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

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ABSTRACT

We continue our study of the effects of pollen and seed migration on the cytonuclear structure of mixed-mating plant populations by analyzing two deterministic continent-island models under the critical assumption of paternal cytoplasmic inheritance. The major results of this study that contrast with our previous conclusions based on maternal cytoplasmic inheritance are (i) pollen gene flow can significantly affect the cytonuclear structure of the island population, and in particular can help to generate cytonuclear disequilibria that greatly exceed the magnitude of those that would be produced by seed migration or mixed mating alone; (ii) with simultaneous pollen and seed migration, nonzero cytonuclear disequilibria will be maintained not only when there is disequilibrium in the immigrant pollen or seeds, but also through a variety of intermigrant admixture effects when the two pools of immigrants differ appropriately in their cytonuclear compositions; (iii) either immigrant pollen or immigrant seeds can generate disequilibria *de novo* in populations with initially random cytonuclear associations, but pollen migration alone generally produces lower levels of disequilibrium than does comparable seed migration, especially at high levels of self-fertilization when the overall fraction of immigrant pollen is low; (iv) the equilibrium state of the island population will be influenced by the rate of pollen gene flow whenever there is either allelic disequilibrium in the immigrant pollen or simultaneous seed migration coupled with different cytoplasmic or nuclear allele frequencies in immigrant pollen and seeds or nonzero allelic disequilibrium in either immigrant pool. The estimation of pollen migration should therefore be facilitated with paternal cytoplasmic inheritance relative to the case of maternal cytoplasmic inheritance. These basic conclusions hold whether the population is censused as seeds or as adults, but with simultaneous pollen and seed migration, the relationship between census time and the ability to detect nonrandom cytonuclear associations is complex. When migration is through pollen alone, however, the cytonuclear structure of the island population is independent of the life stage censused.

THE consideration of joint nuclear and cytoplasmic polymorphisms provides a novel approach to the study of migration in natural populations. For example, gene flow models incorporating a single nuclear locus and a uniparentally inherited, cytoplasmic locus have been used to investigate mitochondrial gene flow between *Drosophila* species (TAKAHATA and SLATKIN 1984) and rates of migration from parental species into hybrid zones of frogs and eels (ASMUSSEN, ARNOLD and AVISE 1989; AVISE *et al.* 1990). Theoretical studies also have shown how cytonuclear frequencies, and especially the nonrandom associations (disequilibria) between the corresponding single-locus frequencies, can identify zones of admixture and can provide estimates of gene flow between one or more random-mating populations (ASMUSSEN and ARNOLD 1991).

The use of cytonuclear data might likewise enhance the study of gene flow in seed plants, which in completely and partially outcrossing species can occur through pollen and seeds. In the first paper of this series, we analyzed a set of continent-island models to delimit the effects of pollen and seed migration on cytonuclear frequencies and disequilibria in random-mating, mixed-mating, and self-fertilizing populations, in which the cytoplasmic DNA was inherited maternally (ASMUSSEN and SCHNABEL 1991). In this case, pollen carries no cytoplasmic genes and seed migration accordingly has the predominant, and pollen migration only a minor, influence on the cytonuclear structure of the plant population.

Although organellar DNA in plants is most commonly maternally inherited, several taxa with paternal inheritance have now been discovered. For example, based on data from several species in three families, chloroplast (cp) DNA appears to be inherited paternally in coniferous gymnosperms (WAGNER *et al.* 1991). More surprising, however, are studies showing paternal inheritance of mitochondrial DNA in the conifer species *Sequoia sempervirens* (NEALE, MARSHALL and SEDEROFF 1989) and *Calocedrus decurrens*

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TABLE 1

Joint nuclear-cytoplasmic genotype frequencies

Cytotype	Nuclear genotype AA	Aa	aa	Total
C	$U_1 = UX + D_1$	$V_1 = VX + D_2$	$W_1 = WX + D_3$	X
c	$U_2 = UY - D_1$	$V_2 = VY - D_2$	$W_2 = WY - D_3$	Y
Total	U	V	W	1.0

TABLE 2

Joint nuclear-cytoplasmic allele frequencies

Cytotype	Nuclear allele A	a	Total
C	$P_1 = PX + D$	$Q_1 = QX - D$	X
c	$P_2 = PY - D$	$Q_2 = QY + D$	Y
Total	P	Q	1.0

(Neale, Marshall and Harry 1991) and of cpDNA in two angiosperm genera (Boblenz, Nothnagel and Metzlaff 1990; Schumann and Hancock 1989), which demonstrate that paternal cytoplasmic inheritance is not limited to cpDNA or to conifers.

Populations in which organelles are inherited paternally should have considerably different features from those with maternal cytoplasmic inheritance. In particular, pollen migration, which is considered to be the main component of gene flow in most seed plants (especially in conifers), should here play an important role in determining the transient and final cytonuclear structure of target populations. The greater dependence of the final cytonuclear structure on pollen migration should, in turn, enhance the power for the independent estimation of pollen and seed migration rates in natural populations relative to the case of maternal cytoplasmic inheritance. In this paper, we investigate these issues by developing and analyzing a set of continent-island models with paternal cytoplasmic inheritance, analogous to those used in our previous cytonuclear study with maternal cytoplasmic inheritance (Asmussen and Schnabel 1991).

CYTONUCLEAR SYSTEM

As outlined in Asmussen and Schnabel (1991), we monitor the cytonuclear structure of a single population of diploid plants with discrete, nonoverlapping generations and no seed dormancy. The nuclear locus, with alleles, A and a, and the cytoplasmic locus, with alleles (cytotypes), C and c, can be combined into six cytonuclear genotypes that have the frequencies shown in Table 1. Note that the marginal values of Table 1 are the frequencies of the nuclear genotypes (U, V and W) and the cytoplasmic alleles (X and Y). Also important in this system are the four cytonuclear allelic combinations, which have the frequencies shown in Table 2, where the marginals here are the frequencies of the nuclear (P and Q) and cytoplasmic alleles. The relations between the joint cytonuclear frequencies in Tables 1 and 2,

$$P_i = U_i + \tfrac{1}{2}V_i \qquad Q_i = W_i + \tfrac{1}{2}V_i, \tag{1}$$

for $i = 1, 2$ mirror the standard relations between nuclear genotype and allele frequencies,

$$P = U + \tfrac{1}{2}V \qquad Q = W + \tfrac{1}{2}V. \tag{2}$$

Tables 1 and 2 also show how the cytonuclear frequencies can be partitioned in terms of nonrandom associations (disequilibria) between cytoplasmic alleles and nuclear alleles or genotypes (Asmussen, Arnold and Avise 1987). In particular, the allelic disequilibrium (D; Table 2) quantifies nonrandom associations between alleles at the nuclear and cytoplasmic loci, and the genotypic disequilibria (D_1, D_2, D_3; Table 1) measure nonrandom associations between the nuclear genotypes and the cytoplasmic alleles, where, for example,

$$D = \text{Freq}(A/C) - \text{Freq}(A)\text{Freq}(C)$$

and

$$D_1 = \text{Freq}(AA/C) - \text{Freq}(AA)\text{Freq}(C).$$

These disequilibria are interrelated by the formulas,

$$D_1 + D_2 + D_3 = 0$$

and

$$D = D_1 + \tfrac{1}{2}D_2, \tag{3}$$

and thus reduce to two independent disequilibrium measures. Although technically unnecessary, we will nonetheless consider the behavior of the full set of disequilibrium measures as this is desirable for a variety of practical reasons (Asmussen, Arnold and Avise 1987; Asmussen and Schnabel 1991).

Because we will be comparing the behavior of the system under two alternative censusing methods, we designate a separate set of variables for each life stage at which censusing will occur (adults and seeds). To do this, we employ uppercase letters for variables in the adult population (as in Tables 1 and 2) and lowercase letters (*e.g.*, u_1, u, x, p_1, p, d_1, d, etc.) for the corresponding variables in the seed population.

CONTINENT-ISLAND FORMULATION

As in our investigation of migration with maternal cytoplasmic inheritance, the underlying formulation for this study is a continent-island model in which the pollen and seed migration rates and the genetic composition of immigrants are assumed to be constant over time. Within the island population, mating follows the assumptions of the mixed-mating model with a fixed probability s of self-fertilization and a probability $1 - s$ of (random) outcrossing (CLEGG 1980), and inheritance of cytoplasmic genes is strictly paternal. At the time of mating, the total outcrossed pollen pool contains a proportion M of immigrant pollen and a proportion $1 - M$ of resident pollen, so that the overall fraction of immigrant pollen per generation is $M(1 - s)$. Following mating and seed maturation, the population undergoes a round of seed migration in which a proportion m of the total seed pool is composed of immigrants and a proportion $1 - m$ is of local origin.

The genetic composition of the immigrant pools is described using the same notation shown in Tables 1 and 2, except for the added superposition of bars, with uppercase associated with immigrant pollen and lowercase with immigrant seeds. The pool of immigrant pollen is characterized by its cytonuclear allele frequencies ($\bar{P}_1$, $\bar{Q}_1$, $\bar{P}_2$, $\bar{Q}_2$) together with its marginal nuclear and cytoplasmic allele frequencies ($\bar{P}$, $\bar{X}$) and its allelic disequilibrium ($\bar{D}$). The pool of immigrant seeds, on the other hand, has analogs to the full set of variables defined in Tables 1 and 2 (*e.g.*, $\bar{u}_1$, $\bar{u}$, $\bar{x}$, $\bar{p}_1$, $\bar{p}$, $\bar{d}_1$, $\bar{d}$). As discussed previously (ASMUSSEN and SCHNABEL 1991), a variety of biological situations could exist that cause the genetic constitution of the immigrant pollen to differ from that of immigrant seeds (*i.e.*, $\bar{P}$, $\bar{X}$ and $\bar{D}$ may not equal $\bar{p}$, $\bar{x}$ and $\bar{d}$). The final assumptions of the model are that no selection, mutation, or genetic drift are operating within the island population.

Beginning with a model in which adults are censused, we investigate the general effects of random and mixed-mating ($0 \leqslant s < 1$) on the cytonuclear structure of the island population when the two immigrant pools are genetically different. We then consider the special case of genetically equivalent immigrant pools ($\bar{X} = \bar{x}$, $\bar{P} = \bar{p}$, $\bar{D} = \bar{d}$), followed by a comparison of the distinct cases of only pollen migration ($m = 0$; $0 < M < 1$) and only seed migration ($0 < m < 1$; $M = 0$). Finally, we briefly discuss differences between this model and one in which seeds are censused. Except where explicitly noted, the results are qualitatively equivalent for mixed-mating ($0 < s < 1$) and random-mating ($s = 0$) populations. The cytonuclear structure of completely self-fertilizing populations is independent of the pattern of cytoplasmic inheritance and is not explicitly discussed, because it has been presented previously (ASMUSSEN and SCHNABEL 1991).

Our approach is first to glean as much qualitative information as possible analytically, and then to use numerical examples to ascertain the practical significance of the analytic results. Of particular interest in the consideration of these models are the relative roles of pollen and seed migration in influencing the transient and final cytonuclear structure of the target population.

ADULT CENSUS MODEL: KEY ANALYTIC RESULTS

The recursion equations for this model are generated following the process outlined in APPENDIX A. In short, we derive a set of interim expressions for the values of all variables in resident seeds following pollen migration, fertilization, and seed maturation and use these to calculate the new values in the next adult generation after seed migration. We then solve for the (explicit) closed-form solutions of the critical variables P_t, V_t, X_t, D_t and $D_2^{(t)}$, which determine the solutions of all remaining resident variables via the relations in Equations 1–3 and Tables 1 and 2. Each solution is usually the sum of one or more convergent geometric terms and a constant term, which is the globally stable equilibrium value to which that variable converges.

Nuclear and cytoplasmic frequencies: The nuclear variables have the same transient and equilibrium behavior described previously (ASMUSSEN and SCHNABEL 1991), since they are unaffected by the mode of cytoplasmic inheritance. The nuclear allele frequency monotonically approaches a weighted average of the two immigrant frequencies, $\bar{p}$ and $\bar{P}$,

$$P_t = \hat{P} + (P_0 - \hat{P})\{(1 - m)[1 - \tfrac{1}{2}M(1 - s)]\}^t \rightarrow$$
$$\hat{P} = \frac{2m\bar{p} + (1 - m)M(1 - s)\bar{P}}{2m + (1 - m)M(1 - s)} \quad \text{as} \quad t \rightarrow \infty, \tag{4}$$

whereas the nuclear heterozygote frequency generally has a more complex trajectory that leads eventually to the equilibrium,

$$\hat{V} = \frac{2m\bar{v} + (1 - m)k_1}{2 - s(1 - m)} \tag{5}$$

where

$$k_1 = 2(1 - s)[M(\hat{P}\bar{Q} + \hat{Q}\bar{P}) + 2(1 - M)\hat{P}\hat{Q}].$$

In contrast, the assumption of paternal cytoplasmic inheritance, and the consequent transmission of cytoplasmic alleles through pollen, naturally has profound effects on the behavior of all cytoplasmic and cytonuclear variables. First, unlike our previous cytonuclear migration models (ASMUSSEN, ARNOLD and AVISE 1989; ASMUSSEN and SCHNABEL 1991), the cytoplasmic (allele) frequency depends on the mating system, and its trajectory is very similar in form to that of the nuclear allele frequency in (4), with

$$X_t = \hat{X} + (X_0 - \hat{X})\{(1 - m)[1 - M(1 - s)]\}^t \rightarrow$$
$$\hat{X} = \frac{m\bar{x} + (1 - m)M(1 - s)\bar{X}}{m + (1 - m)M(1 - s)} \quad \text{as} \quad t \rightarrow \infty. \tag{6}$$

The value of X_t converges monotonically to equilibrium at a constant geometric rate equalling the product of the frequency of resident seeds, $1 - m$, and the overall fraction of resident pollen, $1 - M(1 - s)$. The cytoplasmic frequency therefore reaches its equilibrium at a faster rate than the nuclear allele frequency, because the term due to immigrant pollen, $M(1 - s)$, is given only half-weight in (4) for nuclear genes, which are reduced from diploid to haploid state in gametes. A similar contrast is shown by the final cytoplasmic frequency ($\hat{X}$). This, like the final nuclear allele frequency, is a weighted average of the corresponding frequencies in both immigrant pools, but the weight given to the contribution from immigrant seeds is half that in the nuclear case due to the different ploidy levels of the two genomes in seeds.

Allelic disequilibrium: The effects of gene flow on the population's cytonuclear structure are further evident from analysis of the resident cytonuclear disequilibria. For example, all three geometric terms in the general closed-form solution for the allelic disequilibrium depend on the rates of pollen and seed migration (see APPENDIX B), with the dominant term being $(1 - m)[1 - \frac{1}{2}M(1 - s)]$, as for all the marginal, nuclear variables. Furthermore, the equilibrium value ($\hat{D}$) is a linear combination of the allelic disequilibria in immigrant seeds and pollen and a third, "intermigrant admixture" term that reflects joint nuclear and cytoplasmic allele frequency differences (*intermigrant allele frequency differences*) between the two immigrant pools,

$$\hat{D} = \frac{2m\bar{d} + (1 - m)M(1 - s)\bar{D} + k_2(\bar{P} - \bar{p})(\bar{X} - \bar{x})}{2 - (1 - m)[1 + s - M(1 - s)]} \tag{7}$$

where

$$k_2 = \frac{2m(1 - m)M(1 - s)}{2m + (1 - m)M(1 - s)}.$$

Consequently, with joint pollen and seed migration ($M, m > 0$), any one of three conditions will generate permanent nonrandom associations between nuclear alleles and paternally inherited, cytoplasmic alleles: nonzero allelic disequilibrium in immigrant seeds ($\bar{d} \neq 0$), nonzero allelic disequilibrium in immigrant pollen ($\bar{D} \neq 0$), or unequal nuclear and cytoplasmic allele frequencies in immigrant pollen and seeds ($\bar{P} \neq \bar{p}$ and $\bar{X} \neq \bar{x}$). Nonzero disequilibrium thus can be maintained even if there is no disequilibrium in the immigrants. Moreover, no matter which of the three possible causes of permanent disequilibria are present, the final allelic association in the resident population always depends on the rate of pollen migration.

TABLE 3

Equilibrium values for nonrandom associations between nuclear genotypes and cytoplasmic alleles when adults are censused

$$\hat{D}_1 = \frac{2m\bar{d}_1 + k_3\hat{P}\bar{D} + (1 - m) \cdot [s + 2(1 - s)(1 - M)\hat{P}]\hat{D} + k_4(\hat{P}\bar{P} - \bar{u})(\bar{X} - \bar{x})}{2 - s(1 - m)}$$

$$\hat{D}_2 = \frac{2m\bar{d}_2 + k_3(\hat{Q} - \hat{P})\bar{D} + 2(1 - m)(1 - M) \cdot (1 - s)(\hat{Q} - \hat{P})\hat{D} + k_4(\hat{P}\bar{Q} + \hat{Q}P^{-} - \bar{v})(\bar{X} - \bar{x})}{2 - s(1 - m)}$$

$$\hat{D}_3 = \frac{2m\bar{d}_3 - k_3\hat{Q}\bar{D} - (1 - m) \cdot [s + 2(1 - s)(1 - M)\hat{Q}]\hat{D} + k_4(\hat{Q}\bar{Q} - \bar{w})(\bar{X} - \bar{x})}{2 - s(1 - m)}$$

where

$$k_3 = 2(1 - m)M(1 - s)$$

$$k_4 = \frac{2m(1 - m)M(1 - s)}{m + (1 - m)M(1 - s)}$$

In cases where the two immigrant pools have equal allele frequencies at either locus ($\bar{P} = \bar{p}$ or $\bar{X} = \bar{x}$) but $\bar{d}$ and $\bar{D}$ are nonzero, $\hat{D}$ takes a form similar to $\hat{P}$ and $\hat{X}$: a composite of $\bar{d}$ and $\bar{D}$, with the same *relative* weights as in (4) for the equilibrium nuclear allele frequency ($\hat{P}$). Unlike the allele frequencies, however, the final allelic disequilibrium is less than a weighted average of the corresponding immigrant values, because the denominator in this case exceeds the sum of the two weights. As a result, if immigrant seeds and pollen have equal allele frequencies at either locus and the same sign for their allelic associations, $\hat{D}$ will not only be less in magnitude than the maximum of $|\bar{d}|$ and $|\bar{D}|$ but will often be less than both, and can be substantially less, especially when migration and self-fertilization rates are low. When intermigrant allele frequency differences are present, on the other hand, the magnitude of the final allelic disequilibrium can exceed that in both of the immigrant pools. Based on numerical studies, this scenario appears to be limited to situations in which $\bar{d}$ and $\bar{D}$ are small, reaching its extreme in the case of random allelic associations in immigrant pollen and seeds ($\bar{D} = \bar{d} = 0$), for which $\hat{D}$ reduces to its intermigrant admixture term,

$$\hat{D} = \frac{2m(1 - m)M(1 - s)\,(\bar{P} - \bar{p})(\bar{X} - \bar{x})}{[2m + (1 - m)M(1 - s)] \cdot \{2 - (1 - m)[1 + s - M(1 - s)]\}}. \tag{8}$$

Genotypic disequilibria: The genotypic disequilibria are still more complex. Their usual closed-form solutions involve up to nine convergent geometric terms, of which the dominant term is again $(1 - m)[1 - \frac{1}{2}M(1 - s)]$. Their equilibrium values (Table 3) are each a linear combination of the corresponding genotypic disequilibrium in immigrant seeds ($\bar{d}_i$), the allelic disequilibrium in immigrant pollen ($\bar{D}$), the final allelic disequilibrium ($\hat{D}$), and a genotypic, intermigrant term that can be generated under certain conditions by the "admixture" of immigrant pollen and seeds with different cytoplasmic frequencies. The conditions for permanent genotypic associations are accordingly broader than those for permanent allelic associations in (7). In particular, a final genotypic disequilibrium ($\hat{D}_i$) can be nonzero as a result of cytonuclear disequilibria in immigrant seeds (*i.e.*, at least three of the seed disequilibria, $\bar{d}_1$, $\bar{d}_2$, $\bar{d}_3$, $\bar{d}$, are nonzero), allelic disequilibrium in immigrant pollen ($\bar{D} \neq 0$), or various intermigrant admixture effects between immigrant pollen and seeds. (If $\hat{P} = \frac{1}{2}$, then $\hat{D}_2$ is a somewhat exceptional case in that $\hat{D}_2 \neq 0$ only if $\bar{d}_2 \neq 0$ or if $\bar{X} \neq \bar{x}$ and $\bar{v} \neq \frac{1}{2}$.) Unlike the allelic disequilibrium, the final genotypic disequilibria can be independent of the rate of pollen gene flow, but only when they are generated solely by nonrandom genotypic associations in immigrant seeds.

Several conditions exist under which the intermigrant admixture terms can contribute to the generation of permanent genotypic associations, either by themselves or in conjunction with nonrandom associations in the immigrant pools. Whenever immigrant pollen and seeds differ in both nuclear and cytoplasmic allele frequencies, genotypic disequilibria will be generated through the allelic intermigrant admixture associations in (8); they may be generated simultaneously through the genotypic intermigrant admixture terms shown in Table 3, provided the nuclear genotype frequencies in immigrant seeds differ from those that would result at equilibrium from the random union of resident ovules and immigrant pollen. Alternatively, when immigrant pollen and seeds differ only in their cytoplasmic frequencies (*i.e.*, $\bar{X} \neq \bar{x}$ and $\bar{P} = \bar{p}$) and the immigrant seeds are not in Hardy-Weinberg equilibrium, only genotypic intermigrant effects are present. If in this case no disequilibria exist in either immigrant pool, the final genotypic disequilibria reduce [in analogy to (8)] to their genotypic admixture terms,

$$\hat{D}_1 = \frac{k_4(\bar{p}^2 - \bar{u})(\bar{X} - \bar{x})}{2 - s(1 - m)}$$

$$\hat{D}_2 = \frac{k_4(2\bar{p}\bar{q} - \bar{v})(\bar{X} - \bar{x})}{2 - s(1 - m)} \tag{9}$$

$$\hat{D}_3 = \frac{k_4(\bar{q}^2 - \bar{w})(\bar{X} - \bar{x})}{2 - s(1 - m)},$$

where k_4 is defined in Table 3 and depends on m, M and s.

Disequilibrium patterns: The broad set of conditions for permanent allelic and genotypic disequilibria under random or mixed mating ($0 \leq s < 1$) and joint pollen and seed migration ($0 < M, m < 1$) restrict the number of disequilibrium patterns (ASMUSSEN, ARNOLD and AVISE 1987) likely to be found within an equilibrium island population. The most common situation appears to be completely nonrandom cytonuclear associations ($\hat{D}$, $\hat{D}_1$, $\hat{D}_2$, $\hat{D}_3 \neq 0$), which can be generated through the separate or combined effects of nonzero allelic disequilibrium in immigrant seeds, nonzero allelic disequilibrium in immigrant pollen, or different nuclear and cytoplasmic allele frequencies in the two immigrant pools (with or without nonzero genotypic admixture terms). Conversely, completely random associations ($\hat{D} = \hat{D}_1 = \hat{D}_2 = \hat{D}_3 = 0$) will be found at equilibrium generally only when all disequilibria in the immigrant pools are zero and either immigrant pollen and seeds have identical cytoplasmic frequencies or identical nuclear allele frequencies coupled with Hardy-Weinberg nuclear genotype frequencies in immigrant seeds. The mixed pattern of random allelic associations with nonrandom genotypic associations (*i.e.*, $\hat{D} = 0$; $\hat{D}_1$, $\hat{D}_2$, $\hat{D}_3 \neq 0$) can result in several ways, such as when the corresponding situation exists in the two immigrant pools ($\bar{D} = \bar{d} = 0$; $\bar{d}_1$, $\bar{d}_2$, $\bar{d}_3 \neq 0$) and immigrant pollen and seeds have equal nuclear or cytoplasmic frequencies ($\bar{P} = \bar{p}$ or $\bar{X} = \bar{x}$); this pattern also arises if the genotypic disequilibria are due solely to their intermigrant admixture terms in (9). Although theoretically possible, the three other patterns (with one genotypic disequilibrium zero and the other three disequilibria nonzero) would appear to arise only under very restrictive conditions (see Table 3).

ADULT CENSUS: NUMERICAL RESULTS AND SPECIAL CASES

Further understanding of the cytonuclear effects of gene flow can be obtained through an investigation of four issues of particular biological importance. We present first a numerical analysis of the level of permanent disequilibria generated by intermigrant admixture effects alone and the level and duration of transient disequilibria generated in the absence of factors contributing to permanent associations. We then consider the special case of equivalent immigrant pools ($\bar{X} = \bar{x}$, $\bar{P} = \bar{p}$, $\bar{D} = \bar{d}$), and, finally, we compare the effects of pollen migration alone with those of seed migration alone.

Intermigrant admixture disequilibria: To better understand the intermigrant admixture effects, we will restrict our attention to cases in which the immigrant pollen and seeds have random cytonuclear associations ($\bar{D} = \bar{d} = \bar{d}_i = 0$). In the simplest case where $\bar{X} \neq \bar{x}$, $\bar{P} = \bar{p}$, and immigrant seeds are not in Hardy-Weinberg equilibrium, nonrandom associations are generated solely by the genotypic admixture terms in (9). As illustrated in Figure 1A, the final allelic disequilibrium is then necessarily zero, but substantial genotypic associations can be generated in which the final homozygote disequilibria have the opposite sign and one-half the magnitude of the final heterozygote disequilibrium ($\hat{D}_1 = \hat{D}_3 = -\frac{1}{2}\hat{D}_2$). Furthermore, inspection of (9) shows that the three genotypic admix-

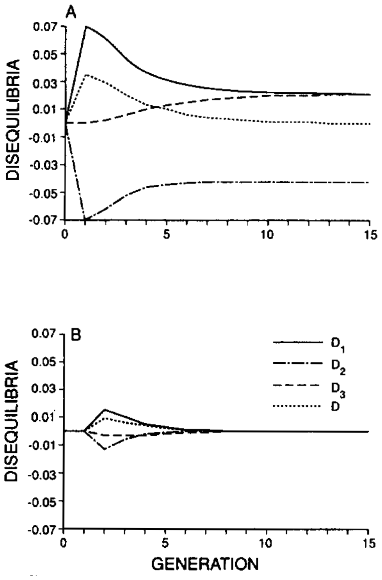

FIGURE 1.—Comparison of admixture disequilibria under adult (A) and seed (B) censusing. In both cases, U_1 (or u_1) = 1 initially, $\bar{v}_2 = 1$, $\bar{P}_1 = \bar{Q}_1 = 0.5$, $m = 0.1$, $M = 0.5$, and $s = 0$.

ture disequilibria increase in magnitude with increasing pollen migration (M) and that the level of pollen gene flow needed to generate a given level of disequilibrium monotonically increases with increasing rates of self-fertilization (Figure 1).

The practical significance of the resulting disequilibria was investigated through a detailed numerical analysis of the cases in which the genotypic intermigrant effects are maximal: $\bar{X} - \bar{x} = 1.0$, $\bar{P} = \bar{p} = 0.5$, and nuclear genotype frequencies deviate maximally from Hardy-Weinberg expectations ($\bar{v} = 0$ or 1). The parameter combinations considered included (i) $0 \leqslant s \leqslant 0.9$ in increments of 0.1, plus $s = 0.99$; and (ii) $0.01 \leqslant M, m \leqslant 0.5$ in increments of 0.1, plus $M, m = 0.001$ and 0.005. A major general result is that the genotypic admixture disequilibria are greatest in predominantly outcrossing populations, with the maximum values found being 0.04 for $|D_1|$ and $|D_3|$ and 0.08 for $|D_2|$.

We also investigated the amount of gene flow necessary to generate genotypic admixture disequilibria with a magnitude greater than 0.01, which we use as an approximate indication of the minimum level of disequilibrium that can be detected experimentally under reasonable sample sizes (FU and ARNOLD 1992). Our results indicate that the pollen migration rate (M) must be at least 0.2 under high selfing ($s = 0.9$), but only 0.03 under low selfing ($s = 0.1$) if the final heterozygote disequilibrium is to exceed 0.01; two- to fourfold higher M values are necessary to ensure that the smaller, homozygote disequilibria are detectable. In contrast, the minimum level of seed migration (m) capable of generating detectable genotypic admixture disequilibria is about 0.05, whatever the level of self-fertilization, and the amount of disequilibrium generated begins to decline when seed migration exceeds 0.42.

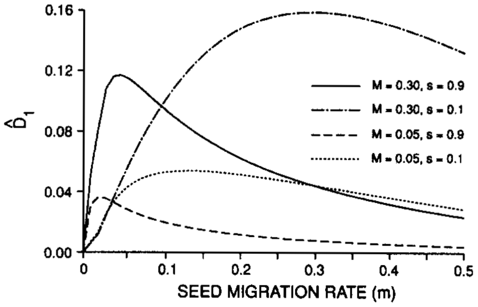

FIGURE 2.—Equilibrium associations under adult censusing between the AA nuclear genotype and the C cytotype ($\hat{D}_1$) for two rates of self-fertilization ($s = 0.1$ and 0.9), two rates of pollen migration ($M = 0.05$ and 0.3), and a series of seed migration rates ($m = 0.0 - 0.5$ in increments of 0.01). In all cases, $\bar{P} - \bar{p} = \bar{X} - \bar{x} = 1$ and $\bar{D} = \bar{d} = \bar{d}_1 = \bar{d}_2 = \bar{d}_3 = 0$, so that $\hat{D}_1$ is generated through the combined effects of the allelic and genotypic intermigrant admixture terms.

The situation is more complicated when the immigrant pools differ in both their nuclear and cytoplasmic allele frequencies (*i.e.*, $\bar{X} \neq \bar{x}$, $\bar{P} \neq \bar{p}$, $\bar{d} = \bar{d}_i = \bar{D} = 0$), because both allelic and genotypic intermigrant effects can be present. In this case (i) the final allelic association is always nonzero due to the intermigrant allele frequency differences; and (ii) nonrandom genotypic associations are generated indirectly through the allelic intermigrant admixture effects and possibly directly through their own intermigrant admixture terms. A wide range of intermigrant allele frequency differences (0.025 − 1.0) and numerous combinations of migration and mating system parameters ($0.001 \leqslant M, m \leqslant 0.5$; $0 \leqslant s \leqslant 0.99$) were explored to better understand the conditions under which potentially detectable disequilibria could be generated and how the magnitudes of the final disequilibria vary with each of the parameters in this case (see *e.g.*, Figure 2).

An important practical result was that the largest amount of allelic disequilibrium generated solely by intermigrant allele frequency differences is about 0.13 across all levels of self-fertilization. The maximum genotypic disequilibria can be greater or less than the maximum allelic disequilibrium, and these maxima vary monotonically with the rate of self-fertilization. For instance, as s increases from 0 to 0.99 when $(\bar{P} - \bar{p})(\bar{X} - \bar{x}) = 1$, $\max|\hat{D}_1|$ decreases from 0.2 to 0.13 and $\max|\hat{D}_2|$ decreases from 0.15 to less than 0.01, while $\max|\hat{D}_3|$ increases from 0.09 to 0.13. Viewed from another perspective, even when allele frequency differences are maximized (*i.e.*, $(\bar{P} - \bar{p})(\bar{X} - \bar{x}) = \pm 1$), the rate of pollen migration must be greater than 1% to generate any potentially detectable cytonuclear disequilibria whatever the other parameter values. On the other hand, if intermigrant allele frequency differences are very small (*e.g.*, $(\bar{P} - \bar{p})(\bar{X} - \bar{x}) = 0.1$), only a limited range of migration rate combinations produces disequilibria detectable under reasonable sample sizes. For example, when $s = 0.1$, both M and m must be about 0.20 or greater, whereas when $s = 0.9$, M must be greater than 0.30 and m must be between 0.02 and 0.10. If $(\bar{P} - \bar{p})(\bar{X} - \bar{x}) < 0.06$, detectable disequilibria were never generated. Additional details regarding joint allelic and genotypic admixture effects are found in APPENDIX C.

Transient disequilibria ($\bar{d} = \bar{d}_i = \bar{D} = 0, \bar{X} = \bar{x}$): Even when the criteria for permanent cytonuclear associations are not met, immigration by pollen and seeds from populations that are genetically distinct from the residents can generate transient cytonuclear disequilibria that are both significantly different from zero and very long lasting. The largest transient associations are generated in the extreme case of fixed nuclear and cytoplasmic differences between immigrants and initial residents (*e.g.*, $\bar{P} = \bar{p} = \bar{X} = \bar{x} = 0$; $P_0 = X_0 = 1$), but even much smaller differences between residents and either or both immigrant pools can lead to significant disequilibria. The resulting associations are usually substantially higher (but in certain circumstances can be substantially lower) than those generated in comparable populations with maternal cytoplasmic inheritance (see Figure 3 in ASMUSSEN and SCHNABEL 1991).

The maximum transient disequilibria attained along a trajectory and the number of generations that the disequilibria remain at detectable levels exhibit the following general patterns. The maximum values tend to (i) increase monotonically with either increasing pollen or seed migration when the other form of gene flow is negligible or absent; (ii) decrease monotonically with increasing pollen migration when seed migration is high (*e.g.*, $m = 0.4$); or (iii) in some cases, initially increase, then decrease in magnitude with increasing M or m. The duration of detectable disequilibria generally decreases as either M or m gets large. These patterns were observed at all levels of self-fertilization, although with high selfing ($s > 0.9$), the effects of pollen migration were often dampened. In general, the effect of s on the magnitudes of the disequilibria is not easily predictable, in that the disequilibria can either increase or decrease with increasing levels of self-fertilization depending on the specific combination of migration rates. Higher selfing, however, generally leads to a longer build-up and a slower decay of the disequilibria, especially at low levels of pollen and seed migration.

Equivalent immigrant pools ($\bar{X} = \bar{x}, \bar{P} = \bar{p}, \bar{D} = \bar{d}$): Although numerous biological scenarios could cause the nuclear and cytoplasmic allele frequencies to differ in immigrant pollen and seeds, there certainly will be situations in nature in which the immigrant pools are effectively equivalent. In this case, each allele frequency converges to the common immigrant value, the final nuclear genotypic frequencies are independent of the rate of pollen flow, and the intermigrant admixture terms of the cytonuclear disequilibria are necessarily all zero. There will thus be permanent disequilibria, and the final state will depend on the rate of pollen migration, only if there are some nonrandom associations in both immigrant pools. The equilibrium allelic association, for instance, is simply a fraction of the immigrants' allelic association,

$$\hat{D} = \frac{[2m + (1 - m)M(1 - s)]\bar{D}}{2 - (1 - m)[1 + s - M(1 - s)]}, \qquad (10)$$

which monotonically increases with both migration rates and the level of self-fertilization, approaching 1 as s or m approaches 1, and a value strictly less than 1 as M approaches 1 (if $s, m < 1$).

To examine this situation more thoroughly, consider an originally monomorphic population (*e.g.*, AA/M) that receives the majority of its immigrants from like populations, but also receives some pollen and seeds from populations that are fixed for alternate nuclear and cytoplasmic alleles (*e.g.*, aa/m). Within this framework, we investigated the final cytonuclear disequilibrium patterns across several pollen migration rates ($M = 0$ through 0.5 in increments of 0.01) under four combinations of seed migration and self-fertilization rates ($m = 0.01$ and 0.05; $s = 0.1$ and 0.9). The results are presented in Figure 3, where, for ease of comparison across parameter combinations, the four curves for each disequilibrium are shown together on a single axis. Note first, that all four cytonuclear disequilibria generally increase in magnitude with increasing rates of pollen and seed migration. The allelic and homozygote disequilibria (Figure 3, A, B and D) attain their greatest magnitudes when high seed migration is coupled with high self-fertilization ($m = 0.05$, $s = 0.9$). The heterozygote disequilibrium (Figure 3C), on the other hand, has a substantially higher magnitude in predominantly outcrossing populations ($s = 0.1$).

Another clear result from these examples is that the relative effect of the seed migration rate is greatest when the pollen migration rate is low. Thus, with all else being equal, the absolute difference in the amount of disequilibrium generated for any two rates of seed migration is reduced as the pollen gene flow rate increases. This point is most clearly illustrated by the heterozygote disequilibrium (Figure 3C), the magnitude of which in our example is almost independent of the seed migration rate when the rate of pollen migration is greater than 0.3.

Pollen migration alone ($0 < M < 1$; $m = 0$) *vs.* seed migration alone ($M = 0$; $0 < m < 1$): With paternal cytoplasmic inheritance, the cytonuclear effects are very similar for either pollen or seed migration alone.

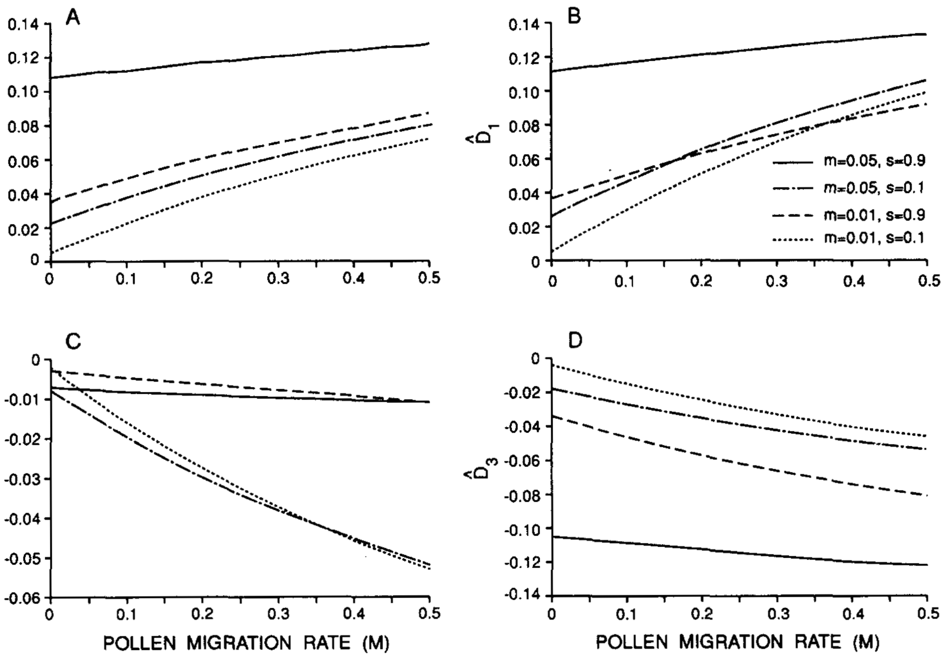

FIGURE 3.—Equilibrium allelic and genotypic associations under adult censusing for two rates of self-fertilization (s = 0.1 and 0.9), two rates of seed migration (m = 0.1 and 0.05), and a series of pollen migration rates (M = 0.0 – 0.5 in increments of 0.01). In all cases, $U_1 = 1$ initially, and the two immigrant pools are equivalent, with $\bar{u}_1 = \bar{P}_1 = 0.7$, and $\bar{w}_2 = \bar{Q}_2 = 0.3$. The disequilibria in immigrant pollen and seeds are $\bar{D} = \bar{d} = \bar{d}_1 = 0.21 = -\bar{d}_3$ and $\bar{d}_2 = 0$.

First, with either single form of gene flow, the nuclear and cytoplasmic allele frequencies converge monotonically to their corresponding frequencies in the immigrants. Second, either pollen or seed migration alone can generate permanent nonrandom associations provided there are nonzero associations in the immigrants ($\bar{D} \neq 0$ or at most one of $\bar{d}$, $\bar{d}_1$, $\bar{d}_2$, $\bar{d}_3$ is zero). Third, gene flow with no disequilibrium in the immigrants ($\bar{D} = 0$ or $\bar{d} = \bar{d}_i = 0$) can in each case lead to significant (although transient) increases over the disequilibria in isolated, mixed-mating populations, and it can generate at least some transient disequilibrium *de novo* when no associations are initially present in the resident population if the cytoplasmic frequencies in the immigrants initially differ from those in the residents ($X_0 \neq \bar{X}$ or $X_0 \neq \bar{x}$).

This latter point is illustrated in Figure 4 for two rates of self-fertilization (s = 0.1 and 0.9). Note first that significant transient disequilibria are generated by both seed and pollen migration, but that seed migration generates larger allelic and homozygote disequilibria than does comparable pollen migration (Figure 4, A *vs.* B and C *vs.* D), especially when s is large. The reverse is true for the heterozygote disequilibrium, at least for low rates of self-fertilization. Second, the duration of the transient associations is greatly increased in predominantly self-fertilizing populations (Figure 4, A *vs.* C and B *vs.* D), especially under pollen migration alone.

Similar contrasts are seen in the final disequilibria under the two forms of gene flow when the immigrants have nonrandom cytonuclear associations. The equilibrium values are given by

$$\begin{aligned}
\hat{D} &= \frac{M\bar{D}}{1+M} \\
\hat{D}_1 &= \frac{[s + 4(1-s)\bar{P}]\hat{D}}{2-s} \\
\hat{D}_2 &= \frac{4(1-s)(\bar{Q}-\bar{P})\hat{D}}{2-s} \\
\hat{D}_3 &= \frac{-[s + 4(1-s)\bar{Q}]\hat{D}}{2-s},
\end{aligned} \tag{11}$$

with only pollen migration ($m = 0$), and by

$$\begin{aligned}
\hat{D} &= \frac{2m\bar{d}}{2-(1-m)(1+s)} \\
\hat{D}_1 &= \frac{2m\bar{d}_1 + (1-m)[s + 2(1-s)\bar{p}]\hat{D}}{2-s(1-m)} \\
\hat{D}_2 &= \frac{2m\bar{d}_2 + 2(1-m)(1-s)(\bar{q}-\bar{p})\hat{D}}{2-s(1-m)} \\
\hat{D}_3 &= \frac{2m\bar{d}_3 - (1-m)[s + 2(1-s)\bar{q}]\hat{D}}{2-s(1-m)}
\end{aligned} \tag{12}$$

with only seed migration ($M = 0$).

The final allelic disequilibrium is in both cases a fraction of its corresponding value in the immigrants, but the value with only seed migration depends on the mating system in addition to the rate of gene flow. Moreover, the magnitude of the final allelic disequilibrium with only pollen migration increases with the level of gene flow up to a maximum of one-half of the immigrant allelic disequilibrium (*i.e.*, $\hat{D}/\bar{D} \rightarrow 1/2$ as $M \rightarrow 1$), whereas with only seed migration, the final

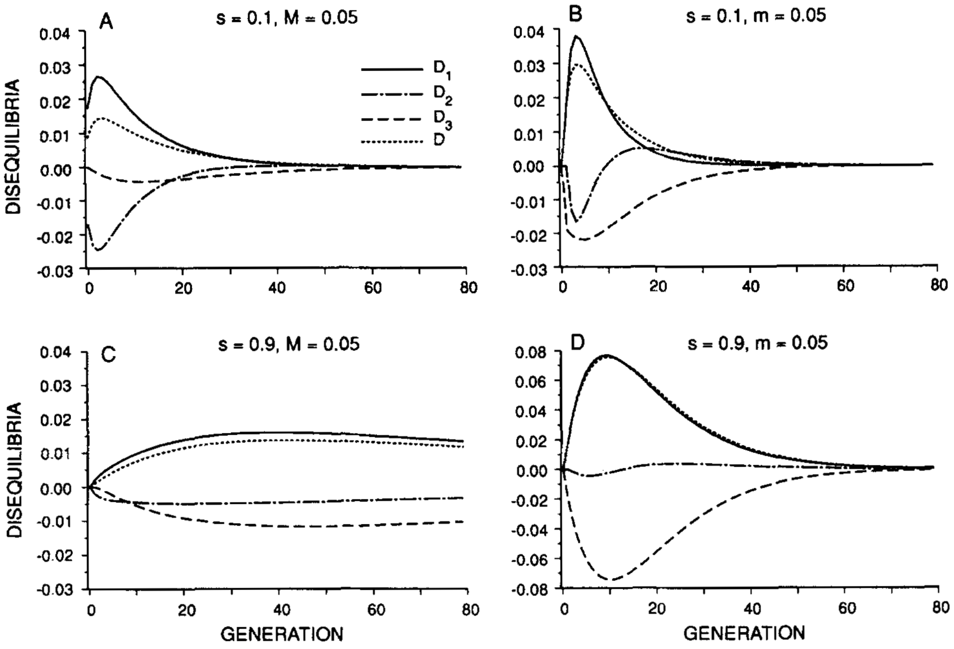

FIGURE 4.—Generation of transient disequilibria by pollen migration alone and by seed migration alone when no disequilibria exist in the immigrants. In all cases, the population is censused as adults, with $X_0 = 0.8$, $P_0 = 1$, $\bar{x} = \bar{X} = 0.4$, and $\bar{p} = \bar{P} = 0$. Note the change of scale in graph D.

allelic association increases to the immigrant value as the rates of either self-fertilization or gene flow increase (*i.e.*, $\hat{D}/\bar{d} \longrightarrow 1$ as s or $m \longrightarrow 1$). Pollen migration can generate at most half the permanent allelic disequilibrium produced by comparable seed migration ($M = m$, $\bar{D} = \bar{d}$), with $\hat{D}_{\text{pollen migration}}/\hat{D}_{\text{seed migration}}$ equalling ½ for $s = 0$, and monotonically decreasing to $M/(1 + M)$ as s increases to 1.

Differences between the final genotypic disequilibria under the two forms of gene flow reflect the difference in ploidy level of the two immigrant pools. Thus, because no genotypic disequilibria are possible in the immigrant pollen pool, the equilibrium genotypic associations under pollen migration are, like the allelic association, fractions of the immigrant allelic disequilibrium, with the exact values depending on the residents' mating system and the immigrants' nuclear allele frequencies in addition to the rate of pollen migration. On the other hand, when gene flow is only through seeds, the final genotypic disequilibria are composites of the genotypic and allelic disequilibria that are possible within a diploid immigrant pool. As a result of these differences, the final genotypic associations under seed migration, like the final allelic disequilibrium in (12) and the transient values shown in Figure 4, can be several times larger (up to an order of magnitude or more) than those under comparable pollen migration ($m = M$, $\bar{d} = \bar{D}$, $\bar{p} = \bar{P}$). These differences are amplified as the rate of self-fertilization increases, because of the consequent decline in the overall fraction of immigrant pollen, $M(1 - s)$.

A final point is that the potential equilibrium structure is more complex under seed migration, with all six patterns of nonrandom associations theoretically possible (ASMUSSEN, ARNOLD and AVISE 1987), as they are with joint pollen and seed migration. The situation is quite different with only pollen migration, however, where because all four disequilibria in (11) are fractions of the allelic disequilibrium in immigrant pollen, the number of possible equilibrium patterns is limited to three: (i) completely nonrandom associations ($\hat{D}$, $\hat{D}_1$, $\hat{D}_2$, $\hat{D}_3 \neq 0$) which occur if and only if $\bar{D} \neq 0$ and $\bar{P} \neq$ ½; (ii) completely random associations ($\hat{D} = \hat{D}_1 = \hat{D}_2 = \hat{D}_3 = 0$) which occur if and only if $\bar{D} = 0$; and (iii) random heterozygote associations but nonrandom allelic and homozygote associations ($\hat{D}$, $\hat{D}_1$, $\hat{D}_3 \neq 0$ but $\hat{D}_2 = 0$) which occur if and only if $\bar{D} \neq 0$ and $\bar{P} =$ ½. This simplified equilibrium structure also allows determination of the relative magnitudes of the final allelic and homozygote disequilibria under pollen migration alone: when $\bar{P} <$ ½, $|\hat{D}_1| < |\hat{D}| < |\hat{D}_3|$; when $\bar{P} >$ ½, $|\hat{D}_3| < |\hat{D}| < |\hat{D}_1|$; and when $\bar{P} =$ ½, $\hat{D}_1 = \hat{D} = -\hat{D}_3$.

SEED CENSUS MODEL

This model assumes that censusing of resident seeds takes place prior to seed dispersal, so that the frequencies and disequilibria in the seed sample each generation are obtained by reversing the steps that yield the adult census model (APPENDIX D). The closed-form solutions for all the marginal nuclear and cytoplasmic variables are equivalent in the number and nature of their geometric terms to those obtained with adult censusing. The equilibrium values of these marginal, as well as all the joint, cytonuclear frequency variables, however, differ under the two census methods in that the final value in resident adults is a weighted average of the corresponding value in immigrant seeds and the equilibrium value in resident seeds [*e.g.*, $\hat{U}_1 = m\bar{u}_1 + (1 - m)\hat{u}_1$].

The cytonuclear disequilibria also have very similar time-dependent solutions and equilibrium expressions under adult and seed censusing (APPENDIX D), with two exceptions. First, the allelic disequilibrium has an additional (nondominant) geometric term corresponding to that for the cytoplasmic frequency. Second, and most significantly, the conditions for permanent nonrandom associations differ in one regard: the genotypic admixture terms are here present under different circumstances due to more complicated forms for their nuclear components. This leads to two important practical distinctions between the two census methods. First, seed-censused populations for which mating is random will never develop permanent genotypic disequilibria solely from intermigrant admixture effects at the genotypic level. Second, random- or mixed-mating populations can have random equilibrium associations in seeds when there are maximal genotypic admixture disequilibria in adults ($\bar{d} = \bar{d}_i = \bar{D} = 0, \bar{X} - \bar{x} = 1, \bar{P} = 0.5, \bar{v} = 1$; Figure 1).

The altered genotypic admixture terms also lead to different conditions for the various equilibrium patterns from those under adult censusing. With seed censusing, for instance, completely random associations will generally be found at equilibrium only when the two immigrant pools have no disequilibria and either (i) equal cytoplasmic frequencies; (ii) equal, monomorphic nuclear allele frequencies; or (iii) equal, polymorphic nuclear allele frequencies combined with random mating in the resident population or only nuclear heterozygotes in the immigrant seeds. Random allelic but nonrandom genotypic associations will be found at equilibrium if the two immigrant pools have (i) this same disequilibrium pattern and equal cytoplasmic or nuclear allele frequencies; or (ii) random cytonuclear associations, different cytoplasmic frequencies, and equal, polymorphic nuclear allele frequencies with some nuclear homozygotes in immigrant seeds, combined with partial self-fertilization in the resident population (in which case genotypic disequilibria are generated solely by their own intermigrant admixture terms).

The final allelic and genotypic disequilibria are related to the corresponding values under adult censusing by the admixture formulas (ASMUSSEN and ARNOLD 1991)

$$
\begin{aligned}
\hat{D} &= m\bar{d} + (1 - m)\hat{d} + m(1 - m) \\
&\quad \cdot(\hat{p} - \bar{p})(\hat{x} - \bar{x}) \\
\hat{D}_1 &= m\bar{d}_1 + (1 - m)\hat{d}_1 + m(1 - m) \\
&\quad \cdot(\hat{u} - \bar{u})(\hat{x} - \bar{x}) \\
\hat{D}_2 &= m\bar{d}_2 + (1 - m)\hat{d}_2 + m(1 - m) \\
&\quad \cdot(\hat{v} - \bar{v})(\hat{x} - \bar{x}) \\
\hat{D}_3 &= m\bar{d}_3 + (1 - m)\bar{d}_3 + m(1 - m) \\
&\quad \cdot(\hat{w} - \bar{w})(\hat{x} - \bar{x}).
\end{aligned}
\tag{13}
$$

Each adult equilibrium value is a weighted average of the corresponding immigrant seed value and the final resident value under seed censusing, plus the equilibrium covariance across these sources between the cytoplasmic frequency and the relevant nuclear frequency.

Because of these potential covariance terms, in the general case one cannot easily predict the relative magnitudes of the disequilibria under the two census schemes. Useful insight into the effect of census time on the magnitude of the disequilibria can, however, be obtained in four special cases. First, when the two immigrant pools have equivalent compositions ($\bar{X} = \bar{x}$, $\bar{P} = \bar{p}$, $\bar{D} = \bar{d}$), the final allelic disequilibrium in seeds is strictly less than that in adults when $s < 1$, with the seed value being at most ½$(1 + s)\bar{d}$. Second, for any given allelic or genotypic association (*e.g.*, d_2), when all intermigrant admixture terms are zero (*e.g.*, $\bar{X} = \bar{x}$) and only the corresponding association in immigrant seeds is zero (*e.g.*, $\bar{d}_2 = 0$; $\bar{d}_1$, $\bar{d}_3$, $\bar{d} \neq 0$), then the final value with seed censusing will always exceed that with adult censusing by a factor of $1/(1 - m)$, with the difference between the two values a steadily increasing function of the seed migration rate. Thus, for the examples in Figure 3 (where $\bar{X} = \bar{x}$ and $\bar{d}_2 = 0$), $\hat{D}_2 = (1 - m)\hat{d}_2$ regardless of the rates of pollen migration or self-fertilization. All other disequilibria in these examples, however, are greater with adult censusing than with seed censusing by as much as 100% when $M = 0.01$, but by as little as 5% when $M = 0.5$. Third, when migration occurs through pollen alone ($m = 0$), the equilibrium state is independent of census time. Fourth, in the contrasting case of seed migration alone, the final allelic disequilibrium under seed censusing is always less·than that under adult censusing by a factor of ½$(1 + s)$, so that $\hat{D} \cong 2\hat{d}$ in predominantly outcrossing populations whereas $\hat{D} \cong \hat{d}$ in predominantly self-fertilizing populations. The relative magnitudes of the genotypic disequilibria in this case are not easily determined analytically.

Census time also has two other important consequences in predominantly outcrossing populations. First, it significantly affects the relative amounts of allelic disequilibrium generated in such populations by pollen or seed migration alone. Whereas with adult censusing, pollen migration generates only half the allelic disequilibrium found under comparable seed migration ($M = m$, $\bar{D} = \bar{d}$) when $s = 0$, with seed censusing, comparable levels of allelic associations are generated by the two forms of gene flow in largely outcrossing populations, with $\hat{d}_{\text{pollen migration}}/\hat{d}_{\text{seed migration}}$ decreasing from 1 to $m/(1 + m)$ as s increases from 0 to 1. Finally, the conditions for permanent genotypic disequilibria are particularly sensitive to census time in highly outcrossing populations. Unlike random-mating populations censused as adults, the associated seeds will develop permanent genotypic disequilibria only under the three conditions that generate permanent allelic disequilibria: nonrandom allelic associations in immigrant seeds or pollen or nonzero intermigrant allele frequency differences. This is because with seed censusing of random-mating populations (APPENDIX D), not only are the final genotypic associations independent of the genotypic associations in immigrant seeds, but the genotypic intermigrant admixture terms are then constant multiples of the intermigrant allele frequency difference, $(\bar{P} - \bar{p})(\bar{X} - \bar{x})$.

DISCUSSION

When gene flow occurs through both pollen and seeds, the cytonuclear structure of plant populations with paternal cytoplasmic inheritance contrasts in three major ways with that of populations with maternal cytoplasmic inheritance (ASMUSSEN and SCHNABEL 1991). First, and most importantly, with paternal cytoplasmic inheritance, pollen migration can (either by itself or in conjunction with seed migration or mixed mating) strongly influence the cytonuclear structure of island populations. In particular, pollen gene flow can help to generate transient and permanent nonrandom associations between cytoplasmic alleles and nuclear alleles or genotypes greatly exceeding those that would be produced by seed migration or mixed mating alone. With maternal cytoplasmic inheritance, on the other hand, pollen migration can only slightly increase or decrease the amount of disequilibrium generated by seed migration or mixed mating; when pollen migration is acting alone, all cytonuclear disequilibria eventually decay to zero, and not even temporary disequilibria can be generated *de novo* if the island population begins with random cytonuclear associations.

A second major difference between the two modes of cytoplasmic inheritance is that the number of ways in which permanent allelic and genotypic disequilibria can be generated is much greater when the cytoplasmic gene is paternally transmitted. In our models with maternal inheritance, nonzero cytonuclear disequilibria can be generated and maintained in the island population if and only if at least some migration occurs each generation through seeds with nonrandom cytonuclear associations. Here we have shown that when cytoplasmic genes are carried by both pollen and seeds, permanent disequilibria can be generated either through disequilibria in one or both immigrant pools, or through the admixture of immigrant pools that differ appropriately in their cytonuclear compositions. These intermigrant admixture effects arise either when the immigrant pollen and seeds differ in both their nuclear and cytoplasmic allele frequencies or when they differ only in their cytoplasmic frequencies and certain nuclear conditions are met. The latter conditions are census specific, and require, if the population is censused as adults, that the immigrant seeds not be in Hardy-Weinberg equilibrium for their nuclear genotypes, or if the population is censused as seeds, that the resident population be partially self-fertilizing and the immigrant pools have a common, polymorphic nuclear allele frequency with at least some nuclear homozygotes among the immigrant seeds. The first (allelic) form of intermigrant admixture contributes to all four cytonuclear disequilibria, whereas the second (genotypic) form contributes only to the three genotypic associations.

The third major difference is that pollen gene flow is more apt to affect the final state of the island population when there is paternal cytoplasmic inheritance. The equilibrium cytonuclear structure of populations with maternal cytoplasmic inheritance depends on the rate of pollen migration only where there is simultaneous seed flow and different nuclear allele frequencies in the two immigrant pools. This latter result is important from a practical standpoint, because it shows that when cytoplasmic inheritance is maternal and there is no seed migration, it is impossible to use the cytonuclear structure of the equilibrium population to estimate rates of pollen migration. Such estimation should be theoretically possible in populations with paternal cytoplasmic inheritance, however, if the immigrant pollen has nonrandom allelic associations. With simultaneous seed gene flow, estimation of both migration rates as well as the rate of self-fertilization should be possible if the two immigrant pools have different nuclear or cytoplasmic allele frequencies or if either immigrant pool has nonrandom allelic associations. (The conditions allowing estimation of seed migration rates alone are much broader under each form of uniparental cytoplasmic inheritance.)

These same general results were obtained regardless of the life stage at which the island population is censused. The disequilibria can depend strongly on the census time, but the life stage that will maximize the chances of detecting nonrandom cytonuclear associations often depends on the mating and migration parameters when cytoplasmic inheritance is strictly paternal. The two census times should, however, give approximately the same result (i) under all rates of self-fertilization and immigrant compositions when the rate of seed migration is low, because this approximates the special case of $m = 0$, for which the equilibrium state is independent of census time; and (ii) across all migration rate combinations when self-fertilization is high ($s > 0.9$), because this approximates the special case of complete self-fertilization, under which the final allelic disequilibrium is independent of census time and the genotypic disequilibria are substantially different between census times only when the quantity $m\bar{d}_2/(1 + m)$, is large (ASMUSSEN and SCHNABEL 1991).

In contrast, census time often significantly affects the conditions under which permanent cytonuclear disequilibria will be generated as well as the ability to detect those associations experimentally in highly outcrossing populations receiving significant gene flow from seeds.

Together the two papers in this series provide a basic theoretical framework for understanding the effects of pollen and seed gene flow on the cytonuclear structure of diploid plant populations in which cytoplasmic inheritance is uniparental (either maternal or paternal). A number of important extensions are still necessary, however, in order to fully employ cytonuclear systems in the empirical study of gene flow in plant populations. The first of these will be to develop statistical methodology for estimating pollen and seed migration rates by the fit of our models to observed cytonuclear frequencies. We hope soon to be able to apply this procedure to nuclear-dicytoplasmic data currently being gathered from a hybrid zone of pines in which the mitochondrial DNA is maternally inherited and the chloroplast DNA is paternally inherited (D. WAGNER, personal communication).

Another important step will be to extend our analysis to encompass joint, nuclear-mitochondrial-chloroplast data, for the full nuclear-dicytoplasmic structure (SCHNABEL and ASMUSSEN 1989) should be especially sensitive to the effects of pollen and seed gene flow, particularly in conifers and other species in which the two organelles are inherited through opposite parents (WAGNER *et al.* 1987, 1991; NEALE and SEDEROFF 1989; SCHUMANN and HANCOCK 1989; HARRISON and DOYLE 1990). Ultimately, systems with biparental cytoplasmic inheritance (KIRK and TILNEY-BASSETT 1978; SEARS 1980; SMITH 1988) should also be examined, as well as ones incorporating the effects of additional evolutionary forces, such as genetic drift and natural selection.

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APPENDIX A

Derivation of the adult census model with joint pollen and seed migration: As for the maternal inheritance model (ASMUSSEN and SCHNABEL 1991), 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 $1 - s$). Although the former are unchanged, the contribution from random outcrossing is reversed with paternal inheritance, being determined by the union of nuclear alleles in resident ovules with the joint, nuclear-cytoplasmic combinations (Table 2) 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 $P[M\bar{P}_1 + (1 - M)P_1]$, corresponding to the fertilization of a resident A-bearing ovule (freq. P) by an A/C pollen grain [freq. $M\bar{P}_1 + (1 - M)P_1$]. Combining these two possibilities shows that the frequency of AA/C among newly formed seeds is

$$u_1 = s(P_1 - \tfrac{1}{4}V_1) + (1 - s)P[M\bar{P}_1 + (1 - M)P_1].$$

Repeating this reasoning shows that the full set of interim cytonuclear genotype frequencies in newly formed seeds is

$$\begin{aligned} u_i &= s(P_i - \tfrac{1}{4}V_i) + (1 - s)P[M\bar{P}_i + (1 - M)P_i] \\ v_i &= \tfrac{1}{2}sV_i + (1 - s)[M(P\bar{Q}_i + Q\bar{P}_i) \\ &\quad + (1 - M)(PQ_i + QP_i)] \qquad (\text{A1}) \\ w_i &= s(Q_i - \tfrac{1}{4}V_i) + (1 - s)Q[M\bar{Q}_i + (1 - M)Q_i], \end{aligned}$$

for $i = 1, 2$. From (A1) and the relations in Tables 1 and 2 and Equation 2, the interim marginal frequencies of the nuclear genotypes and alleles can be shown to be the same as those presented in ASMUSSEN and SCHNABEL (1991) for maternal inheritance:

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

The interim cytoplasmic frequency, however, is now

$$x = M(1 - s)\bar{X} + [1 - M(1 - s)]X, \qquad (\text{A3})$$

and the interim disequilibria are

$$\begin{aligned} d &= \tfrac{1}{2}[1 + s - M(1 - s)]D + \tfrac{1}{2}M(1 - s)\bar{D} \\ &\quad + \tfrac{1}{2}M(1 - s)[1 - M(1 - s)](P - \bar{P})(X - \bar{X}) \\ d_1 &= \tfrac{1}{2}sD_1 + \tfrac{1}{2}[s + 2(1 - s)(1 - M)P]D \\ &\quad + M(1 - s)P\bar{D} + M(1 - s)(u - P\bar{P})(X - \bar{X}) \qquad (\text{A4}) \\ d_2 &= \tfrac{1}{2}sD_2 + (1 - s)(Q - P)[M\bar{D} + (1 - M)D] \\ &\quad + M(1 - s)(v - P\bar{Q} - Q\bar{P})(X - \bar{X}) \\ d_3 &= \tfrac{1}{2}sD_3 - \tfrac{1}{2}[s + 2(1 - s)(1 - M)Q]D \\ &\quad - M(1 - s)Q\bar{D} + M(1 - s)(w - Q\bar{Q})(X - \bar{X}). \end{aligned}$$

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 immigrant seeds (ASMUSSEN and ARNOLD 1991). The new frequencies are therefore simply the weighted averages of those in immigrant (m) and resident $(1 - m)$ seeds, so that the recursions of all single and joint frequency variables, Z, have the form

$$Z' = m\bar{z} + (1 - m)z, \qquad (\text{A5})$$

where $\bar{z}$ is the frequency in immigrant seeds and z is the intermediate frequency in resident seeds. After substituting in the appropriate interim values, we find that the transformations for the three key frequency variables (P, V, and X) are thus

$$\begin{aligned} P' &= m\bar{p} + \tfrac{1}{2}(1 - m)M(1 - s)\bar{P} + (1 - m) \\ &\quad \cdot[1 - \tfrac{1}{2}M(1 - s)]P \\ V' &= m\bar{v} + \tfrac{1}{2}s(1 - m)V + (1 - m)(1 - s) \qquad (\text{A6}) \\ &\quad \cdot[M(P\bar{Q} + Q\bar{P}) + 2(1 - M)PQ] \\ X' &= m\bar{x} + (1 - m)M(1 - s)\bar{X} + (1 - m) \\ &\quad \cdot[1 - M(1 - s)]X. \end{aligned}$$

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:

$$\begin{aligned} D' &= m\bar{d} + (1 - m)d + m(1 - m) \\ &\quad \cdot(p - \bar{p})(x - \bar{x}) \\ D_1' &= m\bar{d}_1 + (1 - m)d_1 + m(1 - m) \\ &\quad \cdot(u - \bar{u})(x - \bar{x}) \qquad (\text{A7}) \\ D_2' &= m\bar{d}_2 + (1 - m)d_2 + m(1 - m) \\ &\quad \cdot(v - \bar{v})(x - \bar{x}) \\ D_3' &= m\bar{d}_3 + (1 - m)d_3 + m(1 - m) \\ &\quad \cdot(w - \bar{w})(x - \bar{x}). \end{aligned}$$

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

APPENDIX B

Time-dependent solution for D_t under joint pollen and seed migration with adults censused: The allele frequency dynamics for X_t and P_t in (4) and (6), coupled with the recursion for D in (A7), show that the value of the allelic disequilibrium is given in any generation $t = 0, 1, 2, \ldots$ by

$$\begin{aligned} D_t &= \hat{D} + b_1\{(1 - m)[1 - \tfrac{1}{2}M(1 - s)]\}^t \\ &\quad + b_2\{(1 - m)^2[1 - \tfrac{1}{2}M(1 - s)] \\ &\quad \cdot[1 - M(1 - s)]\}^t \\ &\quad + (D_0 - \hat{D} - b_1 - b_2) \\ &\quad \cdot \{\tfrac{1}{2}(1 - m)[1 + s - M(1 - s)]\}^t, \\ &\quad \rightarrow \hat{D} \text{ as } t \rightarrow \infty, \end{aligned} \tag{B1}$$

where

$$b_1 = \frac{mM(P_0 - \hat{P})(\bar{X} - \bar{x})}{m + (1 - m)M(1 - s)}$$

$$b_2 = \frac{k[2m + (1 - m)M(1 - s)](P_0 - \hat{P})(X_0 - \hat{X})}{(1 - m)k[2 - M(1 - s)] - s - k},$$

$k = 1 - M(1 - s)$ and $\hat{D}$ is as given in (7).

An exception to the general solution exists when

$$m = \frac{(1 - s)[(1 - M)^2 - sM^2]}{[1 - M(1 - s)][2 - M(1 - s)]}.$$

In this case, the solution for D_t is

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

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

$$b_3 = \frac{k[2m + (1 - m)M(1 - s)](P_0 - \hat{P})(X_0 - \hat{X})}{s + k}.$$

APPENDIX C

Intermigrant admixture disequilibria: When disequilibria are generated by both allelic and genotypic intermigrant admixture effects, we found that in our numerical study the level of nonrandom associations is a monotonically increasing function of the pollen migration rate (M), so that with all else being equal, all disequilibria attain their greatest equilibrium magnitudes when $M = 0.5$. In contrast, the levels of allelic and genotypic associations do not vary monotonically with the seed migration rate (m); for any combination of self-fertilization and pollen migration rates, the level of disequilibrium is maximized at a distinctive rate of seed migration, where this critical m value decreases with increasing self-fertilization and decreasing pollen migration.

This latter situation is illustrated in Figure 2 for $\hat{D}_1$ under a range of seed migration rates ($0 \leqslant m \leqslant 0.5$) and four combinations of pollen migration and self-fertilization rates ($M = 0.05$ and 0.30; $s = 0.1$ and 0.9), where the immigrant pollen and seeds are fixed for different nuclear and cytoplasmic alleles (*i.e.*, $\bar{P} - \bar{p} = \bar{X} - \bar{x} = 1$). Note that for a given rate of self-fertilization, $|\hat{D}_1|$ is maximized at a lower rate of seed migration when $M = 0.05$ than when $M = 0.3$, particularly when s is low. Likewise, for a given rate of pollen migration, $|\hat{D}_1|$ is maximized at a lower rate of seed migration when $s = 0.9$ than when $s = 0.1$, particularly for higher levels of pollen migration. The way in which the admixture disequilibria vary with s, however, depends on the specific migration rates. Although not shown in Figure 2, these same general patterns were observed for the allelic disequilibrium and the other two genotypic disequilibria.

APPENDIX D

Model 2. Seed census: The recursions for this model are generated by reversing the steps outlined in APPENDIX A, and are related to the recursions under adult censusing as shown in (A5) and (A7). The closed-form solutions for p_t and x_t are equivalent to those for P_t and X_t in (4) and (6), with the initial resident adult frequencies replaced by the corresponding initial values among resident seeds, and the equilibrium frequencies altered to

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

$$\hat{x} = \frac{m[1 - M(1 - s)]\bar{x} + M(1 - s)\bar{X}}{m[1 - M(1 - s)] + M(1 - s)},$$

where the denominators are equivalent to those in (4) and (6) under adult census. The dynamics of the heterozygote frequency, v_t, is equivalent to that under maternal cytoplasmic inheritance (ASMUSSEN and SCHNABEL 1991), approaching the equilibrium value

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

The usual closed-form solution of the allelic disequilibrium with seed censusing,

$$\begin{aligned} d_t &= \hat{d} + b_1\{(1 - m)[1 - \tfrac{1}{2}M(1 - s)]\}^t \\ &\quad + b_2\{(1 - m)^2[1 - \tfrac{1}{2}M(1 - s)][1 - M(1 - s)]\}^t \\ &\quad + b_4\{1 - m)[1 - M(1 - s)]\}^t \\ &\quad + (d_0 - \hat{d} - b_1 - b_2 - b_4) \\ &\quad \cdot \{\tfrac{1}{2}(1 - m)[1 + s - M(1 - s)]\}^t, \end{aligned}$$

differs from that presented in (B1) in that it has an extra geometric term, $(1 - m)[1 - M(1 - s)]$, associated with the coefficient

$$b_4 = \frac{-\, mM(1 - s)(\bar{P} - \bar{p})(x_0 - \hat{x})}{2m + (1 - m)M(1 - s)},$$

the coefficients b_1 and b_2 are now

$$b_1 = \frac{mMs(p_0 - \hat{p})(\bar{X} - \bar{x})}{m + (1 - m)M(1 - s)}$$

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

and the final allelic association is now given by

$$\hat{d} = \frac{m(s + k)\bar{d} + M(1 - s)\bar{D} + k_2(\bar{P} - \bar{p})(\bar{X} - \bar{x})}{2 - (1 - m)(s + k)},$$

with k_2 here equaling

$$k_2 = \frac{\begin{array}{r} mM(1 - s)\{[2m + (1 - m)M(1 - s)]k \\ + (1 - m)Ms(1 - s)\} \end{array}}{[m + (1 - m)M(1 - s)][2m + (1 - m)M(1 - s)]},$$

and $k = 1 - M(1 - s)$ as in (B1). The dominant term is still $(1 - m)[1 - \tfrac{1}{2}M(1 - s)]$.

The closed-form solutions for the genotypic disequilibria have the same nine geometric terms, but different coefficients than those under adult censusing. Their limiting values are here

$$\hat{d}_1 = \frac{\begin{array}{l} sm\bar{d}_1 + k_3\hat{P}\bar{D} \\ \quad + [s + 2(1 - M)(1 - s)\hat{P}]\hat{D} + k_4k_5(\bar{X} - \bar{x}) \end{array}}{2 - s(1 - m)}$$

$$\hat{d}_2 = \frac{\begin{array}{l} sm\bar{d}_2 + k_3(\hat{Q} - \hat{P})\bar{D} \\ \quad + 2(1 - M)(1 - s)(\hat{Q} - \hat{P})\hat{D} + k_4k_6(\bar{X} - \bar{x}) \end{array}}{2 - s(1 - m)}$$

$$\hat{d}_3 = \frac{\begin{array}{l} sm\bar{d}_3 - k_3\hat{Q}\bar{D} \\ \quad - [s + 2(1 - M)(1 - s)\hat{Q}]\hat{D} + k_4k_7(\bar{X} - \bar{x}) \end{array}}{2 - s(1 - m)},$$

where the coefficients k_3 and k_4 (Table 3) are altered to

$$k_3 = 2M(1 - s)$$

$$k_4 = \frac{mM(1 - s)}{m + (1 - m)M(1 - s)},$$

and

$$k_5 = s(1 - m)(\hat{u} - \bar{u}) + 2(\hat{P}\bar{P} - \hat{u})$$

$$k_6 = s(1 - m)(\hat{v} - \bar{v}) + 2(\hat{P}\bar{Q} + \hat{Q}\bar{P} - \hat{v})$$

$$k_7 = s(1 - m)(\hat{w} - \bar{w}) + 2(\hat{Q}\bar{Q} - \hat{w}).$$

In random-mating populations ($s = 0$), the latter nuclear components of the genotypic admixture terms reduce to

$$k_5 = -2(1 - M)\hat{P}(\hat{P} - \bar{P})$$

$$k_6 = -2(1 - M)(\hat{Q} - \hat{P})(\hat{P} - \bar{P})$$

$$k_7 = 2(1 - M)\hat{Q}(\hat{P} - \bar{P}),$$

where

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

In general, the genotypic admixture terms contribute to the final genotypic disequilibria found under seed censusing only when the cytoplasmic frequency differs in the two immigrant pools and the equilibrium frequency of the associated nuclear genotype differs from either the corresponding frequency in immigrant seeds or the genotype frequency that would result at equilibrium from the random union of resident ovules and immigrant pollen. These genotypic intermigrant effects will be the sole determinants of the final genotypic disequilibria in the resident seeds if the immigrant pools have no disequilibria ($\bar{d} = \bar{d}_i = \bar{D} = 0$), immigrant seeds and pollen have identical, polymorphic nuclear allele frequencies ($0 < \bar{P} = \bar{p} < 1$) but different cytoplasmic frequencies ($\bar{X} \neq \bar{x}$), the immigrant seed pool contains some nuclear homozygotes ($\bar{v} \neq 1$), and the population is mixed-mating ($0 < s < 1$). Alternatively, the genotypic admixture terms all vanish under two of the same conditions as for adult censusing [$\bar{X} = \bar{x}$ or $\bar{P} = \bar{p} = 0$ or 1; Table 3], as well as when $0 < \bar{P} = \bar{p} < 1$ and either $s = 0$ or $\bar{v} = 1$.