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Population Biology of *Eschscholzia californica* Cham. in Chile. I. Spatial Microheterogeneity in two Populations

Biología de poblaciones de *Eschscholzia californica* Cham. en Chile. I. Microheterogeneidad espacial en dos poblaciones

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ABSTRACT

We investigated spatial patterns of distribution, recruitment, and phenotypes of individuals of *Eschscholzia californica* in two contrasting environments, using a grid point sampling method. In El Arrayán, the more unstable site, we found a low survival rate of adults and a high recruitment rate. We demonstrate that reproduction is uneven, but our tests did not show clearly the heterogeneity in density that was obvious at the site. In Con-Cón, the more stable environment, we found a higher survival rate of adults and a lower recruitment rate. In this population, a number of tests demonstrate that adults and juveniles are aggregated, and that there is no obvious relation between stock and recruitment, but there is more recruitment where there is more germination. We could not demonstrate spatial heterogeneity of genetic-based characters, but could not conclude that it does not exist. The two populations had similar densities, in spite of differences in recruitment, climate, competition, disturbance of habitat, and pattern of spatial microheterogeneity. We conclude that patch size is larger in the more stable site, while patch birth rate and extinction rate are greater in the more unstable site, and that the patterns of spatial microheterogeneity reflect these differences and the disturbances and competition which cause them.

Key words: Ecological strategy, colonization, ruderal species.

RESUMEN

Estudiamos los patrones espaciales de distribución, reclutamiento y fenotipos de individuos de *Eschscholzia californica* en dos ambientes constrastantes, muestreando desde los puntos de un reticulado. En El Arrayán, el sitio más inestable, encontramos una tasa de sobrevivencia baja de adultos, y una de reclutamiento alta. Demostramos que la reproducción es desigual, pero nuestras pruebas no mostraron claramente la heterogeneidad en densidad que era obvia en el terreno. En Con-Cón, el ambiente más estable, encontramos una tasa de sobrevivencia alta de adultos, y una tasa de reclutamiento baja. En esta población, varias pruebas demostraron que tanto los adultos como los juveniles están agregados, que no hay una relación obvia entre "stock" y reclutamiento; sin embargo, que hay más reclutamiento donde hay más germinación. No pudimos demostrar heterogeneidad espacial de caracteres con base genética, pero no se pudo concluir que éstos no existen. Las dos poblaciones tenían densidades similares a pesar de las diferencias en las características de reclutamiento, medio ambiente, competencia, perturbación del "hábitat" y patrón de microheterogeneidad espacial. Concluimos que el tamaño de los manchones es mayor en el sitio más estable, mientras que la tasa de nacimiento y extinción de ellos es mayor en el sitio menos estable. Los patrones de microheterogeneidad espacial reflejan estas diferencias que se habían originado por las perturbaciones y la competencia.

Palabras claves: Estrategia ecológica, colonización, especies "ruderales".

INTRODUCCION

In natural populations of plants, aggregated distributions of individuals are the most common, followed by random distributions; regular (underdispersed) species are infrequent (Goodall 1952). The classical factors postulated to account for aggregated or contagious distributions of individuals were those of limited dispersal

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of propagules and microheterogeneity in the distribution of favorable sites (Feller 1943, Pielou 1960). It is impossible to distinguish between these two causes by analyzing only number of individuals per quadrat; other kinds of sampling information are necessary to distinguish among possible distributions (Feller 1943, Skellam 1952).

More recent theory has considered microheterogeneity as a function of the temporal stability of the local environment. Species which can enter an open area, but cannot survive subsequent competition, are fugitive (Hutchinson 1951) or ruderal (Grime 1977) species. If the environment is stable over several generations, during which competition increases, perennial plants can colonize and should show exploitation selection (Whittaker & Goodman 1979). The r values of the species should be lower in relatively more stable environments (Pianka 1970), but it is not clear what kinds of spatial distributions should be expected.

If sites are available to a species only because of frequent disturbance, Whittaker & Goodman (1979) call this adversity selection; these species are the true weeds or colonizers (Baker 1965).Theory suggests that aggregated distributions should be expected in these r-selected species (Armstrong 1976, Caswell 1982), especially because they must continually re-establish their populations (Connell & Slatyer 1977, Sebens 1982). For a species to survive in an area, the size of the patches produced by disturbance must be small relative to the size of the area; the aggregation of individuals should reflect patch size (Pielou 1974, Levin & Paine 1974).

Local environmental heterogeneity, combined with limited dispersal, is a possible selective mechanism to explain the maintenance of local polymorphisms (Hedrick et al. 1976, Spieth 1979). If this occurs, genotypes should be non-randomly distributed, especially among patches (Gillespie 1974).

According to theory, therefore, we should expect the temporal stability of a population to be reflected in the distribution of individuals and/or in their phenotypes, and in the pattern of regeneration. If a species inhabits sites which differ in their rates of disturbance, we expect greater aggregation and higher recruitment rates in the more unstable sites. In order to test these propositions we used a grid point sampling method, presupposing that distributions would be non-random, to investigate the aggregation and recruitment of a colonizing species, *Eschscholzia californica* Cham, in two contrasting sites.

MATERIAL AND METHODS

Biology of *Eschscholzia californica*

The California poppy was introduced into Chile about 1850 (Frías et al. 1975). Aided by subsequent deliberate scattering of seeds along roads and railroads, it has spread throughout central Chile, also invading some pastures, abandoned fields, slopes, and plantations (*Opuntia*). *E. californica* was classified by Stebbins (1965) as a native species which has become weedy in California and elsewhere, although it lacks many characteristics of ruderals (Eaton 1981)[1]

E. californica is a poor competitor which survives well only in disturbed or marginal areas (Cook 1961). It is an r-selected species with Deevey's (1947) Type IV survival curve; it produces large numbers of seeds and seedlings, of which only a few survive to sexual maturity, and fewer still perenniate (Silva and Eaton, unpublished results). Seeds are small and round, the only dispersal mechanism being the explosive dehiscence of the capsule, which shoots seeds a maximum of 2-3 meters (Cook 1961).

Apparently all Chilean populations are characterized by polymorphisms in the location and amount of orange carotenoid pigments in petals, stamens, and stigmas (Frías et al. 1975, Eaton Gutiérrez & Torres, unpublished data). The most weedy populations in California are among the few in its native habitat in which these polymorphisms are found (Cook 1961, Stebbins, personal communication, April 1981). The genetics of the yellow-orange polymorphisms is complex (Beatty 1936, Douwes 1943) and not completely understood; however, they meet the criteria of Hannan (1981) for genetic-based polymorphisms.

The localities sampled were the following:

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[1] EATON LC (1981) Exito en la colonización de plantas terrestres: El ejemplo de *Eschscholzia californica*. Archivos de Biología y Medicina Experimentales 14 (3): 239-240 (Abstract).

a) Con-Cón, 17/9/1980, 3 km S of the community, along the Con-Cón - Viña del Mar International Highway, 32°59'S, 70° 30' W. Extensive population in pastureland with occasional shrubs, on both sides of the road, about 2 km from the Pacific coast, elevation 100 m. Sample taken on the E side of the road, in nearly flat area with less than 5° slope from SE-NW.

The Con-Cón site is a very gentle slope where walking leaves the soil practically undisturbed except where it is waterlogged. There was apparently only occasional grazing, judging from the growth of grasses and the paucity of fecal deposits. Competition with other species, especially grasses, appeared important here. Our field observations of heterogeneity were of two-dimensional areas of higher and lower density, but these were not well delimited.

b) El Arrayán, 9/9/80. Two km E of the community, on the S side of the road to Farellones, 33°21'S, 71°34'W. Extensive population on the slopes of the Andes foothills, about 130 km from the Coast, elevation 750-800 m, growing with herbs and some shrubs, subject to frequent grazing by cattle and horses. Sample taken in area with about 35° slope S-N, including several erosion-caused washes.

In El Arrayán the soil is loose, and is often dislodged by walking on the steep slope. Rain-produced slides occur in winter, and may be local or follow washes. Frequent grazing leaves criss-cross trails, tramples individuals, and alters the soil. Disturbances are frequent and usually localized, and are due to grazing and slides. We observed that both horses and cattle systematically, but not completely, avoided eating *E. californica.* Although the hooves of the animals destroy many individuals, selective grazing greatly reduces interspecific competition. Field observation indicated that the area was quite heterogeneous with respect to density, plants being notably more dense in narrow "stripes" along the sides of the washes.

Methods

In each area, we established a grid with lines separated by 3 m, using the lattice intersections as sampling points. In Con-Cón, the grid was 20 x 13, and in El Arrayán, 13 x 7. From each point, we measured the distance to the nearest plant; if this was not adult we also measured the distance to the nearest plant in flower, and the distance from the first in flower to its nearest neighbor in flower. For each plant, we noted if it was from the current year or perenniated, the number of flowers, and we collected one flower from each of the two measured. Average densities of perenniated adults were estimated in each population, using ten random 1 m quadrats within the grids.

We counted the number of stamens in each flower, and made the following classification of polymorphic characters:

a) Color of stamens, color of stigmas : Orange, pallid orange, yellow.
b) Relative amount of yellow in petals : Completely orange, narrow border (less than 10% yellow), wide border (10% - 50% yellow), "yellow" (more yellow than orange).
c) Intensity of orange in petals : Strong, brilliant, pale.

To test for non-random distributions of individuals, classes, and phenotypes we used, in addition to common statistical methods:

1. The test of Krishna-Iyer (1949). This method classifies the points or squares of a grid in two classes, and compares the number of adjacent squares of the same class with the expected if the two classes are randomly distributed in space. For an example of its use, see Appendix. We also used this test in cumulative form, succesively adding points according to their densities.

2. The test of Hopkins and Skellam (1954). This method compares the distribution of a sample of point-to-plant and plant-to-plant distances, which are the same if and only if the distribution of individuals is random. Details of these methods are in Pielou (1969); for other tests, see Sokal and Rohlf (1969). Calculations were made using hand calculators and with programs written in BASIC for an Altair 8800 minicomputer.

RESULTS

Basic data for the two populations are summarized in Table 1. While they are similar in mean density and proportion

TABLE 1

Basic data for samples of Con-Cón and El Arrayán, September, 1980. A means plants which germinated in the current year, P means perenniated plants. Average density is ± one standard error.

Datos básicos para muestras de Con-Cón y El Arrayán, septiembre de 1980. A significa plantas que germinaron en el año, y P significa plantas perenniadas. La densidad incluye ± un error estándar.

	Con-Cón		El Arrayán	
Grid sampling points	260		91	
Average density/m^2 (N = 10)	4.4 ±0.6		5.2 ±0.9	
Proportion in flower	0.13		0.11	
Test of Hopkins and Skellam	1.37 (P = .12)		1.58 (P = .17)	
Separation in A and P	A	P	A	P
Proportion of all plants	.47	.53	.91	.09
Proportion of plants in flower	.15	.85	.42	.58
Number of flowers per plant	1.01	1.26	1.11	4.15
Proportion with one flower	.99	.85	.89	.36

of all plants in flower, they are quite different with respect to various measures of season and regeneration. In El Arrayán, 91% of the plants were from the current year (A), but many of them had not yet produced flowers; 58% of the plants in flower were perenniated (P). In Con-Cón there was much less recruitment, A = 47%; most of the plants in flower (85%) were perenniated. In Con-Cón only one A individual had two flowers and only 15% of the P had more than one; while in El Arrayán about 10% of the A had two flowers, and the P showed a roughly exponential distribution with a mean of 4.15 flowers per plant.

These data clearly reflect that the flowering season was more advanced in El Arrayán, even though it was sampled eight days earlier. This is to be expected, since Con-Cón is near the coast; spring days are cloudier and cooler here than inland in the foothills. Although the overall densities are similar, the recruitment rate of the Con-Cón population is much lower. In El Arrayán, perenniated plants were producing nearly four times as many flowers as the recruits, while in Con-Cón the difference was much less-only 7 out of 442 had produced as many as 4 flowers, and only 2 of these had more than 10.

Figure 1 is a graphic representation of the test of Krishna-Iyer applied to the distances point-first plant in flower, for the Con-Cón sample. The expected number of joins (J) and the confidence limits depend only upon the size of the matrix and the number of squares (N) classified

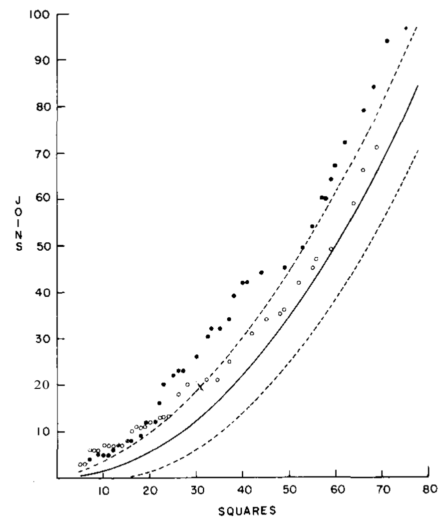

Fig. 1: Krishna-Iyer test applied to point-first plant in flower distances for the Con-Cón sample, in a cumulative form. The solid line is the expected value for the number of joins of a given number of squares; the broken lines are the 95% confidence limits. The solid circles represent squares with greatest distances (lower density); open circles represent squares with higher densities. The areas of least density are clearly grouped, and at least the 30 most dense areas also are.

Prueba de Krishna-Iyer aplicada a las distancias de punto-primera planta con flor, para la muestra de Con-Cón, en forma acumulativa. La línea sólida es el valor esperado para el número de uniones de un número determinado de cuadrados; la línea punteada entrega los límites de confianza de 95%. Los círculos sólidos representan los cuadrados con mayores distancias (menor densidad), y los círculos abiertos representan los cuadrados con mayor densidad. Las áreas de menor densidad están claramente agrupadas, y al menos los 30 puntos más densos también lo están.

TABLE 2

Classification of distances point-first plant (Con-Cón) and point-first plant in flower (El Arrayán), according to whether the plant was from the current year (A) or perenniated (P).

Clasificación de las distancias punto-primera planta (Cón-Cón) y punto-primera planta con flor (El Arrayán) según si la planta fue del año (A) o fue perenniada (P).

Con-Cón

Age	Distance Point-First Plant (cm)						
	0 - 3	4 - 7	8 - 11	12 - 15	16 - 19	20 or more	Total
A	24	40	32	16	4	6	122
P	10	40	32	26	16	13	137
	G (5 d.f.) = 16.6			*P* <.01			

El Arrayán

Age	Distance point-first plant in flower (cm)				
	0 - 20	21 - 40	41 - 60	61 or more	Total
A	4	10	11	12	37
P	10	13	7	24	54
	G (3 d.f.) = 4.86		*P* = .18		

as of one type, so that the significance of any other Krishna-Iyer test for this sample can be determined by inspection from the graph. Figure 1 demonstrates that the areas of least density are clearly grouped, and that at least the 30 most dense points also are. Similar results were obtained using the sum of these distances and plant to neighbor distances, or the maximum (or minimum) of these pairs, for Con-Cón. We conclude that there are patches with more plants in flower, and gaps, with less in flower. In El Arrayán, however, none of these measures gave significant results, as Figure 2 demonstrates, although the six least dense squares were grouped.

Table 2 groups the distances point-first plant (Con-Cón), and point-first plant in flower (El Arrayán), according to whether the plant was A or P. There is a higher concentration of plants in their first year in the more dense areas in Con-Cón. For El Arrayán the test was not significant, but there were few A in flower close to the sampling points. Similar results were obtained applying Mann-Whitney U tests to these sample distributions.

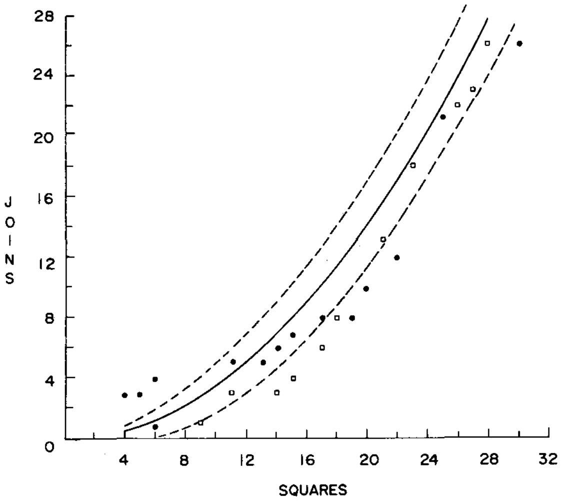

Fig. 2: Cumulative Krishna-Iyer test for point-first plant distances for the El Arrayán sample; explanation as in Figure 1. Only one gap, which joined 4 of the 6 least dense squares, is significant.

Prueba acumulativa de Krishna-Iyer para distancias punto-primera planta en flor, para la muestra de El Arrayán; explicación como en la Figura 1. Sólo un área, que contiene 4 de los 6 cuadros menos densos, es significativa.

Table 3 compares the age of the pairs of plants with flowers. In both populations, there is a significant tendency for the pairs to be both P or both A; therefore there

TABLE 3

Classification of plants in flower nearest the sampling points and their nearest neighbors according to whether they were from the current year (A) or perenniated (P). Both tests of independence have one degree of freedom.

Clasificación de las plantas con flor más cercanas a los puntos de muestreo y de sus vecinos más próximos, según si fueron del año (A) o perenniadas (P). Ambas pruebas de independencia tienen un grado de libertad (d. f.).

		Con-Cón		El Arrayán	
		Neighbor in flower		Neighbor in flower	
		P	A	P	A
First plant	P	197	24	38	15
in flower	A	94	15	13	25
		$G = 16.18$ $P < .001$		$G = 12.84$ $P < .001$	

TABLE 4

Classification of the 3 plants nearest the sampling points according to whether they were from the current year (A) or perenniated (P), for Con-Cón. The 34 cases where the plant nearest the point was in flower were excluded.

Clasificación de las 3 plantas más cercanas a los puntos de muestreo según si fueron del año (A) o perenniadas (P). Los 34 casos en que la planta más cercana al punto tenía flor, se excluyeron.

		Plant nearest sampling point		
		P	A	
Pairs in	P - P	95	75	$N = 226$
flower	A - P	15	31	$X^2_{adj} = 15.02$
	A - A	0	10	$P < .001$ (2 d. f.)

are areas within each population where there is more, and less, recruitment. Table 4 clarifies this for Con-Cón; plants without flowers are more likely to be P if both plants with flowers (from the same point) also are, and are more likely to be A if at least one with flowers is A.

We compared the distances between A-A pairs to those of P-P pairs for El Arrayán, using the Mann-Whitney U test. Areas with greater recruitment have a higher density of plants in flower ($P < .05$). We tested to see if those squares where at least one of the pair had more than one flower were grouped. For Con-Cón, the test of Krishna-Iyer for $N=61$ gave $J=63$ joins, $P < .05$. There are areas where (perennial) plants have more flowers. In El Arrayán, the areas where perennial plants have only one flower are clustered ($P < .05$); there are areas where perennials are less productive. In Con-Cón, the points where one or both flowering plants were A are significantly grouped (see Appendix), which also demonstrates that there are areas of greater recruitment.

We were unable to find any significant associations of morphological characters in space. We tested whether pairs of plants at each point were similar, and for associations of morphology with density. None of these tests gave significant results, although some associations with density were suggestive. The aggregation tests are summarized in Table 5. The two populations are significantly different (G tests, $P < .01$ for each) in their frequencies for each of the morphological yellow-orange flower characters, Con-Cón having more orange in each case. However, El Arrayán has more intense petal color (G test, $P < .01$), and more stamens per flower (Mann-Whitney U, $P < .001$).

We did not use the distance measures to

TABLE 5

Summary of aggregation tests within populations

Resumen de las pruebas de agregación dentro de poblaciones

QUESTION	ANSWER		
	Con - Cón	*El Arrayán*	*Test Used*
A. Related to density of plants			
1. Are there patches and gaps in flowering?	Yes (Fig. 1) $P < .05$	? (Fig. 2) mostly not significant	Krishna-Iyer cumulative
2. Are there more first-year plants in more dense areas?	Yes (Table 2) $P < .01$	? (Table 2) $P = .18$	G independence
	Not tested	Yes (see text)	Mann-Whitney U
B. Related to spatial distribution			
3. Are there patches where flowering plants are older and/or younger?	Yes (Table 3) $P < .001$	Yes (Table 3) $P < .001$	G independence
4. Are there patches where *all* plants are older and/or younger?	Yes (Table 4) $P < .001$	Not tested	X^2 adjusted independence
5. Are there patches with more and/or less flowers per plant?	Yes (for more) $P < .05$	Yes (for less) $P < .05$	Krishna-Iyer
C. Related to polymorphic characters			
6. Are colors of flower parts associated with density?	? ($P = .07$ for petal color)	? ($P = .11$ for stamen color)	Kruskal-Wallace
7. Are nearest neighbors similar? (patches and gaps in morph distributions)	? ($P = .13$ for intensity of petal color)	? ($P = .17$ for stamen color)	G independence

test for randomness of distributions or to estimate densities, since as Pielou (1969) demonstrates, a sample of plants nearest to random points does not give a random sample, but is biased in favor of isolated individuals. It is probably for this reason that the test of Hopkins and Skellam did not give significant results (Table 1, compared to a standard normal variate).

DISCUSSION

In Con-Cón, we found patches and gaps (areas with greater and lesser density) of plants in flower; plants not in flower of the same age group were also aggregated. The more dense squares have more A plants, and there are patches with more A in flower. There are squares with more recruitment, and there is more germination where there is more recruitment. The perenniated plants are more frequent in less dense areas, with less recruitment, although there are patches where they have more flowers.

In El Arrayán, we found a high rate of reproduction and presumably recruitment. Here we could only demonstrate that there are squares with more reproduction and areas where perennials were producing less flowers, and a higher concentration of A-A pairs in more dense sites. Why did the observed heterogeneity not show up more in our tests? First, because the sample size was much smaller in El Arrayán; statistical tendencies in general are more marked in larger samples. Second, as mentioned above, using grid points biases the sample in favor of isolated individuals. A third reason is that the size of the grid was too large to detect the "linear" spatial variation in density present here, where changes were often marked at distances of 1-2 meters.

In spite of these limitations, there is sufficient information to conclude that in both populations there is microheterogeneity in the distribution and flower production of individuals and in recruitment, and that the temporal stability in El Arrayán is much less than in Con-Cón. In El Arrayán, frequent disturbances on a micro level lead to an unpredictable environment with local extinctions and little competition; this is evidenced by the pattern of low survival and high regeneration. In Con-Cón, the relatively more stable environment and longer growing season lead to higher competition, as evidenced in the pattern of greater survival of perennials and less regeneration. Here, *E. californica* "holds on" in the face of increasing competition, until the next disturbance opens up a new patch or site. We also found that the patch size is different in the two populations, being much larger in Con-Cón. The analysis almost missed the smaller, "linear" patches in El Arrayán, while spatial microheterogeneity in the larger, "2-dimensional" patches in Con-Cón was demonstrated for a number of traits.

The average densities of adults were similar in the two populations, in spite of the differences in temporal stability. The local conditions and pattern of disturbances lead to more regeneration and shorter life span in El Arrayán, and to less regeneration and longer life expectancy in Con-Cón. In each case, the persistence of the population depends upon the ability to occupy newly available sites; the difference among populations is the spatio-temporal pattern in which these sites become and remain available.

We could not demonstrate a non-random distribution of phenotypes in either population, which may mean either that such distributions do not exist, or that we were simply unable to detect them. In view of the limitations of the sampling methods, we must leave this an open question. The majority of the tests showed a tendency for similar phenotypes to be clustered, although the results were not statistically significant; we plan to sample populations with more adequate methods in order to provide a more precise test of this hypothesis.

Our results are in agreement with the theoretical predictions outlined in the Introduction, although they do not permit a critical test of the theory. To be more precise, we will need methods to relate patch size with aggregations, and to measure their stability over time.

Concluding, spatial microheterogeneity in these populations is reflected in the aggregated distributions of both juvenile and adult individuals. Areas of different densities and recruitment rates reflect a continual process of colonization and extinction. Although the magnitude and rate of these two events is different in the two populations, this ruderal species is able to persist with similar densities in each.

APPENDIX

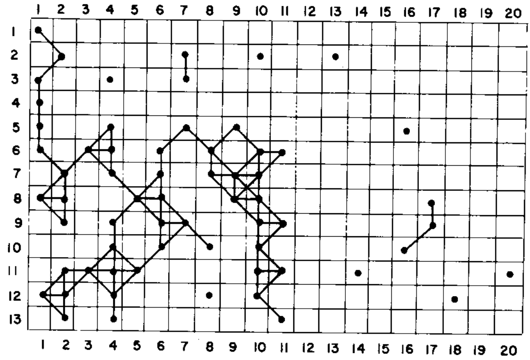

Fig. 3: The method of Krishna-Iyer (1949). Test to see if the squares (N = 63) where at least one of the plants in flower is of the current year (A), are randomly distributed in space. All horizontal or diagonal connections between such squares are counted as joins (J). If the grid is r x c and there are N squares of one type, the expected number of joins is given by:

$$E(J) = \frac{N(N-1)2-3(r+c)+4rc}{rc(rc-1)}$$

The expression for the variance of J is somewhat more complicated; it may be found in Krishna-Iyer (1949) and Pielou (1969). According to these authors, the distribution of J is asymptotically normal. In the present case, using the approximation to the normal distribution, J = 81 joins is significantly greater than expected, E(J) = 54.7, the standard deviation is 6.00, $P < .01$.

El método de Krishna-Iyer (1949). Prueba para ver si los cuadrados (N = 63) en los cuales por lo menos una de las plantas en flor es del año (A), están distribuidos aleatoriamente en el espacio. Se cuentan como uniones (J) todas las conexiones, tanto horizontales como diagonales, entre cuadrados adyacentes. Si el reticulado es de r x c, y hay N cuadrados de un tipo, el número esperado de uniones está dado por la ecuación de arriba. La expresión para la varianza de J es bastante engorrosa; puede encontrarse en Krishna-Iyer (1949), y Pielou (1969). Según estos autores, la distribución de J es asintóticamente normal. En el presente caso, usando la aproximación a la distribución normal, J = 81 uniones es significativamente mayor de lo esperado, E(J) = 54.7, la desviación estándar es 6.00, $P < .01$.

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