Isolation by distance in *Liatris cylindracea*

SEVERAL factors may cause genetic correlation—that is a genetic relationship between individuals within a population—including small population size, self-fertilisation, positive assortative mating or isolation by distance. Isolation by distance occurs when gene dispersal is limited so that distant populations in a series or remote areas within a population become genetically differentiated. Under an isolation-by-distance model of genetic differentiation, spatial distance and genetic correlation between individuals or populations are expected to be negatively related, that is, the greater the distance the smaller the genetic correlation. I wish to present evidence for isolation by distance in the plant, *Liatris cylindracea* Michx. (Compositae), obtained by a genetic distance analysis of gene frequencies at 27 allozyme loci. This analysis revealed genetic differentiation across very small distances and demonstrated that a restriction of gene flow has a profound effect on the spatial distribution of alleles within a population.

Plant species are prime candidates for the study of isolation by distance since they are immobile and gene dispersal in both the pollen and seed phases is often quite restricted. Indeed the earliest study of isolation by distance was on the annual herb *Linanthus parryae*, which shows genetic differentiation for flower colour[1]. *Liatris cylindracea*, a prairie gayfeather, is a perennial, obligately outbreeding herb which grows in undisturbed prairies throughout the mid-west of the United States. A single, dense population[2] on a hillside in Zion, Illinois was divided into a grid 18×33 with 3 m^2 quadrats. Up to 60 plants were collected from each quadrat; the collection totalled 2,258 individuals. Starch gel electrophoresis was performed on the plants for 12 different enzyme systems, encoding 27 genetic loci. Gene frequencies were calculated on a per quadrat basis.

Evidence for isolation by distance was provided by analysis of genetic distance within the Zion population. Genetic distance is an index for measuring the accumulated number of gene differences per locus between groups of organisms. Of several available measures of genetic distance I used Nei's because it uses allozyme gene frequency data and, most importantly for a study of isolation by distance, it is related directly to Malecot's coefficient of kinship, φ. Nei's genetic distance is defined as:

$$D = -\log_e(J_{xy}/\sqrt{(J_x J_y)})$$

where J_x, J_y, and J_{xy} are the arithmetic means of the probabilities of two randomly chosen genes being identical in populations x, y, and x and y. Genetic distance is expressed as codon differences per locus.

Genetic distance in the *L. cylindracea* population was calculated for 103 quadrat pairs which had data from all 27 allozyme loci. Measurements of genetic distance between sample quadrats showed considerable variation. The mean genetic distance averaged from all of the distances computed is 0.0396 ± 0.004 codon differences per locus. Genetic distance between quadrat pairs ranged from 0.0061 to 0.1156.

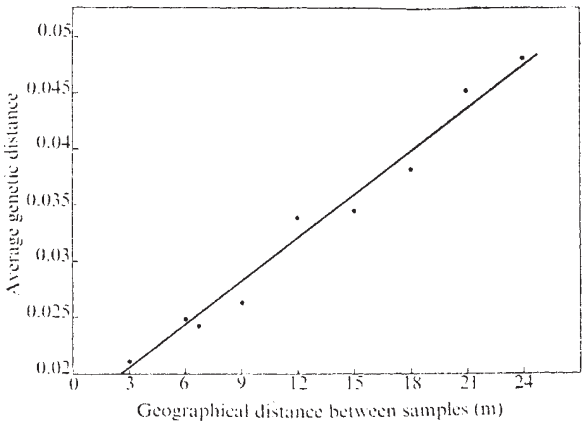

Fig. 1 Genetic distance in *L. cylindracea*. The genetic distance plotted is the average of all quadrat pairs for a given spatial distance. Geographical distance is the distance (m) between sample quadrats.

Considerable local differentiation within the population is indicated by the genetic distance measures. If genetic differentiation is the result of restricted migration, genetic distance would be expected to be related to spatial distance. The average genetic distance measured between sample quadrats is plotted against spatial distance in Fig. 1. As spatial distance increases between sample quadrats, the genetic distance increases proportionately. This linear relationship of spatial and genetic distance suggests that isolation by distance has occurred in the Zion population.

These results are consistent with the population biology of *L. cylindracea*. Both phases of gene dispersal, pollen and seed, are very restricted[4]. Pollen is transferred mainly by bees; field observations on *L. cylindracea* indicate that most moves by pollinators are to the nearest neighbour. Likewise seed dispersal, although by wind, is limited. This restricted gene dispersal is manifested in the spatial variation of gene frequencies within the population. Statistically significant gene frequency differences of as much as 0.2 existed between neighbouring quadrats. Genetic variation at a single locus, however, generally does not correlate to environmental parameters within the population[2]. Genetic divergence over distance appears to be a function of random gene frequency fluctuations. Only when all loci are considered together does the pattern of genetic variation in the Zion population emerge; genetic distance is positively related to spatial distance. This relationship is as predicted for a population in which gene dispersal is limited and genetic differentiation results from isolation by distance.

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Implications of ethylene production by bacteria for biological balance of soil

ETHYLENE in soil causes fungistasis[1], affects the growth of bacteria, actinomycetes and nematodes (unpublished data) and consequently must influence many soil biological processes. *Mucor hiemalis* has been proposed as a major producer of ethylene in soil[2] although earlier work suggested that facultative anaerobes may be involved[3]. Our studies show clearly that the main production of ethylene in soil is by spore-forming bacteria in anaerobic microsites. These bacteria seem to be an integral part of a self-regulating cycle in soil controlling microbial activity and with far-reaching implications for the biological balance of soil.

A high organic matter, basaltic soil (Ashburner[1]), which produces high levels of ethylene, was treated moist for 30 min with aerated steam at 60°, 82° and 100° C to simplify progressively the soil microflora[4]. Samples of treated soil were compared for ethylene production[1] with untreated and autoclaved (60 min at 121° C) samples. Untreated and treated soil samples were dried aseptically at 37° C for 24 h, passed through a 0.2-cm mesh sieve, placed as 5-g lots in four replicate sterile glass vials (14 ml capacity), wetted to 40% water (−0.5 bar water potential) with sterile distilled water, sealed with rubber septa and incubated at 25° C. This is our standardised assess-