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Two-Locus Inbreeding Measures for Recurrent Selection*

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Summary. For a population undergoing recurrent selection, a method is presented for determining the average inbreeding coefficients at the end of each breeding cycle. The coefficients are derived in terms of probability measures that genes are identical by descent. For the one-locus case, two digametic measures are defined and employed in the derivation of a recurrence formula for the inbreeding coefficient. Two further classes of measures, trigametic and quadrigametic, are required for transition from one cycle to the previous one to allow the calculation of the inbreeding function for the two-locus case. Numerical values of the average probability of double identity by descent for populations with various imposed assumptions are listed to illustrate the effects of linkage and population size on the accrual of inbreeding and hence of homozygosity.

Introduction

The use of recurrent selection (RS) procedures in plant breeding is now well established. As Penny *et al.* (1963) point out in their review, the recombination or crossing phase in an RS program slows the rapid approach to homozygosity which limits selection under selfing systems. To monitor the level of homozygosity in RS programs, it is convenient to calculate inbreeding coefficients. These coefficients indicate identity by descent and so do not give a complete description of homozygosity. They do provide lower bounds, however, (Cain and Hinkelmann 1970) and the algebra needed to establish recurrence equations for inbreeding coefficients may also be applied directly to measures of homozygosity.

A one-locus coefficient was calculated by Sprague *et al.* (1952) and a quite detailed discussion of one- and two-locus coefficients was given by Cain and Hinkelmann (1970, 1972). These last two papers contain some errors and, to us, do not seem to follow the most natural development of inbreeding measures. One difficulty with the papers of Cain and Hinkelmann is that they are based on the approach of Shikata (e.g. Shikata 1965) which is of limited application (e.g., Weir 1971).

In this paper we present a one- and two-locus analysis of RS using our digametic, trigametic and quadrigametic measures (Weir and Cockerham 1969a). Such measures provide information on the level of inbreeding and are a subset of a more general set of measures (Cockerham and Weir 1973) which allow the calculation of genotypic frequencies and various disequilibrium quantities.

Mating and Selection Schemes

The population consists of diploid individuals capble of both selfing and intercrossing. There is no restriction on the number of alleles at each of the loci studied. A constant number of progeny per individual is assumed and possible viability effects are ignored. We will base our development on one progeny per mating (self or intercross).

Initially N non-inbred and unrelated individuals are drawn from a source population and selfed. The resulting N offspring are crossed in all possible pairs and then another selfing phase entered. The population size would quickly become unmanageable of course for there would be $M = N(N-1)/2$ individuals at the end of the first intercross phase, $M(M-1)/2$ at the end of the second, and so on.

We will suppose that selection is practised by selecting N individuals at the end of each selfing phase. The basis for this selection will not be discussed, but we note (Cain and Hinkelmann 1970) that our treatment includes such schemes as simple RS

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and RS for specific combining ability. The calculations we make will include all of the M individuals at the end of each intercross phase. Selection will be supposed to be at random, so that we will need to make use of sampling probabilities. Any mating scheme in which there is no choice of mates is expressly excluded from consideration here, but may be analysed by other methods (e.g., Weir and Cockerham 1969a). Most of the discussion will be for the case where N individuals are chosen quite at random from the M at the end of each selfing phase, and so would be appropriate for a control population. We will follow Cain and Hinkelmann (1970), however, and also consider two schemes of random selection with constraints. These are the so called "minimum" and "maximum" inbreeding schemes. In the former case, each of the selected individuals contributes exactly two gametes to the next group of selected individuals. In the latter case, one of the selected individuals contributes N-1 gametes, two contribute two gametes while the remaining N-3 individuals each contribute exactly one gamete to the next group of selected individuals. The mating and selection schemes are illustrated for N = 4 in Fig.1. Random selection is when the four individuals selected in generation 1 of a cycle are selected without regard to gametic contributions in the previous cycle.

We wish to calculate the average inbreeding coefficient for the intercross and selfed populations, so that all members of these populations must be considered whether or not they contribute to succeeding generations.

One-Locus Case: Digametic Measures

For a single locus with genes a, the descent status of pairs of genes a, a' is needed. Specifically we wish to know whether or not the two genes are identical by descent and must distinguish the two cases according to whether or not the gametes carrying the two genes unite. The probability that gametes uniting to form individual X carry identical genes is written as F_X, the inbreeding coefficient of X. If the two gametes are from individuals Y and Z, they carry identical genes with probability θ_{YZ}, the coancestry of Y and Z. Evidently $F_X = \theta_{YZ}$ when X is the offspring of Y and Z.

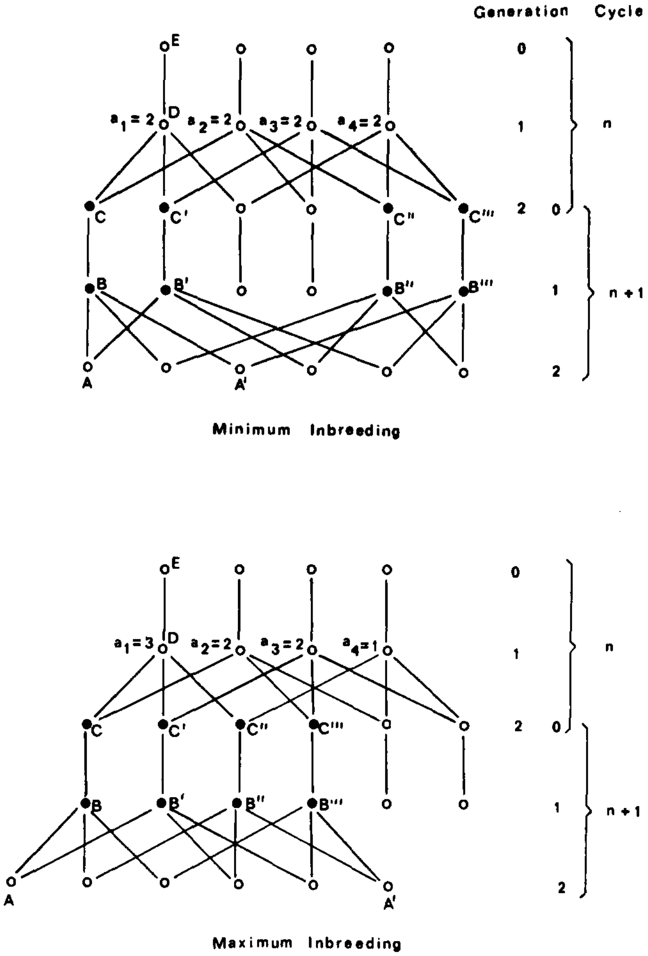

Fig.1. Mating and selection schemes for N = 4. Selected individuals are shown as solid circles

The inbreeding coefficient of a random one of the M members, say A, of generation 2 (intercrossed generation) of cycle n can be written as F_A or as $F_{(2,n)}$. As not all members of this generation have the same pedigree, F_A is an average measure. We express F_A as $\theta_{BB'}$, the coancestry of two of the N distinct individuals B and B' chosen at random from generation 1 (selected selfed generation) of cycle n. The process of tracing gametes back in time continues until a set of transition equations is established which allow the calculation of F_A and of F_B.

Sampling Probabilities for One-Locus-Case

If C and C' are the parents of B and B', respectively, they are distinct members of the selected intercross population (generation 2 of cycle n-1) and

$$F_A = \theta_{BB'} = \theta_{CC'} \ . \qquad (1)$$

The selected intercross population refers to the parents of the selected selfed population. Further expansion back in time requires account to be taken of whether C and C' have a common parent, with probability P_{211}, or whether they have four distinct parents, with probability P_{1111}. For both schemes in Fig. 1, individual A has grandparents C, C' with a common parent D, while the grandparents of individual A' do not have a common parent. In general, when a set of 2m gametes received by m members of generation 2 of cycle n is considered, $P_{t_1 t_2 \ldots t_r}$ is the probability that these gametes are from r individuals in generation 1 of cycle n and that the ith of these individuals contributed t_i of the gametes. This requires that the t_i sum to 2m.

The four gametes received by distinct individuals C, C' necessarily come from three or four individuals unless N, the selected population size, is equal to 2. This provides

$$P_{211} + P_{1111} = 1,\ N \geqslant 3;\ P_{22} = 1,\ N = 2 .$$

For the unrestricted random sampling scheme, $N \geqslant 3$, the sampling probabilities may be taken to refer to four gametes uniting to form any two of the M crossed offspring in generation 2 of a cycle. The number of such pairs of offspring is $\binom{M}{2}$ and, since selection is random, the number of ways in which three distinct parents can be chosen for a pair is $\binom{N}{3}$. Finally, the number of ways in which one of the three parents can be chosen to contribute two gametes, and become the common parent to the pair of individuals, is $\binom{3}{1}$ so that

$$P_{211} = \binom{N}{3}\binom{3}{1}\Big/\binom{M}{2} = \frac{4}{N+1},\ P_{1111} = \frac{N-3}{N+1},\quad N \geqslant 3 . \tag{2}$$

For the restricted random selection schemes, we follow Cain and Hinkelmann and let a_i be the number of gametes contributed by the ith selected individual to the next generation of selected individuals. These a_i must satisfy

$$1 \leqslant a_i \leqslant N - 1,\ \sum_{i=1}^{N} a_i = 2N$$

and may be regarded as the number of gametes the ith selected selfed individual contributes to the follow generation of selected intercrossed individuals. Now P_{211} can be regarded as the probability that a pair of individuals from the selected intercross population have a common parent in the preceding selected self population. There are $\binom{N}{2}$ such pairs of individuals and $\sum_i a_i(a_i - 1)/2$ pairs of gametes from a single parent, so that

$$P_{211} = \sum_i a_i(a_i - 1)/N(N - 1) . \tag{3}$$

In Fig. 1 we show the a_i's for the case $N = 4$. For minimum inbreeding, $a_i = 2$ for $i = 1, 2, \ldots N$ so that

$$P_{211} = 2/(N - 1),\ N \geqslant 3$$

while for maximum inbreeding we may write $a_1 = N - 1$, $a_2 = a_3 = 2$, $a_i = 1$ for $i = 4, 5, \ldots N$ and hence

$$P_{211} = (N^2 - 3N + 6)/N(N - 1),\ N \geqslant 4 \tag{4}$$

Note that, as expected, P_{211} for unrestricted random selection is greater than that for minimum inbreeding and less than that for maximum inbreeding for all $N \geqslant 4$.

Recurrence Formulae for $N \geqslant 4$ for One-Locus Case

We maintain the convention that primes denote distinct random individuals and continue the expansion of Eq. (1)

$$\theta_{CC'} = P_{211}(\theta_{DD} + 3\theta_{DD'})/4 + P_{1111}\theta_{DD'} . \tag{5}$$

From the usual result for the coancestry of an individual with itself

$$\begin{aligned} \theta_{DD} &= (1 + F_D)/2 \\ F_D &= \theta_{EE} = (1 + F_E)/2 \end{aligned} \tag{6}$$

and these expressions may be substituted into (5) which, with $\theta_{DD'}$ written as F_C, gives

$$F_A = 3P_{211}/16 + (3P_{211} + 4P_{1111})F_C/4 + P_{211}F_E/16 . \tag{7}$$

Recall that D, D' are any two of the selected selfed individuals, while C in F_C refers to any of the M offspring obtained by crossing these.

In general then, the average inbreeding for the whole of the intercross generations follows from (7) as

$$F_{(2,n)} = 3P_{211}/16 + (1-P_{211}/4)F_{(2,n-1)} + + P_{211}F_{(2,n-2)}/16 \qquad (8)$$

and that for the whole of the selfed generations follows from (6) as

$$F_{(1,n)} = (1 + F_{(2,n-1)})/2 \, . \qquad (9)$$

While any initial conditions at all may be accommodated, it is usual to take $F_{(2,0)} = F_{(2,1)} = 0$, where $F_{(2,0)}$ is for the initial N individuals.

For unrestricted random selection, substitution of P_{211} from (2) into (8) gives

$$F_{(2,n)} = \frac{3}{4(N+1)} + \frac{N}{N+1} F_{(2,n-1)} + \frac{1}{4(N+1)} F_{(2,n-2)} \qquad (10)$$

which corrects Eqs.(3.1), (3.2) of Cain and Hinkelmann (1970).

For restricted random selection, if P_{211} from (3) is substituted into (8) we recover a result similar to that in Eq.(6.1) of Cain and Hinkelmann (1970), who refer to this case as effective directional selection. In their Eq.(6.2), however, these authors give a result which differs from Eq.(9) above.

In the maximum inbreeding case there is the unusual result that average inbreeding increases with population size. This is because, for $N \geqslant 6$, P_{211} is an increasing function of N. As N increases, there is a greater chance that any two members of the selected intercross generation have a common parent. This extreme case is less likely to occur by chance under unrestricted random selection as N increases, however.

Recurrence Formulae for N < 4 for the One-Locus Case

For a population to be maintained at size less than four, there can be no selection since $M \leqslant N$ and the situation is really outside the scope of this paper. For N = 1 we are back to the simple selfing case with no scope for intercrossing. For N = 3 each individual always contributes exactly two gametes to succeeding generations, and, from either (2) or (3), $P_{211} = 1$. Eq.(8) does reduce to

$$F_{(2,n)} = \frac{3}{16} + \frac{3}{4} F_{(2,n-1)} + \frac{1}{16} F_{(2,n-2)} \qquad (11)$$

as given in (4.3) of Cain and Hinkelmann (1970).

To maintain a population of size N = 2, it would be necessary for the pair of individuals in each intercrossing phase to leave two offspring instead of one. The system then reduces to one of alternating selfing and full sib mating, for which the appropriate recurrence formula is

$$F_{(2,n)} = \frac{3}{8} + \frac{1}{2} F_{(2,n-1)} + \frac{1}{8} F_{(2,n-2)} . \qquad (12)$$

Eq.(9) is still to be used in conjuction with (11) and (12).

Two-Locus Case: Di-, Tri- and Quadrigametic Measures

For two loci with genes a and b, respectively, the descent status of two pairs of genes, a,a' and b,b' is needed. The usual procedure (e.g., Shikata 1965) is to define a four component vector for these gene pairs as

$$\underline{X}(ab,a'b') = \begin{bmatrix} X_{11}(ab,a'b') \\ X_{10}(ab,a'b') \\ X_{01}(ab,a'b') \\ X_{00}(ab,a'b') \end{bmatrix} = \begin{bmatrix} \text{prob}(a \equiv a',\ b \equiv b') \\ \text{prob}(a \equiv a',\ b \not\equiv b') \\ \text{prob}(a \not\equiv a',\ b \equiv b') \\ \text{prob}(a \not\equiv a',\ b \not\equiv b') \end{bmatrix}$$

where the equivalence sign $\equiv$ means identity by descent.

To evaluate such two-locus inbreeding measures we found it necessary (Weir and Cockerham 1969a) to distinguish the cases where the pairs of genes are carried on two, three or four gametes. There are two digametic measures, just as there are in the one-locus case:

$\underline{F}_A = \underline{X}$(ab, a'b': ab, a'b' are on the two gametes uniting to form individual A),

$\underline{\theta}_{YZ} = \underline{X}$(ab, a'b': ab, a'b' are on two gametes taken from individuals Y and Z, respectively).

The trigametic and quadrigametic measures are written as $\underline{\gamma}$ and $\underline{\delta}$, respectively:

$\underline{\gamma}_{W,YZ} = \underline{X}$(ab, a'b': ab, a', b' are on three gametes taken from individuals W, Y and Z, respectively),

$\underline{\delta}_{VW,YZ} = \underline{X}$(ab, a'b': a, b, a', b' are on four gametes taken from individuals V, W, Y and Z, respectively).

One-locus measures may be found by summing appropriate components of two-locus measures. In Table 1, for example, we show that the one-locus inbreeding coefficient for an individual, A, can be found from the two-locus measure $\underline{F}_A$. In that table, identity by descent at the a and b loci has probabilities $F_{1.A}$ and $F_{.1A}$, respectively, but as we seldom envisage different inbreeding at different loci we simply write the one-locus coefficient as F_A. Once this latter coefficient is known, the table demonstrates that only one component of the two-locus measure need be calculated in order to determine the whole measure. For convenience we work with the components X_{00} for double non-identity.

Table 1. Relationship between one- and two-locus inbreeding coefficients

F_{11A} F_{01A}	F_{10A} F_{00A}	$F_{1.A} = F_A$ $F_{0.A} = 1 - F_A$
$F_{.1A} = F_A$	$F_{.0A} = 1 - F_A$	1

For further convenience we define the following average measures

$$\underline{\gamma}_{W,\overline{YZ}} = (\underline{\gamma}_{W,YZ} + \underline{\gamma}_{W,ZY})/2,$$

$$\underline{\delta}_{VW,\overline{YZ}} = (\underline{\delta}_{VW,YZ} + \underline{\delta}_{VW,ZY})/2$$

$$\underline{\delta}_{\overline{VW},\overline{YZ}} = (\underline{\delta}_{VW,YZ} + \underline{\delta}_{VW,ZY} + \underline{\delta}_{WV,YZ} + \underline{\delta}_{WV,ZY})/4 .$$

The final notational convention is our use of λ as the linkage parameter, where λ is one minus twice the recombination coefficient so that $0 \leqslant \lambda \leqslant 1$.

Selfing Phase Expansions for Two-Locus Case

The general method of calculating $\underline{F}$ for any generation follows that for the one-locus coefficient F. We start with a random member A of generation 2 of cycle n and express $\underline{F}_A$ as the two-locus coancestry coefficient of its distinct parents

$$\underline{F}_A = \theta_{BB'} \quad \text{and} \quad F_{00A} = \theta_{00BB'} \,.$$

The tracing of the genes received by A back through the selfing phase is now more complicated since the four genes may be carried on two, three or four gametes in that phase. In particular, if individual B receives gametes $a_C b_C$, $a'_C b'_C$ from its single parent C and transmits gamete $a_B b_B$ to individual A, then we trace $a_B b_B$ back to the array

$$\frac{1+\lambda}{4} a_C b_C + \frac{1+\lambda}{4} a'_C b'_C + \frac{1-\lambda}{4} a'_C b_C + \frac{1-\lambda}{4} a_C b'_C$$

and similarly for the gamete transmitted from B' to A. The two arrays may be written as the margins of a two way table, as in Table 2, and the values of $\theta_{00BB'}$ in each of the sixteen cases written in the body of the table. Collecting terms in this table shows that

$$\theta_{00BB'} = \frac{(1+\lambda)^2}{4} \theta_{00CC'} + \frac{1-\lambda^2}{2} \gamma_{00C,C'C'} + \frac{(1-\lambda)^2}{4} \delta_{00CC,C'C'} \qquad (14)$$

where, once again, primes are used to denote distinct rather than particular individuals.

Further expansion, now through the intercross phase, will require the use of sampling probabilities as previously and then we will be faced with another round of expansions through a selfing phase. These selfing expansions will evidently be for genes received by two, three or four individuals (in generation 1 of cycle n-1). We now list all of the other selfing phase expansions required in this study. Futher details of the method of obtaining them are given in Weir and Cockerham (1969a).

$$\theta_{00BB} = \frac{1+\lambda^2}{4} \theta_{00CC} \qquad (15)$$

$$\gamma_{00B,BB} = \frac{1}{4} \theta_{00CC} \qquad (16)$$

$$\gamma_{00B,B'B'} = \frac{1+\lambda}{4} \theta_{00CC'} + \frac{1}{2} \gamma_{00C,C'C'} + \frac{1-\lambda}{4} \delta_{00CC,C'C'} \qquad (17)$$

Table 2. Expansion of $\theta_{00BB'}$

		$\underline{a_B b_B}$			
		$\frac{1+\lambda}{4}$	$\frac{1+\lambda}{4}$	$\frac{1-\lambda}{4}$	$\frac{1-\lambda}{4}$
	$\theta_{00BB'}$	$a_C b_C$	$a'_C b'_C$	$a_C b'_C$	$a'_C b_C$
$\underline{a_{B'} b_{B'}}$	$\frac{1+\lambda}{4}\ a_{C'} b_{C'}$	$\theta_{00CC'}$	$\theta_{00CC'}$	$\gamma_{00C',CC}$	$\gamma_{00C',CC}$
	$\frac{1+\lambda}{4}\ a'_{C'} b'_{C'}$	$\theta_{00CC'}$	$\theta_{00CC'}$	$\gamma_{00C',CC}$	$\gamma_{00C',CC}$
	$\frac{1-\lambda}{4}\ a_{C'} b'_{C'}$	$\gamma_{00C,C'C'}$	$\gamma_{00C,C'C'}$	$\delta_{00CC,C'C'}$	$\delta_{00CC,C'C'}$
	$\frac{1-\lambda}{4}\ a'_{C'} b_{C'}$	$\gamma_{00C,C'C'}$	$\gamma_{00C,C'C'}$	$\delta_{00CC,C'C'}$	$\delta_{00CC,C'C'}$

$$\gamma_{00B,\overline{BB}'} = \frac{1}{2}\gamma_{00C,\overline{CC}'} \tag{18}$$

$$\gamma_{00B,B'B''} = \frac{1+\lambda}{2}\gamma_{00C,C'C''} + \frac{1-\lambda}{2}\delta_{00CC,C'C''} \tag{19}$$

$$\delta_{00BB,BB} = \frac{1}{4}\theta_{00CC} \tag{20}$$

$$\delta_{00BB,B'B'} = \frac{1}{4}\theta_{00CC'} + \frac{1}{2}\gamma_{00C,C'C'} + \frac{1}{4}\delta_{00CC,C'C'} \tag{21}$$

$$\delta_{00BB',BB'} = \frac{1}{4}\delta_{00CC',CC'} \tag{22}$$

$$\delta_{00BB,B'B''} = \frac{1}{2}\gamma_{00C,C'C''} + \frac{1}{2}\delta_{00CC,C'C''} \tag{23}$$

$$\delta_{00\overline{BB}',\overline{BB}''} = \frac{1}{2}\gamma_{00C,C'C''} + \frac{1}{2}\delta_{00CC,C'C''} \tag{24}$$

$$\delta_{00BB',B''B'''} = \delta_{00CC',C''C'''} \tag{25}$$

These equations may be manipulated more easily in matrix form. For the selfed generation of cycle n we write the twelve measures needed as a vector $\underline{u}_{(1,n)}$

$$\underline{u}'_{(1,n)} = [\theta_{00BB},\ \theta_{00BB'},\ \gamma_{00B,BB},\ \gamma_{00B,B'B'},\ \gamma_{00B,\overline{BB}'},\ \gamma_{00B,B'B''},\ \delta_{00BB,BB},\ \delta_{00BB,B'B'},\ \delta_{00BB',BB'},\ \delta_{00BB,B'B''},\ \delta_{00\overline{BB}',\overline{BB}''},\ \delta_{00BB',B''B'''}]$$

and the ten measures needed for the intercross generation of cycle n-1 are written as $\underline{v}_{(2,n-1)}$ or as $\underline{v}_{(0,n)}$

$$\underline{v}'_{(2,n-1)} = [\theta_{00CC},\ \theta_{00CC'},\ \gamma_{00C,C'C'},\ \gamma_{00C,\overline{CC}'},\ \gamma_{00C,C'C''},\ \delta_{00CC,C'C'},\ \delta_{00CC',CC'},\ \delta_{00CC,C'C''},\ \delta_{00\overline{CC}',\overline{CC}''},\ \delta_{00CC',C''C'''}]\ .$$

Equations (14) - (25) become

$$\underline{u}_{(1,n)} = \Psi\,\underline{v}_{(2,n-1)} = \Psi\,\underline{v}_{(0,n)} \tag{26}$$

where the 12×10 matrix Ψ has elements defined by those equations.

Sampling Probabilities for Two-Locus Case

The previous section showed that account must be taken of gametes received by two, three or four individuals in generation 1 of a cycle. The four genes of interest on these gametes can be traced back to genes on up to four gametes received by individuals in generation 2 of the previous cycle. Sampling probabilities are needed for these intercross gametes. To take proper account of the restrictions on mating in the intercross phase, we define sampling probabilities for all 2m gametes received by m individuals ($m = 2, 3, 4$). Appropriate sums of these probabilities are then taken to give the required probabilties for up to four gametes.

The sampling probabilities are given in Table 3. The derivations of these values is illustrated by reference to P_{21111}, the probability that the six gametes received by three of the N selected members of the intercross generation descend from five members of the selected self generation in the previous cycle in such a way that one of the five gives two gametes. For the unrestricted random selection case, we can consider the six gametes received by any three of the M members of the whole intercross generation so that P_{21111} will have a denominator of $\binom{M}{3}$. For the numerator we note that there are $\binom{N}{5}$ ways of choosing the five members of the self generation and $\binom{5}{1}$ ways of choosing one of them to give two gametes. There are then $\binom{4}{2}$ ways of choosing two from the remaining four individuals to provide the gametes which unite with the two from the first individual chosen and so

$$\begin{aligned} P_{21111} &= \binom{5}{1}\binom{4}{2}\binom{N}{5}/\binom{M}{3} \qquad && N \geqslant 5 \\ &= 0 \,. && N < 5 \end{aligned}$$

We are unable to express the probabilities for the restricted selection schemes in terms of a_i, the numbers of gametes contributed to the selected intercross individuals by the ith selected selfed individual, as did Cain and Hinkelmann. When the probabilities involve a choice of more than one member of the self generation (in contrast to the one needed for P_{211} in the one-locus case), we need knowledge of the mating pattern between members of this generation. Such knowledge is not provided by the a_i.

For either restricted selection scheme we can choose the three intercross individuals for which P_{21111} is defined in $\binom{N}{3}$ ways. In the minimum inbreeding case two of these three can be chosen to have a common parent in N ways. The third can be chosen not to have a parent in common with either of the first two in (N-4) ways. These three individuals then receive six gametes satisfying the definition of P_{21111} so that

$$\begin{aligned} P_{21111} &= N(N-4)/\binom{N}{3} \qquad && N \geqslant 5 \\ &= 0 \,. && N < 5 \end{aligned}$$

In the maximum inbreeding case the common parent for two out of the selected intercross individuals must be the selfed individual which contributes (N-1) gametes. Two out of these (N-1) gametes must unite with gametes from the two selfed individuals which contribute two gametes, which means that the two selected intercross individuals with a common parent can be chosen from (N-3) such individuals. The third individual for which P_{21111} is specified is then determined and

$$\begin{aligned} P_{21111} &= \binom{N-3}{2}/\binom{N}{3} \qquad && N \geqslant 5 \\ &= 0 \,. && N < 5 \end{aligned}$$

We make a restriction in the case of minimum inbreeding not mentioned by Cain and Hinkelmann. We will assume that the minimum inbreeding scheme, in the intercross phase, is equivalent to circular mating (Kimura and Crow 1963) for N individuals. This means, for example, that it is not possible to select two sets of N/2 offspring that have disjoint sets of N/2 parents.

The notation for the sampling probabilities in Table 3 has been extended in two places to prevent ambiguities. We use $P_{22211(i)}$ and $P_{22211(ii)}$ according to whether or not each of the three individuals giving two gametes mates with the other two. Similarly $P_{221111(i)}$ and $P_{221111(ii)}$ distinguish the cases of whether or not the two individuals giving two gametes mate.

In Table 3 also, and for the remainder of this paper, we restrict attention to the case of $N \geqslant 4$. When sampling probabilities involve gametes from r parents, we obviously assume that $N \geqslant r$, or that the probability is zero if $r > N$.

Intercross Phase Expansions for Two-Locus Case

The intercross phase expansions amalgamate two steps. After expanding through the selfing phase of

Table 3. Gametic sampling probabilities†

Numbers of			Selection Scheme		
Gametes(2m)	Parents(r)	Symbol	Unrestricted*	Minimum Inbreeding**	Maximum Inbreeding***
4	3	P_{211}	$\binom{3}{1}$	1	$(N^2 - 3N + 6)/2$
	4	P_{1111}	$\binom{3}{1}$	$\frac{1}{2}\binom{N-3}{1}$	$\binom{N-3}{1}$
6	3	P_{222}	1	0	1
	4	P_{2211}	$\binom{4}{2}\binom{2}{1}$	1	$2\binom{N-3}{1}$
	4	P_{3111}	$\binom{4}{1}$	0	$\binom{N-1}{3}$
	5	P_{21111}	$\binom{5}{1}\binom{4}{2}$	$\binom{N-4}{1}$	$\binom{N-3}{2}$
	6	P_{111111}	$\binom{5}{1}\binom{3}{1}$	$\frac{1}{3}\binom{N-4}{2}$	0
8	4	P_{2222}	$\binom{3}{1}$	0(1 if N=4)	0
	4	P_{3221}	$\binom{4}{1}\binom{3}{1}$	0	$\binom{N-3}{1}$
	5	$P_{22211(i)}$	$\binom{5}{3}$	0	0
	5	$P_{22211(ii)}$	$\binom{5}{3}\binom{3}{1}\binom{2}{1}$	1	0
	5	P_{32111}	$\binom{5}{1}\binom{4}{1}\binom{3}{1}$	0	$2\binom{N-3}{2}$
	5	P_{41111}	$\binom{5}{1}$	0	$\binom{N-1}{4}$
	6	P_{311111}	$\binom{6}{1}\binom{5}{3}$	0	$\binom{N-3}{3}$
	6	$P_{221111(i)}$	$\binom{6}{2}\binom{4}{2}$	$\binom{N-5}{1}$	0
	6	$P_{221111(ii)}$	$\binom{6}{2}\binom{4}{1}\binom{3}{1}$	$\frac{1}{2}\binom{N-5}{1}$	0
	7	P_{211111}	$\binom{7}{1}\binom{6}{2}\binom{3}{1}$	$\binom{N-5}{2}$	0
	8	$P_{11111111}$	$\binom{7}{1}\binom{5}{1}\binom{3}{1}$	$\frac{1}{4}\binom{N-5}{3}$	0

*divide by $\binom{M}{m}/\binom{N}{r}$ **divide by $\binom{N}{m}/N$

***divide by $\binom{N}{m}$

†Assumes that $N \geq r$ in any line and that $N \geq 4$.

cycle n, we had a set of measures $\underline{v}_{(2,n-1)}$ involving gametes from members of the intercross generation of the previous cycle. These gametes must first be related to gametes received by that intercross generation and then to gametes from the preceeding self generation (i.e., to $\underline{u}_{(1,n-1)}$). The first step takes account of recombination and the second step of gametic sampling.

The simplest expansion is for the digametic measure θ_{00CC}. Double non-identity can be maintained only if the four genes on the two gametes from C descend from four distinct genes on two gametes received by C. This occurs with probability $(1+\lambda^2)/4$ and these last two gametes necessarily descend from distinct individuals D, D' so that

$$\theta_{00CC} = \frac{1+\lambda^2}{4}\,\theta_{00DD'} \; . \tag{27}$$

The two gametes for which the other digametic measure $\theta_{00CC'}$ is defined trace back to two, three or four gametes received by C and C', and then back to two, three or four distinct individuals D, D', D'' and D'''. When both gametes from C, C' are recombinant and trace back to four gametes from the parents of C and C', the sampling probabilities in Table 3 may be used directly. If either or both of the gametes from C, C' are parental though, various sums of those probabilities must be used. New notation is needed for these marginal probabilities and we say that ${}_mQ_{t_1t_2\ldots t_s}$ is for a subset of q of the 2m gametes received by m members of generation 2 (offspring) of a cycle from generation 1 of that cycle (parents). The q gametes are from s of the parents in such a way that the ith parent contributed t_i gametes. This requires that the t_i sum to q and that $q \geqslant m$. We need only consider cases with $q \leqslant 4$ since we are never concerned with more than four genes, and hence never more than four gametes. All of the marginal probabilities required are shown in Table 4.

The expansion for $\theta_{00CC'}$ is then

$$\begin{aligned}\theta_{00CC'} = {} & \left(\frac{1+\lambda}{2}\right)^2 ({}_2Q_2\,\theta_{00DD} + {}_2Q_{11}\,\theta_{00DD'}) \\ & + \frac{1-\lambda^2}{2}({}_2Q_{21}\,\gamma_{00D,\overline{DD'}} + {}_2Q_{111}\,\gamma_{00D,D'D''}) \\ & + \left(\frac{1-\lambda}{2}\right)^2 [{}_2Q_{211}(\delta_{00DD,D'D''} + \\ & + \delta_{00DD',DD''})/2 + {}_2Q_{1111}\,\delta_{00DD',D''D'''}] \; .\end{aligned} \tag{28}$$

Use has been made here of some equalities among quadrigametic measures

$$\delta_{00VW,YZ} = \delta_{00VZ,YW} = \delta_{00WV,ZY} \; .$$

Equation (28) also provides the expansions for $\gamma_{00C,C'C'}$ and $\delta_{00CC,C'C'}$. For the trigametic measure the three recombination coefficients are $(1+\lambda)/4$, $1/2$ and $(1-\lambda)/4$ while for the quadrigametic measure they are 1/4, 1/2 and 1/4.

In expanding $\gamma_{00C,\overline{CC'}}$ we must trace back to three gametes to preserve double non-identity

$$\begin{aligned}\gamma_{00C,\overline{CC'}} = {} & \frac{1}{2}[{}_2Q_{21}(\gamma_{00D,\overline{DD'}} + \gamma_{00D,D'D'})/2 + \\ & + {}_2Q_{111}\,\gamma_{00D,D'D''}] \; .\end{aligned} \tag{29}$$

For the final trigametic measure we trace back to three or four gametes

$$\begin{aligned}\gamma_{00C,C'C''} = {} & \frac{1+\lambda}{2}[{}_3Q_3\,\gamma_{00D,DD} + {}_3Q_{21}(2\gamma_{00D,\overline{DD'}} + \\ & + \gamma_{00D,D'D'})/3 + {}_3Q_{111}\,\gamma_{00D,D'D''}] \\ & + \frac{1-\lambda}{2}[{}_3Q_{31}\,\delta_{00DD,\overline{DD'}} + \\ & + {}_3Q_{22}(\delta_{00DD,D'D'} + \delta_{00DD',DD'})/2 \\ & + \left(\frac{1}{2}P_{222} + \frac{1}{4}P_{3111} + \frac{5}{12}P_{2211} + \right. \\ & \left. + \frac{1}{4}P_{21111}\right)\delta_{00DD,D'D''} \\ & + \left(\frac{1}{4}P_{222} + \frac{1}{4}P_{3111} + \frac{1}{4}P_{2211} + \right. \\ & \left. + \frac{1}{6}P_{21111}\right)\delta_{00DD',DD''} \\ & + {}_3Q_{1111}\,\delta_{00DD',D''D'''}] \; .\end{aligned} \tag{30}$$

If the recombination coefficients are changed from $(1+\lambda)/2$, $(1-\lambda)/2$ in (30) to 1/2, 1/2 then (30) provides the expansion for $\delta_{00CC,C'C''}$. The expansions for the remaining three quadrigametic measures are now listed.

$$\begin{aligned}\delta_{00CC',CC'} = {} & \frac{1}{4}({}_2Q_{211}\,\delta_{00DD,D'D''} + \\ & + {}_2Q_{1111}\,\delta_{00DD',D''D'''}) \; .\end{aligned} \tag{31}$$

$$\begin{aligned}\delta_{00CC',CC''} = {} & \frac{1}{2}[{}_3Q_{31}\,\delta_{00DD,DD'} + {}_3Q_{22}\,\delta_{00DD,D'D'} \\ & + \left(\frac{1}{2}P_{222} + \frac{1}{2}P_{3111} + \frac{1}{2}P_{2211} + \right. \\ & \left. + \frac{1}{3}P_{21111}\right)\delta_{00DD,D'D''} \\ & + \left(\frac{1}{4}P_{222} + \frac{1}{6}P_{2211} + \right. \\ & \left. + \frac{1}{12}P_{21111}\right)\delta_{00DD',DD''} + \\ & + {}_3Q_{1111}\,\delta_{00DD',D''D'''}] \; .\end{aligned} \tag{32}$$

Table 4. Marginal gametic sampling probabilities

Gametic Subset Numbers of				Marginal Probabilities
Offspring	Gametes	Parents		
2	2	1	$_2Q_2$	$= \frac{1}{4} P_{211}$
		2	$_2Q_{11}$	$= \frac{3}{4} P_{211} + P_{1111}$
	3	2	$_2Q_{21}$	$= \frac{1}{2} P_{211}$
		3	$_2Q_{111}$	$= \frac{1}{2} P_{211} + P_{1111}$
	4	3	$_2Q_{211}$	$= P_{211}$
		4	$_2Q_{1111}$	$= P_{1111}$
3	3	1	$_3Q_3$	$= \frac{1}{8} P_{3111}$
		2	$_3Q_{21}$	$= \frac{1}{2} P_{2211} + \frac{1}{4} P_{21111} + \frac{3}{4} P_{222} + \frac{3}{8} P_{3111}$
		3	$_3Q_{111}$	$= P_{111111} + \frac{3}{4} P_{21111} + \frac{1}{2} P_{2211} + \frac{1}{4} P_{222} + \frac{1}{2} P_{3111}$
	4	2	$_3Q_{31}$	$= \frac{1}{4} P_{3111}$
		2	$_3Q_{22}$	$= \frac{1}{4} P_{222} + \frac{1}{12} P_{2211}$
		3	$_3Q_{211}$	$= \frac{1}{2} P_{3111} + \frac{3}{4} P_{222} + \frac{2}{3} P_{2211} + \frac{5}{12} P_{21111}$
		4	$_3Q_{1111}$	$= \frac{1}{4} P_{3111} + \frac{1}{4} P_{2211} + \frac{7}{12} P_{21111} + P_{111111}$
4	4	1	$_4Q_4$	$= \frac{1}{16} P_{41111}$
		2	$_4Q_{22}$	$= \frac{1}{8} P_{3221} + \frac{1}{8} P_{2222} + \frac{1}{16} P_{32111} + \frac{1}{16} P_{22211(ii)}$
				$+ \frac{1}{16} P_{221111(ii)}$
		2	$_4Q_{31}$	$= \frac{1}{4} P_{41111} + \frac{1}{8} P_{3221} + \frac{1}{8} P_{32111} + \frac{1}{8} P_{311111}$
		3	$_4Q_{211}$	$= \frac{3}{8} P_{41111} + \frac{5}{8} P_{3221} + \frac{3}{4} P_{2222} + \frac{1}{2} P_{32111}$
				$+ \frac{3}{4} P_{22211(i)} + \frac{5}{8} P_{22211(ii)} + \frac{3}{8} P_{311111}$
				$+ \frac{3}{8} P_{221111(ii)} + \frac{1}{2} P_{221111(i)} + \frac{1}{4} P_{2111111}$
		4	$_4Q_{1111}$	$= \frac{5}{16} P_{41111} + \frac{1}{8} P_{3221} + \frac{1}{8} P_{2222} + \frac{5}{16} P_{32111}$
				$+ \frac{1}{4} P_{22211(i)} + \frac{5}{16} P_{22211(ii)} + \frac{1}{2} P_{311111}$
				$+ \frac{9}{16} P_{221111(ii)} + \frac{1}{2} P_{221111(i)} + \frac{3}{4} P_{2111111}$
				$+ P_{11111111}$

$$
\begin{aligned}
\delta_{00CC',C''C'''} = {}& {}_4Q_4\, \delta_{00DD,DD} + {}_4Q_{31}\, \delta_{00DD,\overline{DD'}} + \\
& + {}_4Q_{22}(2\delta_{00D,D'D'} + \delta_{00DD',DD'})/3 \\
& + {}_4Q_{211}(2\delta_{00DD,D'D''} + \delta_{00DD',DD''})/3 \\
& + {}_4Q_{1111}\, \delta_{00DD',D''D'''} \,. \qquad (33)
\end{aligned}
$$

All of the intercross expansions may now be collected together as

$$\underline{v}_{(2,n-1)} = \Omega\, \underline{u}_{(1,n-1)} \qquad (34)$$

where the 10×12 matrix Ω has elements defined by Equations (27)-(33). A set of transition equations between successive self generations or between successive intercross generations is now very easily obtained as

$$\underline{u}_{(1,n)} = \Psi\, \Omega\, \underline{u}_{(1,n-1)} \qquad (35)$$

$$\underline{v}_{(2,n)} = \Omega\, \Psi\, \underline{v}_{(2,n-1)} \,. \qquad (36)$$

Discussion

Numerical results obtained by using the transition Equations (35), (36) are shown in Tables 5, 6 and 7. As mentioned above, the initial generation is assumed to be non-inbred and unrelated so that for these initial individuals, prior to any selfing,

$$\underline{v}'_{(0,1)} = \left[\frac{1+\lambda^2}{4}, 1, 1, 1/2, 1, 1, 1/4, 1, 1/4, 1\right]$$

and $\underline{u}_{(1,1)}$ follows from equation (26).

As shown in these tables, linkage has a complicated effect on inbreeding at two loci. For complete

Table 5. Progress of the two-locus inbreeding coefficient (F_{11}) in intercross generation and the corresponding value of identity disequilibrium (η_{11}) under random selection scheme for varying population sizes (N) and varying linkage parameters (λ). Individuals in the source population are non-inbred and unrelated

			Recurrent Cycle Number											
N	λ		1	2	3	4	5	6	7	8	9	10	20	100
2	1.00	F_{11}	.000	.375	.563	.703	.797	.861	.905	.935	.956	.970	.999	1.000
		η_{11}	.000	.234	.246	.209	.162	.119	.086	.061	.042	.029	.001	.000
	0.75	F_{11}	.000	.232	.394	.549	.671	.764	.833	.882	.918	.943	.999	1.000
		η_{11}	.000	.092	.078	.055	.036	.022	.013	.008	.004	.003	.000	.000
	0.25	F_{11}	.000	.145	.320	.497	.636	.743	.820	.875	.914	.941	.999	1.000
		η_{11}	.000	.005	.003	.002	.001	.001	.000	.000	.000	.000	.000	.000
	0.00	F_{11}	.000	.141	.316	.494	.635	.742	.820	.875	.914	.941	.999	1.000
		η_{11}	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
3	1.00	F_{11}	.000	.188	.328	.445	.542	.622	.688	.742	.787	.824	.974	1.000
		η_{11}	.000	.152	.221	.247	.248	.235	.215	.191	.168	.145	.025	.000
	0.75	F_{11}	.000	.112	.194	.278	.362	.442	.517	.585	.646	.700	.950	1.000
		η_{11}	.000	.077	.086	.080	.068	.055	.044	.034	.027	.020	.001	.000
	0.25	F_{11}	.000	.048	.116	.205	.299	.390	.476	.553	.621	.680	.949	1.000
		η_{11}	.000	.013	.009	.007	.005	.003	.003	.002	.001	.001	.000	.000
	0.00	F_{11}	.000	.035	.108	.198	.294	.387	.473	.551	.620	.679	.949	1.000
		η_{11}	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000

(continued)

Table 5. (continued)

			Recurrent Cycle Number											
N	λ		1	2	3	4	5	6	7	8	9	10	20	100
4	1.00	F_{11}	.000	.150	.270	.374	.462	.539	.604	.660	.708	.750	.946	1.000
		η_{11}	.000	.128	.197	.234	.249	.249	.239	.224	.207	.188	.051	.000
	0.75	F_{11}	.000	.090	.156	.222	.289	.355	.420	.481	.539	.592	.897	1.000
		η_{11}	.000	.067	.083	.083	.075	.065	.055	.046	.038	.031	.002	.000
	0.25	F_{11}	.000	.038	.086	.151	.223	.297	.370	.440	.505	.565	.895	1.000
		η_{11}	.000	.016	.014	.011	.009	.007	.006	.004	.003	.003	.000	.000
	0.00	F_{11}	.000	.028	.077	.143	.216	.292	.366	.437	.503	.563	.894	1.000
		η_{11}	.000	.006	.004	.003	.003	.002	.002	.001	.001	.001	.000	.000
10	1.00	F_{11}	.000	.068	.130	.188	.242	.293	.340	.384	.425	.463	.730	.999
		η_{11}	.000	.064	.113	.153	.184	.207	.224	.237	.244	.249	.197	.001
	0.75	F_{11}	.000	.041	.070	.096	.122	.148	.175	.203	.232	.262	.551	.998
		η_{11}	.000	.036	.053	.061	.063	.062	.060	.056	.052	.047	.018	.000
	0.25	F_{11}	.000	.017	.031	.049	.071	.097	.126	.156	.189	.222	.536	.998
		η_{11}	.000	.013	.014	.014	.013	.012	.010	.009	.008	.007	.002	.000
	0.00	F_{11}	.000	.013	.025	.043	.066	.092	.121	.152	.185	.218	.535	.998
		η_{11}	.000	.008	.009	.008	.007	.006	.006	.005	.005	.004	.001	.000
25	1.00	F_{11}	.000	.029	.057	.084	.110	.135	.160	.184	.207	.230	.424	.943
		η_{11}	.000	.028	.053	.077	.098	.117	.134	.150	.164	.177	.244	.054
	0.75	F_{11}	.000	.017	.029	.039	.047	.055	.063	.071	.079	.088	.203	.890
		η_{11}	.000	.016	.026	.032	.035	.037	.037	.037	.036	.035	.023	.000
	0.25	F_{11}	.000	.007	.001	.015	.020	.026	.033	.041	.050	.059	.183	.890
		η_{11}	.000	.007	.008	.008	.008	.008	.008	.007	.007	.007	.004	.000
	0.00	F_{11}	.000	.005	.009	.012	.017	.023	.030	.038	.047	.057	.182	.890
		η_{11}	.000	.005	.005	.005	.005	.005	.005	.004	.004	.004	.002	.000
100	1.00	F_{11}	.000	.007	.015	.022	.029	.037	.044	.051	.058	.065	.132	.521
		η_{11}	.000	.007	.015	.022	.029	.035	.042	.048	.054	.061	.114	.250
	0.75	F_{11}	.000	.004	.008	.010	.011	.013	.014	.015	.016	.017	.029	.275
		η_{11}	.000	.004	.007	.009	.011	.011	.012	.012	.012	.012	.011	.004
	0.25	F_{11}	.000	.002	.003	.003	.004	.004	.005	.005	.006	.007	.020	.272
		η_{11}	.000	.002	.002	.003	.003	.003	.003	.003	.003	.003	.002	.001
	0.00	F_{11}	.000	.001	.002	.002	.003	.003	.004	.004	.005	.006	.019	.272
		η_{11}	.000	.001	.002	.002	.002	.002	.002	.002	.002	.002	.001	.000

Table 6. Progress of the two-locus inbreeding coefficient (F_{11}) in intercross generation and the corresponding value of identity disequilibrium (η_{11}) under minimum inbreeding selection scheme for varying population sizes (N) and varying linkage parameters (λ). Individuals in the source population are non-inbred and unrelated

			Recurrent Cycle Number											
N	λ		1	2	3	4	5	6	7	8	9	10	20	100
4	1.00	F_{11}	.000	.125	.229	.321	.402	.474	.536	.592	.641	.683	.912	1.000
		η_{11}	.000	.109	.177	.218	.240	.249	.249	.242	.230	.216	.081	.000
	0.75	F_{11}	.000	.075	.128	.180	.234	.289	.344	.398	.451	.501	.835	1.000
		η_{11}	.000	.059	.076	.077	.072	.065	.056	.048	.041	.034	.005	.000
	0.25	F_{11}	.000	.032	.067	.115	.171	.232	.294	.355	.414	.470	.831	1.000
		η_{11}	.000	.016	.014	.012	.009	.007	.006	.005	.004	.003	.000	.000
	0.00	F_{11}	.000	.023	.059	.108	.166	.227	.290	.352	.412	.468	.830	1.000
		η_{11}	.000	.008	.006	.005	.004	.003	.002	.002	.001	.001	.000	.000
10	1.00	F_{11}	.000	.042	.081	.119	.155	.190	.223	.255	.286	.315	.550	.984
		η_{11}	.000	.040	.075	.105	.131	.154	.173	.190	.204	.216	.248	.016
	0.75	F_{11}	.000	.025	.042	.056	.069	.082	.095	.109	.124	.139	.323	.969
		η_{11}	.000	.023	.036	.042	.045	.046	.045	.044	.042	.040	.021	.000
	0.25	F_{11}	.000	.011	.017	.024	.034	.045	.058	.073	.088	.106	.305	.969
		η_{11}	.000	.009	.010	.010	.010	.009	.008	.008	.007	.006	.003	.000
	0.00	F_{11}	.000	.008	.013	.020	.030	.041	.055	.069	.086	.103	.304	.969
		η_{11}	.000	.006	.007	.006	.006	.005	.005	.005	.004	.004	.002	.000
25	1.00	F_{11}	.000	.016	.031	.046	.061	.075	.090	.104	.118	.132	.258	.788
		η_{11}	.000	.015	.030	.044	.057	.070	.082	.093	.104	.114	.191	.167
	0.75	F_{11}	.000	.009	.016	.021	.024	.028	.031	.034	.037	.040	.084	.623
		η_{11}	.000	.009	.015	.018	.021	.022	.023	.023	.023	.022	.018	.002
	0.25	F_{11}	.000	.004	.006	.007	.009	.011	.013	.015	.018	.022	.069	.621
		η_{11}	.000	.004	.005	.005	.005	.005	.005	.005	.004	.004	.003	.000
	0.00	F_{11}	.000	.003	.004	.005	.007	.009	.011	.014	.017	.020	.068	.621
		η_{11}	.000	.003	.003	.003	.003	.003	.003	.003	.003	.003	.002	.000
100	1.00	F_{11}	.000	.004	.008	.011	.015	.019	.023	.026	.030	.034	.070	.313
		η_{11}	.000	.004	.008	.011	.015	.018	.022	.026	.029	.032	.065	.215
	0.75	F_{11}	.000	.002	.004	.005	.006	.006	.007	.007	.007	.008	.011	.101
		η_{11}	.000	.002	.004	.005	.006	.006	.006	.006	.007	.007	.006	.004
	0.25	F_{11}	.000	.001	.001	.002	.002	.002	.002	.002	.002	.003	.006	.099
		η_{11}	.000	.001	.001	.001	.001	.001	.001	.001	.001	.001	.001	.001
	0.00	F_{11}	.000	.001	.001	.001	.001	.001	.001	.002	.002	.002	.006	.098
		η_{11}	.000	.001	.001	.001	.001	.001	.001	.001	.001	.001	.001	.000

Table 7. Progress of the two-locus inbreeding coefficient (F_{11}) in intercross generation and the corresponding value of identity disequilibrium (η_{11}) under maximum inbreeding selection scheme for varying population sizes (N) and varying linkage parameters (λ). Individuals in the source population are non-inbred and unrelated

			Recurrent Cycle Number											
N	λ		1	2	3	4	5	6	7	8	9	10	20	100
4	1.00	F_{11}	.000	.156	.280	.386	.476	.554	.619	.675	.723	.764	.952	1.000
		η_{11}	.000	.132	.202	.237	.249	.247	.236	.219	.200	.180	.046	.000
	0.75	F_{11}	.000	.093	.163	.233	.302	.371	.438	.501	.559	.613	.909	1.000
		η_{11}	.000	.069	.085	.084	.075	.065	.054	.045	.036	.029	.003	.000
	0.25	F_{11}	.000	.040	.092	.160	.236	.313	.389	.460	.526	.586	.907	1.000
		η_{11}	.000	.015	.013	.011	.009	.007	.005	.004	.003	.003	.000	.000
	0.00	F_{11}	.000	.029	.082	.152	.229	.308	.385	.457	.524	.584	.906	1.000
		η_{11}	.000	.005	.004	.003	.002	.002	.001	.001	.001	.001	.000	.000
10	1.00	F_{11}	.000	.158	.283	.390	.481	.558	.624	.680	.728	.769	.954	1.000
		η_{11}	.000	.133	.203	.238	.250	.247	.235	.218	.198	.178	.044	.000
	0.75	F_{11}	.000	.095	.169	.242	.314	.384	.451	.513	.571	.624	.913	1.000
		η_{11}	.000	.069	.089	.090	.083	.072	.061	.051	.041	.033	.003	.000
	0.25	F_{11}	.000	.040	.096	.166	.243	.321	.397	.469	.535	.594	.910	1.000
		η_{11}	.000	.015	.015	.014	.012	.010	.008	.006	.005	.004	.000	.000
	0.00	F_{11}	.000	.030	.085	.156	.234	.314	.392	.464	.531	.592	.910	1.000
		η_{11}	.000	.005	.004	.004	.003	.002	.002	.002	.001	.001	.000	.000
25	1.00	F_{11}	.000	.174	.307	.420	.514	.593	.659	.715	.761	.800	.966	1.000
		η_{11}	.000	.144	.213	.244	.250	.241	.225	.204	.182	.160	.033	.000
	0.75	F_{11}	.000	.104	.186	.267	.346	.422	.492	.557	.616	.669	.935	1.000
		η_{11}	.000	.074	.092	.091	.082	.070	.058	.047	.037	.029	.002	.000
	0.25	F_{11}	.000	.044	.109	.189	.275	.360	.441	.516	.583	.643	.933	1.000
		η_{11}	.000	.014	.014	.013	.010	.008	.007	.005	.004	.003	.000	.000
	0.00	F_{11}	.000	.033	.097	.178	.266	.353	.436	.511	.580	.640	.933	1.000
		η_{11}	.000	.002	.002	.002	.002	.001	.001	.001	.001	.001	.000	.000
100	1.00	F_{11}	.000	.184	.323	.439	.535	.614	.680	.735	.780	.818	.972	1.000
		η_{11}	.000	.150	.219	.246	.249	.237	.218	.195	.171	.149	.027	.000
	0.75	F_{11}	.000	.110	.197	.283	.366	.445	.516	.584	.643	.696	.947	1.000
		η_{11}	.000	.076	.093	.091	.080	.067	.055	.044	.034	.027	.002	.000
	0.25	F_{11}	.000	.047	.117	.204	.295	.385	.469	.545	.612	.671	.945	1.000
		η_{11}	.000	.013	.013	.011	.009	.007	.006	.004	.003	.003	.001	.000
	0.00	F_{11}	.000	.035	.105	.193	.286	.378	.463	.541	.609	.669	.945	1.000
		η_{11}	.000	.001	.001	.001	.001	.000	.000	.000	.000	.000	.000	.000

linkage, $\lambda = 1$, the Eqs.(35), (36) do reduce correctly to the appropriate one-locus results. When $\lambda = 0$, and the loci segregate independently, Cain and Hinkelmann (1970) claimed that the inbreeding coefficient $F_{11}(\lambda = 0)$ was the square of the one-locus coefficient $F_1 = F_{11}(\lambda = 1)$. This is not the case here, or whenever there is a choice of mates, and for general λ we have earlier (Weir and Cockerham 1969b) defined an identity disequilibrium $\eta_{11}(\lambda)$ by

$$\eta_{11}(\lambda) = F_{11}(\lambda) - (F_1)^2 .$$

Values for the identity disequilibrium are also shown in Tables 5, 6, 7. The quantity is positive in early generations, reaches a maximum, and decreases to zero with complete inbreeding. For completely specified pedigrees, however, such as afforded by the cases of N = 2 or N = 3, there is no identity disequilibrium.

In general, population size is seen to delay the accrual of inbreeding, and allow selection to be practised for a longer period. As N increases, the minimum and maximum inbreeding schemes become more extreme. As noted above, the maximum inbreeding scheme actually permits inbreeding to increase with N. The increasing divergence in inbreeding levels between the minimum inbreeding scheme and unrestricted random selection shows that the latter scheme falls further behind in exploiting fully the advantages of the intercross phase in this respect.

As Cain and Hinkelmann (1970, 1972) point out, the plant breeder is likely to be more concerned with homozygosity than with measures of inbreeding. If the initial population is completely heterozygous, the homozygosity by descent indicated by inbreeding measures is likely to be close to total homozygosity. It is safer to regard F_1, F_{11} as providing lower bounds on the homozygosity at one and two loci, however. A complete discussion of this problem requires knowledge of gene frequencies and would need to take into account the effects of the selection program on gene frequencies.

This paper has demonstrated the effects of linkage and population size on levels of inbreeding at one and two loci in recurrent selection schemes. The development has been straightforward and has avoided the intricacies and, hopefully, the inaccuracies of earlier treatments.

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