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The genetics of selfing with concurrent backcrossing in breeding hybrid sugar beet (*Beta vulgaris altissima* L.)

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Abstract Sugar beet hybrids are produced by crossing a cytoplasmic male-sterile (CMS) line with a pollinator. New CMS lines are produced by crossing a fertile plant to an existing CMS line. The fertile plant is also selfed. In the following generation, one of the selfed, fertile progeny is paired and isolated with one of the crossed, CMS progeny, to give a second generation of selfing and crossing. Over a series of such crosses and selfs, a new fertile inbred line and its corresponding, near-isogenic CMS partner are produced. Selection among lines takes place at one or more stages of the backcrossing programme. A method is presented here for calculating the genetic variances and covariances within and between lines and generations based on a derivation of additive genetic relationships modified from an approach widely employed in animal breeding. The genetic variances and covariances are used to predict response to selection from varying strategies, from which optimum schemes can be determined. Results suggest that selection should generally take place after three generations of backcrossing when the fertile plant used to initiate the backcrossing process is not inbred, but can take place after generation two when the fertile plant is inbred. Doubled haploid production is unlikely to provide an extra advantage that would be

worthwhile in such a system. The method developed here can be used to explore a wide range of more complex breeding systems.

Key words Hybrid selection · Concurrent backcrossing · Additive genetic relationship · Doubled haploids · Inbreeding

Introduction

Sugar beet hybrids are produced by crossing a cytoplasmic male-sterile (CMS) line with a pollinator (Bosemark 1993; Ford-Lloyd 1995; Poehlman 1986). An important part of any sugar beet breeding programme is therefore the development of new CMS lines. These lines are typically developed by a modified system of backcrossing as shown in Fig. 1. In the starting generation a fertile plant is crossed to a plant from an existing male-sterile line. At the same time, the fertile plant is selfed. Provided that the fertile plant is a non-restorer or O-type (Bosemark 1993; Ford-Lloyd 1995; Poehlman 1986; Owen 1945), then the crossed progeny, harvested on the CMS plant, will themselves be sterile. In the following generation, one of the selfed, fertile progeny is paired and isolated with one of the crossed, CMS progeny, giving a second generation of selfing and crossing. Over a series of such crosses and selfs, a new fertile inbred line and its corresponding, near-isogenic CMS partner are produced. At some stage during this process selection on performance between new CMS lines occurs, usually by the evaluation of test-crosses of these new CMS lines to one or more pollinator lines. Following selection, the inbreeding and backcrossing process may be continued for the selected lines, or may be stopped, with the selected lines thereafter being maintained by multiplication in isolated bulk populations of the O-type and corresponding CMS.

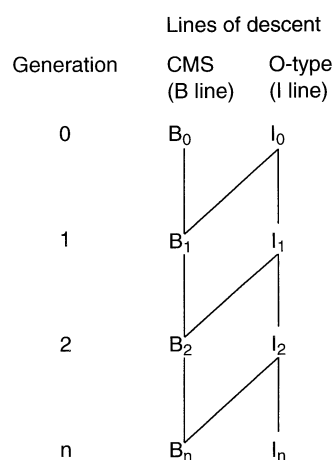
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Fig. 1 Generation of cytoplasmic male-sterile (CMS) lines by selfing with concurrent backcrossing to a non-restorer (*O-type*) line



can be used to predict responses to single and multi-stage selection in any generation.

Theory

Outline

Inbreeding coefficients and genetic (co)variances are derived from the additive genetic relationships among all relevant individuals. Additive genetic relationships are twice the coefficient of coancestry or coefficient of kinship (Falconer and Mackay 1996). Here, additive genetic relationships are derived by the recursive method commonly used in animal breeding, attributed by Emik and Terrill (1949) to J. L. Lush, and easily adapted to calculation with computer spreadsheets. The description in the section below is taken from Henderson (1976), with the addition of some rules to simplify the handling of selfed families.

This process differs from conventional backcrossing in that there is no true recurrent parent. Rather, the male-sterile line of descent is backcrossed to the fertile, selfing line of descent in each generation. As far as the authors are aware, there have been no publications which study the genetic consequences of the breeding programme described above, which we shall refer to as selfing with concurrent backcrossing. This analysis is important to allow informed decisions to be made on the number of backcrosses required before selection and the number of backcrosses before new lines are sufficiently stable and uniform for commercial use.

In this paper, we calculate inbreeding coefficients and additive genetic (co)variances for selfing with concurrent backcrossing and show how these components

Calculations of additive genetic relationships

A square matrix, *A*, of additive genetic relationships a_{ij} between individuals *i* and *j*, is constructed as described below. A small example matrix is given in Table 1, for the case of two selfed (S_1) individuals crossed to an inbred CMS tester in the initial generation.

It is a requirement of the method to order individuals so that parents precede their progeny and the matrix is completed from top left to bottom right. Here, relationships for the selfing lines of descent are calculated and listed first, followed by relationships for the backcrossing lines of descent. Since backcrossed individuals are never used as parents for selfing, the requirement that parents always precede their progeny in the matrix is still met.

For a diagonal element of the matrix, representing the relationship of an individual with itself, the relationship is:

$$a_{ii} = 1 + \frac{1}{2} (a_{pq}), \quad (1)$$

Table 1 Additive genetic relationships amongst a set of selfed plants with concurrent backcrossing (n/a not applicable)

Line of descent ^a	I ₁ ⁱ	I ₂ ⁱ	I ₁	I ₂	I ₁	I ₂	B ₁ ^f	B ₂ ^f	B ₁	B ₂	B ₁	B ₂
Generation ^b	0	0	1	1	2	2	0	0	1	1	2	2
Plant no. ^c	1	2	3	4	5	6	7	8	9	10	11	12
Parent plants ^d	n/a	n/a	1 selfed	2 selfed	3 selfed	4 selfed	n/a	n/a	1×7	2×8	3×9	4×10
1	1.500	0.000	1.500	0.000	1.500	0.000	0.000	0.000	0.750	0.000	1.125	0.000
2	0.000	1.500	0.000	1.500	0.000	1.500	0.000	0.000	0.000	0.750	0.000	1.125
3	1.500	0.000	1.750	0.000	1.750	0.000	0.000	0.000	0.750	0.000	1.250	0.000
4	0.000	1.500	0.000	1.750	0.000	1.750	0.000	0.000	0.000	0.750	0.000	1.250
5	1.500	0.000	1.750	0.000	1.875	0.000	0.000	0.000	0.750	0.000	1.250	0.000
6	0.000	1.500	0.000	1.750	0.000	1.875	0.000	0.000	0.000	0.750	0.000	1.250
7	0.000	0.000	0.000	0.000	0.000	0.000	2.000	2.000	1.000	1.000	0.500	0.500
8	0.000	0.000	0.000	0.000	0.000	0.000	2.000	2.000	1.000	1.000	0.500	0.500
9	0.750	0.000	0.750	0.000	0.750	0.000	1.000	1.000	1.000	0.500	0.875	0.250
10	0.000	0.750	0.000	0.750	0.000	0.750	1.000	1.000	0.500	1.000	0.250	0.875
11	1.125	0.000	1.250	0.000	1.250	0.000	0.500	0.500	0.875	0.250	1.375	0.125
12	0.000	1.125	0.000	1.250	0.000	1.250	0.500	0.500	0.250	0.875	0.125	1.375

^a Line of descent: two fertile plants are selfed and concurrently backcrossed, giving rise to two selfed (I) lines of descent with two corresponding backcrossed (B) lines of descent

^b Generation: results for three generations of selfing, and the corresponding three generations of backcrossing are shown

^c Plant no: an arbitrary number to identify each plant

^d Parent plants: the parent plant number(s) of each plant

^e Fertile I plants in generation 0 are from unrelated S_1 families

^f CMS B plants in generation 0 are from a single inbred line, unrelated to the I plants

where p and q are the male and female parents of i . Where an individual has been produced by selfing:

$$a_{ii} = 1 + \frac{1}{2} (1 + F_p) \quad (2)$$

where F_p is the inbreeding coefficient of the parent p . For an off-diagonal element, the relationship is:

$$a_{ij} = \frac{1}{2} (a_{ip} + a_{iq}) \quad (3)$$

where p and q are the parents of j .

Relationships, a_{ij} , for the initial generation take values which depend on the family structure from which the plants i and j have been selected. These equal the coefficients of between-family additive genetic variance tabulated in various standard texts (e.g. Hallauer 1981; Falconer and Mackay 1996). a_{ii} for an individual in the initial generation is:

$$a_{ii} = 1 + F_i \quad (4)$$

where F_i is the inbreeding coefficient of that individual.

The CMS source is usually unrelated to the O-type source, so that, for generation zero:

$$a_{i0}, B_{0j} = 0 \quad (5)$$

for individuals i and j in generation 0 in the I and B lines of descent, respectively.

Calculation of inbreeding coefficients, genetic variances, covariances and correlations

Inbreeding coefficients of any individual are given as half the genetic relationship between the parents or equivalently:

$$F_i = a_{ii} - 1 \quad (6)$$

In considering genetic variances and covariances, we must distinguish between I and B lines of descent which have been derived from common I parents in each generation, and I and B lines which have been derived from different parent plants. We shall use the term 'backcross pedigree' to refer to an I line of descent and its B line partner. To avoid excessive use of subscripts in formulae we shall make the following simplifications. Where subscripts are identical for I and B lines, these refer to the same backcross pedigree. Where subscripts are different, the I and B lines are from different backcross pedigrees. Where subscripts are different for a pair of I lines or a pair of B lines, these refer to plants from different lines of descent, not to plants within a line of descent.

To calculate responses to selection we require genetic variances between- and within-backcross pedigrees for I and B lines of descent considered separately, and covariances between I and B lines of descent within-backcross pedigrees. These are most simply produced by deriving the A matrix, using the method described above, for a single representative plant at each generation, of each of the I and B lines from two separate backcross pedigrees. The A matrix therefore consists of four individuals in each generation, as shown in Table 1. Variances and covariances between these individuals, and between the families of which these plants are the single representative member, are derived from the elements of A using Eqs. 7–10 below.

Within a generation, the expectations of additive genetic variance among I and among B plants from different backcross pedigrees are:

$$V_I = (a_{I_i, I_i} - a_{I_i, I_j}) V_A \quad (7)$$

$$V_B = (a_{B_i, B_i} - a_{B_i, B_j}) V_A \quad (8)$$

where V_A is the additive genetic variance of the base population from which the lines have been derived.

These variances are made up of two parts. The first has the coefficient of a_{ii} , the leading diagonal of the additive genetic relationship matrix A, and is the coefficient of V_A if the parents of the current generation are unrelated. The second part has the coefficient of $-a_{ij}$ and represents the reduction in genetic variance in the current generation if the parents are related.

The covariance W between individuals in the I and B lines in the same backcross pedigree, in the same generation, takes a similar form:

$$W_{IB} = (a_{B_i, I_i} - a_{B_i, I_j}) V_A \quad (9)$$

To get within-family variances in any generation, additional sibs within families could be added to the A matrix and the variance amongst those sibs computed using formulae 7 and 8 with subscripts redefined. A simpler method for the B lines of descent is to calculate the diagonal element of matrix A for the generation under study as if it were an off-diagonal element. The difference between the true value and this new value is the coefficient of the within-family variance:

$$V_{B(\text{within})} = [a_{B_i, B_i} - 0.5 (a_{B_i, I_p} + a_{B_i, B_q})] V_A \quad (10)$$

where p and q are the parents of i .

For the I line of descent the within-family variance is also the difference between the total variances in the current and preceding generations (Mather and Jinks 1982).

Between-family variances can be found as the difference between the total genetic variance and the within-family variance.

Covariances, between B and I lines within families, are zero, since these represent deviations from family means due to Mendelian segregation within families which are independent for different families. The covariance given by Eq. 9 is therefore the covariance between B and I family means within backcross pedigrees.

Equations 6–10 allow the calculation of genetic and phenotypic correlations between B and I lines at any generation and the calculation of response to selection in any single generation. To calculate responses to multistage selection in different generations, we must also calculate covariances across generations. These are:

$$W_{IxIy} = (a_{Ix_i, Iy_i} - a_{Ix_i, Iy_j}) V_A \quad (11)$$

$$W_{BxB_y} = (a_{Bx_i, B_y_i} - a_{Bx_i, B_y_j}) V_A$$

$$W_{BxIy} = (a_{Bx_i, Iy_i} - a_{Bx_i, Iy_j}) V_A$$

$$W_{IxBy} = (a_{Ix_i, B_y_i} - a_{Ix_i, B_y_j}) V_A$$

where I and B are selfs and backcrosses, and x and y are two different generations, $x < y$. Once again, all covariances are between-family means within-backcross pedigrees.

Results

Approach to homozygosity

Table 2 lists inbreeding coefficients of the I and B lines for a range of values of inbreeding coefficient of the single fertile plant used to initiate the selfing and backcrossing process. $F = 0, 0.5, 0.75,$ and 1 represent typical starting values for plants extracted from full or half-sib, $S_1, S_2,$ and doubled-haploid based recurrent selection schemes, respectively. Recurrent selection schemes based on these family types have been reported in sugar beet (Bosemark 1993; Ford Lloyd 1995). As expected, the approach to homozygosity in

Table 2 Inbreeding coefficient in successive generations for lines derived by selfing with concurrent selection

Generation	I_0 outcrossed		I_0 selfed once		I_0 selfed twice		I_0 fully inbred	
	Selfs	Backcross	Selfs	Backcross	Selfs	Backcross	Selfs	Backcross
0	0.000	1.000	0.500	1.000	0.750	1.000	1.000	1.000
1	0.500	0.000	0.750	0.000	0.875	0.000	1.000	0.000
2	0.750	0.250	0.875	0.375	0.938	0.438	1.000	0.500
3	0.875	0.500	0.938	0.625	0.969	0.688	1.000	0.750
4	0.938	0.688	0.969	0.781	0.984	0.828	1.000	0.875
5	0.969	0.813	0.984	0.875	0.992	0.906	1.000	0.938
6	0.984	0.891	0.992	0.930	0.996	0.949	1.000	0.969
7	0.992	0.938	0.996	0.961	0.998	0.973	1.000	0.984
8	0.996	0.965	0.998	0.979	0.999	0.985	1.000	0.992
Infinity	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000

the CMS (B) line increases as the degree of inbreeding of the I_0 plants increases. To make decisions on the use of CMS lines while ignoring the inbreeding status of the I_0 plants or by applying the well-known results from $F_{I_0} = 1$ (corresponding to a fully inbred non-recurrent parent) to all other values of F_{I_0} will therefore be misleading. In the case of $F_{I_0} = 0$, even after four generations of selfing with recurrent backcrossing, F_{B_4} is only 0.69.

Response to one-stage selection

We assume selection is on test-cross performance of B_k family means, in the k th generation of backcrossing. We also assume family size to be sufficiently large that the effect of within-family genetic variation on between-family heritability can be ignored. This assumption can be dropped, but in practice it is usually justified and it makes for a clearer presentation of the results.

The character we are interested in is improving test-cross hybrid performance itself, which can be treated as being controlled by predominantly additive gene action – we are in essence testing the performance of gametes from the B line in a background determined by the test-cross pollinator(s). Melchinger (1987) and Gallais (1991) have studied the theoretical aspects and practical utility of this model more extensively. With the character so defined, the only possible source of non-additive gene action is through additive \times additive interactions, which we shall assume to be negligible. We also assume that genetic heterogeneity in the tester causes negligible genetic variation between test-cross progenies. Finally, we assume no linkage.

Response to selection should not be measured by the direct response of the B_k families unless these families are to be used directly in commercial hybrid production. Here we measure the correlated response in the B_∞ generation. This is a simplification. In practice, if selection first takes place amongst the B_k , it is possible that the line will be used commercially from the

$B_{(k+1)}$ onwards, although for a more successful line, the bulk of income from the line will not be achieved until a later generation of backcrossing. For the simple genetic model used here, the measurement of response to selection in the B_∞ is equivalent to measuring the correlated response to selection amongst the $I_{(k-1)}$ single plants or amongst the $I_{(k)}$ families. Calculation of correlated responses to selection in any of these generations by the formulae given in Falconer and Mackay (1996), for example, gives identical results.

Table 3 presents genetic parameters and responses to selection with environmental and genetical variances V_E and V_A equal to 2 and 1, respectively. This gives a heritability of family means of 50% for fully inbred lines. Responses to selection have been calculated for selection at generations 1–4 and ∞ for lines derived from I_0 plants with inbreeding coefficients of 0, 0.5, 0.75 and 1.0.

As expected, response to selection rises as the number of generations of backcrossing rises and as the degree of inbreeding of the initial I_0 plant rises. The optimum generation for selection will depend on the interaction between late selection giving a greater response and early selection giving a reduced response but a faster introduction of the new product to the market. In addition, the optimum will vary with heritability. The lower the heritability, the greater the relative response from later generations (data not shown). This is analogous to the effect of heritability on the optimum generation for selection in a classical selfing programme in an inbreeding crop (Pooni and Jinks 1985; Cornish 1990a).

Response to multistage selection

Any discussion of multiple-stage selection programmes in plant breeding must take into account the reduction in genetic variance caused by selection. (Curnow 1961; Cornish 1990b; Mackay and Gibson 1993). Formulae for the reduction in genetic variation in the later

Table 3 Population and selection parameters and response to a single round of selection on backcrossed family means at different generations

	F_{10} ^a	Generation of selection				
		1	2	3	4	∞
V_{B_r} ^b	0	0.250	0.750	1.219	1.523	2.000
	0.5	0.375	0.938	1.406	1.664	2.000
	0.75	0.438	1.031	1.500	1.734	2.000
	1	0.500	1.125	1.594	1.805	2.000
h^2	0	0.111	0.273	0.379	0.432	0.500
	0.5	0.158	0.319	0.413	0.454	0.500
	0.75	0.179	0.340	0.429	0.464	0.500
	1	0.200	0.360	0.443	0.474	0.500
Response to selection	0	0.333	0.603	0.766	0.866	1.000
	0.5	0.487	0.729	0.847	0.914	1.000
	0.75	0.560	0.790	0.885	0.938	1.000
	1	0.632	0.849	0.923	0.961	1.000

^a F_{10} inbreeding coefficient of the unrelated plants used to initiate the selfing and backcrossing process

^b V_{B_r} variance between backcrossed family means

Table 4 Population parameters and response to two-stage selection on backcrossed family means under selfing with concurrent selection. All lines are derived from unrelated, non-inbred individuals from a population with a genetic variance of 1.0. Environmental variance for the first stage of selection: 2.0. Environmental variance for the second stage of selection 0.5. The best 10% of lines are selected at each stage

1st cycle ^a	V_{B_r} ^b	h_1^2 ^c	R_1 ^d	V_∞ ^a	h_2^2 ^c	R_2 ^d	R_{tot} ^d	V_∞ ^e
1	0.250	0.111	0.585	1.908	0.792	2.158	2.743	0.653
2	0.750	0.273	1.058	1.698	0.773	2.010	3.068	0.609
3	1.219	0.379	1.345	1.512	0.752	1.871	3.216	0.569
4	1.523	0.432	1.519	1.378	0.734	1.765	3.284	0.539
∞	2.000	0.500	1.755	1.170	0.701	1.589	3.344	0.490

^a 1st cycle: generation of first cycle of selection, second cycle of selection is at ∞

^b V_{B_r} : genetic variance between backcrossed family means

^c h_1^2, h_2^2 : heritabilities of backcrossed family means at the first and second cycles of selection, respectively

^d R_1, R_2, R_{tot} : response to selection in the first cycle and second cycle and total response, respectively

^e V_∞, V'_∞ : genetic variation between family means in generation ∞ , before and after second cycle of selection, respectively

generations can be found using the methods described in Mackay and Gibson (1993). These can be used to optimise the selfing and backcrossing programme in a manner analogous to that used by Cornish (1990a, b) in the optimisation of a selfing programme within an F_2 population. Here, for purposes of illustration, we have restricted ourselves to two-stage selection where the second stage takes place when the backcrossing process is complete; that is, at generation infinity. We also assume that after the first stage of selection, lines of descent are progressed by further generations of selfing with concurrent backcrossing. Calculations could be computed for cases where, after the first round of selection, selected lines are maintained as family bulks, as described in the Introduction, but this scheme will give a lower response to selection from the second stage of selection and has therefore not been pursued.

Table 4 tabulates responses to selection and genetic variation in generation B_∞ following prior selection in one of generations 1–4, or ∞ . All lines have been derived from unrelated individuals in a non-inbred population. V_A in the base populations was 1.0. V_E was taken to be 2.0 at the first stage of selection and 0.5 at

the second stage. The proportion selected was fixed at 10% for each stage. V_E was reduced for the second stage of selection to mimic an increase in replication of test crosses at the second stage of selection. This strategy follows from the principles of Curnow (1961) and Finney (1966). However, all parameters have been used for illustrative purposes only and are unlikely to be optimal.

Results in Table 4 show that in the absence of any constraints, selection is best delayed until the latest possible generation – the maximum response to selection comes from both stages of selection occurring at generation ∞ . However, in practice, delayed selection is more expensive than selection during earlier generations. Where selfed lines are derived by single-seed descent, with 10% selection at each stage, we must have a minimum of 100 families before selection at generation infinity for two stages of selection is possible. With early generation selection, we only need carry forward 10 families from the first stage of selection to the second. Thus, the genetically less efficient two, stage selection programmes could be carried out more cheaply. Early generation selection also gives the opportunity to

produce sublimes after the first stage of selection. In the extreme case, 1 family could be selected from 10 at the first stage of selection, with a further 10 lines being derived from the single selected family for the second stage of selection. The method described in this paper can also be used to study responses to selection from such schemes and optimise the selection process, along the same lines as Cornish (1990b) has done for pedigree selection in inbreeding species.

We should note in passing that responses to all two-stage selection programmes will be overestimated due to the failure of the assumption of normal distributions of genetic values at the second stage of selection. This failure will be greatest when the first stage of selection takes place in later generations, since there is less opportunity for subsequent segregational variance to make the distribution in the second stage more normal. However, the effect of non-normality will be slight, at least for two-stage selection (Curnow 1961; Bulmer 1980). Cornish (1990b) found simulated and predicted responses agreed well in pedigree schemes including up to five stages of selection.

Comparison of inbred and F₁ cytoplasmic male-sterile donor lines

All results presented so far have been calculated on the assumption that an inbred CMS line is used to initiate the backcrossing line of descent. Many sugar beet breeders use an F₁ CMS rather than an inbred because the F₁ line has better sterility and monogermity. However, in addition, the use of an F₁ will generate more variation within families in the first generation of backcrossing due to segregational variance within the B line of descent. This within-family variation makes the backcrossing process easier since it allows easier matching of flowering time when selecting pairs of plants from the selfing and backcrossing lines within-backcross pedigrees. In later generations, as the lines become increasingly similar, their flowering times converge and the problem disappears.

The use of an F₁ CMS unrelated to the initial plants used in selfing will have no effect on the rate of

inbreeding of the B line: in both cases the first generation has an inbreeding coefficient of zero, and successive generations have identical inbreeding coefficients. However, between- and within-family variances are affected, and therefore responses to selection will also vary.

Table 5 shows an example where non-inbred, unrelated plants from a source population are backcrossed to an F₁ or inbred CMS source. Variation within the backcrossed families is greater for an F₁ source for the first generation only. In subsequent generations, variation within families is identical for both CMS sources. Therefore, there is considerable benefit to be gained from using an F₁ CMS source if matching flowering time is likely to be a problem, although this benefit is available in the first generation only.

Variation between families is greater among backcrossed families derived from an F₁ source although the effect is slight apart from generation 2. Equally, correlations between the selfed and backcrossed family means are greater for lines derived from an inbred CMS source than for lines derived from an F₁ CMS, although the difference is large for generation 2 only. These two effects tend to cancel out so that responses to selection are very similar for both CMS sources. The choice between an inbred or CMS source can therefore be made purely on their relative practical merits as seed parents.

Discussion

This paper uses a method common in animal breeding research to calculate inbreeding coefficients and responses to selection using a practical problem in sugar beet as an example. The theory described here may be of use for other crops where the female components of hybrids are derived by backcrossing to a fertile maintainer. Examples are swedes, where backcrossing is to lines with strong self-incompatibility (Bradshaw 1989), and onions and carrots, where CMS systems similar to that in sugar beet are employed in hybrid production (Peterson and Simon 1986; Pike 1986).

Table 5 Comparison of F₁ and inbred CMS for initiation of backcrossing programme

Generation	V _{Bf} ^a within families		V _{Bf} ^a between families		r _{fam} ^b		Response to selection ^c	
	CMS type: Inbred	F ₁	Inbred	F ₁	Inbred	F ₁	Inbred	F ₁
1	0.250	0.500	0.250	0.250	1.000	1.000	0.585	0.585
2	0.375	0.375	0.750	0.813	0.943	0.906	1.058	1.046
3	0.250	0.250	1.219	1.234	0.942	0.936	1.345	1.342
4	0.156	0.156	1.523	1.527	0.961	0.960	1.519	1.518
∞	0.000	0.000	2.000	2.000	1.000	1.000	1.755	1.755

^a V_{Bf}: variance between and within backcrossed families, respectively

^b r_{fam}: correlation between selfing and backcrossing families

^c Response to selection: response to a single stage of selection; same parameters as Table 3

Although we have not attempted to optimise particular breeding programmes in this paper, we can make the following conclusions about the likely form that such an optimised programme would take:

1) Doubled haploid production for female lines is unlikely to be cost-effective. Once the doubled haploids are produced, they must be backcrossed as normal to a male-sterile source. Ovule culture, the only published means of producing doubled haploids in sugar beet with any degree of success (Bossoutrot and Hosemans 1985; Van Geyt et al. 1987; Lux et al. 1990), takes at least 1 and probably 2 years. Although the backcrossing process takes longer for outcrossed material than for fully homozygous material, the time taken to produce the doubled haploids largely cancels out this disadvantage (Tables 2 and 3). Given the greater expense of producing doubled haploids compared to the cost of selfing with concurrent backcrossing, doubled haploids might give a slightly greater response to selection, but at a considerably higher cost.

2) Selection after only one round of backcrossing is unlikely to be optimum under any conditions. For outcrossed material, selection should be delayed until after the third round of backcrossing. For inbred starting material, from S_1 or S_2 families, selection can occur following the second stage of backcrossing.

The theory described in this paper will also allow the development of optimum breeding plans for the production of new CMS lines in sugar beet. If inbreeding does not occur by single-seed descent, but by pedigree inbreeding, with several plants being carried forward from each selfed individual from the previous generation, or if the set of plants used to initiate the selfing and backcrossing programme are grouped into full, half-sib, or S_1 families, then expectations for variances between and within pedigrees can be calculated by altering the values of a_{ij} to those appropriate for the family type under consideration. All (co)variances calculated for the current and subsequent generations are then (co)variances within the corresponding pedigree. (Co)variances between pedigrees are calculated by the difference between values for the whole population of lines and the values within pedigree.

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References

- Bosemark N (1993) Genetics and plant breeding. In: Cooke DA, Scott RK (eds) The sugar beet crop. Chapman and Hall, London, pp 67–119
- Bossoutrot D, Hosemans D (1985) Gynogenesis in *Beta vulgaris* L.: from in vitro culture of unpollinated ovules to the production of doubled haploid plants in soil. *Plant Cell Rep* 4: 300–303
- Bradshaw JE (1989) The relative merits of lines versus hybrids in swedes (*Brassica napus* L. ssp. *rapifera*). In: Honne BI (ed) Biometrics in plant breeding. (Proc 7th Meet EUCARPIA Sect Biometrics Plant Breed). Norwegian State Agricultural Stations, Ås, Norway, pp 47–57
- Bulmer MG (1980) The mathematical theory of quantitative genetics. Clarendon Press, Oxford
- Cornish MA (1990a) Selection during a selfing programme. I. The effects of a single round of selection. *Heredity* 65: 201–211
- Cornish MA (1990b) Selection during a selfing programme. II. The effects of two or more rounds of selection. *Heredity* 65: 213–220
- Curnow RN (1961) Optimal programmes for varietal selection. *J R Stat Soc Ser B* 23: 282–318
- Emik LO, Terrill CE (1949) Systematic procedures for calculating inbreeding coefficients. *J Hered* 40: 51–55
- Falconer DS, Mackay TFC (1996) Introduction to quantitative genetics, 4th edn. Longman, London
- Finney DJ (1966) An experimental study of certain screening processes. *J R Stat Soc Ser B* 28: 88–109
- Ford-Lloyd BV (1995) Sugarbeet, and other cultivated beets. In: Smartt J, Simmonds NW (eds) Evolution of crop plants, 2nd edn. Longman Scientific & Technical, London, pp 35–40
- Gallais A (1991) A general approach for the study of a population of testcross progenies and consequences for recurrent selection. *Theor Appl Genet* 81: 493–503
- Hallauer AR (1981) Selection and breeding methods. In: Frey KJ (ed) Plant breeding II. Iowa State University Press, Ames, Iowa, pp 3–55
- Henderson CR (1976) A simple method for computing the inverse of a numerator relationship matrix used in prediction of breeding values. *Biometrics* 32: 69–83
- Lux H, Herrmann L, Wetzel C (1990) Production of haploid sugar beet (*Beta vulgaris* L.) by culturing unpollinated ovules. *Plant Breed* 104: 177–183
- Mackay IJ, Gibson JP (1993) The effect of gametic-phase disequilibrium on the prediction of response to recurrent selection in plants. *Theor Appl Genet* 87: 152–160
- Mather K, Jinks JL (1982) Biometrical genetics, 3rd edn. Chapman and Hall, London
- Melchinger AE (1987) Expectation of means and variances of testcrosses produced from F_2 and backcross individuals and their selfed progenies. *Heredity* 59: 105–115
- Owen FV (1945) Cytoplasmically inherited male-sterility in sugar beets. *J Agric Res* 71: 423–440
- Peterson CE, Simon PW (1986) Carrot breeding. In: Bassett MJ (ed) Breeding vegetable crops. Avi Publ Co, Westport, Conn., pp 322–356
- Pike LM (1986) Onion breeding. In: Bassett MJ (ed) Breeding vegetable crops. Avi Publ Co, Westport, Conn., pp 357–394
- Poehlman JM (1986) Breeding field crops, 3rd edn. Van Nostrand Reinhold, New York
- Pooni HS, Jinks JL (1985) Retrospective selection and sources of superior inbreds amongst pedigree inbred families of *Nicotiana rustica*. *Heredity* 54: 225–260
- Van Geyt J, Speckmann GJ Jr, D'Halluin KD, Jacobs M (1987) In vitro induction of haploid plants from unpollinated ovules and ovaries of the sugarbeet (*Beta vulgaris* L.) *Theor Appl Genet* 73: 920–925