Theoretical and Applied Genetics 46, 201-212 (1975)

Identity Coefficients and Covariances between Relatives in a Parent-Offspring Inbreeding System*

P.L. Cornelius
Departments of Agronomy and Statistics, University of Kentucky, Lexington, Kentucky (USA)

Summary. A one-locus "operator" for a younger parent-offspring inbreeding system is obtained by a generation matrix method in which 14 "classes" of matings are defined. The eigenvalues and a set of eigenvectors for the generation matrix and, also, the general solution for the frequencies of mating classes among descendants of an original mating of genotypes ab × cd are given. The operator gives the genotypic array of descendants of a given mating an arbitrary number of generations later. Using this operator, an algorithm is developed for calculating identity coefficients between any two relatives in a possibly branching younger parent-offspring mating system. Application to obtaining covariances between relatives for a one-locus model is illustrated.

Introduction

In plant or animal breeding programs which utilize inbred lines, an important consideration is the method of inbreeding used to obtain the lines. Ordinarily the breeder will want to do some selection during the inbreeding process. Therefore, predictions of response to selection under various inbreeding systems would be an important consideration in choosing an inbreeding system. Predictions of response to selection under selfing and full-sib mating in maize (*Zea mays* L.) were made by Cornelius (1972) using methods which depend on covariances between individuals in the generation of applied selection and in the generation in which it is hoped to observe a response to the prior selection. In some cases these may be several generations apart. The mathematical expressions for the covariances depend on probabilities (coefficients of identity) of alleles being alike by descent in the individuals concerned (Cockerham, 1971; Gillois, 1965; Harris, 1964).

Parent-offspring inbreeding (with mating of offspring always to the younger parent) is impossible in an annual plant species such as maize, but could be used with an animal species or a perennial plant species. This paper deals with obtaining the identity coefficients and covariances for any given pair of relatives in a younger parent-offspring inbreeding system.

There are 15 possible "identity states" (Gillois, 1965) of allelic genes of inbred relatives. For most applications, however, it is sufficient to define nine "condensed identity states" (Jacquard, 1972; Harris, 1964; Cockerham, 1971) which, for inbred relatives X and Y, we may formalize as follows:

Identity State X	Y	Probability (Identity Coefficient)
aa	aa	δ_1
aa	bb	δ_2
aa	ab	δ_3
aa	bc	δ_4
ab	aa	δ_5
bc	aa	δ_6
ab	ab	δ_7
ab	ac	δ_8
ab	cd	δ_9

In the designation of an identity state, the allele represented by a given letter is arbitrary, letters which are the same indicate genes which are identical by descent, and unlike letters represent genes which are not identical by descent (but may or may not be alike in state). General procedures for calculating the identity coefficients have been suggested by Harris (1964), Cockerham (1971), Jacquard (1966), and Nadot and Vaysseix (1973). In regular systems of inbreeding, for cases where X and Y have the same relationship as mated individuals, obtaining their identity coefficients is just a reformulation of the generation matrix problem applied to mating types (Fisher, 1965; Kempthorne, 1957, Ch.6).

Kempthorne (1963), in discussing the role of system of mating in determining means, variances and covariances in genetic populations, introduced the concept of

---

* Journal article (74-3-73) of the Kentucky Agricultural Experiment Station published with approval of the Director.

an "operator" for a particular mating system and gave explicit expressions for random mating and selfing operator. The operator when applied to a genotype or set of genotypes generates the array of progeny. When applied m times, i.e., to the mth power, the operator generates the array of progeny after m generations of the particular system. If one obtains the appropriate operator for a given system of inbreeding, a simplified procedure can be developed for obtaining identity coefficients for any relatives in the given system. This was done by Cornelius and Dudley (1975) for the case of full-sib mating.

The explicit expression for the mth power of a full-sib mating operator may be written

$$FS^m(ab \times cd) = F_{m+1}\bar{z}_1 + (F_{m+1} - F_m)\bar{z}_2 + (1 + F_m - 2F_{m+1})\bar{z}_3 \qquad (1)$$

where

$\bar{z}_1 = (aa + bb + cc + dd)/4$

$\bar{z}_2 = (ab + cd)/2$

$\bar{z}_3 = (ac + ad + bc + bd)/4$

and F_m is the coefficient of inbreeding in the mth generation given by

$F_0 = 0$

$F_1 = 0$

$$F_m = (1 + F_{m-2} + 2F_{m-1})/4, \quad m \geq 2. \qquad (2)$$

In (1) the argument, ab × cd, is intended to mean that the operator is applied to the family generated by that mating.

Horner (1956) derived expressions for the covariances of parent and offspring and of full-sibs under younger parent-offspring inbreeding for a one-locus model restricted to two alleles at the locus. These covariances for the case of multiple alleles could readily be obtained from Fisher's (1965) work, but to obtain covariances between more distant relatives, such as grandparent-grandoffspring, uncle-nephew, or cousins in a branching system, a simple procedure for obtaining identity coefficients for any relatives in the system is useful.

This paper extends the methods of Cornelius and Dudley (1975) to the case of younger parent-offspring inbreeding and to a more general class of identity coefficients. (The previous paper dealt only with a set of 5 condensed coefficients necessary to obtain covariances between relatives.) The operator analogous to (1) is obtained and applied to the calculation of identity coefficients and obtaining covariances between any relatives in the system. The genotypic distribution of matings among descendants of a given initial mating is also obtained.

Derivation of the Younger Parent-Offspring Mating Operator

We presume that in generation zero all matings are at random and, thereafter, one (or more, thus allowing the system to branch) randomly chosen offspring is (are) always mated to the younger parent. In generation zero, which parent is actually younger is irrelevant, but we will define the "younger" generation zero parent to be the one chosen to be used again in generation 1. Let a given generation zero mating be designated ab × cd, and let ab be the genotype of the "younger" parent.

For the case of sib-mating, Cornelius and Dudley defined three sets of genotypes involving the genes a, b, c and d:

$z_1 = \{aa, bb, cc, dd\}$

$z_2 = \{ab, cd\}$

$z_3 = \{ac, ad, bc, bd\}$.

For the parent-offspring case, it will be necessary to partition sets z_1 and z_2 into disjoint subsets as follows:

$z_{11} = \{aa, bb\}$

$z_{12} = \{cc, dd\}$

$z_{21} = \{ab\}$

$z_{22} = \{cd\}$.

This leads to the following formal expression of genotypic arrays:

$\bar{z}_{11} = (aa + bb)/2$

$\bar{z}_{12} = (cc + dd)/2$

$\bar{z}_{21} = ab$

$\bar{z}_{22} = cd$

$\bar{z}_3 = (ac + ad + bc + bd)/4$

Table 1. Symbolic expression of mating classes under parent offspring inbreeding, their frequencies, and genotypic arrays of offspring

	Younger Parent	Older Parent	Frequency	Genotypic Array of Offspring from All Matings of Given Class
1.	ii ε z_{11}*	ii** ε z_{11}	f_1	$\bar{z}_{11}$
2.	ii ε z_{12}	ii ε z_{12}	f_2	$\bar{z}_{12}$
3.	ij ε z_{21}	ij ε z_{21}	f_3	$(\bar{z}_{11} + \bar{z}_{21})/2$
4.	ij ε z_3	ij ε z_3	f_4	$(\bar{z}_{11} + \bar{z}_{12} + 2\bar{z}_3)/4$
5.	ii ε z_{11}	ij ε z_{21}	f_5	$(\bar{z}_{11} + \bar{z}_{21})/2$
6.	ii ε z_{11}	ij ε z_3	f_6	$(\bar{z}_{11} + \bar{z}_3)/2$
7.	ii ε z_{12}	ij ε z_3	f_7	$(\bar{z}_{12} + \bar{z}_3)/2$
8.	ij ε z_{21}	ii ε z_{11}	f_8	$(\bar{z}_{11} + \bar{z}_{21})/2$
9.	ij ε z_3	ii ε z_{11}	f_9	$(\bar{z}_{11} + \bar{z}_3)/2$
10.	ij ε z_3	ii ε z_{12}	f_{10}	$(\bar{z}_{12} + \bar{z}_3)/2$
11.	ij ε z_{21}	ik ε z_3	f_{11}	$(\bar{z}_{11} + \bar{z}_{21} + 2\bar{z}_3)/4$
12.	ij ε z_3	ik ε z_3	f_{12}	$(\bar{z}_{12} + \bar{z}_{21} + 2\bar{z}_3)/4$
13.	ij ε z_3	ik ε z_{21}	f_{13}	$(\bar{z}_{11} + \bar{z}_{21} + 2\bar{z}_3)/4$
14.	ij ε z_{21}	kℓ ε z_{22}	f_{14}	$\bar{z}_3$

* The symbol ε is used to indicate to which set a genotype belongs and may be read "is in". For definiton of z_{11}, z_{12}, z_{21}, z_{22} and z_3, see text.

** Letters in common in younger and older parent genotypes indicate identity situations between the two parents, e.g., Mating Class 1 consists of matings of identical homozygotes (by descent) subject to the restriction that this homozygous genotype is in set z_{11}.

Cornelius and Dudley subdivided Fisher's (1965, p. 23) seven mating types* into 13 classes, such that the various possible matings within any given class are always equally frequent, but matings which are of the same type, but in different classes occur with differing frequency. For the parent-offspring case there are 14 classes of matings (Table 1). Mating Classes 1 and 2 both conform to Fisher's (1965, p. 58) mating type aa × aa; i.e., Classes 1 and 2 are disjoint sets of matings of type aa × aa; Classes 3 and 4 are disjoint sets of type ab × ab; Classes 5, 6 and 7 are disjoint sets of type aa × ab; Classes 8, 9 and 10 are disjoint sets of type ab × aa; Classes 11, 12 and 13 are disjoint sets of type ab × ac. Class 14 consists only of the given generation zero mating ab × cd and cannot occur in any later generation. It should be noted that Class 12 consists of only 2 possible matings, ac × bc and ad × bd, the mating ac × ad, for example, is impossible because after generation zero the genes c and d can never again come together in the same mating. Also, the genotype cd can never reappear, so the only need to define the set z_{22} is to characterize Class 14 and to obtain identity coefficients of descendents with the generation zero "older" parent.

Let $f_i^{(m)}$ be the frequency of the ith mating class in generation m, and let

$$\mathbf{f}^{(m)} = \left[f_1^{(m)}, f_2^{(m)}, \ldots, f_{14}^{(m)} \right]',$$

be the column vector of these frequencies. Then

$$\mathbf{f}^{(m)} = \mathbf{A}^m \mathbf{f}^{(0)}$$

where A is the 14 × 14 generation matrix (Table 2) and

$$\mathbf{f}^{(0)} = [0,0,0,0,0,0,0,0,0,0,0,0,0,1]',$$

---

* Fisher's original concept of mating type was not based on the concept of identity by descent. However, his work is valid regardless of whether the mating types represent situations of identity or merely situations of alikeness in state of genes in individuals mated. Throughout this paper a mating type should be regarded as a situation of identity.

Table 2. Generation matrix (frequencies of generation m mating classes among offspring of a given generation m-1 mating class)

Generation m Mating Class	Generation m-1 Mating Class													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14
1	1	0	0	0	1/2	1/2	0	0	0	0	0	0	0	0
2	0	1	0	0	0	0	1/2	0	0	0	0	0	0	0
3	0	0	1/2	0	0	0	0	1/2	0	0	1/4	0	0	0
4	0	0	0	1/2	0	0	0	0	1/2	1/2	0	1/4	1/4	0
5	0	0	1/2	0	0	0	0	1/2	0	0	1/4	0	0	0
6	0	0	0	1/4	0	0	0	0	1/2	0	0	0	1/4	0
7	0	0	0	1/4	0	0	0	0	0	1/2	0	1/4	0	0
8	0	0	0	0	1/2	0	0	0	0	0	0	0	0	0
9	0	0	0	0	0	1/2	0	0	0	0	0	0	0	0
10	0	0	0	0	0	0	1/2	0	0	0	0	0	0	0
11	0	0	0	0	0	0	0	0	0	0	0	1/4	1/4	0
12	0	0	0	0	0	0	0	0	0	0	0	1/4	1/4	0
13	0	0	0	0	0	0	0	0	0	0	1/2	0	0	1
14	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Table 3. Eigenvalues of **A** and a solution for $\mathbf{g}^{(0)}$ and $\mathbf{C}^{-1}$ for parent-offspring inbreeding generation matrix

Eigenvalue	$\mathbf{g}^{(0)}$	Column of $\mathbf{C}^{-1}$											
		1	2	3(4)*	5(6)*	7	8	9	10	11	12	13	14
1	1	2/3	-1/6	$-(1+\psi)/5$	$(1-4\psi)/5$	-1/4	-1/12	0	0	1/2	0	0	0
1	0	1/3	1/6	$-(1+\psi)/5$	0	1/4	1/12	0	0	0	0	0	0
ψ**	2	0	0	0	$2(3\psi-2)/5$	0	0	1	0	-1/6	-1/3	0	0
ψ'	2	0	0	$(3-2\psi)/5$	0	0	0	0	1	-1/3	1/3	0	0
ψ	1	0	0	0	$2(3\psi-2)/5$	0	0	0	0	-1/6	-1/3	0	0
ψ'	1	0	0	$(3-2\psi)/10$	0	1/4	1/4	0	0	-1/3	1/3	0	0
1/2	2	0	0	$(3-2\psi)/10$	0	-1/4	-1/4	0	0	0	0	0	0
-1/2	2	0	0	0	$(7-8\psi)/5$	0	0	-1	0	-1/6	2/3	0	1
0	0	0	0	$(3\psi-2)/5$	0	1/4	-1/4	0	-1/2	-1/3	-2/3	-1/2	-1
0	0	0	0	$(3\psi-2)/5$	0	-1/4	1/4	0	-1/2	0	0	1/2	1
1/2	2	0	0	0	0	0	0	0	0	1/3	-1/3	0	-2
-1/4	-4	0	0	0	0	0	0	0	0	1/3	-1/3	-1	-2
0	0	0	0	0	0	0	0	0	0	1/3	2/3	1	2
0	1	0	0	0	0	0	0	0	0	0	0	0	1

* Column 4 can be obtained from column 3 and column 6 from column 5 by replacing ψ with ψ'.

** $\psi = (1+\sqrt{5})/4$, $\psi' = (1-\sqrt{5})/4$.

since the given generation zero mating, by definition, is in Class 14. To obtain a solution for $\mathbf{f}^{(m)}$ we need a transformation of the type

$$\mathbf{f}^{(m)} = \mathbf{C}^{-1}\mathbf{g}^{(m)} = \mathbf{C}^{-1}(\mathbf{CAC}^{-1})^{m}\mathbf{g}^{(0)}$$

where $\mathbf{CAC}^{-1}$ is diagonal. Solutions for $\mathbf{C}^{-1}$, $\mathbf{g}^{(0)}$ and the diagonal elements of $\mathbf{CAC}^{-1}$ (which are the eigenvalues of A) are given in Table 3. The resulting general solutions for the elements of $\mathbf{f}^{(m)}$ are in Table 4.

Cornelius and Dudley (1975), in applying a similar technique to the case of sib-mating, obtained an eigenvalue, -1/4, which is not an eigenvalue of Fisher's (1965, Ch. III) generation matrix for sib-mating. The same thing happens in the present case, i.e., an eigenvalue, -1/4, is found which is not an eigenvalue of Fisher's (1965, Section 18) (or Horner's (1956)) generation matrix for parent-offspring inbreeding. This indicates that the 14 × 14 matrix contains information concerning the structure of the mating system which is not obtainable from Fisher's work.

The desired operator for parent-offspring inbreeding powered m times generates the generation m + 1 genotypic array of offspring of the given generation zero mating. This is obtained by applying the mating class frequencies to the genotypic arrays in Table 1 and collecting terms in $\bar{z}_{11}$, $\bar{z}_{12}$, $\bar{z}_{21}$, and $\bar{z}_{3}$, giving

Table 4. Frequencies of mating classes in generation m

Mating Class	Frequency
1	$F_m + u/2 - (1+v/2)/3$*
2	$2F_{m+1} - F_m - 1 + u/2 + (1+v/2)/3$
3	$6F_{m+1} - 5F_m - 1 - (u-4w)/3$
4	$2(1+3F_m - 4F_{m+1}) - 2(u+2w)/3$
5	$6F_{m+1} - 5F_m - 1 - (u-4w)/3$
6	$1+3F_m - 4F_{m+1} - u/6 + v/2 - 4w/3$
7	$1+3F_m - 4F_{m+1} - (u+v)/2$
8	$2(1+4F_m - 5F_{m+1}) - (u+8w)/3 + 0^{m}$**
9	$6F_{m+1} - 5F_m - 1 - u/6 - v/2 + 8w/3 - 0^m$
10	$6F_{m+1} - 5F_m - 1 - (u-v)/2 + 0^m$
11	$2[(u+2w)/3 - 0^m]$
12	$2[(u+2w)/3 - 0^m]$
13	$2[(u-4w)/3 + 0^m]$
14	0^m

* $u = (1/2)^m$, $v = (-1/2)^m$, $w = (-1/4)^m$ and F_m is the coefficient of inbreeding in generation m.

** $0^m \begin{cases} = 1 \text{ if } m=0 \\ = 0 \text{ if } m>0 . \end{cases}$

Table 5. Mating types, their frequencies and sets of genotypes generated by each type

Mating type	Frequency in generation n–1	z_{11}	z_{12}	z_{21}	z_{22}	z_3
1. aa × aa	$2F_n - 1 + (1/2)^{n-1}$	{aa,aa}	{aa,aa}	{aa}	{aa}	{aa,aa,aa,aa}
2. ab × ab	$1 + F_{n-1} - 2F_n - (1/2)^{n-1}$	{aa,bb}	{aa,bb}	{ab}	{ab}	{aa,ab,ab,bb}
3. aa × ab	$1 + F_{n-1} - 2F_n - (1/2)^{n-1}$	{aa,aa}	{aa,bb}	{aa}	{ab}	{aa,ab,aa,ab}
4. ab × aa	$2(F_n - F_{n-1}) - (1/2)^{n-1} + 0^{n-1}$*	{aa,bb}	{aa,aa}	{ab}	{aa}	{aa,aa,ab,ab}
5. ab × ac	$(1/2)^{n-2} - 2(0^{n-1})$	{aa,bb}	{aa,cc}	{ab}	{ac}	{aa,ac,ab,bc}
6. ab × cd	0^{n-1}	{aa,bb}	{cc,dd}	{ab}	{cd}	{ac,ad,bc,bd}

$*0^a \begin{cases} = 1 \text{ if } a = 0 \\ = 0 \text{ if } a > 0 . \end{cases}$

$$\begin{aligned} PO^m(ab \times cd) &= \{F_m/2 + [1-(-1/2)^m]/6\}\bar{z}_{11} \\ &+ \{F_{m+1} - F_m/2 - [1-(-1/2)^m]/6\}\bar{z}_{12} \\ &+ (F_{m+1} - F_m)\bar{z}_{21} + (1 + F_m - 2F_{m+1})\bar{z}_3 . \end{aligned} \quad (3)$$

The coefficients of inbreeding F_m, $m \geqslant 0$, may be obtained from equations (2) since coefficients of inbreeding by parent-offspring inbreeding follow the same recurrence relations as do coefficients of inbreeding under full-sib mating (Kempthorne, 1957, p. 83).

Some interesting comparisons of (3) with (1) can be made. The last term is exactly the same in both expressions. Comparing the second term of (1) with the third term of (3) we see that the recovery of parental genotypes occur with the same frequency in either system, but such recoveries are divided equally among genotypes ab and cd under sib-mating whereas only genotype ab is recovered in a parent-offspring system. In (1) the genotypes aa, bb, cc, and dd are equally frequent whereas in (3), except when m=0, aa and bb occur with greater frequency than cc and dd. For $m \geqslant 1$, an equivalent expression for the coefficient of $\bar{z}_{12}$ is

$$\{F_{m-1}/2 + [1-(1-1/2)^{m-1}]/6\}/2$$

which shows that the frequency of cc and dd is always half the frequency of aa and bb in the previous generation. The asymptotic distribution is $(2\bar{z}_{11} + \bar{z}_{12})/3$, i.e., when complete homozygosity is reached two-thirds of the descendants are of genotype aa or bb and one-third are cc or dd.

Given any mating in an arbitrary generation, say generation n - 1, the genotypic array of descendants from that mating in generation n+m may be obtained by applying the operator (3) to that mating. In so doing, we relax the restriction that the genes a, b, c, d be nonidentical by descent and instead let them assume the identity situation of a particular generation n - 1 mating. In particular, under parent-offspring inbreeding, the mating types, their frequencies in generation n - 1 if all matings are of type ab × cd (a, b, c, d nonidentical) in generation zero, and the sets z_{11}, z_{12}, z_{21}, z_{22}, and z_3 conditional on the identity situation of the generation n - 1 parents are as shown in Table 5.

Identity Coefficients Between Relatives

Consider two relatives, X and Y, in a possibly branching system of parent-offspring inbreeding. To obtain the identity coefficients between them it is necessary to trace their relationship to a set of parents in some generation, say generation n - 1, in which *both* parents are common ancestors of X and Y. Note that if X and Y are not generation n individuals, they will have one (the younger generation n - 1 parent used again in generation n), but not both, generation n ancestors in common. If both parents in generation n are common ancestors of X and Y, then generation n - 1 is not correctly identified. Let n + m and n + k be the indices of the generations of X and Y, respectively. In the case where X is an ancestor of Y, n - 1 will be the mating generation in which X is a younger parent. Then m will be equal to -1 and we will define $F_{-1} = -1$. The reason for doing this is that we want m = -1 to give a coefficient of unity for $\bar{z}_{21}$ in (3) and zero coefficients for $\bar{z}_{11}$, $\bar{z}_{12}$, and $\bar{z}_3$. This may at first seem illogical. However, given $F_0 = F_1 = 0$ and defining $P_n = 1 - F_n$, the recurrence relation for P_n (Kempthorne, 1957, p.84) actually generates $P_{-1} = 2$, thus giving $F_{-1} = 1$. This result, of course, has no probabilistic interpretation and the only rationale for its use is that it happens to give the desired result for m = -1 in (3) and makes it unnecessary to deal with the case of X an ancestor of Y as a special case unless X is the "older" generation zero parent. Note that, from (3) and (1) we can now define

$$PO^{-1}(ab \times cd) = ab$$

$$FS^{-1}(ab \times cd) = (ab + cd)/2.$$

For example, consider the path diagram in Fig. 1. We can summarize this diagram as follows:

Generation	Matings	Offspring
0	A × B	C, D
1	C × A	E, G
	D × A	H, I
2	E × C	J, K
	G × C	L, M
	H × D	N, Q
	I × D	R, S

Now consider the following possible choices of X and Y, the most recent mating where both parents are common ancestors of X and Y and the resulting values of n - 1, m and k.

X	Y	n-1	Generation n-1 mating	m	k
J	K	2	E × C	0	0
J	L	1	C × A	1	1
L	N	0	A × B	2	2
E	N	0	A × B	1	2
C	N	0	A × B	0	2
E	G	1	C × A	0	0
C	D	0	A × B	0	0
A	J	0	A × B	-1	2
A	C	0	A × B	-1	0
C	L	1	C × A	-1	1

Denoting the younger ancestor of X and Y in the generation n - 1 mating by A_1 and the older ancestor in that mating as A_2, the genotype of X is a random choice from the distribution of genotypes given by $PO^m(A_1 \times A_2)$. Similarly Y is randomly chosen from $PO^k(A_1 \times A_2)$. Clearly, if the genotypes of A_1 and A_2 are known or if only the state of identity between them is known, we

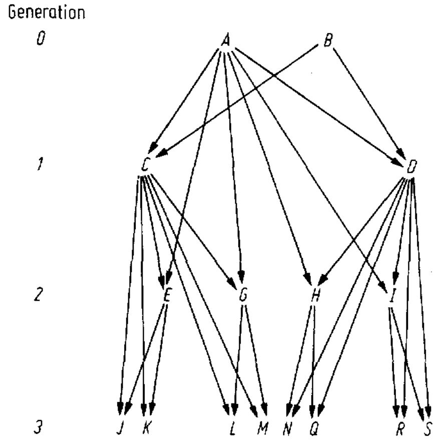

Fig. 1. Path diagram of parent-offspring inbreeding system with branching

can easily obtain the probability of any state of identity between X and Y. The usual situation, however, is that the state of identity of A_1 and A_2 is unknown, but is randomly chosen from a known or assumed distribution of identity states. In our case this would be the generation n - 1 distribution of mating types. The probability of a particular state of identity between X and Y can be obtained by finding that probability for each possible identity state for A_1 and A_2 and then taking the weighted mean of these probabilities over the distribution of identity states (mating types) of A_1 and A_2.

Let $\delta_{s(ij)M}$ be the identity coefficient, δ_s, $s = 1, 2, \ldots, 9$, conditional on X being a random member of set z_i and Y a random member of set z_j, $i,j = 11, 12, 21, 3$; z_i and z_j being conditional on a given generation n - 1 mating type, M. (Note that for the z's which have two subscripts, i or j represents the double subscript.) Form the $\delta_{s(ij)M}$ into a 4×4 matrix, $\mathbf{\Delta}_{sM}$. Removing the conditional membership of X and Y in given sets,

$$\delta_{s(\cdot,\cdot)M} = \mathbf{c}'_X \mathbf{\Delta}_{sM} \mathbf{c}_Y \tag{4}$$

where

$$\mathbf{c}'_X = \{F_m/2+[1-(-1/2)^m]/6,\ F_{m+1}-F_m/2-[1-(-1/2)^m]/6,\ F_{m+1}-F_m,\ 1+F_m-2F_{m+1}\} \tag{5}$$

and $\mathbf{c}_Y$ has the same form as $\mathbf{c}_X$ with m replaced by k. Finally, removing the conditioning on mating type,

$$\delta_s = \sum_{M=1}^{6} f_M^{(n-1)} \mathbf{c}'_X \mathbf{\Delta}_{sM} \mathbf{c}_Y = \mathbf{c}'_X \mathbf{\Delta}_s^{(n)} \mathbf{c}_Y \tag{6}$$

where $f_M^{(n-1)}$ is the frequency of mating type M in generation n-1 (Table 5), and

$$\mathbf{\Delta}_s^{(n)} = \sum_{M=1}^{6} f_M^{(n-1)} \mathbf{\Delta}_{sM}. \tag{7}$$

We will denote the (i,j)th element of $\mathbf{\Delta}_s^{(n)}$ by $\delta_{s(ij)}^{(n)}$.

The $\delta_{s(ij)M}$ can be written down by inspection of Table 5. For example for $i = 11$, $j = 11$, we have

Mating type (M)	$\delta_{1(11,11)M}$	$\delta_{2(11,11)M}$
1. aa × aa	1	0
2. ab × ab	1/2	1/2
3. aa × ab	1	0
4. ab × aa	1/2	1/2
5. ab × ac	1/2	1/2
6. ab × cd	1/2	1/2

and $\delta_{s(11,11)M} = 0$ for $s = 3, \ldots, 9$ for all M.

Taking means over the generation n-1 distribution of mating types, we get

$$\delta_{1(11,11)}^{(n)} = (1 + F_{n-1})/2$$

$$\delta_{2(11,11)}^{(n)} = (1 - F_{n-1})/2$$

$$\delta_{s(11,11)}^{(n)} = 0,\ s = 3, \ldots, 9.$$

All of the elements of the $\mathbf{\Delta}_s^{(n)}$ matrices are found in this manner. The resulting formulae are given in the Appendix. The matrices $\mathbf{\Delta}_1^{(n)}$, $\mathbf{\Delta}_2^{(n)}$, $\mathbf{\Delta}_7^{(n)}$, $\mathbf{\Delta}_8^{(n)}$, and $\mathbf{\Delta}_9^{(n)}$ are symmetric, whereas $\mathbf{\Delta}_3^{(n)}$ and $\mathbf{\Delta}_4^{(n)}$ are the transposes of $\mathbf{\Delta}_5^{(n)}$ and $\mathbf{\Delta}_6^{(n)}$ respectively.

The δ's for the case where X is the "older" generation zero parent and Y is a generation k+1 offspring are not obtainable from (6). However these are easily obtained from (3) as

$$\delta_1 = \delta_2 = \delta_3 = \delta_4 = \delta_7 = 0$$

$$\delta_6 = F_k/2 + [1 - (-1/2)^k]/6$$

$$\delta_5 = F_{k+1} - \delta_6$$

$$\delta_8 = 1 + F_k - 2F_{k+1}$$

$$\delta_9 = F_{k+1} - F_k.$$

Any other case involving an older parent can be obtained from (6) because, for $n \geqslant 1$, the older parent in generation n is the younger parent in generation $n-1$.

The algorithm for obtaining the identity coefficients between relatives X and Y can now be summarized:

1. First determine generation $n-1$, i.e., find the most recent mating in which *both* parents are common ancestors of X and Y. Then generation $n-1$ is the generation of the younger parent in that mating. That is, n is the generation of the offspring of the mating so identified. If X is an ancestor of Y, then $n-1$ is the generation to which X belongs.

2. Determine the generations, $n+m$ and $n+k$, of X and Y respectively, and solve for m and k.

3. Obtain the matrices $\Delta_s^{(n)}$, $s = 1, 2, \ldots, 9$, which depend on n.

4. Using (5) obtain the vectors $\mathbf{c}_X$ and $\mathbf{c}_Y$ which depend only on m and k, respectively. If m or $k = -1$ (which will happen if one relative is an ancestor of the other), set F_{-1} equal to -1.

5. Calculate the identity coefficients using (6).

To illustrate, consider a generation 4 uncle (X) and generation 8 nephew (Y). Then $n=4$, $m=0$, $k=4$. From (2) the inbreeding coefficients needed are:

$$F_n = 1/2$$
$$F_{n-1} = 3/8$$
$$F_m = 0$$
$$F_{m+1} = 0$$
$$F_k = 1/2$$
$$F_{k+1} = 19/32$$
$$F_{n+k} = 201/256\,.$$

The $\Delta_s^{(n)}$ matrices, using the equations from the Appendix,

$$\Delta_1^{(4)} = \begin{bmatrix} 11/16 & 1/2 & 3/8 & 3/8 \\ & 5/8 & 1/4 & 11/32 \\ & & 3/8 & 1/4 \\ \text{sym.} & & & 17/64 \end{bmatrix}$$

$$\Delta_2^{(4)} = \begin{bmatrix} 5/16 & 1/2 & 0 & 1/8 \\ & 3/8 & 1/8 & 7/32 \\ & & 0 & 0 \\ \text{sym.} & & & 1/32 \end{bmatrix}$$

$$\Delta_3^{(4)} = \Delta_5^{(4)\prime} = \begin{bmatrix} 0 & 0 & 5/8 & 7/16 \\ 0 & 0 & 1/2 & 3/8 \\ 0 & 0 & 0 & 1/8 \\ 0 & 0 & 1/4 & 3/16 \end{bmatrix}$$

$$\Delta_4^{(4)} = \Delta_6^{(4)\prime} = \begin{bmatrix} 0 & 0 & 0 & 1/16 \\ 0 & 0 & 1/8 & 1/16 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 1/64 \end{bmatrix}$$

$$\Delta_7^{(4)} = \begin{bmatrix} 0 & 0 & 0 & 0 \\ & 0 & 0 & 0 \\ & & 5/8 & 1/4 \\ \text{sym.} & & & 13/64 \end{bmatrix}$$

$$\Delta_8^{(4)} = \begin{bmatrix} 0 & 0 & 0 & 0 \\ & 0 & 0 & 0 \\ & & 0 & 1/8 \\ \text{sym.} & & & 3/32 \end{bmatrix}$$

$$\Delta_9^{(4)} = \text{zero matrix.}$$

Using (5):

$$\mathbf{c}_X' = (0, 0, 0, 1);$$
$$\mathbf{c}_Y' = (13/32,\ 3/16,\ 3/32,\ 5/16).$$

$$\delta_1 = \mathbf{c}_X' \Delta_1^{(4)} \mathbf{c}_Y = 331/1024$$
$$\delta_2 = \mathbf{c}_X' \Delta_2^{(4)} \mathbf{c}_Y = 13/128$$
$$\delta_3 = \mathbf{c}_X' \Delta_3^{(4)} \mathbf{c}_Y = 21/256$$
$$\delta_4 = \mathbf{c}_X' \Delta_4^{(4)} \mathbf{c}_Y = 5/1024$$
$$\delta_5 = \mathbf{c}_X' \Delta_5^{(4)} \mathbf{c}_Y = 163/512$$
$$\delta_6 = \mathbf{c}_X' \Delta_6^{(4)} \mathbf{c}_Y = 43/1024$$
$$\delta_7 = \mathbf{c}_X' \Delta_7^{(4)} \mathbf{c}_Y = 89/1024$$
$$\delta_8 = \mathbf{c}_X' \Delta_8^{(4)} \mathbf{c}_Y = 21/512$$
$$\delta_9 = 0\,.$$

Covariances Between Relatives

Using a model described by Cornelius and Dudley (1975) which provides for additive and dominance effects but assumes no epistasis or linkage, the covariance between relatives X and Y is

$$\mathrm{Cov}(X,Y) = \delta_1\sigma_\infty^2 + (\delta_1 + \delta_2 - F_X F_Y)\mu_\infty^2 + [(\delta_3 + \delta_5)/2]C + (\delta_7 + \delta_8/2)\sigma_A^2 + \delta_7\sigma_D^2 \tag{8}$$

where

F_X, F_Y are the coefficients of inbreeding of X and Y, respectively;

σ_A^2 and σ_D^2 are the additive genetic variance and dominance variances, respectively, in the original random mating population;

σ_∞^2 is the (additive) genetic variance in a completely homozygous population resulting from inbreeding the original population without selection;

C is twice the sum over loci of the covariance of the effect of a gene at a given locus in the homozygous population with its additive effect in the original population; and

$$\mu_\infty^2 = \sum_{\text{loci}} \left(\sum_i p_i d_{ii} \right)^2$$

where the p_i are gene frequencies and d_{ii} is the dominance deviation of genotype A_iA_i in the original population. The quantity $\sum_i p_i d_{ii}$ is the contribution of the given locus to the difference between the mean of original and completely homozygous populations.

Formula (8) follows immediately from the definitions of the components and the identity states. A lengthier derivation is given by Cornelius and Dudley (1975). They also relate the parameters in (8) to a parameterization developed by Harris (1964). The covariance components in (8) were previously described by Kempthorne (1957, Section 17.11). His V_∞ is our σ_∞^2.

In the covariance of generation 4 uncle and generation 8 nephew (example of previous section):

$$\begin{aligned}
\text{coefficient of } \sigma_\infty^2 &= \delta_1 = 331/1024;\\
\text{coefficient of } \mu_\infty^2 &= \delta_1 + \delta_2 - F_4F_8\\
&= 331/1024 + 13/128 - (1/2)(201/256)\\
&= 33/1024;\\
\text{coefficient of } C &= (\delta_3 + \delta_5)/2\\
&= (21/256 + 163/512)/2\\
&= 205/1024\\
\text{coefficient of } \sigma_A^2 &= \delta_7 + \delta_8/2\\
&= 89/1024 + (21/512)(1/2)\\
&= 110/1024;\\
\text{coefficient of } \sigma_D^2 &= \delta_7 = 89/1024.
\end{aligned}$$

So the covariance of generation 4 uncle and generation 8 nephew in a parent-offspring inbreeding system is

$$(331/1024)\sigma_\infty^2 + (33/1024)\mu_\infty^2 + (205/1024)C + (110/1024)\sigma_A^2 + (89/1024)\sigma_D^2.$$

For a one-locus model with two alleles, A and a, with gene frequencies p and q = 1 - p, respectively,

$$\begin{aligned}
\sigma_\infty^2 &= pqy^2\\
\mu_\infty^2 &= \sigma_D^2 = p^2q^2x^2\\
C &= pqy^2 + pq(p-q)xy\\
\sigma_A^2 &= [pqy^2 + 2pq(p-q)xy + pq(p-q)^2x^2]/2
\end{aligned} \tag{9}$$

where

$$y = AA - aa$$
$$x = AA + aa - 2Aa$$

in which, to calculate y and x, genotypic values are substituted for the genotypes (Kempthorne, 1957, Chapter 17; Cornelius and Dudley, 1975). Using (9) it has been verified that Horner's results for the covariances of parent and offspring and of full sibs agree with (8) with the identity coefficients calculated by the algorithm developed here.

Covariances Useful in Applications

The utility of estimates of the covariance components is discussed by Cornelius and Dudley (1975) and applied by Cornelius (1972) to problems of predicting response to selection in an inbreeding program and choosing an inbreeding system. For similar applications in regard to a parent-offspring inbreeding system some useful covariances are:

1. Covariance of a generation n - 1 younger parent and completely homozygous descendants:

$$\lim_{m\to\infty} \mathrm{Cov}(PO^{-1}(M_{n-1}), PO^m(M_{n-1})) = \{F_{n-1} - [(1+F_{n-1} - 2F_n)/2 - (1/2)^n]/3\}\sigma_\infty^2 + [(1-F_{n-1})/2 - (1/2)^n/3]C \tag{10}$$

where M_{n-1} is a randomly chosen generation n-1 mating.

2. Covariance of the mean of a generation n full-sib family and its completely homozygous descendants (equivalent to covariance of generation n uncle and generation ∞ nephew):

$$\begin{aligned}\lim_{m\to\infty} \mathrm{Cov}\,(PO^0(M_{n-1}),PO^m(M_{n-1}))=&\{(4F_n-1+0^{n-1}/4)/3\\ &+(1/2)^{n+1}\}\,\sigma^2_\infty+\{(F_n-F_{n-1}-(1/2)^n+0^{n-1}/2)/3\}\,\mu^2_\infty\\ &+\{[(3+F_{n-1}-4F_n)/2-(1/2)^n]/3\}\,C \qquad (11)\end{aligned}$$

3. Covariance of mid-parent value in generation n-1 and completely homozygous descendants:

$$\begin{aligned}\lim_{m\to\infty} \mathrm{Cov}[FS^{-1}(M_{n-1}),PO^m(M_{n-1})]=&[(22F_n-3F_{n-1}-7)/12\\ &+(1/2)^{n+1}+0^{n-1}/3]\sigma^2_\infty\\ &+[(3+F_{n-1}-4F_n)/4-(1/2)^{n+1}\\ &-0^{n-1}/4]\,C \qquad (12)\end{aligned}$$

Covariances involving average genotypic values of progeny (general combining ability) resulting from mating an individual or a family at random with the population are also of interest. The array of progeny of such matings may be represented by Kempthorne's random mating operator $R(\cdot)$ in which the argument may be any given array of genotypes and the operator generates the array of progeny when that array of genotypes is mated at random with the population. In particular, $R(PO^{-1}(M_{n-1}))$ is the array of progeny resulting from mating a randomly chosen generation n - 1 younger parent at random with the population. $R(FS^{-1}(M_{n-1}))$ generates the array of progeny resulting from taking both parents of a randomly chosen generation n - 1 mating and mating them at random with the population. $R(PO^0(M_{n-1}))$ generates the array of progeny resulting from taking a randomly chosen generation n family of full sibs and mating them at random to the population. In general, it is easily seen from the definition of the δ's and the covariance components that, for relatives X and Y

$$\mathrm{Cov}(X,R(Y)) = (\delta_1/2+\delta_3/4)C + [(\delta_5+\delta_7)/2+\delta_8/4]\,\sigma^2_A \qquad (13)$$

$$\mathrm{Cov}(X,R(X)) = (F_X/2)C + [(1-F_X)/2]\,\sigma^2_A \qquad (14)$$

These are general formulae which apply to any system of inbreeding. (Note that $\mathrm{Cov}(R(X),Y)$ is obtained by interchanging δ_3 and δ_5 in (13).) Thus, if a plant or animal breeder is selecting on the basis of inbred performance of individuals or families, but wishes to predict response in general combining ability as a result of selection, obtaining the relevant covariances is reduced to the problem of obtaining the δ's.

Numerical Results

A FORTRAN IV program has been written to generate identity coefficients and coefficients of the components of covariance for all possible relatives (ancestor-descendant, uncle-nephew removed by one or more generations, full sibs, cousins) up to the eighth generation of a younger parent-offspring inbreeding system. The program or its results are available to interested readers.

Literature

Cockerham, C.C.: Higher order probability functions of identity of alleles by descent. Genetics 69, 235-246 (1971)

Cornelius, P.L.: Quantitative genetic evaluation of full sib mating and selfing as methods of inbreeding in *Zea mays* L. Unpublished Ph.D. thesis, University of Illinois Library, Champaign, Illinois (1972)

Cornelius, P.L.; Dudley, J.W.: Theory of inbreeding and covariances between relatives under full-sib mating in diploids. Biometrics 31, 169-181 (1975)

Fisher, R.A.: The Theory of Inbreeding, Second Ed. New York: Academic Press 1965

Gillois, M.: Relation d'identité en génétique. I. Postulats et axiomes mendeliens. II. Corrélation génétique dans le cas de dominance. Ann. Inst. Henri Poincaré, B. II, 1-94 (1965)

Harris, D.L.: Genotypic covariances between inbred relatives. Genetics 50, 1319-1348 (1964)

Horner, T.W.: Parent-offspring and full-sib correlations under a parent-offspring mating system. Genetics 41, 460-468 (1956)

Jacquard, A.: Logique de calcul des coéfficients d'identité. Population Paris 21, 751-776 (1966)

Jacquard, A.: Genetic information given by a relative. Biometrics 28, 1101-1114 (1972)

Kempthorne, O.: An Introduction to Genetic Statistics. New York: Wiley 1957

Kempthorne, O.: The role of system of mating in the determination of means, variances, and covariances in genetic populations. In: Statistical Genetics and Plant Breeding, NAS-NRC Pub. 982, pp. 21-23 (1963)

Nadot, R.; Vaysseix, G.: Apparentement et identité. Algorithme du calcul des coéfficients d'identité. Biometrics 29, 347-359 (1973)

Appendix

The $\Delta_s^{(n)}$ matrices in (6) and (7) are of the form

$$\begin{bmatrix} \delta^{(n)}_{s(11,11)} & \delta^{(n)}_{s(11,12)} & \delta^{(n)}_{s(11,21)} & \delta^{(n)}_{s(11,3)} \\ \delta^{(n)}_{s(12,11)} & \delta^{(n)}_{s(12,12)} & \delta^{(n)}_{s(12,21)} & \delta^{(n)}_{s(12,3)} \\ \delta^{(n)}_{s(21,11)} & \delta^{(n)}_{s(21,12)} & \delta^{(n)}_{s(21,21)} & \delta^{(n)}_{s(21,3)} \\ \delta^{(n)}_{s(3,11)} & \delta^{(n)}_{s(3,12)} & \delta^{(n)}_{s(3,21)} & \delta^{(n)}_{s(3,3)} \end{bmatrix}$$

We have already noted that Δ_1, Δ_2, Δ_7, Δ_8, and Δ_9 are symmetric, and

$\Delta_3 = \Delta_5'$

$\Delta_4 = \Delta_6'$.

Therefore only the upper triangle of each matrix will be given. Let $u = (1/2)^n$. Then we have:

For $\boldsymbol{\Delta}_1^{(n)}$:

$$\delta^{(n)}_{1(11,11)} = (1 + F_{n-1})/2;$$
$$\delta^{(n)}_{1(11,12)} = F_n;$$
$$\delta^{(n)}_{1(11,21)} = F_{n-1};$$
$$\delta^{(n)}_{1(11,3)} = (4F_n + F_{n-1} - 1 + 2u)/4;$$
$$\delta^{(n)}_{1(12,12)} = 2F_n - F_{n-1} + 0^{n-1}/2;$$
$$\delta^{(n)}_{1(12,21)} = (2F_n + F_{n-1} - 1 + 2u)/2;$$
$$\delta^{(n)}_{1(12,3)} = (4F_n - F_{n-1} - 1 + u)/2 + 0^{n-1}/4;$$
$$\delta^{(n)}_{1(21,21)} = F_{n-1};$$
$$\delta^{(n)}_{1(21,3)} = (2F_n + F_{n-1} - 1 + 2u)/2;$$
$$\delta^{(n)}_{1(3,3)} = (14F_n - F_{n-1} - 5)/8 + u + 0^{n-1}/8 .$$

For $\boldsymbol{\Delta}_2^{(n)}$:

$$\delta^{(n)}_{2(11,11)} = (1 - F_{n-1})/2;$$
$$\delta^{(n)}_{2(11,12)} = 1 - F_n;$$
$$\delta^{(n)}_{2(11,21)} = \delta^{(n)}_{2(21,21)} = \delta^{(n)}_{2(21,3)} = 0;$$
$$\delta^{(n)}_{2(11,3)} = (1 - F_{n-1})/4 - u/2;$$
$$\delta^{(n)}_{2(12,12)} = 1 + F_{n-1} - 2F_n - 0^{n-1}/2;$$
$$\delta^{(n)}_{2(12,21)} = (1 + F_{n-1} - 2F_n)/2 - u;$$
$$\delta^{(n)}_{2(12,3)} = (1 - F_{n-1})/2 - 3u/2 + 0^{n-1}/4;$$
$$\delta^{(n)}_{2(3,3)} = \delta^{(n)}_{2(12,21)}/4 .$$

For $\boldsymbol{\Delta}_3^{(n)}$:

$$\delta^{(n)}_{3(i,j)} = 0 \text{ if } j = 11 \text{ or } 12;$$
$$\delta^{(n)}_{3(11,21)} = 1 - F_{n-1};$$
$$\delta^{(n)}_{3(11,3)} = 1 - F_n - u;$$
$$\delta^{(n)}_{3(12,21)} = 1 - F_{n-1} - 2u;$$
$$\delta^{(n)}_{3(12,3)} = 1 + F_{n-1} - 2F_n;$$
$$\delta^{(n)}_{3(21,21)} = 0;$$
$$\delta^{(n)}_{3(21,3)} = (1 + F_{n-1} - 2F_n)/2 - u;$$
$$\delta^{(n)}_{3(3,3)} = (1 - F_n)/2 - u.$$

For $\boldsymbol{\Delta}_4^{(n)}$:

$$\delta^{(n)}_{4(i,j)} = 0 \text{ if } i = 21 \text{ or } j = 11 \text{ or } 12;$$
$$\delta^{(n)}_{4(11,21)} = 0;$$
$$\delta^{(n)}_{4(11,3)} = u;$$
$$\delta^{(n)}_{4(12,21)} = 2u;$$
$$\delta^{(n)}_{4(12,3)} = u - 0^{n-1}/2;$$
$$\delta^{(n)}_{4(3,3)} = (2u - 0^{n-1})/8.$$

For $\boldsymbol{\Delta}_5^{(n)}$:

$$\delta^{(n)}_{5(i,i)} = \delta^{(n)}_{3(i,i)}, \; i = 11,\ 12,\ 21,\ 3;$$
$$\delta^{(n)}_{5(i,j)} = 0 \text{ if } i = 11 \text{ or } 12;$$
$$\delta^{(n)}_{5(21,3)} = (1 - F_{n-1})/2 - u.$$

For $\boldsymbol{\Delta}_6^{(n)}$:

The only non-zero element in the upper triangle is

$$\delta^{(n)}_{6(3,3)} = \delta^{(n)}_{4(3,3)}.$$

For $\boldsymbol{\Delta}_7^{(n)}$:

$$\delta^{(n)}_{7(i,j)} = 0 \text{ if } i \text{ or } j = 11 \text{ or } 12;$$
$$\delta^{(n)}_{7(21,21)} = 1 - F_{n-1};$$
$$\delta^{(n)}_{7(21,3)} = (1 - F_{n-1})/2 - u;$$
$$\delta^{(n)}_{7(3,3)} = (1 - F_n)/2 - 3u/4 + 0^{n-1}/8.$$

For $\boldsymbol{\Delta}_8^{(n)}$:

$$\delta^{(n)}_{8(i,j)} = 0 \text{ if } i \text{ or } j = 11 \text{ or } 12;$$
$$\delta^{(n)}_{8(21,21)} = 0;$$
$$\delta^{(n)}_{8(21,3)} = 2u;$$
$$\delta^{(n)}_{8(3,3)} = (6u - 0^{n-1})/4.$$

For $\boldsymbol{\Delta}_9^{(n)}$:

All elements are zero except
$$\delta^{(n)}_{9(3,3)} = 0^{n-1}/4.$$

Also of possible use are cases where X or $Y \varepsilon z_{22}$ (e.g. in finding covariances involving mid-parent values). Consideration of these possibilities is equivalent to augmenting the $\boldsymbol{\Delta}_s^{(n)}$ matrices with another row and column. The additional columns are

$\boldsymbol{\Delta}_1^{(n)}$:

$$\delta^{(n)}_{1(11,22)} = 3F_n - F_{n-1} - 1 + u + 0^{n-1}/2;$$
$$\delta^{(n)}_{1(12,22)} = \delta^{(n)}_{1(22,22)} = 4F_n - 2F_{n-1} - 1 + 0^{n-1};$$
$$\delta^{(n)}_{1(21,22)} = 2F_n - 1 + 2u;$$
$$\delta^{(n)}_{1(3,22)} = 3F_n - F_{n-1} - 1 + u + 0^{n-1}/2.$$

$\Delta_2^{(n)}$:

$\delta^{(n)}_{2(11,22)} = F_n - F_{n-1} - u + 0^{n-1}/2;$

$\delta^{(n)}_{2(i,22)} = 0,\ i = 12,\ 21,\ 3,\ 22.$

$\Delta_3^{(n)}$:

$\delta^{(n)}_{3(11,22)} = 2(1 + F_{n-1} - 2F_n) - 2u - 0^{n-1};$

$\delta^{(n)}_{3(12,22)} = \delta^{(n)}_{3(11,22)} + 2u;$

$\delta^{(n)}_{3(21,22)} = 1 + F_{n-1} - 2F_n - 2u;$

$\delta^{(n)}_{3(3,22)} = \delta^{(n)}_{3(11,22)}/2;$

$\delta^{(n)}_{3(22,22)} = 0.$

$\Delta_4^{(n)}$:

$\delta^{(n)}_{4(11,22)} = 2u;$

$\delta^{(n)}_{4(i,22)} = 0,\ i = 12,\ 21,\ 3,\ 22.$

$\Delta_5^{(n)}$:

$\delta^{(n)}_{5(i,22)} = 0,\ i = 11,\ 12,\ 22;$

$\delta^{(n)}_{5(21,22)} = 2(F_n - F_{n-1}) - 2u + 0^{n-1};$

$\delta^{(n)}_{5(3,22)} = \delta^{(n)}_{5(21,22)}/2.$

$\Delta_6^{(n)}$:

$\delta^{(n)}_{6(i,22)} = 0,\ i = 11,\ 12,\ 21,\ 3,\ 22.$

$\Delta_7^{(n)}$:

$\delta^{(n)}_{7(i,22)} = 0,\ i = 11, 12;$

$\delta^{(n)}_{7(21,22)} = 1 + F_{n-1} - 2F_n - 2u;$

$\delta^{(n)}_{7(3,22)} = 1 + F_{n-1} - 2F_n - u + 0^{n-1}/2;$

$\delta^{(n)}_{7(22,22)} = 2(1 + F_{n-1} - 2F_n) - 0^{n-1}.$

$\Delta_8^{(n)}$:

$\delta^{(n)}_{8(i,22)} = 0,\ i = 11, 12, 22;$

$\delta^{(n)}_{8(21,22)} = 4u - 2(0^{n-1});$

$\delta^{(n)}_{8(3,22)} = 2u.$

$\Delta_9^{(n)}$:

$\delta^{(n)}_{9(i,22)} = 0,\ i = 11,\ 12,\ 3,\ 22;$

$\delta^{(n)}_{9(21,22)} = 0^{n-1}.$

The reader may easily verify that

$$\sum_{i=1}^{9} \Delta_i^{(n)}$$

is a matrix with all elements equal to unity.

Received November 15, 1974/
February 10, 1975
Communicated by R.W. Allard

Dr. Paul L. Cornelius
Department of Agronomy
University of Kentucky
Lexington, Kentucky 40506 (USA)