

Comparative Effects of Pollen and Seed Migration on the Cytonuclear Structure of Plant Populations. I. Maternal Cytoplasmic Inheritance

Marjorie A. Asmussen and Andrew Schnabel

Department of Genetics, University of Georgia, Athens, Georgia 30602

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ABSTRACT

We explicitly solve and analyze a series of deterministic continent-island models to delimit the effects of pollen and seed migration on cytonuclear frequencies and disequilibria in random-mating, mixed-mating and self-fertilized populations. Given the critical assumption of maternal cytoplasmic inheritance, five major findings are (i) nonzero cytonuclear disequilibria will be maintained in the island population if and only if at least some migration occurs each generation through seeds with nonrandom cytonuclear associations; (ii) immigrant seeds with no cytonuclear disequilibria can strongly affect the genetic structure of the island population by generating significant and long-lasting transient associations; (iii) with all else being equal, substantially greater admixture disequilibria are generally found with higher rates of seed migration into, or higher levels of self-fertilization within, the island population (with the possible exception of the heterozygote disequilibrium); (iv) pollen migration can either enhance or reduce the cytonuclear disequilibria caused by seed migration, or that due to mixed-mating in the absence of seed migration, but the effect is usually small and appears primarily to make a noticeable difference in predominantly outcrossing populations; and (v) pollen migration alone cannot generate even transient disequilibria *de novo* in populations with completely random associations. This same basic behavior is exhibited as long as there is some random outcrossing in the island population. Self-fertilized populations represent a special case, however, in that they are necessarily closed to pollen migration, and nonzero disequilibria can be maintained even in the absence of seed migration. All of these general results hold whether the population is censused as adults or as seeds, but the ability to detect nonrandom cytonuclear associations can depend strongly on the life stage censused in populations with a significant level of random outcrossing. We suggest how these models might be used for the estimation of seed and pollen migration.

JOINT nuclear-cytoplasmic frequencies and the statistical associations (disequilibria) between the corresponding single-locus frequencies represent a new and extremely useful tool for the study of natural populations. The special utility of cytonuclear systems stems from the juxtaposition of the uniparental inheritance of haploid, cytoplasmic genes against the biparental inheritance of diploid, nuclear genes. This is perhaps most obvious in the delineation of certain nonrandom mating patterns, where it has been shown both empirically and theoretically that joint nuclear-cytoplasmic data allow biological inferences and mating parameter estimates that are unobtainable from surveys of nuclear loci alone (LAMB and AVISE 1986; ASMUSSEN, ARNOLD and AVISE 1987; ARNOLD, ASMUSSEN and AVISE 1988).

An important practical by-product of the underlying mating system models is that the sign pattern of observed cytonuclear disequilibria may itself convey much information concerning the mating system in a population. This is because of the critical discovery that substantial nonrandom cytonuclear associations

can be generated by nonrandom mating even in the absence of natural selection, migration and genetic drift. The resulting disequilibria will be transient in the case of partial self-fertilization, partial assortative mating based on nuclear genotype, or partial assortative mating in hybrid zones based on an interaction between the cytotype and the multilocus nuclear genotype characteristic of the pure parental species (ASMUSSEN, ARNOLD and AVISE 1987; SCHNABEL and ASMUSSEN 1989). Permanent cytonuclear disequilibria can be produced, however, under an assortative mating pattern based on an interaction between cytotype and genotype at a single nuclear locus (ARNOLD, ASMUSSEN and AVISE 1988).

Recent theoretical studies indicate that cytonuclear data also offer a novel perspective on the study of gene flow into a hybrid zone and other zones of admixture (ASMUSSEN, ARNOLD and AVISE 1989; ASMUSSEN and ARNOLD 1991). The first of these investigations demonstrated how joint cytonuclear frequencies allow particularly sensitive estimates of the migration rates from the two parental species into a

hybrid zone, as well as of the rate at which pure species females preferentially mate with conspecific males in the zone (ASMUSSEN, ARNOLD and AVISE 1989). An important concurrent finding was that continued immigration from two genetically distinct parental species will generate permanent cytonuclear disequilibria in a hybrid zone, whether or not pure parental females mate assortatively. This theoretical framework has recently been extended beyond the context of hybrid zones to show how cytonuclear frequencies and disequilibria can help identify zones of admixture as well as provide estimates of gene flow between one or more random-mating populations (ASMUSSEN and ARNOLD 1991). The latter investigation also revealed how cytonuclear disequilibria can be generated by population subdivision, admixture, and continued migration into or between random-mating populations.

Here we expand the study of the cytonuclear effects of migration to the special case of seed plants, where not only may there be complete or partial self-fertilization, but gene flow has both diploid (seed) and haploid (pollen) components. The latter distinction is noteworthy for two major biological reasons. First, although several cases of biparental and paternal organelle inheritance are known (SEARS 1980; BOBLENZ, NOTHNAGEL and METZLAFF 1990; SMITH 1988; SCHUMANN and HANCOCK 1989; NEALE, MARSHALL and SEDEROFF 1989), the majority of plant species appear to exhibit strictly maternal inheritance of mitochondria and chloroplasts, in which case their pollen does not transmit cytoplasmic genes. The two forms of gene flow would therefore be expected to have different effects on the cytonuclear structure of most species. Second, for partially or fully outcrossing species, gene flow via pollen is generally believed to occur at much greater rates than gene flow via seed (LEVIN and KERSTER 1974; HANDEL 1983). The two forms of gene flow would, however, be expected to be more comparable in highly selfing species and in species with seeds that are dispersed long distances by water or highly mobile animals (BULLOCK and PRIMACK 1977; LANNER and VANDER WALL 1980; DARLEY-HILL and JOHNSON 1981; SCHNEIDER and SHARITZ 1988).

The present paper examines and contrasts the separate and joint effects of these two types of gene flow on the cytonuclear dynamics within single random-mating, mixed-mating, and self-fertilized populations, based on a continent-island formulation. Paralleling previous migration studies (ASMUSSEN, ARNOLD and AVISE 1989; ASMUSSEN and ARNOLD 1991), we also examine the extent to which the two standard census times for plants (adults *vs.* seeds) affect the ability to detect and utilize nonrandom cytonuclear associations.

TABLE 1

Joint nuclear-cytoplasmic genotype frequencies

Cytotype	Nuclear genotype			Total
	AA	Aa	aa	
C	U_1	V_1	W_1	X
c	U_2	V_2	W_2	Y
Total	U	V	W	1.0

CYTONUCLEAR SYSTEM

Consider a population of diploid, strictly annual plants with no seed dormancy, in which we monitor a single nuclear locus with two alleles, *A* and *a*, and a single cytoplasmic locus with two haplotypes, *C* and *c*. The frequencies of the six resulting two-locus cytonuclear genotypes are denoted as in Table 1. Note that the individual cytotype frequencies, *X* and *Y*, are obtained by summing across each row, whereas summation down each column gives the nuclear genotype frequencies, *U*, *V* and *W*. Other critical frequency variables include the four joint, cytonuclear allele frequencies,

$$\begin{aligned} P_1 &= \text{Freq}(A/C) = U_1 + \frac{1}{2}V_1 \\ P_2 &= \text{Freq}(A/c) = U_2 + \frac{1}{2}V_2 \\ Q_1 &= \text{Freq}(a/C) = W_1 + \frac{1}{2}V_1 \\ Q_2 &= \text{Freq}(a/c) = W_2 + \frac{1}{2}V_2, \end{aligned} \quad (1)$$

and the nuclear allele frequencies,

$$P = \text{Freq}(A) = P_1 + P_2 = U + \frac{1}{2}V \quad (2)$$

and

$$Q = \text{Freq}(a) = Q_1 + Q_2 = W + \frac{1}{2}V.$$

The remaining variables reflect the nonrandom associations in the population at the level of both genotypes and alleles as defined by ASMUSSEN, ARNOLD and AVISE (1987). Although as in nuclear systems (*e.g.*, WEIR and WILSON 1986) many other forms of cytonuclear disequilibria could be defined, we focus on these measures because of their demonstrated utility in interpreting cytonuclear data (*e.g.*, ASMUSSEN, ARNOLD and AVISE 1989; AVISE *et al.* 1990). Under this formulation, nonrandom associations between the three nuclear genotypes (*AA*, *Aa*, *aa*) and the two cytoplasmic haplotypes (*C*, *c*) are measured by the *genotypic disequilibria*.

$$\begin{aligned} D_1 &= U_1 - UX & D_2 &= V_1 - VX \\ D_3 &= W_1 - WX, \end{aligned} \quad (3)$$

where, for instance,

$$D_2 = \text{Freq}(Aa/C) - \text{Freq}(Aa)\text{Freq}(C).$$

The corresponding *allelic disequilibrium*, D , similarly quantifies nonrandom associations between alleles at the nuclear and cytoplasmic loci:

$$D = \text{Freq}(A/C) - \text{Freq}(A)\text{Freq}(C) = P_1 - PX. \quad (4)$$

The genotypic and allelic disequilibria are interrelated by the formulas

$$D_1 + D_2 + D_3 = 0 \quad (5)$$

and

$$D = D_1 + \frac{1}{2}D_2,$$

and thus reduce to two independent disequilibrium measures.

Whereas all the variables defined by Table 1 and Equations 1–4 are useful in cytonuclear analyses, it should be emphasized that only five independent variables are actually required to describe the full, six-genotype system. Particularly useful parameterizations are based on the two allele frequencies (X , P), one nuclear genotype frequency (*e.g.*, V), and two of the cytonuclear disequilibria. The latter can include either the allelic disequilibrium and one genotypic disequilibrium, such as D and D_2 , or two genotypic disequilibria, such as D_1 and D_2 . Although technically redundant, it is nonetheless desirable to consider the behavior of the full set of allelic and genotypic disequilibria in order to detect distinctive, joint sign patterns, which have proven useful in the interpretation of cytonuclear data (*e.g.*, ASMUSSEN, ARNOLD and AVISE 1987; ARNOLD, ASMUSSEN and AVISE 1988; AVISE *et al.* 1990).

To complete our parameterization of the system, it is helpful to designate a separate set of variables for each of the two life stages at which the plant population might be censused (Figure 1). This is accomplished here by reserving uppercase letters [as shown in (1)–(5) and Table 1] for frequency and disequilibrium variables in the adult population, and lowercase letters (*i.e.*, u_1 , u , p , x , d , d_1 , etc.) for the corresponding values in the seed population.

MIGRATION MODELS

The migration models considered below examine the cytonuclear dynamics within a population in which mating is a mixture of selfing, with probability s , and random outcrossing, with probability $1 - s$, in accordance with the assumptions of the mixed-mating model (CLEGG 1980). We incorporate gene flow into the system by allowing pollen and seed to enter this (island) population from a large constant source (continent) in two distinct stages (Figure 1). In each generation, the total pool of outcrossed pollen consists of a proportion M of immigrant pollen and a proportion $1 - M$ of resident pollen. The overall fraction of

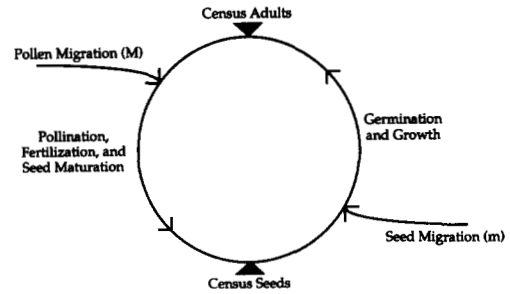


FIGURE 1.—Alternate census times within the life cycle of a plant population receiving immigrant pollen and seeds.

immigrant pollen per generation is thus the product, $M(1 - s)$. After fertilization and seed maturation, seed migration occurs such that a proportion m of the total seed pool comes from the source population and the remaining fraction $1 - m$ is of local origin. Both migration rates, M and m , are assumed constant through time.

The variables describing the genetic constitution of the two migrant pools are notationally distinguished by the superposition of bars, with lowercase again associated with seeds and uppercase here describing pollen. Specifically, immigrant pollen is characterized by its nuclear allele frequency, \bar{P} , whereas the frequencies and disequilibria in immigrant seed are described by \bar{u}_1 , \bar{u} , \bar{x} , \bar{p} , \bar{d} , and so on. Although the composition of both migrant pools is assumed constant over time, the nuclear gene frequencies need not be equal in the two dispersal stages due to different genetic factors influencing pollen and seed dispersal or the operation of selection or other evolutionary forces within the life cycle of the source population. The separate \bar{p} and \bar{P} parameters also allow for the possibility of multiple source populations with different frequencies, which contribute differentially to the two migrant pools. The final general assumptions are that the cytoplasmic locus is inherited maternally and that no selection, mutation, or genetic drift are operating within the island population.

Within this basic framework, we investigate two primary models, based on the two standard census times of plant populations. The first model assumes that the island is censused each generation in the adult stage, whereas the second assumes censusing involves mature seeds sampled prior to seed dispersal. In terms of actual field work, adult censusing has the practical advantage of almost always being feasible and is required for traits that are only expressed in adults. Seed censusing, on the other hand, may not always be possible, but it is necessary for studies of demographic genetics, mating systems, and pollen migration (*e.g.*, CLEGG, KAHLER and ALLARD 1978; RITLAND and JAIN 1981; ELLSTRAND and MARSHALL 1985) and in some cases is preferable due to ease of tissue storage, small size of adult plants, and small population sizes.

For both census methods, recursion equations for the resident frequency and disequilibrium variables are generated via a two-step process. First, a set of expressions is derived for the interim variables following the initial round of migration by pollen (seeds). These expressions are then used to calculate the new resident values in the next generation following the second round of migration by seeds (pollen). We will first examine the general effects of mixed-mating ($0 < s < 1$) in conjunction with both pollen and seed migration (*i.e.*, $0 < M < 1$ and $0 < m < 1$) assuming different nuclear gene frequencies in immigrant pollen and seeds ($\bar{P} \neq \hat{p}$). We will then discuss several special cases, including pollen migration alone ($m = 0$), seed migration alone ($M = 0$), equal nuclear gene frequencies in the two migrant pools ($\bar{P} = \hat{p}$), complete random mating ($s = 0$), and complete self-fertilization ($s = 1$).

Model 1. Adult census: When adults are censused, each generation cycle begins with pollen migration, followed by pollination, fertilization and seed maturation, and concludes with seed migration, germination, and growth to reproductive maturity (Figure 1). Close examination of the complete model (APPENDIX A) reveals several important points. First, the island cytoplasmic frequency is independent of both pollen migration and the rate of self-fertilization, being affected only by the rate of seed migration (m), the cytotype frequency in immigrant seeds (\bar{x}), and the initial resident frequency (X_0). The explicit solution for the value of the cytotype frequency in any generation $t \geq 1$,

$$X_t = \bar{x} + (X_0 - \bar{x})(1 - m)^t \tag{6}$$

shows that X_t remains constant in the island population (*i.e.*, $X_t = X_0$ for $t = 0, 1, 2, \dots$) if either the resident frequency initially equals that in immigrant seeds ($X_0 = \bar{x}$) or there is no seed migration ($m = 0$). Otherwise, the resident cytoplasmic frequency converges monotonically at the geometric rate of $1 - m$ per generation to the cytoplasmic frequency in immigrant seeds.

In contrast, the nuclear gene frequency trajectory depends on the level of self-fertilization and both migration rates, as well as on the nuclear allele frequencies in immigrant seeds (\hat{p}), immigrant pollen (\bar{P}), and the initial residents (P_0):

$$P_t = \hat{P} + (P_0 - \hat{P})\left\{(1 - m)\left[1 - \frac{1}{2}M(1 - s)\right]\right\}^t, \tag{7}$$

where

$$P_t \rightarrow \hat{P} = \frac{2m\hat{p} + (1 - m)M(1 - s)\bar{P}}{2m + (1 - m)M(1 - s)} \text{ as } t \rightarrow \infty.$$

Although both gene frequencies converge monotonically to equilibrium, the nuclear gene frequency does so at a faster geometric rate (*i.e.*, $(1 - m)\left[1 - \frac{1}{2}M(1 - s)\right] < 1 - m$), because nuclear alleles enter the

resident population through both pollen and seeds. This latter fact is also reflected in the equilibrium gene frequency, \hat{P} , which is a weighted average incorporating the frequency of nuclear alleles entering the population through migrant pollen but reaching the adult stage via resident seeds $[(1 - m)M(1 - s)\bar{P}]$, and the frequency of nuclear alleles entering the population via immigrant seeds ($2m\hat{p}$).

Unlike the simple geometric convergence of the two gene frequencies, the allelic disequilibrium's closed-form solution is considerably more complex, usually equaling its equilibrium value,

$$\hat{D} = \frac{2m\bar{d}}{2 - (1 - m)(1 + s)} \tag{8}$$

plus three convergent geometric terms (see APPENDIX B). The island's allelic association can thus change sign or direction along its trajectory, depending on the residents' initial allelic association (D_0) and the migration and mating system parameters.

Detailed inspection of the complete solution for D_t reveals that seed migration has a major, and pollen migration only a limited, effect on the allelic disequilibrium in the island population. For instance, the dominant geometric term, which determines the asymptotic rate of approach to equilibrium, is $(1 - m)^t$, and thus depends only on the rate of seed migration; only one of the smaller geometric terms includes the (outcrossed) pollen migration rate, M . The final allelic association (\hat{D}) is, in fact, independent of pollen migration, being determined solely by the rate of seed migration (m), the level of self-fertilization (s), and the allelic disequilibrium in immigrant seeds (\bar{d}). Even more importantly, we see from (8) that the island population will develop permanent nonrandom allelic associations (*i.e.*, $\hat{D} \neq 0$) if and only if there is seed migration from a source with nonzero allelic disequilibrium (*i.e.*, $m > 0$ and $\bar{d} \neq 0$). If these conditions are met, the ultimate allelic disequilibrium in the island will have the same sign as, but a smaller magnitude than, the allelic disequilibrium in immigrant seeds (\bar{d}). Moreover, \hat{D} monotonically increases in magnitude with both the rate of seed migration and self-fertilization (Figure 2), approaching \bar{d} as either m or s increases toward unity.

Proceeding, we find that the gene frequency and allelic disequilibrium solutions (X_t, P_t, D_t), coupled with that in APPENDIX B for the frequency of nuclear heterozygotes (V_t), allow us to solve for the dynamics of all remaining variables. Of particular interest are those for the genotypic disequilibria, which are similar to, but more complex than, the allelic disequilibrium solution in that (i) each is usually the sum of its equilibrium value (\hat{D}_i) and a large number of convergent geometric terms ($D_i^{(j)}$, for instance, generally has eight geometric terms); (ii) the dominant term is again

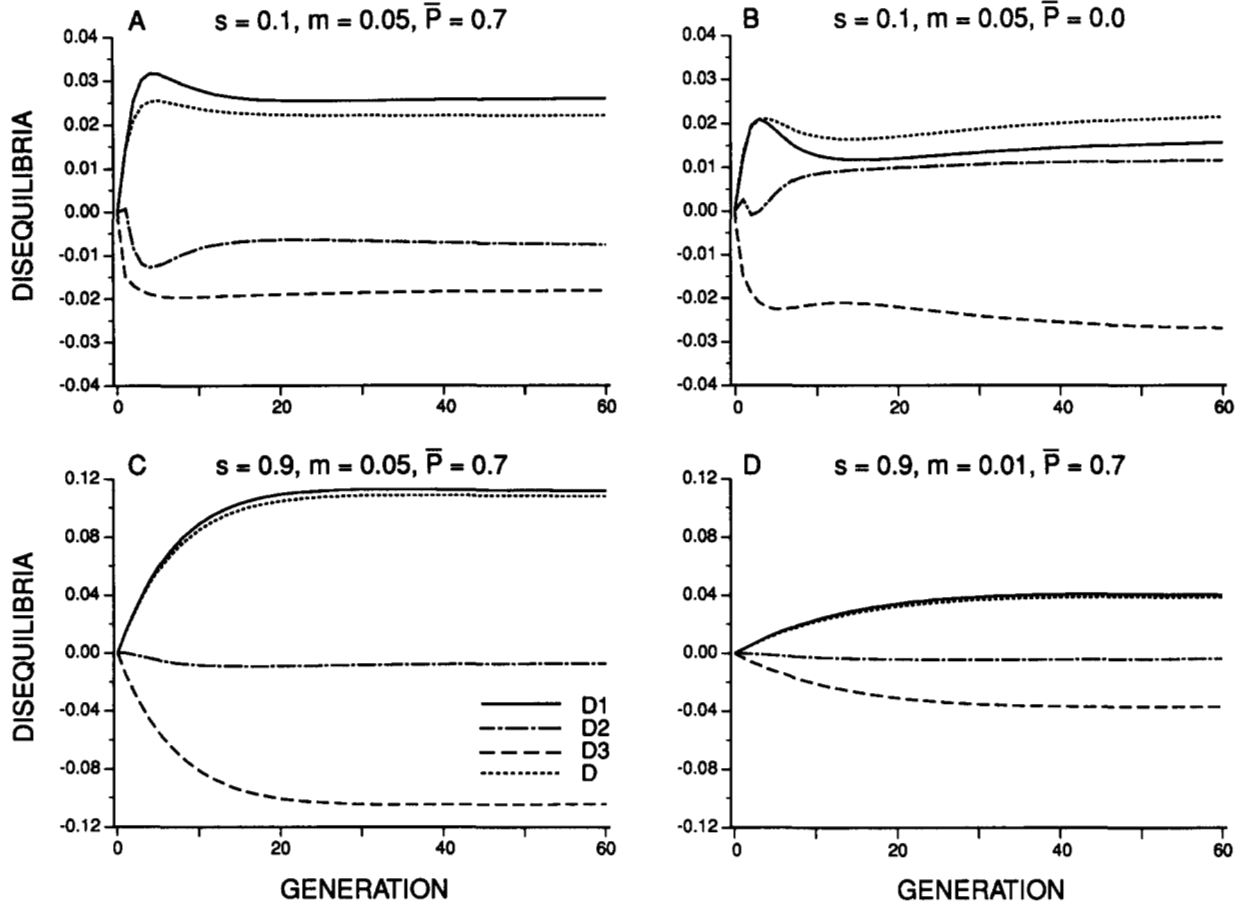


FIGURE 2.—Generation of permanent cytonuclear disequilibria by migrant seeds with nonrandom associations. In all cases the population is censused as adults, with $U_1^{(0)} = 1$, $\hat{u}_1 = 0.7$, $\hat{w}_2 = 0.3$, and $M = 0.2$. The disequilibria in the migrant seeds are $\bar{d}_1 = \bar{d} = 0.21 = -\bar{d}_3$, $\bar{d}_2 = 0$.

$(1 - m)^t$, which depends only on the seed migration rate; and (iii) the pollen migration rate only appears in some of the smaller, nondominant terms.

The relative roles of pollen and seed migration are further reflected in the island's limiting genotypic associations,

$$\begin{aligned} \hat{D}_1 &= \frac{2m\bar{d}_1 + (1 - m)}{s + 2(1 - s)[M\bar{P} + (1 - M)\hat{P}]} \hat{D} \\ \hat{D}_2 &= \frac{2m\bar{d}_2 + 2(1 - m)(1 - s)}{[M(\bar{Q} - \bar{P}) + (1 - M)(\hat{Q} - \hat{P})]} \hat{D} \\ \hat{D}_3 &= \frac{2m\bar{d}_3 - (1 - m)}{s + 2(1 - s)[M\bar{Q} + (1 - M)\hat{Q}]} \hat{D} \end{aligned} \quad (9)$$

which are determined by the two rates of gene flow, the nuclear gene frequencies in the two migrant pools, the cytonuclear disequilibria in immigrant seeds, and the selfing rate. These formulas show first that seed migration is necessary for the maintenance of nonrandom genotypic associations, just as it is for nonrandom

allelic associations. This is because $m = 0$ implies that $2m\bar{d}_1$, $2m\bar{d}_2$, $2m\bar{d}_3$ and \hat{D} are zero, which ensures \hat{D}_1 , \hat{D}_2 and \hat{D}_3 are zero as well. Another critical observation is that a permanent genotypic association simply requires some nonrandom cytonuclear associations in immigrant seeds. This is because each final genotypic disequilibrium is a composite of the migrant allelic and genotypic associations. As a result, a given nuclear genotype may eventually be nonrandomly associated with the two cytotypes even without such an association in the dispersed seeds, provided the other three immigrant disequilibria are nonzero (e.g., as seen in Figure 2, \hat{D}_2 may be nonzero when $\bar{d}_2 = 0$, if \bar{d} , \bar{d}_1 and \bar{d}_3 are all nonzero).

Numerical examples indicate that the final disequilibria will generally be only a small fraction of those found in the migrant seeds unless the selfing rate or the seed migration rate is moderately large. Figure 2 shows how nonzero disequilibria are generated in four different cases corresponding to an originally monomorphic population ($U_1^{(0)} = 1$) that receives the majority of its immigrants from like populations, but also receives some pollen and seeds from genetically distinct populations. In each instance, significant per-

manent disequilibria are generated *de novo* in the resident population as a result of nonrandom associations in the immigrant seeds, which are due solely to the migrant seeds themselves being the admixture of seeds from two sources with different nuclear and cytoplasmic frequencies (ASMUSSEN and ARNOLD 1991).

Note first that the allelic and homozygote disequilibria are substantially higher if the population is predominantly self-fertilizing ($s = 0.9$, $m = 0.05$, Figure 2C) than if it is predominantly outcrossing ($s = 0.1$, $m = 0.05$, Figure 2A). The final heterozygote disequilibrium, on the other hand, was generally small in the examples considered (even in cases where \bar{d}_2 was large), and it, as well as the full D_2 trajectory, varied less and in a more complex way with the selfing rate. Second, with all else being equal, increases in the rate of seed migration usually impart substantially greater disequilibrium values to the resident population (compare Figure 2, C and D). If, instead, the population is both predominantly outcrossing and receives only a small amount of seed migration (*e.g.*, $s = 0.1$ and $m = 0.01$, not shown), the disequilibria quickly stabilize below 0.01 in magnitude and are thus unlikely to be detected experimentally (FU and ARNOLD 1991).

Although pollen gene flow cannot generate permanent cytonuclear disequilibria, it can enhance or reduce the ultimate genotypic disequilibria in populations receiving migrant seeds with some nonrandom cytonuclear associations, if the nuclear gene frequency differs in immigrant seeds and pollen. Pollen migration can similarly influence all transient cytonuclear disequilibria as long as the nuclear gene frequencies in the two migrant pools do not equal the initial resident frequency. The net effect of pollen migration on the magnitude of the disequilibria appears to be small, however, typically ranging from changes of 0.01–0.03 in predominantly outcrossing populations to often undetectable changes in highly selfing populations where migrant pollen necessarily has a limited impact.

Our numerical study thus suggests that pollen migration is most apt to be an important force for predominantly outcrossing populations (and to a lesser degree for the heterozygote disequilibrium at any level of random outcrossing). More generally, a significant effect appears largely restricted to cases where the disequilibria are low, in which migrant pollen with a substantially different nuclear gene frequency from the residents or migrant seeds can sometimes determine the detectability or sign of nonrandom associations. A graphical example is given in Figure 2, where although the disequilibrium trajectories when $\bar{P} = \bar{p}$ (Figure 2A) are virtually indistinguishable from those with no pollen migration (not shown), the same frac-

tion of migrant pollen carrying a substantially different nuclear frequency (Figure 2B, corresponding to pollen gene flow from only the genetically distinct populations) slightly increases $|D_3|$, slightly reduces $|D_1|$ and $|D|$ (but not $|\hat{D}|$), and perhaps most interestingly, causes a sign change in D_2 . These effects of pollen migration can be magnified by higher seed migration rates.

Gene flow can significantly affect the cytonuclear structure of the resident population when immigrant seeds do not have cytonuclear disequilibria. As illustrated in Figure 3, seed migration rates of just 1–3% can generate experimentally detectable and long-lasting transient disequilibria *de novo*. The transient associations in such cases are due primarily to the admixture of immigrant and resident seeds with different nuclear and cytoplasmic frequencies (ASMUSSEN and ARNOLD 1991). Simultaneous pollen migration generally has only a small effect, the nature of which is similar to that described above when migrant seeds have nonrandom associations.

The effects of self-fertilization and seed migration (Figure 3) also parallel those when permanent disequilibria are generated. For instance, with all else being equal, higher selfing rates tend to produce greater and longer-lasting transient homozygote and allelic disequilibria, while often (but not always) decreasing the heterozygote disequilibrium (see Figure 3, A and C). Higher seed migration rates again generate greater associations, but these are of shorter duration (especially the homozygote and allelic disequilibria), because the higher gene flow causes the resident population to reach its final equilibrium state more quickly (see Figure 3, C and D). Note that the examples in Figure 3 represent the most favorable case where the migrants and initial residents are fixed for opposite cytonuclear genotypes. The levels of transient disequilibria will be less when the cytonuclear composition of the migrant seeds is more similar to that of the residents. Small transient associations can build up, however, even when the migrant seeds have the same nuclear genotypic frequencies as the resident seeds, provided these are not the (inbreeding) equilibrium frequencies in the resident population and the cytoplasmic frequency differs in the migrants and residents. In such cases, admixture disequilibria develop, because the mating system alters the resident nuclear genotype frequencies, causing them to deviate from those in the migrant seeds.

Returning to the final cytonuclear structure, we see from (8)–(9) and the interrelations in (5) that all six possible disequilibrium patterns (ASMUSSEN, ARNOLD and AVISE 1987) could conceivably be found in the equilibrium island population. In particular, there may eventually be (i) completely nonrandom cytonuclear associations, which require $m > 0$ and $\bar{d} \neq 0$ (and

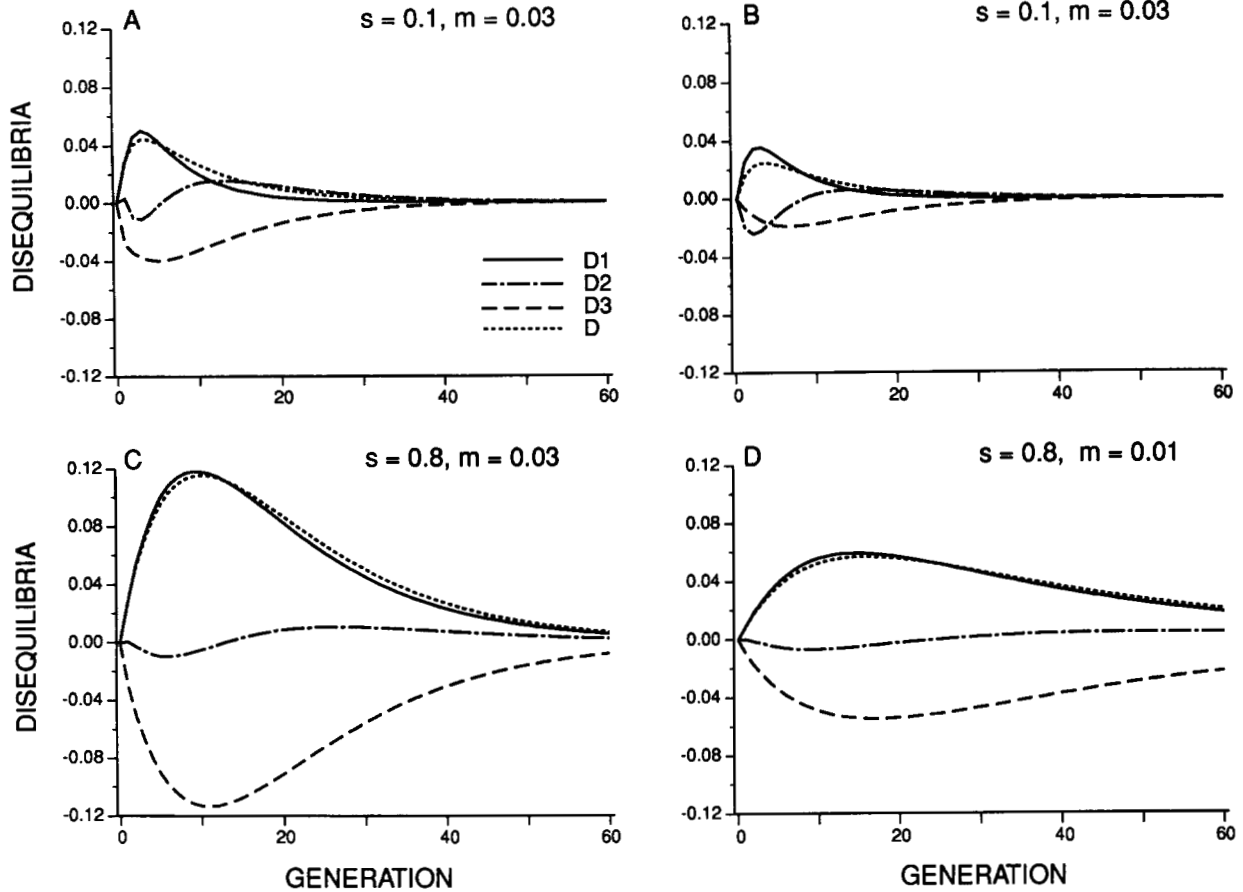


FIGURE 3.—Generation of transient cytonuclear disequilibria by migrant seeds with random associations. The population is censused as seeds in graph B and as adults in the others. In all cases, $U_1^{(0)}$ (or $u_1^{(0)}$) = 1, $\hat{w}_2 = 1$, $M = 0.1$, and $\bar{P} = 0$.

consequently at most one genotypic association can be zero in immigrant seeds); (ii) completely random associations, which necessarily occur only when there is no seed migration or there are cytonuclear disequilibria in immigrant seeds (*i.e.*, $\bar{d}_1 = \bar{d}_2 = \bar{d}_3 = \bar{d} = 0$); (iii) a random allelic association ($\hat{D} = 0$) but completely nonrandom genotypic associations ($\hat{D}_1, \hat{D}_2, \hat{D}_3 \neq 0$), provided $m > 0$, $\bar{d} = 0$, and $\bar{d}_1, \bar{d}_2, \bar{d}_3 \neq 0$; or (iv) possibly a single random genotypic association, with all the other three associations nonzero (*e.g.*, $\hat{D}_1 = 0$ and $\hat{D}_2, \hat{D}_3, \hat{D} \neq 0$), which might occur when $m > 0$ and $\bar{d} \neq 0$, given the appropriate combination of parameter values.

To complete the island's equilibrium structure, we note that the ultimate genotypic frequencies ($\hat{U}_1, \dots, \hat{W}_2$) can be calculated from the limiting gene frequencies and cytonuclear associations in (6)–(9) and the limiting frequency of nuclear heterozygotes,

$$\hat{V} = \frac{\{2m\bar{v} + 2(1 - m)(1 - s) \cdot [M(\hat{P}\hat{Q} + \hat{Q}\hat{P}) + 2(1 - M)\hat{P}\hat{Q}]\}}{2 - s(1 - m)}, \quad (10)$$

via the cytonuclear relations in Table 1 and (2)–(3).

In the general case where $0 < s, m, M < 1$ and $\bar{P} \neq \bar{p}$, the final, overall cytonuclear constitution of the island population is thus a function of the selfing rate, the two migration rates, the nuclear gene frequency in immigrant pollen, and the overall cytonuclear constitution of immigrant seeds.

Additional insight regarding the relative effects of the mating system and the two forms of gene flow is provided by an examination of the behavior in the nested models of no seed migration ($m = 0$), no pollen migration ($M = 0$), equal nuclear gene frequencies in the two migrant pools ($\bar{P} = \bar{p}$), complete random mating ($s = 0$), and complete self-fertilization ($s = 1$).

Pollen migration without seed migration ($0 < M < 1; m = 0$): Populations receiving only immigrant pollen have distinctly different cytonuclear dynamics from those described above, further indicating that seed migration has a major impact on the resident population. For instance, the cytoplasmic frequency is constant ($X_t \equiv X_0$), whereas the nuclear frequency monotonically approaches the frequency in immigrant pollen ($P_t \rightarrow \bar{P}$). The two most striking differences in the absence of seed migration are that all cytonuclear disequilibria are always ultimately zero, and not even

transient disequilibria can be generated *de novo* in populations with completely random allelic and genotypic associations.

In further contrast to the case with simultaneous pollen and seed migration, the transient allelic disequilibria are here entirely independent of any pollen migration; when $m = 0$, D_i has the trajectory characteristic of isolated, mixed-mating populations, monotonically decaying to zero at the constant geometric rate of $\frac{1}{2}(1 + s)$ per generation. The initial decay or transient increase in the genotypic associations due to mixed-mating (ASMUSSEN, ARNOLD and AVISE 1987) can be slightly enhanced or reduced by pollen migration whenever the nuclear frequency in migrant pollen differs from the residents' initial value, in much the same way pollen migration affects the disequilibria with simultaneous seed migration. In this case, any net effect seems short-lived, however, and requires some initial nonrandom associations in the resident population. Ultimately, all three genotypic disequilibria always ultimately decay to zero at the asymptotic rate of $\frac{1}{2}(1 + s)$ characteristic of an isolated, mixed-mating population regardless of the rate of pollen gene flow or its nuclear gene frequency.

Populations receiving only pollen migration are also unusual in that their final state is independent of the actual rate of pollen flow. The ultimate cytonuclear constitution ($\hat{U}_1, \dots, \hat{W}_2$) is determined solely by the selfing rate, the residents' initial cytoplasmic frequency, and the nuclear gene frequency in immigrant pollen. Interestingly, the equilibrium frequencies for both nuclear and joint cytonuclear genotypes are equivalent to those in isolated, mixed-mating populations (e.g., HEDRICK 1985; ASMUSSEN, ARNOLD and AVISE 1987), with immigrant pollen frequencies in place of the residents' initial nuclear gene frequencies. The complete time-dependent solutions and equilibria for this case are given in APPENDIX C.

Seed migration without pollen migration ($0 < m < 1$; $M = 0$): This is the only case (other than the trivial one where $P_0 = \hat{P}$) in which the nuclear gene frequency trajectory is independent of the level of self-fertilization. The nuclear dynamics in (7) become equivalent to the cytoplasmic dynamics in (6), with P_i monotonically approaching the immigrant seed frequency, \hat{p} , at the constant geometric rate of $1 - m$ per generation. Otherwise, the qualitative results with only seed migration closely parallel those above under both forms of gene flow, with only somewhat minor simplifications in the joint cytonuclear dynamics, the equilibrium genotype frequencies, and the equilibrium genotypic associations,

$$\hat{D}_1 = \frac{2m\bar{d}_1 + (1 - m)[s + 2(1 - s)\hat{p}]\hat{D}}{2 - s(1 - m)}$$

$$\hat{D}_2 = \frac{2m\bar{d}_2 + 2(1 - m)(1 - s)(\bar{q} - \hat{p})\hat{D}}{2 - s(1 - m)} \quad (11)$$

$$\hat{D}_3 = \frac{2m\bar{d}_3 - (1 - m)[s + 2(1 - s)\bar{q}]\hat{D}}{2 - s(1 - m)}$$

(As indicated in the discussion of the general case above, the quantitative differences between the disequilibria in (11) and those in (9) for simultaneous pollen and seed migration tend to be small and primarily of significance for highly outcrossed populations.) The cytoplasmic trajectory (6) and the equilibrium allelic association (8) are unchanged, since both are independent of pollen migration. The fact that the island population exhibits almost the same qualitative behavior with or without pollen migration provides final confirmation that seed migration is by far the most influential form of gene flow in this system.

Equal nuclear gene frequencies in immigrant pollen and seeds ($\bar{P} = \hat{p}$): When nuclear gene frequencies are equal in the two migrant pools, the equilibrium state is independent of pollen migration and is equivalent to that above with $M = 0$. Pollen migration thus only affects the final outcome when the nuclear frequencies are different in immigrant pollen and seeds. The time-dependent solutions for the nuclear and cytonuclear variables are simplified somewhat when $\bar{P} = \hat{p}$, but retain their (transient) dependence on M . The solution for D_i , for instance, involves only two geometric terms, and the nuclear gene frequency solution is only simplified in that it approaches the common frequency in the two migrant pools. The cytoplasmic trajectory in (6) is, of course, unchanged, since it is independent of the nuclear frequencies.

Complete random mating ($s = 0$): The results under random mating are qualitatively equivalent to those under partial self-fertilization. One technical difference is that the full dynamics are completely determined by those of the resident gene frequencies and allelic disequilibrium in conjunction with the various migration parameters. Practically speaking, however, this only slightly simplifies the explicit solutions and equilibria for the nuclear and cytonuclear variables. The limiting cytonuclear associations in (8)–(9), for instance, reduce to

$$\begin{aligned} \hat{D} &= \frac{2m\bar{d}}{1 + m} \\ \hat{D}_1 &= m\bar{d}_1 + (1 - m)[M\bar{P} + (1 - M)\hat{P}]\hat{D} \\ \hat{D}_2 &= m\bar{d}_2 \\ &\quad + (1 - m)[M(\bar{Q} - \bar{P}) + (1 - M)(\hat{Q} - \hat{P})]\hat{D} \\ \hat{D}_3 &= m\bar{d}_3 - (1 - m)[M\bar{Q} + (1 - M)\hat{Q}]\hat{D}, \end{aligned} \quad (12)$$

where the equilibrium nuclear gene frequency is

$$\hat{p} = \frac{2m\bar{p} + (1 - m)M\bar{P}}{2m + (1 - m)M}. \quad (13)$$

The most noteworthy difference is that the equilibrium allelic association, \hat{D} , is here more obviously a simple fraction of the allelic disequilibrium in immigrant seeds. The qualitative behavior in mixed-mating populations is therefore primarily a reflection of the random-mating component, although, as seen in Figures 2 and 3, the level of self-fertilization strongly influences the actual magnitude of the cytonuclear disequilibria. [The complete time-dependent solutions for random-mating populations with only seed migration are equivalent to the solutions under the continent-island model censused before mating in ASMUSSEN and ARNOLD (1991).]

Complete self-fertilization with seed migration ($s = 1$; $0 < m < 1$): Self-fertilized populations are distinctive, because they are independent of pollen migration and can maintain cytonuclear disequilibria even in the absence of seed migration. As a result their dynamics are both simpler and qualitatively different from those under mixed-mating. The nuclear gene frequency trajectory, for instance, is analogous to that in (6) for the cytoplasmic frequency, while the trajectory of the allelic disequilibrium becomes

$$D_t = \bar{d} + [D_0 - \bar{d} + (P_0 - \bar{p})(X_0 - \bar{x})](1 - m)^t - (P_0 - \bar{p})(X_0 - \bar{x})(1 - m)^{2t}. \quad (14)$$

The nuclear frequency and allelic disequilibrium thus both approach the corresponding values in immigrant seeds, whatever the seed migration rate, at the constant and asymptotic rate, respectively, of $1 - m$ per generation. Another noteworthy feature of self-fertilized populations is that their limiting genotypic associations depend only on the gene flow from, and the cytonuclear associations in, immigrant seeds, with

$$\begin{aligned} \hat{D}_1 &= \bar{d} - \frac{m\bar{d}_2}{1 + m} \\ \hat{D}_2 &= \frac{2m\bar{d}_2}{1 + m} \\ \hat{D}_3 &= -\bar{d} - \frac{m\bar{d}_2}{1 + m}. \end{aligned} \quad (15)$$

[Note that these equilibrium values do not apply when $m = 0$, for then $D_t \equiv D_0$, $\hat{D}_2 = 0$, and $\hat{D}_1 = -\hat{D}_3 = D_0$.]

Aside from their greater simplicity, the major qualitative difference from those in (9) under mixed-mating is that the final heterozygote disequilibrium, \hat{D}_2 , is a simple fraction of the migrant association and thus is zero if and only if nuclear heterozygotes are randomly associated with the cytoplasmic alleles in immigrant seeds. It is also easier, in this case, to predict

the precise equilibrium patterns of the cytonuclear associations. These patterns, as well as the full dynamical solutions for a self-fertilized population, can be found in APPENDIX D.

Model 2. Seed census: Under the alternative census method, mature seeds are regularly censused in the resident population prior to seed migration. From the recursions for this new model, we note first that the cytoplasmic frequency has equivalent dynamics under both census schemes and is the only variable with this property. Although the transformations of the other variables depend on the life stage censused, the basic functional form of their time-dependent solutions (*i.e.*, the number and nature of their geometric terms) appear to be the same in both cases, with only the coefficients and final equilibrium values depending on the census time. The equilibria for the two life stages are, in fact, directly connected by the phase shift between the generation cycle under the two models. For each nuclear or cytonuclear variable, z , the equilibrium value in resident adults (\hat{Z}) is a weighted average of the equilibrium value in resident seeds (\hat{z}) and the corresponding value in immigrant seeds (\bar{z}):

$$\hat{Z} = m\bar{z} + (1 - m)\hat{z}. \quad (16)$$

This relation implies that the two equilibrium values for a given variable are each both less than, both greater than, or both equal to the corresponding value in immigrant seeds, with the adult equilibria generally closer to the immigrant seed values than are the seed equilibria (*i.e.*, $\hat{z} < \hat{Z} < \bar{z}$, $\bar{z} < \hat{Z} < \hat{z}$, or $\bar{z} = \hat{Z} = \hat{z}$).

The intercensus relationship in (16) is of practical importance for the detection of nonrandom allelic associations, because the ultimate allelic disequilibrium among seeds,

$$\hat{d} = \frac{m(1 + s)\bar{d}}{2 - (1 - m)(1 + s)}, \quad (17)$$

is always less in magnitude than that in (8) among adults (\hat{D}), as long as there is some random outcrossing in the population. Specifically, \hat{d} is reduced by the factor $\frac{1}{2}(1 + s)$ below \hat{D} , which despite the intervening pollen migration is precisely the reduction in allelic disequilibrium after mating within an isolated population. The gap between the equilibrium allelic associations in the two life stages is greatest in predominantly outcrossing species, where $\hat{D} \cong 2\bar{d}$, and steadily declines as the rate of self-fertilization increases to one, becoming negligible in primarily self-fertilized populations where $\hat{D} \cong \hat{d} \cong \bar{d}$. Further inspection of (17) reveals that like \hat{D} , \hat{d} increases in magnitude with both s and m , with the important difference that the final allelic association in seeds cannot exceed $\frac{1}{2}(1 + s)\bar{d}$.

Seed censusing has a more complicated effect on the detection of nonrandom genotypic associations, because the relative magnitudes of the final genotypic disequilibria in the two life stages depend on the precise migration and mating system parameters. The one clear-cut analytic difference arises in self-fertilized populations where the final heterozygote disequilibrium in adults (\hat{D}_2) is always twice that in seeds (\hat{d}_2). For the numerical examples in Figures 2 and 3, adult censusing consistently resulted in higher allelic and homozygote disequilibria, but either lower or higher heterozygote disequilibria, depending on its sign. The differences were negligible in populations with high rates of self-fertilization but quite substantial in highly outcrossed populations, where the disequilibria are generally lower. A specific example showing the contrasting trajectories with adult and seed census is given by Figure 3, A and B, where the maximum values of $|d_1|$, $|d_3|$ and $|d|$ are, respectively, 72, 46 and 58% of the maximum values of $|D_1|$, $|D_3|$ and $|D|$, while the maximum for $|d_2|$ is only 44% that of $|D_2|$ when positive, but over twice that of $|D_2|$ over the negative range.

Otherwise, the two census times have qualitatively equivalent equilibrium properties, including the same general factors leading to permanent cytonuclear disequilibria, with one important exception. In random-mating populations, the conditions for nonrandom genotypic associations are strongly dependent on the life stage censused, as is evident from a comparison of the final adult values in (12)–(13) with the corresponding equilibrium associations in seeds:

$$\begin{aligned}\hat{d} &= \frac{m\bar{d}}{1+m} \\ \hat{d}_1 &= 2[M\bar{P} + (1-M)\hat{P}]\hat{d} \\ \hat{d}_2 &= 2[M(\bar{Q} - \bar{P}) + (1-M)(\hat{Q} - \hat{P})]\hat{d} \\ \hat{d}_3 &= -2[M\bar{Q} + (1-M)\hat{Q}]\hat{d}.\end{aligned}\quad (18)$$

[Note that these formulas have been simplified by writing them in terms of the equilibrium nuclear gene frequencies in adults (\hat{P} , \hat{Q}) via the intercensus relation in (16).]

Inspection of (18) reveals three important features specific to random-mating populations censused as seeds. First, the equilibrium cytonuclear associations have a distinctive sign pattern, which is similar to the transient sign pattern in isolated, random-mating populations (ASMUSSEN, ARNOLD and AVISE 1987). Second, permanent allelic and genotypic disequilibria will be found if and only if the population receives immigrant seeds from a source with nonrandom allelic associations. Third, there are only three possible equilibrium patterns: (1) completely random associations (if and only if $m = 0$ or $\bar{d} = 0$); (2) completely

nonrandom associations [if and only if $m > 0$, $\bar{d} \neq 0$, and $(1-M)(\hat{Q} - \hat{P}) \neq -M(\bar{Q} - \bar{P})$]; or (3) completely nonrandom associations except for heterozygotes [if and only if $m > 0$, $\bar{d} \neq 0$, and $(1-M)(\hat{Q} - \hat{P}) = -M(\bar{Q} - \bar{P})$]. The gene frequency condition in the last two cases reduces to whether or not \bar{p} equals $\frac{1}{2}$ if nuclear gene frequencies are equal in the two migrant pools or if the population receives no immigrant pollen.

The simplified equilibrium structure under (18), as well as the overriding role played in this case by the allelic association in immigrant seeds, stands in strong contrast to the corresponding adult equilibrium structure under (12). This is because not only can all six standard equilibrium patterns conceivably be found among adults; but the actual adult pattern is strongly influenced by both the allelic and genotypic disequilibria in immigrant seeds. Seed censusing of random-mating populations is also distinctive in that the trajectories of the nuclear and cytonuclear genotypic frequencies are independent of the genotypic frequencies and genotypic disequilibria in immigrant seeds. Further technical details of the seed census model can be found in APPENDIX E.

DISCUSSION

We have developed and analyzed a series of deterministic continent-island models to delimit the cytonuclear effects of pollen and seed migration on random-mating, mixed-mating and self-fertilized populations in which cytoplasmic inheritance is strictly maternal. All models are selectively neutral and assume a sufficiently large population size that the effects of random genetic drift can be ignored. Several lines of evidence indicate that seed migration plays the dominant role in shaping the overall cytonuclear structure of such populations. First, the cytoplasmic frequency is necessarily independent of pollen migration. Second and more importantly, continuous seed migration is necessary for the maintenance of nonrandom cytonuclear associations in the island population. Whereas the ultimate genotypic disequilibria are composites of the allelic and genotypic associations in immigrant seeds, the final allelic disequilibrium is a fraction of, and thus a direct reflection of, the corresponding immigrant seed value. The two exceptions to these general properties occur in (i) seeds censused from random-mating populations, where the development of permanent genotypic disequilibria hinges solely on the existence of nonrandom allelic associations in immigrant seeds; and (ii) self-fertilized populations, where the allelic disequilibrium converges to the migrant value, and the heterozygote disequilibrium to a simple fraction of the migrant heterozygote disequilibrium. Provided the cytoplasmic frequency in the

migrant seeds differs sufficiently from the initial frequency in the residents, substantial and long-lasting transient disequilibria can nonetheless be generated when immigrant seeds have random cytonuclear associations.

Further evidence for the predominant role of seed migration comes from the analysis of special cases, which show, first of all, that pollen migration affects the limiting values of the genotypic disequilibria, as well as the ultimate genotypic and nuclear gene frequencies, only when the two migrant pools have different nuclear gene frequencies. Moreover, although populations with only seed migration have essentially the same basic cytonuclear properties as those experiencing both forms of gene flow, populations with only pollen migration are distinctly different. These latter populations closely resemble isolated populations, because their cytoplasmic frequency is constant, and all their cytonuclear associations eventually decay to zero. Pollen migration, however, can enhance or reduce the cytonuclear disequilibria caused by seed migration or by mixed-mating in the absence of seed migration, but the impact is usually small, especially on the allelic and homozygote disequilibria when the island population has a high level of self-fertilization.

The results of this investigation have practical implications for the likelihood of observing nonrandom associations between nuclear genes and maternally inherited cytoplasmic genes in natural populations. Based both on direct observations of pollen and seed dispersal (*e.g.*, LEVIN and KERSTER 1974) and on correlations between pollination or seed dispersal syndromes and patterns of genetic structure (GOVINDARAJU 1988; HAMRICK and GODT 1989), pollen migration is generally considered to be the primary component of gene flow in most outcrossed and partially self-fertilized species. Regardless of the level of pollen migration, seed migration rates among established populations of most species are generally believed to be low (LEVIN 1981; HANDEL 1983). If these generalizations are correct, then the great majority of gene flow entering most seed plant populations will have minimal effect on their cytonuclear structure. Moreover, only small disequilibria will be generated unless the population has very high levels of self-fertilization or neighboring populations have well-developed seed dispersal mechanisms (*e.g.*, LANNER and VANDER WALL 1980; SCHNEIDER and SHARITZ 1988), and then only if the immigrant seeds themselves have significant disequilibria or a substantially different nuclear and cytoplasmic composition from the resident population.

The detection of these admixture disequilibria will therefore require careful experimental design. One critical issue is the size of the data set to be collected. In this regard, FU and ARNOLD (1991) have developed

tables showing the exact sample sizes necessary for the detection of nonzero allelic (or gametic) disequilibrium based on the gene frequencies at the two loci. Further work is under way to extend these results to the detection of the interrelated genotypic disequilibria.

A second experimental design issue arises from our demonstration that the observed level of nonrandom cytonuclear associations can be strongly dependent on the life stage censused. In general, adult censusing is recommended, especially in predominantly outcrossing populations, where the nearly twofold increase over the seed value can significantly increase the ability to detect nonrandom allelic associations. This advantage steadily diminishes as the level of self-fertilization increases, with the final allelic disequilibrium being comparable among seeds and adults of highly self-pollinated species. Although the effect of census timing on the magnitude of the genotypic disequilibria is less clear, our simulations consistently showed the homozygote disequilibria to be larger under the adult census model, again with the greatest effect appearing in populations with little self-fertilization. Moreover, in cases where permanent disequilibria are generated, adult censusing of largely self-fertilized populations will report twice the final heterozygote disequilibrium found in seeds. Figure 3, A and B, clearly shows, however, that the effect of census timing on transient heterozygote disequilibrium can be mixed.

In conclusion, our results shed considerable light on the separate and joint effects of pollen and seed migration on the cytonuclear structure of plant populations. At the same time, the underlying models provide a new theoretical framework from which to assess these two forms of gene flow in natural populations: by adapting the statistical methodology developed by ASMUSSEN, ARNOLD and AVISE (1989) and fitting the appropriate census model to either observed nuclear-mitochondrial or nuclear-chloroplast frequencies, estimates and standard errors of pollen and seed migration rates can possibly be obtained for many of the plant species with maternal cytoplasmic inheritance. In principle, this should be feasible as long as there is some cytonuclear variation in the resident population, the cytonuclear (nuclear) composition of the migrant seeds (pollen) contributed by the source population(s) is known, and the model's equilibrium state depends on the parameter(s) to be estimated. This does not necessarily require any nonrandom cytonuclear associations in the resident or source population. The primary limitation is that with strictly maternal cytoplasmic inheritance, pollen migration can only be estimated when migrant pollen and seeds have different nuclear gene frequencies, because if these coincide, the final equilibrium state is independent of pollen gene flow.

The subsequent paper in this series will develop an analogous framework for utilizing nuclear-cytoplasmic data from those species whose plastids or mitochondria appear to be inherited paternally (*e.g.*, NEALE, MARSHALL and SEDEROFF 1989). With the exception of populations that are completely self-fertilized or otherwise closed to pollen migration, the behavior in these systems is expected to be qualitatively different from that found here, because immigrant pollen can then directly affect the cytonuclear structure of the recipient population. From a practical standpoint, paternal cytoplasmic inheritance should therefore facilitate the estimation of pollen gene flow. These same considerations apply to species with biparental cytoplasmic inheritance (*e.g.*, SMITH 1988).

In order to complete our understanding of the extent to which pollen and seed migration shape the cytonuclear structure of plant populations, still more complex systems must be modeled, which incorporate the effects of natural selection and genetic drift. Another important, further step will be to extend the migration models to encompass nuclear-mitochondrial-chloroplast systems (SCHNABEL and ASMUSSEN 1989), for the nuclear-dicytoplasmic structure should be especially sensitive to the effects of pollen and seed migration, particularly in those species in which all three genomes have different modes of inheritance. We are hopeful that the necessary cytonuclear data (D. WAGNER, M. ARNOLD, personal communications) will soon be available for practical applications of this theory.

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LITERATURE CITED

- ARNOLD, J., M. A. ASMUSSEN and J. C. AVISE, 1988 An epistatic mating system model can produce permanent cytonuclear disequilibria in a hybrid zone. *Proc. Natl. Acad. Sci. USA* **85**: 1893-1896.
- ASMUSSEN, M. A., and J. ARNOLD, 1991 The effects of admixture and population subdivision on cytonuclear disequilibria. *Theor. Pop. Biol.* (in press).
- ASMUSSEN, M. A., J. ARNOLD and J. C. AVISE, 1987 Definition and properties of disequilibrium statistics for associations between nuclear and cytoplasmic genotypes. *Genetics* **115**: 755-768.
- ASMUSSEN, M. A., J. ARNOLD and J. C. AVISE, 1989 The effects of assortative mating and migration on cytonuclear associations in hybrid zones. *Genetics* **122**: 923-934.
- AVISE, J. C., W. S. NELSON, J. ARNOLD, R. K. KOEHN, G. C. WILLIAMS and V. THORSTEINSSON, 1990 The evolutionary genetic status of icelandic eels. *Evolution* **44**: 1254-1262.
- BOBLENZ, K., T. NOTHNAGEL and M. METZLAFF, 1990 Paternal inheritance of plastids in the genus *Daucus*. *Mol. Gen. Genet.* **220**: 489-491.
- BULLOCK, S. H., and R. B. PRIMACK, 1977 Comparative experimental study of seed dispersal on animals. *Ecology* **58**: 681-686.
- CLEGG, M. T., 1980 Measuring plant mating systems. *Bioscience* **30**: 814-818.
- CLEGG, M. T., A. L. KAHLER and R. W. ALLARD, 1978 Estimation of life cycle components of selection in an experimental plant population. *Genetics* **89**: 765-792.
- DARLEY-HILL, S., and W. C. JOHNSON, 1981 Acorn dispersal by the blue jay (*Cyanocitta cristata*). *Oecologia* **50**: 231-232.
- ELLSTRAND, N. C., and D. L. MARSHALL, 1985 Interpopulation gene flow by pollen in wild radish, *Rhaphanus sativus*. *Am. Nat.* **126**: 606-616.
- FU, Y. X., and J. ARNOLD, 1991 A table of exact sample sizes for use with Fisher's exact test for 2 x 2 tables. *Biometrics* (in press).
- GOVINDARAJU, D. R., 1988 Relationship between dispersal ability and levels of gene flow in plants. *Oikos* **52**: 31-35.
- HAMRICK, J. L., and M. J. W. GODT, 1989 Allozyme diversity in plant species, pp. 43-63 in *Plant Population Genetics, Breeding and Genetic Resources*, edited by A. H. D. BROWN, M. T. CLEGG, A. L. KAHLER and B. S. WEIR. Sinauer, Sunderland, Mass.
- HANDEL, S. N., 1983 Pollination ecology, plant population structure, and gene flow, pp. 163-211 in *Pollination Biology*, edited by L. REAL. Academic Press, New York.
- HEDRICK, P. W., 1985 *Genetics of Populations*. Jones & Bartlett, Boston.
- LAMB, T., and J. C. AVISE, 1986 Directional introgression of mitochondrial DNA in a hybrid population of tree frogs: the influence of mating behavior. *Proc. Natl. Acad. Sci. USA* **83**: 2526-2530.
- LANNER, R. M., and S. B. VANDER WALL, 1980 Dispersal of limber pine seed by Clark's nutcracker. *J. For.* **78**: 637-639.
- LEVIN, D. A., 1981 Dispersal versus gene flow in plants. *Ann. Mo. Bot. Gard.* **68**: 233-253.
- LEVIN, D. A., and H. W. KERSTER, 1974 Gene flow in seed plants. *Evol. Biol.* **7**: 139-220.
- NEALE, D. B., K. A. MARSHALL and R. R. SEDEROFF, 1989 Chloroplast and mitochondrial DNA are paternally inherited in *Sequoia sempervirens* D. Don Endl. *Proc. Natl. Acad. Sci. USA* **86**: 9347-9349.
- RITLAND, K., and S. K. JAIN, 1981 A model for the estimation of outcrossing rate and gene frequencies using *n* independent loci. *Heredity* **47**: 35-52.
- SCHNABEL, A., and M. A. ASMUSSEN, 1989 Definition and properties of disequilibria within nuclear-mitochondrial-chloroplast and other nuclear-dicytoplasmic systems. *Genetics* **123**: 199-215.
- SCHNEIDER, R. L., and R. R. SHARITZ, 1988 Hydrochory and regeneration in a bald cypress-water tupelo swamp forest. *Ecology* **69**: 1055-1063.
- SCHUMANN, C. M., and J. F. HANCOCK, 1989 Paternal inheritance of plastids in *Medicago sativa*. *Theor. Appl. Genet.* **78**: 863-866.
- SEARS, B. B., 1980 Elimination of plastids during spermatogenesis and fertilization in the plant kingdom. *Plasmid* **4**: 233-255.
- SMITH, S. E., 1988 Biparental inheritance of organelles and its implications in crop improvement. *Plant Breed. Rev.* **6**: 361-393.
- WEIR, B. S., and S. R. WILSON, 1986 Log-linear models for linked loci. *Biometrics* **42**: 505-523.

APPENDIX A

Recursions for adult census under joint pollen and seed migration: The cytonuclear frequencies at the interim seed stage are the weighted averages of those from self-fertilization of resident ovules (probability s) and those from random outcrossing (probability $1 - s$). The contribution from selfing depends on the resident adult frequencies of the six cytonuclear genotypes (Table 1) in accordance with the cytonuclear recursions for an isolated, self-fertilized population (ASMUSSEN, ARNOLD and AVISE 1987). The contribution from random outcrossing, on the other hand, is determined by the joint nuclear-cytoplasmic allele frequencies in resident ovules (1) and the nuclear gene frequency in the combined resident-migrant pollen pool.

To illustrate how the intermediate seed frequencies are derived, consider the production of AA/C seeds within the island population. An AA/C seed results from selfing with probability $U_1 + \frac{1}{4}V_1 (= P_1 - \frac{1}{4}V_1)$, corresponding to the self-fertilization of resident AA/C or Aa/C individuals. Alternatively, an AA/C seed is produced by random outcrossing with probability $P_1[M\bar{P} + (1 - M)P]$, corresponding to the fertilization of a resident A/C ovule (Freq P_1) by an A -bearing pollen grain [Freq $M\bar{P} + (1 - M)P]$. Combining these two possibilities shows that the frequency of AA/C among newly formed seeds is $u_1 = s(P_1 - \frac{1}{4}V_1) + (1 - s)P_1[M\bar{P} + (1 - M)P]$. Repeating this reasoning shows that the full set of interim cytonuclear genotype frequencies in newly formed seeds is

$$\begin{aligned} u_i &= s(P_i - \frac{1}{4}V_i) + (1 - s)P_i[M\bar{P} + (1 - M)P] \\ v_i &= \frac{1}{2}sV_i + (1 - s) \\ &\quad \cdot [M(P_i\bar{Q} + Q_i\bar{P}) + (1 - M)(P_iQ + Q_iP)] \\ w_i &= s(Q_i - \frac{1}{4}V_i) + (1 - s)Q_i[M\bar{Q} + (1 - M)Q], \end{aligned} \quad (A1)$$

for $i = 1, 2$. The interim marginal frequencies can then be calculated for the nuclear genotypes

$$\begin{aligned} u &= s(P - \frac{1}{4}V) + (1 - s)P[M\bar{P} + (1 - M)P] \\ v &= \frac{1}{2}sV \\ &\quad + (1 - s)[M(P\bar{Q} + Q\bar{P}) + 2(1 - M)PQ] \\ w &= s(Q - \frac{1}{4}V) + (1 - s)Q[M\bar{Q} + (1 - M)Q], \end{aligned} \quad (A2)$$

and the nuclear and cytoplasmic alleles

$$\begin{aligned} p &= \frac{1}{2}M(1 - s)\bar{P} + [1 - \frac{1}{2}M(1 - s)]P \\ x &= X, \end{aligned} \quad (A3)$$

via the relations in Table 1 and (2). The seed frequencies in turn allow derivation of the interim disequili-

bria from the definitions in (3)–(4):

$$\begin{aligned} d &= \frac{1}{2}(1 + s)D \\ d_1 &= \frac{1}{2}sD_1 \\ &\quad + \{\frac{1}{2}s + (1 - s)[M\bar{P} + (1 - M)P]\}D \\ d_2 &= \frac{1}{2}sD_2 \\ &\quad + (1 - s)[M(\bar{Q} - \bar{P}) + (1 - M)(Q - P)]D \\ d_3 &= \frac{1}{2}sD_3 \\ &\quad - \{\frac{1}{2}s + (1 - s) \cdot [M\bar{Q} + (1 - M)Q]\}D. \end{aligned} \quad (A4)$$

Since we have assumed no selection, the cytonuclear constitution of the new generation of adults is precisely that due to admixture of the resident and migrant seeds (ASMUSSEN and ARNOLD 1991). The new frequencies are therefore simply the weighted averages of those in immigrant (m) and resident ($1 - m$) seeds, as illustrated by the recursions for the cytonuclear genotypes

$$\begin{aligned} U'_i &= m\bar{u}_i + (1 - m)u_i \\ &= m\bar{u}_i + (1 - m)\{s(P_i - \frac{1}{4}V_i) \\ &\quad + (1 - s)P_i[M\bar{P} + (1 - M)P]\} \\ V'_i &= m\bar{v}_i + (1 - m)v_i \\ &= m\bar{v}_i + (1 - m)\{\frac{1}{2}sV_i \\ &\quad + (1 - s)[M(P_i\bar{Q} + Q_i\bar{P}) \\ &\quad + (1 - M)(P_iQ + Q_iP)]\} \\ W'_i &= m\bar{w}_i + (1 - m)w_i \\ &= m\bar{w}_i + (1 - m)\{s(Q_i - \frac{1}{4}V_i) \\ &\quad + (1 - s)Q_i[M\bar{Q} + (1 - M)Q]\}, \end{aligned} \quad (A5)$$

for $i = 1, 2$. From these we obtain the transformations for the nuclear genotypes, which are equivalent to those in (A5) with subscripts removed, and the gene frequency recursions,

$$\begin{aligned} P' &= m\bar{p} + (1 - m)p \\ &= m\bar{p} + \frac{1}{2}(1 - m)M(1 - s)\bar{P} \\ &\quad + (1 - m)[1 - \frac{1}{2}M(1 - s)]P \end{aligned} \quad (A6)$$

$$X' = m\bar{x} + (1 - m)x = m\bar{x} + (1 - m)X.$$

The new adult cytonuclear disequilibria equal the weighted average of those in the immigrant and resident seeds, plus the covariance across these sources between the cytoplasmic frequency and the relevant

nuclear frequency:

$$\begin{aligned}
 D' &= m\bar{d} + (1 - m)d \\
 &\quad + m(1 - m)(p - \bar{p})(x - \bar{x}) \\
 D'_1 &= m\bar{d}_1 + (1 - m)d_1 \\
 &\quad + m(1 - m)(u - \bar{u})(x - \bar{x}) \\
 D'_2 &= m\bar{d}_2 + (1 - m)d_2 \\
 &\quad + m(1 - m)(v - \bar{v})(x - \bar{x}) \\
 D'_3 &= m\bar{d}_3 + (1 - m)d_3 \\
 &\quad + m(1 - m)(w - \bar{w})(x - \bar{x}).
 \end{aligned} \tag{A7}$$

Substitution of the interim values from (A2)–(A4) into these admixture formulas yields the final disequilibrium recursions

$$\begin{aligned}
 D' &= m\bar{d} + \frac{1}{2}(1 - m)(1 + s)D \\
 &\quad + m(1 - m)\{[1 - \frac{1}{2}M(1 - s)]P \\
 &\quad + \frac{1}{2}M(1 - s)\bar{P} - \bar{p}\}(X - \bar{x}) \\
 D'_1 &= m\bar{d}_1 + \frac{1}{2}s(1 - m)D_1 \\
 &\quad + (1 - m)\{\frac{1}{2}s + (1 - s)[M\bar{P} + (1 - M)P]\}D \\
 &\quad + m(1 - m)\{s(P - \frac{1}{4}V) \\
 &\quad + (1 - s)P[M\bar{P} + (1 - M)P] - \bar{u}\}(X - \bar{x}) \\
 D'_2 &= m\bar{d}_2 + \frac{1}{2}s(1 - m)D_2 \\
 &\quad + (1 - m)(1 - s)\{M(\bar{Q} - \bar{P}) + (1 - M)(Q - P)\}D \\
 &\quad + m(1 - m)\{\frac{1}{2}sV + (1 - s)[M(P\bar{Q} + Q\bar{P}) \\
 &\quad + 2(1 - M)PQ] - \bar{v}\}(X - \bar{x}) \\
 D'_3 &= m\bar{d}_3 + \frac{1}{2}s(1 - m)D_3 \\
 &\quad - (1 - m)\{\frac{1}{2}s + (1 - s)[M\bar{Q} + (1 - M)Q]\}D \\
 &\quad + m(1 - m)\{s(Q - \frac{1}{4}V) + (1 - s)Q \\
 &\quad + [M\bar{Q} + (1 - M)Q] - \bar{w}\}(X - \bar{x}).
 \end{aligned} \tag{A8}$$

APPENDIX B

Time-dependent solutions for D_t and V_t under joint pollen and seed migration with adults censused: The gene frequency dynamics for X_t and P_t in (6)–(7), coupled with the recursion for D in (A8), show that the value of the allelic disequilibrium is given in any generation $t = 0, 1, 2, \dots$ by

$$\begin{aligned}
 D_t &= \hat{D} + b_1(1 - m)^t + b_2\{(1 - m)^2[1 - \frac{1}{2}M(1 - s)]^t \\
 &\quad + (D_0 - \hat{D} - b_1 - b_2)[\frac{1}{2}(1 - m)(1 + s)]^t\}
 \end{aligned} \tag{B1}$$

where

$$\begin{aligned}
 b_1 &= \frac{2mM(\bar{P} - \bar{p})(X_0 - \bar{x})}{2m + (1 - m)M(1 - s)} \\
 b_2 &= \frac{m[2 - M(1 - s)](P_0 - \hat{P})(X_0 - \bar{x})}{(1 - m)[2 - M(1 - s)] - (1 + s)}
 \end{aligned}$$

and

$$D_t \rightarrow \hat{D} = \frac{2m\bar{d}}{2 - (1 - m)(1 + s)} \text{ as } t \rightarrow \infty. \tag{B2}$$

An exception to the general solution in (B1) exists when $M = (1 - s - 2m)/[(1 - m)(1 - s)]$. In this case, the solution for D_t is

$$\begin{aligned}
 D_t &= \hat{D} + b_1(1 - m)^t \\
 &\quad + (D_0 - \hat{D} - b_1 + tb_3)[\frac{1}{2}(1 - m)(1 + s)]^t,
 \end{aligned} \tag{B3}$$

where b_1 and \hat{D} are as before, and

$$b_3 = [m/(1 - m)](P_0 - \hat{P})(X_0 - \bar{x}).$$

The time-dependent solution for the frequency of nuclear heterozygotes is similarly found to be

$$\begin{aligned}
 V_t &= \hat{V} + k_1\{(1 - m)[1 - \frac{1}{2}M(1 - s)]\}^t \\
 &\quad + k_2\{(1 - m)[1 - \frac{1}{2}M(1 - s)]\}^{2t} \\
 &\quad + (V_0 - \hat{V} - k_1 - k_2)[\frac{1}{2}s(1 - m)]^t
 \end{aligned} \tag{B4}$$

where

$$\begin{aligned}
 k_1 &= \frac{2(1 - s)[M(\bar{Q} - \bar{P}) + 2(1 - M)(\hat{Q} - \hat{P})](P_0 - \hat{P})}{2 - s - M(1 - s)} \\
 k_2 &= \frac{-8(1 - M)(1 - s)(P_0 - \hat{P})^2}{(1 - m)[2 - M(1 - s)]^2 - 2s}
 \end{aligned}$$

and \hat{V} is defined in (10). This solution applies except in the unlikely event that $m = 1 - 2s/[2 - M(1 - s)]^2$, when

$$\begin{aligned}
 V_t &= \hat{V} + k_1\{(1 - m)[1 - \frac{1}{2}M(1 - s)]\}^t \\
 &\quad + (V_0 - \hat{V} - k_1 + tk_3)[\frac{1}{2}s(1 - m)]^t,
 \end{aligned} \tag{B5}$$

where k_1 and \hat{V} are as before, and

$$k_3 = -4[(1 - s)/s](1 - M)(P_0 - \hat{P})^2.$$

APPENDIX C

Complete solutions for adult census with only pollen migration ($0 < M < 1$; $m = 0$): When $m = 0$, the new adult frequencies and disequilibria are given by the interim expressions shown in (A1)–(A4) for joint pollen and seed migration. The gene frequency dynamics in this case reduce to

$$X_t \equiv X_0 \text{ for } t = 0, 1, 2, \dots,$$

and

$$P_t = \bar{P} + (P_0 - \bar{P})[1 - \frac{1}{2}M(1-s)]^t \rightarrow \bar{P} \quad \text{as } t \rightarrow \infty. \quad (C1)$$

The trajectory of the nuclear heterozygote frequency is obtained by setting $m = 0$ in the general solution shown in (B4)–(B5), with the main simplification being that

$$V_t \rightarrow \hat{V} = 4[(1-s)/(2-s)]\bar{P}\bar{Q} \quad \text{as } t \rightarrow \infty. \quad (C2)$$

Turning to the cytonuclear disequilibria, we see from (A8) that the allelic disequilibrium has the simple closed-form solution,

$$D_t = D_0[\frac{1}{2}(1+s)]^t, \quad (C3)$$

which, when combined with the solution for P_t in (C1), can be used to derive the complete trajectory for the heterozygote disequilibrium,

$$D_2^{(t)} = k_3[\frac{1}{2}(1+s)]^t + k_4\{\frac{1}{4}(1+s)[2-M(1-s)]\}^t + (D_2^{(0)} - k_3 - k_4)(\frac{1}{2}s)^t, \quad (C4)$$

where

$$k_3 = 2(1-s)(\bar{Q} - \bar{P})D_0$$

$$k_4 = \frac{-8(1-s)(1-M)(P_0 - \bar{P})D_0}{2 - M(1-s^2)}.$$

The solutions for all remaining variables can now be obtained from those for the five key variables ($X_t, P_t, V_t, D_t, D_2^{(t)}$) via the basic cytonuclear relations in Table 1 and (1)–(5). The dynamics of the nuclear homozygote frequencies, for instance, are

$$U_t = P_t - \frac{1}{2}V_t \rightarrow \hat{U} = \bar{P} - \frac{1}{2}\hat{V} \quad (C5)$$

$$W_t = Q_t - \frac{1}{2}V_t \rightarrow \hat{W} = \bar{Q} - \frac{1}{2}\hat{V},$$

while the trajectories of the homozygote disequilibria are determined by

$$D_1^{(t)} = D_t - \frac{1}{2}D_2^{(t)}$$

and

$$D_3^{(t)} = -D_t - \frac{1}{2}D_2^{(t)}. \quad (C6)$$

The cytonuclear genotype frequencies are similarly found to be

$$U_1^{(t)} = U_t X_0 + D_1^{(t)} \rightarrow \hat{U}_1 = \hat{U}X_0$$

$$U_2^{(t)} = U_t Y_0 - D_1^{(t)} \rightarrow \hat{U}_2 = \hat{U}Y_0$$

$$V_1^{(t)} = V_t X_0 + D_2^{(t)} \rightarrow \hat{V}_1 = \hat{V}X_0$$

$$V_2^{(t)} = V_t Y_0 - D_2^{(t)} \rightarrow \hat{V}_2 = \hat{V}Y_0$$

$$W_1^{(t)} = W_t X_0 + D_3^{(t)} \rightarrow \hat{W}_1 = \hat{W}X_0$$

$$W_2^{(t)} = W_t Y_0 - D_3^{(t)} \rightarrow \hat{W}_2 = \hat{W}Y_0. \quad (C7)$$

APPENDIX D

Complete solutions for purely selfing populations with adults censused: Under the limiting case of complete self-fertilization ($s = 1$; $0 < m < 1$), the dynamics of the single-locus gene frequencies (P_t, X_t), as well as the two-locus allelic frequencies ($P_1^{(t)}, P_2^{(t)}, Q_1^{(t)}, Q_2^{(t)}$), have the form

$$Z_t = \bar{z} + (Z_0 - \bar{z})(1-m)^t$$

monotonically approaching the corresponding immigrant frequency at the constant geometric rate of $1 - m$ per generation. Direct solution of the recursions for the frequencies of the heterozygous cytonuclear genotypes in turn yields

$$V_i^{(t)} = \hat{V}_i + (V_i^{(0)} - \hat{V}_i)[\frac{1}{2}(1-m)]^t \rightarrow \hat{V}_i = 2m\bar{v}_i/(1+m), \quad (D1)$$

and thus the trajectories for the homozygous cytonuclear genotypes are

$$U_i^{(t)} = P_i^{(t)} - \frac{1}{2}V_i^{(t)} \rightarrow \hat{U}_i = \bar{p}_i - [m\bar{v}_i/(1+m)]$$

$$W_i^{(t)} = Q_i^{(t)} - \frac{1}{2}V_i^{(t)} \rightarrow \hat{W}_i = \bar{q}_i - [m\bar{v}_i/(1+m)], \quad (D2)$$

for $i = 1, 2$. The equilibrium marginal genotypic frequencies at the nuclear locus have the same form as those in (D1)–(D2) with the subscripts deleted.

The allelic disequilibrium approaches the immigrant value, \bar{d} , along the trajectory given in (14), while the heterozygote disequilibrium has the solution

$$D_2^{(t)} = \hat{D}_2 - \hat{V}(X_0 - \bar{x})(1-m)^t + [D_2^{(0)} - \hat{D}_2 + V_0(X_0 - \bar{x})][\frac{1}{2}(1-m)]^t - (V_0 - \hat{V})(X_0 - \bar{x})[\frac{1}{2}(1-m)^2]^t, \quad (D3)$$

where

$$D_2^{(0)} \rightarrow \hat{D}_2 = 2m\bar{d}_2/(1+m) \quad \text{as } t \rightarrow \infty.$$

The dynamics and equilibria for the homozygote associations are thence obtained by the relations in (C6).

Because the equilibrium cytonuclear associations are simple functions of \bar{d} , \bar{d}_2 , and m , we can precisely define all possible equilibrium patterns among the four disequilibria. Assuming $m > 0$, these are 1) completely random associations, if and only if immigrant seeds have completely random cytonuclear associations; 2) $\hat{D} = 0$ and $\hat{D}_1 = \hat{D}_3 = -\frac{1}{2}\hat{D}_2 = -m\bar{d}_2/(1+m) \neq 0$, if and only if $\bar{d} = 0$ and $\bar{d}_2 \neq 0$; 3) $\hat{D}_1 = 0$ and $\hat{D}_2 = \frac{1}{2}\hat{D}_3 = -\frac{1}{2}\hat{D}_3 = \bar{d} \neq 0$, if and only if $\bar{d} = m\bar{d}_2/(1+m) \neq 0$; 4) $\hat{D}_2 = 0$ and $\hat{D}_1 = \hat{D}_3 = -\hat{D}_3 = \bar{d} \neq 0$, if and only if $\bar{d}_2 = 0$ and $\bar{d} \neq 0$; 5) $\hat{D}_3 = 0$ and $\hat{D}_1 = \frac{1}{2}\hat{D}_2 = -\frac{1}{2}\hat{D}_2 = \bar{d} \neq 0$, if and only if $\bar{d} = -m\bar{d}_2/(1+m) \neq 0$; or 6) completely nonrandom cytonuclear associations, if and only if $\bar{d} \neq 0$ and $\bar{d}_2 \neq 0$, with $\bar{d} \neq \pm m\bar{d}_2/(1+m)$.

Note finally that the dynamics and equilibria in the absence of seed dispersal equal those in an isolated, self-fertilizing population (SCHNABEL and ASMUSSEN

1989) and cannot all be obtained by simply setting $m = 0$ in the above solutions.

APPENDIX E

Model 2. Seed census dynamics: The new seed frequencies and disequilibria after a complete generation cycle are obtained by reversing the steps leading to the adult census model. In short, the admixture formulas from (A5)–(A7) here form (with primes removed) the interim values, which can then be substituted into (A1)–(A4) (with primes added on the left) to yield the full set of seed census recursions. The seed gene frequency dynamics are equivalent to those in (6)–(7) for adults, with the resident adult frequencies ($X_b, X_0; P_b, P_0, \hat{P}$) replaced by the corresponding resident seed frequencies ($x_b, x_0; p_b, p_0, \hat{p}$), where only the nuclear equilibrium frequency in seeds,

$$\hat{p} = \frac{m[2 - M(1 - s)]\bar{p} + M(1 - s)\bar{P}}{m[2 - M(1 - s)] + M(1 - s)},$$

differs from that in adults. The trajectory of the allelic disequilibrium is equivalent to the adult trajectories in (B1)–(B3), with the resident adult variables (D_b, D_0) replaced by the resident seed variables (d_b, d_0), \hat{D} replaced by $\hat{d} = \frac{1}{2}(1 + s)\hat{D}$, and the coefficients altered to

$$b_1 = \frac{mM(1 + s)(\bar{P} - \bar{p})(x_0 - \bar{x})}{2m + (1 - m)M(1 - s)}$$

$$b_2 = \frac{m(1 + s)(p_0 - \hat{p})(x_0 - \bar{x})}{(1 - m)[2 - M(1 - s)] - (1 + s)}$$

and $b_3 = m(p_0 - \hat{p})(x_0 - \bar{x})$. The solution for v_i is similarly equivalent to the adult solution in (B4)–(B5) with the resident adult frequencies replaced by the corresponding resident seed frequencies, k_2 and k_3 additionally multiplied by $1 - m$, and \hat{V} replaced by the seed equilibrium

$$\hat{v} = \frac{sm\bar{v} + 2(1 - s)[M(\hat{P}\bar{Q} + \hat{Q}\bar{P}) + 2(1 - M)\hat{P}\hat{Q}]}{2 - s(1 - m)}.$$

The genotypic disequilibria again have much more complicated dynamics than the other basic variables, with each solution usually equalling the limiting value

$$\hat{d}_1 = \frac{sm\bar{d}_1 + \{s + 2(1 - s)[M\bar{P} + (1 - M)\hat{P}]\}\hat{D}}{2 - s(1 - m)}$$

$$\hat{d}_2 = \frac{sm\bar{d}_2 + 2(1 - s)[M(\bar{Q} - \bar{P}) + (1 - M)(\hat{Q} - \hat{P})]\hat{D}}{2 - s(1 - m)}$$

$$\hat{d}_3 = \frac{sm\bar{d}_3 - \{s + 2(1 - s)[M\bar{Q} + (1 - M)\hat{Q}]\}\hat{D}}{2 - s(1 - m)}$$

plus eight convergent geometric terms, where in the latter we have used the intercensus relation in (16) for $\hat{d}, \hat{D}; \hat{p}, \hat{P};$ and \hat{q}, \hat{Q} .

Special cases: The nested models of only pollen or only seed dispersal, equal nuclear frequencies in the two migrant pools, and complete self-fertilization have the same qualitative features found under adult censusing. In the case of pollen migration without seed migration, the dynamics and equilibria are, in fact, equivalent to those in APPENDIX C under adult censusing (given the appropriate replacements of resident seed for resident adult variables). Under complete self-fertilization, the explicit solutions for all seed variables are equivalent to those for adults in APPENDIX D, but seeds have different equilibrium genotypic associations,

$$\hat{d}_1 = \bar{d} - \frac{\frac{1}{2}m\bar{d}_2}{1 + m}$$

$$\hat{d}_2 = \frac{1}{2}\hat{D}_2 = \frac{m\bar{d}_2}{1 + m}$$

$$\hat{d}_3 = -\bar{d} - \frac{\frac{1}{2}m\bar{d}_2}{1 + m},$$

and nuclear and cytonuclear genotypic frequencies,

$$\hat{u}_i = \bar{p}_i - \frac{\frac{1}{2}m\bar{v}_i}{1 + m} \quad \hat{v}_i = \frac{1}{2}\hat{V}_i = \frac{m\bar{v}_i}{1 + m}$$

$$\hat{w}_i = \bar{q}_i - \frac{\frac{1}{2}m\bar{v}_i}{1 + m},$$

for $i = 1, 2$ or with no subscripts. The two census methods thus differ for self-fertilized populations in that (i) once equilibrium is achieved, the heterozygote frequencies and heterozygote disequilibrium are all reduced by $\frac{1}{2}$ in seeds relative to their values in adults; and (ii) the conditions under which the homozygote disequilibria reach zero are $\bar{d} = \pm\frac{1}{2}m\bar{d}_2/(1 + m)$ in seeds, as opposed to $\bar{d} = \pm m\bar{d}_2/(1 + m)$ in adults.

The major qualitative distinction of seed censusing arises in the case of random-mating populations, where, as indicated in the text, the conditions for permanent genotypic disequilibria are qualitatively different from those in the other cases considered. If such populations receive only seed migration, the time-dependent solutions are equivalent to those for censusing after mating in the continent-island model of ASMUSSEN and ARNOLD (1991).