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Effect of spatially restricted pollen flow on spatial genetic structure of an animal-pollinated allogamous plant population

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The consequences of population genetic structure under different degrees of restriction of pollen flow in an animal-pollinated allogamous plant species were investigated through computer simulations. A single locus with two alleles in a population of self-incompatible, bisexual diploid plants was considered. The formula $f \propto e^{-Kd}$ was adopted to describe pollen flow patterns where f is the probability of mating, d is the distance from the pollen source, and K is a constant. Values of K estimated by fitting the formula to data in the literature for different plant species varied from 0.076 to 0.787 for gene flow through pollen and from 0.652 to 2.805 for pollinator movement. Starting with randomly distributed genotypes with equal allele frequencies, simulation runs up to the 200th generation were made for different values of K in the range from 0.06 to 3.00. Even with the highest empirically based value of $K(=3.00)$, the decrease in heterozygosity and development of patch structure in our simulations were less than those of the 'relaxed' model by Turner *et al.* (1982) and were similar to the 'neighborhood' model by Sokal & Wartenberg (1983) and Epperson (1990). Local differentiation was very sensitive to the degree of gene dispersal. We conclude that one cannot ascribe any local differentiation observed solely to restriction of gene flow unless one explicitly examines whether the degree of restriction is sufficiently severe to produce the differentiation.

Keywords: animal-pollinated plant, gene flow, genetic structure, pollen flow, spatial structure.

Introduction

Theoretical studies on differentiation among local populations were pioneered by Wright (1931, 1938). The simplest model explored was an 'island model' (Wright, 1969), which assumes that a total population is divided into many isolated subgroups, within which mating is at random, except for a certain proportion of migrants drawn at random from the whole. But if there is a complete continuity of the spatial distribution of the total population, this island model is not valid. Genetic divergence among different areas occurs even in a large continuously distributed population if gene flow is sufficiently restricted. At the opposite extreme from the island model, Wright (1940, 1943) presented his 'isolation by distance model' to analyse this type of divergence. It was assumed in the model that each plant can be considered to be surrounded by parents with which mating occurs with a probability that follows a bivariate normal distribution and that mating is in principle at random within an area defined as a 'neighbourhood'. In this model a number of factors, including pollen dispersal, and the varying densities of interbreeding individuals, may result in panmictic areas, neighbourhoods, which are more limited than the whole population. Wright's aim was to describe a neighbourhood size *Ne*, where *Ne* is the number of individuals responsible for a decay in genetic variance equal to that in a model population of size *N*. Many theoretical studies have been based on this model (Wright, 1946, 1951; Li, 1955; Kerster & Levin, 1968; Rohlf & Schnell, 1971; Endler, 1977; Sokal & Wartenberg, 1983; Epperson, 1990), assuming random mating within a neighbourhood. Malécot (1969, 1973) studied a similar model and obtained the asymptotic solutions for a spatially distributed population.

The assumptions of many neighbourhood-sized areas and random mating within a neighbourhood in the isolation by distance model were originally introduced to simplify the mathematical treatment of the

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model, but do not seem to be exactly realistic, especially in plant populations. To examine the dispersal process and its consequences for the population structure under spatially restricted gene flow, Monte Carlo computer simulations in which actual pollen and seed dispersal patterns are introduced may be more justifiable.

The first simulation studies where pollen and seed dispersal patterns were explicitly taken into account were made by Turner *et al.* (1982). They investigated the problem quantitatively for two specific cases of spatially restricted pollen flow, i.e. a 'strict' model and a 'relaxed' model without assuming a 'neighbourhood' or 'deme'. In the strict model the four nearest plants had an equal probability of serving as male parent, while in the relaxed model the 12 nearest neighbours of the female parent had probabilities of serving as male parent according to their distance from the female. Rapid decreases of heterozygosity and the development of patches of homozygous genotypes were observed under both models.

In this study, although they attempted to introduce pollen flow pattern and seed dispersal pattern into their simulation models, Turner *et al.*'s pollen flow models seem too simple to reflect mating schemes in nature.

Since it is known that pollen flow distance markedly varies with plant species and pollen can reach over two or more plant intervals in most cases (Bateman, 1947a, b; Levin & Kerster, 1968, 1969, 1974; Schaal, 1974, 1975, 1980; Price & Waser, 1979; Handel, 1983a, b; Bos and Van der Haring, 1988), introduction of more generalized pollen flow patterns than used by Turner *et al.* seems justified.

We investigated the effect of spatially restricted pollen flow on the spatial genetic structure of a population, that is, change of heterozygosity and development of patch structure, through computer simulations using a simple but generalized formula for animal-pollination. Spatial genetic structure is analysed using patchiness indices and spatial autocorrelation analysis. The former is modified from Turner *et al.*'s patchiness index. The latter has only recently been applied to the study of genetic structure within plant populations (Sokal & Oden, 1978a, b; Sokal & Wartenberg, 1983; Epperson & Clegg, 1986; Waser, 1987; Dewey & Heywood, 1988; Schoen & Latta, 1989; Epperson, 1990).

Methods

A computer program was written to simulate the change in population structure with generations of an allogamous plant species. The program was coded in N88-BASIC and C for a NEC microcomputer. The flow diagram of the simulation model is presented in Fig. 1. Simulations were conducted under the following conditions. The simulated plants were annual, bisexual, self-incompatible diploids and animal-pollinated. A single locus with two alleles (A and a) was considered. Selection and mutation were assumed to be absent. The initial populations were essentially in a Hardy–Weinberg equilibrium with equal allele frequencies i.e. $1AA$: $2Aa$: $1aa$. The plants were uniformly distributed at the intersections of a square grid of 100×100 positions. Population size was set to be a constant 10,000 through generations. Synchronized flowering and reproduction of all plants and hence no overlapping of generations were assumed.

Our simulation model is basically similar to that of Turner *et al.* (1982) but differed in that the pollen flow was expressed by a generalized equation.

We assumed that pollen flow follows a negative exponential formula which was first presented by Brownlee (1911):

$$f(D) = Ke^{-Kd},$$

where $f(D)$ is the probability density function for fertilization by a pollen from source, D is the distance from pollen source measured on the scale of the inter-plant interval, and K is a parameter. K is determined by several factors such as plant species, kinds of animal pollinators, plant density and pollinator pools.

Here we consider a 2-dimensional situation. In this situation, we integrated the formula (1) and introduced a probability distribution function $\Phi(d)$ for a continuous variable d defined by the following equation:

$$\Phi(d) = \int_0^d f(D) \cdot 2\pi D \, dD \Big/ \int_0^\infty f(D) \cdot 2\pi D \, dD$$

$$= 1 - (1 + Kd)e^{-Kd}. \qquad (2)$$

The value of $\Phi(d)$ was the probability that a plant at or less than a fixed distance, d, was chosen as the pollen donor of the female parent. First, by generating a series of pseudorandom numbers on a computer, we determined the $\Phi(d)$, and the distance from the female parent (d) was calculated by solving (2) for d. Here, individuals closer to a female parent had a higher probability of being selected as donor candidates. These candidates were located at the same distance from a female parent in all directions. Next the direction was decided by using another pseudorandom number from a uniform distribution. The plant which was the nearest one to a point decided by distance and direction as mentioned above was chosen as a pollen donor. If the point selected was outside the population we repeated selection of distance and direction until

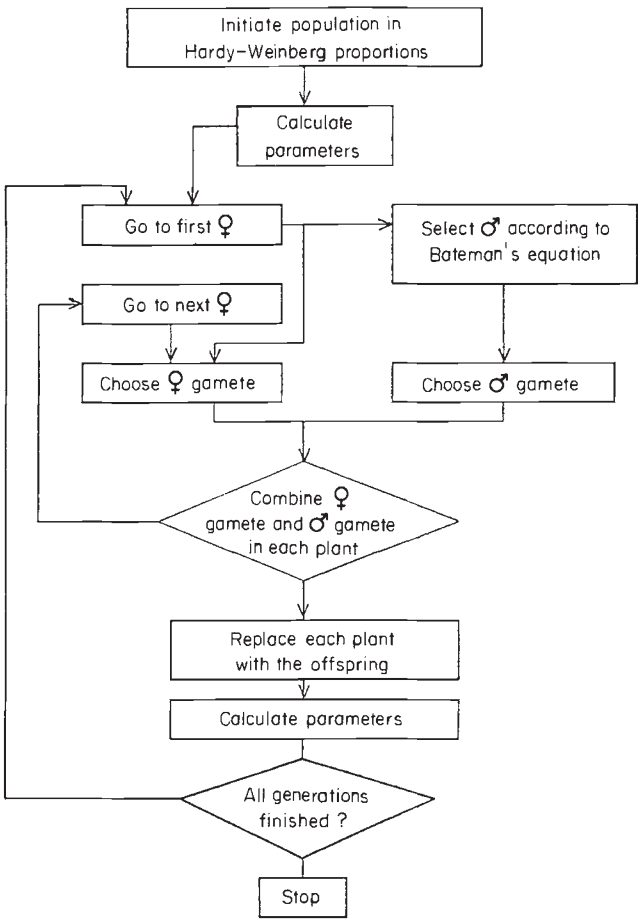

Fig. 1. A flow diagram of the simulation model.

the point was inside the population. For the sake of brevity of expression we include the effect of carryover of pollen in the term 'pollen flow'. A gamete from a female parent was crossed with a gamete from a male parent, producing a seed. When a parent was a heterozygote a pseudorandom number was used to choose which allele took part in the fertilization.

Seed dispersal pattern followed the model of Turner *et al.* (1982). Namely, plants were either replaced by their own maternally derived seed with a probability of 0.8 or by a seed formed from one of the four nearest plants with a probability of 0.2.

Prior to running simulations we determined what values of K have been observed for actual pollen flow in different animal-pollinated species growing under natural conditions. We collected data for 11 species on pollen flow distance, and data for 10 species on pollinator movement. The effect of carryover of pollen is included in the former but not in the latter. K was estimated from published values in each case by least squares nonlinear regression (SAS procedure NLIN, SAS Institute, 1991). Distance from the pollen source in published studies was measured by taking the between-plant interval as one unit.

Based on the range of K values obtained from gene flow and pollinator movement in actual populations, we ran simulations for eight different values of K: 0.12, 0.25, 0.50, 0.75, 1.00, 1.50, 2.00 and 3.00. Lower values of K represent wider pollen dispersal. To compare our results with those of the previous studies, we also simulated three specific cases, namely (i) Turner *et al.*'s relaxed pollen flow model (re438, mentioned later) in which three kinds of neighbours have the probability of being a male parent of 0.2125, 0.025 and 0.0125, respectively; (ii) a random pollen flow model (random) in which all individuals in the population have equal probabilities of being male parents; and (iii) a neighbourhood model (Rohlf & Schnell, 1971; Sokal & Wartenberg, 1983; Epperson, 1990) in which the pollen donor was taken at random from a square neighbourhood of individuals centered on the individual to be replaced, and there was no seed dispersal. Every pollen flow pattern was simulated in 20 replicate populations of 200 generations.

Characteristics of genetic population structure were measured by heterozygosity, patchiness indices and spatial autocorrelation in each generation. Heterozygosity is the proportion of the heterozygous genotype (Aa).

Two types of patchiness indices were used to describe spatial differentiation. Patchiness index 1 (pid1) is, as Turner *et al.* (1982) defined, the fraction of homozygous plants whose four nearest neighbours are of the same genotype, which is a little smaller than the total number of plants contained in different patches. Patchiness index 2 (pid2) reflects the maximum size of patches developed in the population, with each patch size measured as the number of times the outermost layer can be removed successively until further removal would leave no individual included in the patch.

Spatial autocorrelations according to Epperson (1990) were calculated on some of the genotypic surfaces of simulations for each 20 generation increment of each simulation run. First, the allele frequency was calculated for the lattice of 10,000 genotypes. Then, the lattice was subdivided into 400 contiguous quadrats of size 5×5, and the allele frequency, q_i, in each quadrat i was calculated and recorded along with quadrat location in the 20 by 20 matrix or lattice of quadrats, also referred to as a gene frequency surface. Pairs of quadrats were grouped by the Euclidean distances between the quadrat centres. Thus class k contained all pairs of quadrats that were separated by $k-0.5$ to $k+0.5$ (for $k=1, 2, —, 27$) quadrat length (that is, $5k-2.5$ to $5k+2.5$ unit lengths between adja-

cent plants on the original genotypic lattice). Moran's *I*-statistic for the *k*th distance class was calculated by:

$$I_k = n \sum_i \sum_j z_i z_j / (W_k \sum_i z_i^2),$$

where $z_i = q_i - q$, and q is the mean of quadrat allele frequencies in the population (Sokal & Oden, 1978a).

The summation was taken over all pairs of quadrats that fall into distance class k. Graphs of the *I*-statistics for each of the distance classes are termed correlograms.

Results

There is much debate about pollen flow patterns and no single formula seems to show a good fit to observed data. Bateman (1947b) reported that $f = Ke^{-Kd}$ or $f = ye^{-Kd}/d$, where y is a constant dependent on K appeared suitable to describe the pollen flow pattern of insect-pollinated species. We found by statistical analysis of different data from literature including his that the latter simple form $f = Ke^{-Kd}$ showed a better fit to most of the observed data in animal-pollinated species. So this equation was employed to determine the pollen flow pattern in the present simulations. The estimated values of K are shown in Tables 1 and 2. From the literature survey it was found that the estimated values of K were in the range of 0.076 to 0.787 for gene flow through pollen and 0.652 to 2.805 for pollinator movement. The latter group of data is based on the measurement of distance of a single flight of insects and does not include the effect of carryover of pollen by insects or other animals. That may be the reason why the estimated values of K were much higher for pollinator movement. The maximum of the estimated K was 0.787 for *Ipomopsis aggregata* and the minimum 0.076 for *Cucumis melo*. We also found that the 'relaxed' model of Turner *et al.* (1982) corresponded to a case of

Table 1 The estimated values of K from gene flow for 11 animal-pollinated species

Species	Estimated values	Literature
Cucumis melo L.	0.076*	Handel (1982)
Brassica campestris	0.114	Bateman (1947a)
Lupinus texensis	0.153	Schaal (1980)
Brassica napus	0.290	Ohsawa & Namai (1988)
Delphinium nelsonii	0.378	Campbell (1985)
Raphanus sativus	0.441	Bateman (1947a)
Brassica campestris	0.478	Bateman (1947a)
Fagopyrum esculentum	0.528	Namai (1986)
Raphanus sativus	0.533	Crane & Mather (1943)
Corchorus olitorius	0.713	Datta *et al.* (1982)
Ipomopsis aggregata	0.787	Campbell (1985)

*K was estimated by the least squares method for non-linear regression.

Table 2 The estimated values of K from pollinator movement for 10 animal-pollinated species

Species	Pollinators	Estimated values	Literature
Cucumis melo L.	Bumblebees	0.652*	Handel (1982)
Lupinus texensis	Bumblebees, Honeybees	0.817	Schaal (1980)
Phlox drummondi	Swallowtail butterflies	0.999	Levin (1981)
Senecio integerrimus	Butterflies	1.228	Schmitt (1980)
Fagopyrum esculentum	Flower flies	1.391	Namai (1986)
Delphinium nelsonii	Hummingbirds	1.590	Price & Waser (1979)
Epilobium angustifolium	Bees	1.941	Bulter *et al.* (1943)
Primula veris	Bumblebees	2.313	Richard (1986)
Delphinium nelsonii	Bumblebees	2.242	Price & Waser (1979)
Senecio integerrimus	Bumblebees	2.805	Schmitt (1980)

*K was estimated by the least-squares method for non-linear regression.

K= 1.00

0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
0	0	0	0	2	3	1	7	0	2	3	0	0	0	0
0	0	1	5	4	11	5	15	15	7	7	2	0	0	0
0	0	3	6	14	23	39	39	30	17	10	5	3	0	0
0	3	7	7	26	39	65	81	102	41	19	9	9	3	0
0	5	13	18	43	119	185	243	171	121	44	19	6	3	0
0	4	15	21	90	214	452	676	476	194	80	32	14	3	0
0	1	6	36	87	246	658	★	685	229	106	38	11	3	0
0	4	9	27	74	210	456	649	438	200	80	33	10	7	0
0	4	4	31	65	98	207	243	208	86	52	19	3	2	0
0	1	9	15	24	47	72	92	85	31	31	19	6	1	0
0	0	2	6	13	23	38	37	24	21	16	6	6	0	0
0	0	1	3	9	9	10	19	6	7	5	3	0	0	0
0	0	0	0	0	0	10	5	8	2	1	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Fig. 2. The probability (× 10,000) distribution of individuals serving as male parent to female plant (star mark in centre) in a representative simulation with $K = 1.00$.

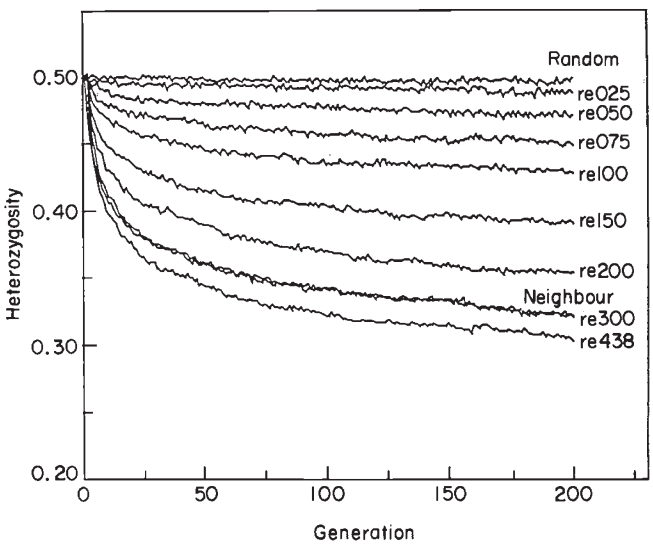

Fig. 3. The change in heterozygosity up to the 200th generation. The values represent averages over 20 runs of simulation. re025 in the figure, for example, means relaxed model with $K = 0.25$.

$K = 4.38$ in our pollen flow model. An example of the resulting probability distribution of a plant serving as male parent for a female plant in the centre of the grid is presented in Fig. 2 for the cases of $K = 1.00$.

The effects of spatially restricted pollen flow on heterozygosity up to generation 200 for different values of K are shown in Fig. 3. In each case the figure is based on the average over 20 replicate simulations. The variability of heterozygosity between 20 replicates was quite small, with variances less than 0.001. When pollen flow was restricted, there was a monotonic decrease in heterozygosity through successive generations, especially in the first 20 generations. The magnitude of the decrease in heterozygosity at a particular generation depended on the value of K. For instance, heterozygosity at generation 200 was 0.4718, 0.4264, 0.3536 and 0.3212 for $K = 0.50$, 1.00, 2.00 and 3.00, respectively. Table 3 shows the differences among simulations at generation 200. In the random pollen flow model, heterozygosity was kept nearly constant at 0.5 throughout 200 generations. The case of $K = 4.38$, which is the same as Turner's relaxed model showed significantly lower heterozygosity than a case of $K = 3.00$. Heterozygosity in the neighbourhood model was similar to the value resulting from $K = 3.00$.

Restriction of pollen flow caused the development of patches of the homozygotes *AA* or *aa*. In the random pollen flow model, no sign of growth of genotypic patches was observed even after 200 generations. On the other hand, when pollen flow was restricted, small patches rapidly grew for the first five generations. They grew, aggregated with each other and developed into a relatively small number of large patches. The patches persisted for many generations once they formed, although their shapes often changed. Different patches containing different homozygotes were separated by zones where heterozygotes were predominant. General features in the development of patch structures were quite similar to those reported by Turner *et al.* (1982). Endler (1977) also reported a similar result but his model is different from ours with respect to gene flow pattern.

To compare the spatial differentiation of the population quantitatively between different pollen flow types, the development of the patches was measured by pid1 and pid2 (Figs 4 and 5). Both pid1 and pid2 showed a relatively steady increase across generations, although the latter showed somewhat larger fluctuation. When $K = 0.12$ and 0.25, patchiness growth was rarely observed until generation 200. Conspicuous growth of patch structure was observed only when K was around 2 or more. Differences in both pid1 and pid2 among pollen flow types at generation 200 are shown in Table 2. When $K = 4.38$, pid1 was 0.2267 at generation 200, showing that about 2300 individuals were included in patches, and pid2 was about 6.70. If we assume that the largest patch was circular, then it follows that it would possess a radius of around 6.70 and contain about 140 individuals. Pid1 was clearly higher for $K = 4.38$ than for $K = 3$, while no significant difference was recognized in pid2. When K values were low, $K = 0.12$ and $K = 0.25$, neither pid1 nor pid2 differed significantly from values in the random pollen flow model. The pid1 for the neighbour model was lower than for $K = 3.00$.

The spatially restricted pollen flow resulted in statistically significant spatial autocorrelations. Figure 6

Table 3 Summary of differences among pollen flow types at generation 200 of 20 replicates

	Pollen flow type*								
	Random	$K = 0.12$	$K = 0.25$	$K = 0.50$	$K = 0.75$	$K = 1.00$	$K = 1.50$	$K = 2.00$	$K = 3.00$	$K = 4.38$	Neighbour
Heterozygosity	0.4949a	0.4899a	0.4879a	0.4718b	0.4500c	0.4264d	0.3918e	0.3536f	0.3212g	0.3041h	0.3219g
Patch index 1	0.0064i	0.0082i	0.0100i	0.0208h	0.0392g	0.0599f	0.1051e	0.1571d	0.2047b	0.2267a	0.1775c
Patch index 2	2.00 g	2.05 g	2.35 g	2.90 f	3.60 e	4.15 d	5.20 c	6.25 b	7.10 a	6.70 ab	6.20 b
Spatial autocorrelation											
$I - 1$**	0.0069g	0.0786f	0.2568e	0.4668d	0.5267a	0.5350a	0.5107abc	0.5201ab	0.4822bcd	0.4753cd	0.4695d
$I - 2$	0.0026f	0.0609e	0.1822d	0.3214ab	0.3537a	0.3243ab	0.2771bc	0.2647c	0.2072d	0.1938d	0.2055d

*Pollen flow types sharing the same letter do not have significantly different means using ANOVA and Duncan's multiple range test.
**Values of $I - 1$ and $I - 2$ were Moran's I statistics for the first and second distance class, respectively.

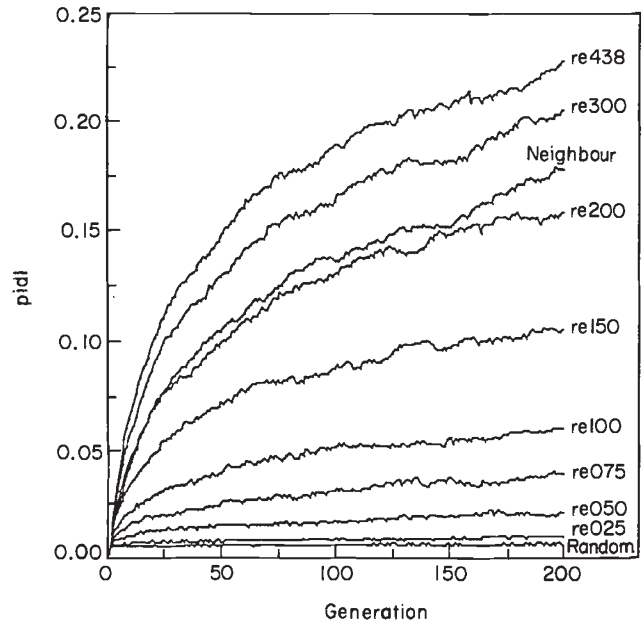

Fig. 4. Change in patchiness index 1 with generation.

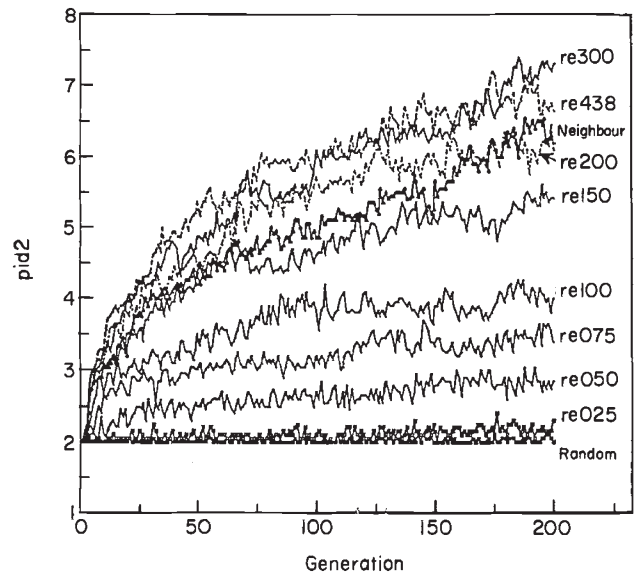

Fig. 5. Change in patchiness index 2 with generation.

shows the average correlogram for each simulation over the first eight distance classes at generation 200. The expected values for the case of no autocorrelation are close to zero, -0.025, so that most of the I-statistics are statistically significant when tested against the null hypothesis that sample I does not differ from its expected value, $-1/(n-1)$, using the test procedure given by Sokal & Oden (1978a) and Cliff & Ord (1981). The significance of most of I-statistics except for the random pollen flow model is attributed to the

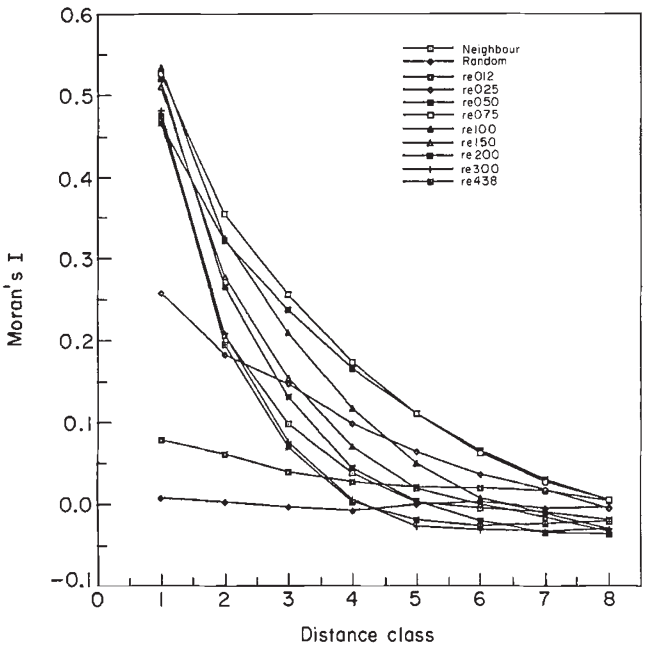

Fig. 6. Average *I*-correlograms (average of Moran's *I*-statistics for each of the first eight distance classes) for the 20 replicate simulations in each pollen flow type.

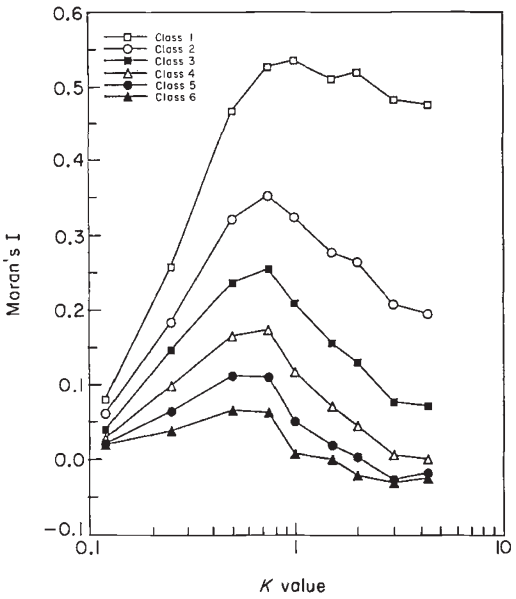

Fig. 7. Relations between *K* values and Moran's *I* for each of the first six distance classes.

unusually large number of grid points ($n = 400$) in this study. These results indicate areas of homogeneity representing the hills and valleys of gene frequency surface. As *K* takes larger values, the hills become higher and the valleys become lower. That is, similarity between nearby quadrats was low when the pollen dispersal was short. The simulations of our neighbour model are essentially identical to simulations 'set 1A and 1B' of Epperson (1990) and 'set 1 and 2' of Sokal & Wartenberg (1983), and these correlograms are very similar. The correlogram for the neighbour model in our simulations was very similar to that for $K = 3.00$ or Turner *et al.*'s model ($K = 4.38$), up to distance class three but subsequently became close to the correlogram for $K = 2.00$. Patterns of variation in the *I*-statistics with *K* were different from that of heterozygosity, pid1 and pid2. The magnitude of the increase or decrease in the latter clearly depended on the value of *K*. On the other hand, the *I*-statistics increased with increasing *K* values up to $K = 0.75$, beyond which the values decreased again (Fig. 7, Table 3). We found significant differences between the *I*-statistics for simulations with the low *K* values and those for the random pollen flow model, unlike the other statistics.

Discussion

The results of simulations in the present study indicate that spatially restricted pollen flow exerts an influence on genetic structure of animal-pollinated allogamous plant populations. Many theoretical and simulation studies have been carried out on the effects of restriction of gene flow on genetic structure. Most of them have been based on Wright's 'Isolation by distance' model, and involved 'neighbourhoods' or 'demes' in the model. In the models the species is distributed continuously in two dimensions, and each individual is considered to be at the centre of a bivariate model distribution of parent–offspring distances from which parents may have been drawn at random. They have shown that spatially limited gene flow combined with genetic sampling drift within a neighbourhood can give rise to differentiation. The assumptions of 'demes' or 'neighbourhoods' within which both parents are assumed to be vagile simplifies the mathematical analysis of genetic structure. However, it seems to be worthwhile to do simulation studies where actual pollen and seed dispersal patterns are explicitly taken into account. It is still difficult to solve for genetic structure analytically without simplifying assumptions. So a simulation approach is very valuable.

Restricted pollen flow has been reported in various animal-pollinated species (Kerster & Levin, 1968; Beattie & Culver, 1979; Schaal, 1980; Waser & Price, 1983; Ellstrand & Marshall, 1985), and has frequently been considered as a major factor promoting local genetic differentiation of populations (Handel, 1983b; Hamrick & Godt, 1990).

By simulation studies, Turner *et al.* (1982) showed that homozygote patches developed rapidly when pollen flow was very restricted. However, those authors

investigated only two specific cases i.e. strict and relaxed models. It is known that the range of pollen dispersal varies substantially among plant species (Hamrick, 1982). To cover a wide range of cases, introduction of more generalized pollen flow patterns into the simulation model is required.

From the literature survey it was found that the estimated values of K were in the range of 0.076 to 0.787 for gene flow through pollen and 0.652 to 2.805 for pollinator movement. Although the collected data are limited in number and the gene flow distance of a particular species may vary because of environmental conditions, coexistence of competitive species, or plant density (Levin & Kerster, 1969, 1975; Levin, 1979), the range of K estimated in the present study may well reflect actual situations.

Turner *et al.* (1982) showed that in their relaxed model with initial gene frequency $P=0.5$ that the value of Wright's fixation index F increased up to 0.36 at generation 140 (fig. 3 of their paper) which corresponds to a heterozygosity of 0.320. In our models heterozygosity at the same generation for the highest $K(=3)$ was a little higher (0.331). We compared the values of heterozygosity with those of Epperson (1990) and Sokal & Wartenberg (1983). Epperson showed that the value of F for generation 200 was 0.33 in his 'set 1' and Sokal & Wartenberg (1983) showed that F for generation 200 in their 'sets 1 and 2' was 0.302 and 0.294, respectively. Heterozygosity in our results can be converted to Wright's F, which in our neighbour model is 0.356, a little higher than previous results. The values of heterozygosity for the neighbour model anyway lie in the range for larger K values.

Since Turner *et al.* did not present the detailed data for their patchiness index in their paper, we cannot directly compare our results with theirs, for the growth speed and final size of patch structure. But the relaxed model nearly corresponds to a case of $K=4.38$ in our model as judged by gene flow distances. In fact, the heterozygosity at generation 140 for $K=4.38$ was 0.312 and near to the value obtained for their relaxed model, showing that the relaxed model can be reasonably approximated by our model of $K=4.38$. Growth of patch structure as measured by pid1 was distinctly smaller for $K=3$ and much smaller for $K=1$ or less, as compared with $K=4.38$. pid2 showed no difference between $K=3$ and 4.38, but was much smaller for $K=1$ or less.

The problem of local differentiation was also studied by Malécot (1969, 1973) in terms of change in correlation with distance. He showed that individuals living nearby tend to be more alike than those living far apart. Our results support Malécot's works. Spatial autocorrelation coefficients increased with K value up to a threshold ($K=0.75$), beyond which they decreased again. Sokal & Wartenberg (1983) explained why the coefficients should be higher with larger neighbourhood size and lower overall fixation and variance. They mentioned that, for any distance class, proportionately more of the point pairs within this class occurred in the same area when homogeneous areas were larger. A higher proportion of within-area distances for a given distance class resulted in higher spatial autocorrelation for that class. In our simulations, the explanation is essentially the same as theirs. The threshold value of K was 0.75. For that value, all quantities that we investigated were moderate. However, in our results, even when $K=0.50$ or $K=0.75$, spatial structures were recognizable. Although there were no large patches of homozygotes, we could see spatial density gradients of gene frequency.

Turning to pollen flow pattern in nature, moderate K values such as $K=0.50$ and 0.75 are not unrealistic. Our results indicate the possibility that spatially restricted pollen flow changes the spatial structure of animal-pollinated plant pollination. It can be concluded that genetic diversity caused solely by restriction of pollen flow is much less conspicuous in actual animal-pollinated plant populations than postulated by Turner *et al.* (1982) in their relaxed and strict models. Their two models would both be extremes which can hardly be realistic in nature. In previous studies (Rohlf & Schnell, 1971; Sokal & Wartenberg, 1983; Epperson, 1990, etc.) based on a neighbourhood model, the effects of restriction of pollen flow may have been overestimated, because the results were very similar to those with $K=2.00$ or more. We do not see such large values except in the estimated values from pollinator movement which do not involve the effect of carryover.

When one observes both spatially restricted gene flow and local differentiation of a population, one should be careful in ascribing the latter to the former. Since growth of patch structure is very sensitive to actual gene flow distances, one must examine if the gene flow pattern in the population can quantitatively account for the observed differentiation.

The simulation model adopted here can be extended to wind-pollinated species (Tonsor, 1985) for which pollen is generally more far-reaching and follows different patterns (Okubo, 1989) from insect-pollinated species. There are many other parameters which should be taken into account in the study of local differentiation, e.g. size and shape of the total population, polyploidy of the plants, or multiple loci, with or without linkage. Introduction of these parameters into the present model would be interesting.

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