haploids: the single doubled haploid descent recurrent selection

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Summary. Different methods of line development using doubled haploids in recurrent selection are presented. They are divided into two types: recurrent selection with progeny testing and recurrent selection on the phenotype of lines. It is shown that one of the best methods of line development is based on "single doubled haploid descent recurrent selection". Only one line is studied per plant of the population, and the best lines are intercrossed. Using this method it is very easy to extract lines for variety development.

Key words: Breeding methods – Recurrent selection – Doubled haploids – Quantitative genetics – Line breeding

Doubled haploids (DH) are being used more and more in plant breeding to develop lines, in *Hordeum vulgare* (crossing with *Hordeum bulbosum* or by androgenesis), in rapeseed (*Brassica napus*), and in several solanacea. We will assume that the production of DH is well controlled, and that a DH line derived from a genotype can be considered a random line among all possible derivable lines.

The use of DH in line development has been discussed by several authors: Griffing (1975) and Gallais (1978) in recurrent selection, and Feyt and Pelletier (1976) and Snape (1976) for extraction of the best line from a cross. We have already shown (Gallais 1978) that the best strategy for developing lines is to combine population improvement for line value and line development in such a way that a line, as a variety, is a co-product of recurrent selection.

In recurrent selection they are two fundamental ways to use DH: (1) DH are used to produce progenies (set of lines), and the selected mother plants or their progenies are intermated to produce the new population; this is a progeny test; (2) DH are used to produce lines which are evaluated separately. The best lines, taken on the basis of their phenotypic values, are intermated to produce the new population; this is a phenotypic selection.

We will consider briefly different modalities of these types of recurrent selections using DH, after recalling the concept of line value and the definition of genetic effects for line value (Gallais 1978).

Definition of genetic effects for line value

Line value of a population can be considered as the expected value of all lines which can be derived from this population. Line value of a genotype is the expected value of all lines which can be derived from this genotype. For a genotype $A_i A_j$ belonging to a random mating population and reduced to one locus, it would fit the following model, where μ_L is the line value of the population and ${}_L\alpha_i$ (or ${}_L\alpha_j$) is the additive effect for line value (Gallais 1979):

$$L_{ij} = \mu_L + {}_L\alpha_i + {}_L\alpha_j,$$

It is the expected value of lines which can be derived from genotypes with allele A_i (or A_j):

$${}_L\alpha_i = E_j(L_{ij}) - \mu_L .$$

Note that by definition there are no dominance effects for line value. Dominance effects between identical genes are integrated in the additive effects for line value. Indeed, for a homozygous genotype $A_i A_i$:

$$L_{ii} = \mu_L + 2\,{}_L\alpha_i = \mu + 2\alpha_i + \beta_{ii},$$

μ being the mean of the random mating population, α_i

the classical additive effect, and β_{ii} the residue of dominance for a homozygous genotype:

$${}_L\alpha_i = \alpha_i + 1/2\,[\beta_{ii} - E(\beta_{ii})].$$

Additive × additive epistatic effects could also be defined.

It is possible to associate a variance with each effect. With a random mating population, the genotype variance in line value will be, in the absence of epistasis:

$$\sigma^2_{G_L} = \sigma^2_{A_L}$$

and the variance among all lines derivable from a population will be $2\,\sigma^2_{A_L}$ (Gallais 1978).

Recurrent selection by progeny testing

The aim of recurrent selection is to improve the ability of the population to give good lines. It is then natural to select genotypes for their line value and to recombine the best genotypes. In this case the response to selection will be:

$$\Delta G = i\,\frac{\theta\,\mathrm{co}\,P_L\,O_L}{\sqrt{\mathrm{var}\,P_L}}$$

where P_L is the phenotypic line value of the parents and O_L the genotypic line value of offspring. Thus

$$\mathrm{cov}\,P_L\,O_L = 1/2\,\sigma^2_{A_L}.$$

Note that the genotypic value of a parent is A_L and the expected value of its offspring is $1/2\,A_L$, so the genetic correlation between parent and offspring for line value is unity. Also θ will be equal to 2 with selection on both sexes, and var P_L is the phenotypic variance among evaluated progenies according to the test system. Two types of tests can be envisaged: either lines from a plant are tested separately or they are tested together. If they are tested separately (method 1), the evaluation of the line value of a plant will be very expensive, because it will be necessary to have several lines per plant. In this case:

$$\mathrm{var}\,P_{L(1)} = \sigma^2_{A_L} + \frac{1}{l}\,\sigma^2_{A_L} + \frac{1}{bl}\left[\sigma^2_p + \frac{1}{n}\,\sigma^2_e\right] \qquad (1)$$

l being the number of derived lines per plant, b the number of repetitions, σ^2_p the plot error, n the number of plants per plot, and σ^2_e the environmental variance at the level of one plant within the plot. This experimental structure allows the direct derivation of lines as variety, but at the expense of selection intensity i.

The other procedure is to mix all lines from a plant in order to form only one progeny per plant and to directly evaluate its line value (method 2). This is justified with a great number of lines for each plant and in the absence of competition. In this case:

$$\mathrm{var}\,P_{L(2)} = \sigma^2_{A_L} + \frac{1}{b}\left[\sigma^2_p + \frac{1}{n}\,(\sigma^2_{A_L} + \sigma^2_e)\right] \qquad (2)$$

with a low heritability such a variance can be greater than that in method (1), however this effect can be counterbalanced by a greater selection intensity. The main disadvantage of such a procedure is that it does not give a new line as quickly.

Recurrent selection on the line phenotype

It is possible to test several DH lines per plant separately (method 3). Selection can then be performed between and within plants. Noting the same variance between and within plants ($\sigma^2_{A_L}$), the genetic advance will be:

$$\Delta G = i_B\,\frac{\sigma^2_{A_L}}{\sqrt{\mathrm{var}\,B_F}}\,c_B + i_W\,\frac{\sigma^2_{A_L}}{\sqrt{\mathrm{var}\,W_F}}\,c_W$$

where var B_F is the phenotypic variance among plants defined by expression (1); var W_F is the phenotypic variance within plants:

$$\mathrm{var}\,W_F = \sigma^2_{A_L} + \frac{1}{b}\left[\sigma^2_p + \frac{1}{n}\,\sigma^2_e\right],$$

and $\quad c_B = (l+1)/l, \quad c_W = (l-1)/l.$

The best procedure is to compute an index of family value and of line/family value. It is a particular case of combined selection. However, having several DH lines per plant decreases the selection intensity at the level of the plant. To maximize this selection intensity and to minimize the risk of inbreeding development, it is possible to study only one DH line per plant (method 4), (Fig. 1). In this case the expression of genetic advance will be:

$$\Delta G = i\,\frac{2\,\sigma^2_{A_L}}{\sqrt{\mathrm{var}\,P_L}}.$$

Indeed in method 4 the covariance between the value of the parents and the line value of its offspring is $\sigma^2_{A_L}$. Another way to obtain this result is to define the total variance among evaluated lines as $2\,\sigma^2_{A_L}$. As the correlation between the line value of the parent and that of offspring is 1, the expression of genetic advance for the evaluated lines gives the expression of genetic advance after intercrossing of the selected lines. In this case

$$\mathrm{var}\,P_L = \sigma^2_{A_L} + \frac{1}{b}\left[\sigma^2_p + \frac{1}{n}\,\sigma^2_e\right]. \qquad (3)$$

This variance will be greater than variance (2), but as the numerator of genetic advance is multiplied by 2,

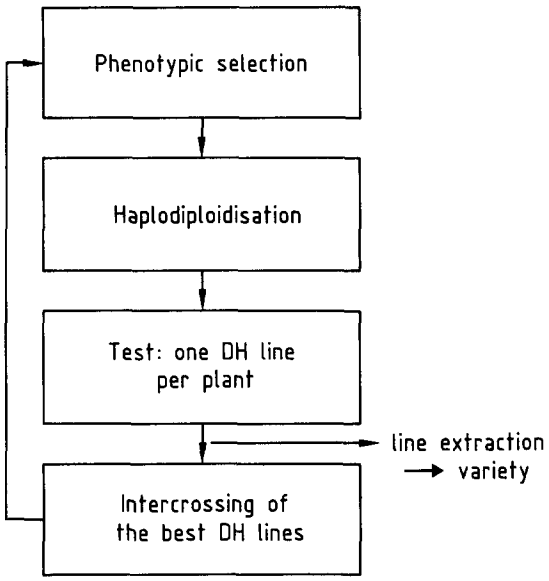

Fig. 1. Single doubled haploid descent recurrent selection

this method will be much more efficient than method 2. The ratio of expected genetic advance with method 4 to that of method 2 will be nearly $\sqrt{2}$ with no environmental effects. This degree of superiority will tend to increase slightly with low heritabilities (the heritability being defined by the ratio $\sigma^2_{A_L}/(\sigma^2_{A_L}+\sigma^2_p+\sigma^2_e)$. That means that method 4 will be more efficient than method 2 by at least 41.4% in one cycle and would be one of the best methods for recurrent selection using DH. An advantage with methods 3 and 4 is the possibility of a direct line extraction for variety development. This is a good illusration of how population improvement and varietal development must be connected in such a way that varietal development is nearly a co-product of population improvement. A practical advantage of the method 4 is to need only one doubled haploid per plant.

Note that the principle of only one line per plant is similar to the principle of single seed descent (S.S.D.) (Park et al. 1976). Such a procedure allows the maximum conservation of genetic variance in the breeding population. We propose to call this procedure "single doubled haploid descent recurrent selection" (S.D.H. – R.S.) (Fig. 1).

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