A model of kin-migration in plants

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Summary. Migrants between plant populations may represent a random sample of the donor population or may be related, being identical in the extreme. There is considerable potential for kin-structured migration in many plant species through the co-dispersal of seeds from single individuals. Through simulation experiments we have shown that the greater the level of relatedness of migrants, the less a given level of migration counterbalances the effect of genetic drift among populations.

Key words: Kinship – Migration – Genetic Drift – Population structure

Introduction

Migration is a prime factor shaping the organization of genetic variation within species, because it counterbalances the dispersive effects of selection and genetic drift on gene frequencies. The greater the level of migration, the more similar will be the gene frequencies of populations. The homogenizing effect of migration depends not only on the level of migration but on the relationship of the migrants, as shown by Fix (1978) and Rogers (1987) (Rogers and Jorde 1987). The greater the level of relatedness among migrants leaving one population and entering another, the less a given level of migration counterbalances genetic drift. Kin-structured migration has been reported in human populations (Fix 1975, 1978), Rhesus macaques (Chepko-Sade and Sade 1979; Colvin 1983), Japanese macaques (Furuya 1968; Lee 1983), vervet monkeys (Cheney 1983), baboons (Nash 1976), and lions (Bygott et al. 1979).

Kin-structured migration has not been reported in plants, but the potential for such is considerable. In many

species the unit of dispersal is a multiseeded fruit (van der Pijl 1972). The transport of such fruits to another population would constitute kin-structured migration. In other species the unit of dispersal is a single seed. If many seeds from one plant were eaten by or attached to a given vector and deposited in another population, migration would be kin-structured. Even the transport of propagules from neighboring plants may result in kin-migration, because neighboring plants are often related (Coles and Fowler 1976; Waser and Price 1983; Park and Fowler 1982; Levin 1984). In this case, the migrants would be more distantly related than if they had a common parent.

Outcrossed seeds on a plant would be full sibs if they shared a sire or half sibs if they did not. The coefficient of relationship between full sibs when parents are non-inbred and unrelated is 0.50; between half sibs it is 0.25 (Wright 1922; Squillace 1974). The coefficient of relationship will be even higher in plants with restricted recombination. If the seeds were the product of self-fertilization the coefficient of relationship would be 0.67, and if seeds were the product of apomixis it would be 1.00.

Kin-structured migration would also occur if pollen carried from one population to another came from one or a small number of plants. This pattern of pollen flow is fostered by animal pollination. Most of the pollen on single pollinators foraging on plants with numerous flowers is likely to be from the last plant visited. In many plant species, kin-migration is assured because pollen is dispersed in pollinia or in aggregates (Faegri and van der Pijl 1979; Richards 1986).

Data on pollen and seed dispersion and on the spread of genetic markers suggest that migration between populations of herbaceous plants one or more kilometers apart involves only a few pollen grains or seeds per generation (Levin 1984). This view is supported by indirect

estimates of gene flow obtained from electrophoretic data (Hamrick 1987). When the number of pollen or seed immigrants is small, there is a high probability that most or some are from the same pollen or seed parent, because a dispersal agent is likely to carry more than one pollen grain or seed. Thus, when migration is infrequent and effected by animals, kin-structured migration may be the norm. The purpose of this paper is to demonstrate the effect of kin-structured migration as it might occur in plants on the genetic population structure when selection is absent.

The simulation model

The roles of kin-structured migration in genetic differentiation were studied using Monte Carlo stimulation. The basic model is a linear stepping-stone system (see Fix 1978, for a similar model).

In these experiments, intergenerational random genetic drift was mimicked by randomly determining gene frequencies for each population each generation of the runs. The new gene frequency was chosen from a normal distribution with the expected value being the old gene frequency with a variance of $pq/2N$. Following the drift procedure, migration between adjacent populations in the linear array was simulated. In contrast to the drift procedure, which was invariant for all runs, different migration algorithms were used to simulate deterministic, random, and various degrees of kin-structuring of migrant groups. For all conditions, migrants moved to the two populations adjacent to the source population only. For all runs the migration rate was 10% from source populations of 200 individuals.

The five migration algorithms listed were: (1) Identical (run set I). This procedure simulated the case where all migrants were genetically identical (as for apomictic species). The procedure randomly determined a single genotype (based on the gene frequency in the donor population) and assigned that genotype to all the migrants that moved to one of the adjacent populations. The procedure was then repeated to determine the genotype of the migrants moving to the opposite adjacent population. Each generation for each population i, two clonal migrant groups moved to the ith $+1$ and the ith -1 populations (except for the end populations of the array which sent and received one group only). (2) Full sibs (run set II). Genotypes for migrant groups comprised of full siblings were generated by first randomly choosing parental genotypes (based on the donor population gene frequencies), then randomly choosing the migrant sibs genotypes based on the probabilities set by the parents' genotypes. For clonal migrant groups, the procedure was repeated twice for each population each generation. (3) Half sibs (run set III). The procedure was the same as for full sibs except that only one parental genotype remained constant for all the migrants in one group. A second parent was chosen randomly for each offspring. It would, therefore, be possible that none of the migrants shared both parents. (4) Random individuals (run set IV). The procedure was as described above except each individual migrant was randomly chosen. (5) Deterministic (run set V). Rather than choosing migrant groups according to random procedure, migration among populations was simulated according to:

$$q'_i = (1-m)q_i + 0.5\,m\,q_{i-1} + 0.5\,m\,q_{i+1}$$

i.e., the gene frequency in the next generation in population i (q'_i) was a function of the current gene frequency (q_i), the migration rate (m), and gene frequencies in the adjacent populations (q_{i-1} and q_{i+1}).
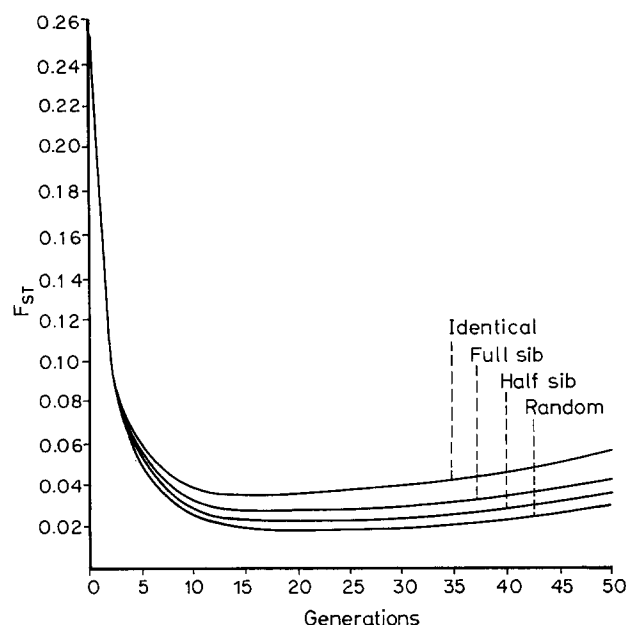

Fig. 1. The effect of the relatedness of migrants on the development of gene frequency heterogeneity among populations

Table 1. Reduction of total drift variance by migration *

Run set	Migrant relatedness	Migrant F_{ST}/ Drift F_{ST}	Percentage reduction	Average F_{ST} Generation 50
I	Clone	0.976	2.4	0.053
II	Full sib	0.960	4.0	0.042
III	Half sib	0.948	5.2	0.036
IV	Random	0.929	7.1	0.030
V	Deterministic	0.919	8.1	0.029

* Averages of 10 replicate runs calculated for the last 20 generations of the runs to avoid initial effects. See text for further details

Results

In all, ten different sets of ten replicate runs were made (Table 1). Each run began with a linear array of 25 populations with initial gene frequencies alternating between 0.25 and 0.75 so that the average gene frequency for the array as a whole was 0.49 (since the number of populations in the array was not even). Run duration was 50 generations.

The principal dimension of comparison was the degree of kin-structuring of migrant groups and its effect on genetic variation among the populations in the array. Figure 1 shows the relationship between Wright's F_{ST} (averages over the ten replicate runs for each set) and kin-structuring for four conditions. Since initial gene frequencies were highly differentiated, F_{ST} declined rapidly for the first ten generations of all runs. The high rate of

migration among populations caused considerable homogenization. However, in the absence of systematic forces such as stabilizing selection or long-range migration, genetic differentiation due to intergenerational genetic drift increased slowly in following generations for all run sets.

There is a clear relationship between the degree of migrant group kin-structuring and the maintenance of genetic variation among populations. The deterministic migration runs (set V) showed least differentiation (average F_{ST} after 50 generations = 0.029). Random migration introduced sampling error; however, since the number of migrants per generation was high ($N_{Mig} = 20$), overall F_{ST} remained low (average F_{ST} at generation 50 = 0.030). Average F_{ST} at generation 50 was 0.036, 0.042, and 0.053 (in the ratio 1.00:1.17:1.47) for half sibs, full sibs, and identical migrants, respectively. Thus kin-structured migration of groups allowed considerable variation to persist in these populations.

Another way to assess the role of kin-structuring of migration is to measure the degree to which migration counterbalances the variation generated by genetic drift. In each generation during each simulation run, F_{ST} was calculated after genetic drift occurred (drift F_{ST}) and a second value of F_{ST} was calculated following migration (migration F_{ST}). The expectation is that drift F_{ST} would be greater than migration F_{ST}. However, the amount by which drift F_{ST} is reduced varied depending on the degree of kin-structuring.

Table 1 shows the average percentage reduction of drift F_{ST} after migration. It may be noted that since F_{ST} declines rapidly over the first 10 generations of each run set (Fig. 1), the values in Table 1 are based on the last 20 generations of the runs; thus, each value in Table 1 is the average of 200 values (20 generations for 10 runs).

Substantial differences in the effect of migration on genetic variation exist among the run sets in Table 1. Deterministic migration of 10% reduced F_{ST} by an average of 8.1% each generation; clonal migration, on the other hand, was less than a third as effective (average 2.4%). The greater the degree of kin-structuring, the less effective was migration in reducing genetic variation.

Discussion

We have seen that the extreme forms of kin-structuring of migration possible in plant populations strongly affect F_{ST}. Indeed, almost a doubling of F_{ST} was shown between identical migrant (run set I) and random migrant (run set IV) conditions. We did not simulate the co-migration of the products of self-fertilization. With each generation of selfing, the progeny of single plants increase in similarity, and after several generations become identical. Thus the results would be similar to that with identical migrants.

Recently Rogers (1987) has developed a model of kin-structured migration. Because predictions of Rogers' model apply to equilibrium values which were not attained in our simulations, direct comparison with this model cannot be made. However, Rogers (personal communication) has suggested a method to evaluate the consistency of our results after 50 simulated generations with his equilibrium predictions. If

$$G = F_{ST}/(1 - F_{ST})$$

then for the four run sets I, II, III, and IV at generation 50

$$G_I = 0.0560$$
$$G_{II} = 0.0438$$
$$G_{III} = 0.0373$$
$$G_{IV} = 0.0309 .$$

Rogers' model implies that at equilibrium

$$G_{KSM} = G_{NoKSM}(1 + 2\,m_e\,\theta)$$

where G_{KSM} is the value of G under kin-structured migration, G_{NoKSM} is the value with no kin-structuring of migration, m_e is a measure of effective migration rate, and θ measures the intensity of kin-structuring (see Rogers [1987] for details). For the present case, the relevant portions of θ have to do with k, the coefficient of relationship within families; these are 1.0, 0.5, 0.25, and 0.0 for run sets I, II, III and IV respectively.

Since our results are not equilibrium values, they are not directly comparable to Roger's predictions. But a comparison of relative expectations may be accomplished by considering the quantity

$$H_i = G_{KSM}/G_{NoKSM} \qquad i = I, II, III$$

which equal $2\,m_e\,\theta$ at equilibrium. H_i is basically the proportional increase in G due to kin-structuring of migration. Since our run set IV modeled random migrant groups, we may use G_{IV} as an estimate of G_{NoKSM}. Based on generation 50 values:

	$2\,m_e\,\theta$	k
H_I = 0.8107	0.2064	1.00
H_{II} = 0.4188	0.1032	0.50
H_{III} = 0.2071	0.0516	0.25

The values of $2\,m_e\,\theta$, the equilibrium predictions on Rogers' model, are directly proportional to k in keeping with theory. Interestingly, the proportionality at generation 50 in our simulation results is almost as exact and the actual effect is considerably stronger (nearly four times that expected at equilibrium). We may conclude that kin-structuring may show strong effects and be manifest in populations far from equilibrium.

We have explored the effects of different degrees of kin-structuring in these simulation experiments. A variety of other sources of variation have not been considered. So, for instance, we considered only one rate of migration (10%) and one population size ($N = 200$). Insofar as our model is consistent with Rogers' (1987) model, we might note that he found that the impact of kin-structured migration was greater at higher migration rates. Many populations may well experience higher rates than the 10% used in this set of simulations; our results should not be viewed as extremes in this sense. Population size, according to the findings of Rogers and Jorde (1987), seems not to have a significant effect on variation due to migration.

The impact of kin-structured migration depends in part on the fixation indices of populations. The lower the fixation indices within a population system, the less heterozygous individuals will be on average, and the greater will be the genetic similarity among full sibs, half sibs, etc. Given that the sampling error of a population's gene frequencies increases with the genetic similarity of relatives, the impact of kin-migration will be the greatest in population systems with the highest fixation indices, all else being equal including gene diversity (= expected heterozygosity). The impact of kin-structured migration is, thus, likely to be the greatest in populations of plants where self-fertilization is common or where there is considerable genetic structure due to narrow transport of pollen and seeds.

The impact of kin-structured migration also depends on the organism's ploidal level. We assumed that the simulated populations were diploid; however, they could be polyploid. The number of genomes present in a specified kin group of size n will be greater in a polyploid than in diploid species. Accordingly, the sampling error of a population's gene frequencies will be less in the aforementioned kin group within a polyploid species, and, consequently, so will be the impact of kin-structured migration.

Thus far kin migration has been considered in terms of counterbalancing the effects of genetic drift among populations. It is important to recognize that kin migration may also affect that rate of spread of an advantageous gene among populations. In the case of a linear array of discontinuous populations, advantageous genes would progress in a wave-like fashion, with the velocity being a function of the migration rate and time to fixation within populations (Slatkin 1976). Fix (1981) demonstrated that kin-structured migration increased the rate of spread of advantageous genes among populations above that with deterministic migration. This is because kin-structured migration increases the initial frequency of advantageous genes compared to migration by unrelateds, and as a consequence the probability of their loss by chance is reduced. The rate of spread will be a positive function of migrant relatedness. Initial gene frequencies would be elevated the most if all migrants are identical and are homozygous for the gene in question.

Individuals may move from one population to another or may emigrate and found a new population. The formation of new populations by relatives promotes interpopulation differentiation, especially when the rate of colonization is high, relatives have a high genetic correlation, and migration between established populations is infrequent (Neel and Salzano 1967; Smouse et al. 1981; Fix 1985; Cheverud and Dow 1985). Kin-structured founding of populations has been documented in humans and other primates (Neel and Salzano 1967; Fix 1975; Duggleby 1977; Cheverud et al. 1978; Chepko-Sade and Sade 1979; O'Rourke and Bach Enciso 1982). It has not been demonstrated in plants, but it must be a common phenomenon in weedy species in which seeds are dispersed actively or passively in aggregates. We might expect that the extreme degree of kin-structuring possible for plants provides the potential for extreme local variability due to kin-based extinction and recolonization.

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