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A DIFFUSION MODEL FOR DISPERSAL OF *OPUNTIA IMBRICATA* (CHOLLA) ON RANGELAND

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SUMMARY

(1) The dispersal of *Opuntia imbricata* (cholla) on rangeland may be directly or indirectly affected by the presence of livestock and wildlife. Overgrazing creates gaps or open spaces for seeds or stems that fall to the ground to become established (passive dispersal). In addition, livestock or wildlife may cause stems and fruits to fall to the ground (active dispersal).

(2) A theoretical model is formulated for the dispersal of plants based on the diffusion equation which assumes one or more mechanisms of dispersal (e.g. passive and active dispersal). The χ^2 goodness-of-fit test is used to determine whether the data may be explained by one or by two mechanisms of dispersal. Methods for estimating the model parameters are presented based on the χ^2 method and the method of moments.

(3) The model and analytical techniques are applied to field data on the spatial distribution of *Opuntia imbricata* in four different pastures.

(4) The results indicate that dispersal of cholla can be attributed to two dispersal mechanisms. Passive dispersal alone cannot account for the current spread of cholla on some of the pastures.

INTRODUCTION

Opuntia imbricata (Haw) D. C., commonly called cholla or walkingstick cholla, is a native cactus in Texas and New Mexico. Usually the species is present in low frequencies on rangeland. However, for reasons not well understood, *O. imbricata* can dramatically increase its density and act as a range weed, interfering with livestock grazing and handling (Kunst 1988). *O. imbricata* reproduces from seeds and from detached stems or joints (Kunst 1988, 1990), with asexual reproduction representing the dominant method by which the species spreads in rangelands (Brown 1950; Glendening 1952; Humphrey & Mehikoff 1958; Pieper, Rea & Fraser 1974). Livestock and wildlife may play a dual role in the dispersal of cholla. Overgrazing creates open spaces in the herbaceous vegetation in which detached stems (joints) may establish new plants (passive dispersal). The availability of gaps is assumed to be a key factor in the success of cholla invasion (Pieper, Rea & Fraser 1974). Animals may also cause joints to fall to the ground (Humphrey & Mehikoff 1958; Laycock & Mihlbacher 1987). In addition, animals may help the dispersal by trans-

porting stems (e.g. joints may become lodged on their body and drop off later) or by ingesting the fruits and depositing the seeds through defecation (active dispersal).

There are two important variables in the dispersal of cholla which have implications for range management: the rate of dispersal and the density eventually attained by the species. If either one of these variables is low, cholla can be easily controlled or poses no serious range problem. Therefore, it is useful to be able to estimate these variables for various range conditions. The density eventually attained by cholla is easily estimated, but the rate at which cholla disperses is much more difficult to assess. Assuming that dispersal of cholla can be modelled by a diffusion process (discussed in the next section), then this dispersal can be quantified by estimating diffusion coefficients. As mentioned above, however, more than one type of dispersal mechanism may be present, and a simple diffusion process with a single diffusion coefficient may be inadequate to explain or predict the rate of spread of cholla. In this paper, the dispersal of cholla by diffusion is generalized to take into account more than one dispersal mechanism. After the formulation of a theoretical dispersal model, a method is presented to test if empirical data can be explained by one or more mechanisms of dispersal, assuming that the dispersal is by diffusion. The model and techniques are applied to four pastures in Texas and New Mexico with cholla infestations.

MODEL FORMULATION

The diffusion equation provides a theoretical framework for determining the spatial distribution of plants away from a source. Skellam (1951) was one of the first to use it to model the spatial spread of a population and to apply it to particular plant and animal populations. Andow *et al.* (1990) applied the diffusion equation to three introduced species (*Ondatra zibethica* (muskrat), *Oulema melanopus* (cereal leaf beetle) and *Pieris rapae* (small cabbage white butterfly)) to estimate their asymptotic rate of spread. The diffusion equation has served as a useful starting point for many models of population dispersal or spread (e.g. Okubo 1980; Liddle, Parlange & Bulow-Olsen 1987; Banks, Kareiva & Zia 1988; Edelman-Keshet 1988; Hengeveld 1988, 1989; Moody & Mack 1988; Murray 1989; Okubo & Levin 1989).

For our purposes, mechanisms of dispersal can be divided into two categories: active and passive. Okubo (1980) defines 'active diffusion' as the diffusion of objects, primarily animals, which perform motion by themselves and 'passive diffusion' as the diffusion of objects that are not capable of performing random motion without the help of environmental turbulence. The term 'passive diffusion' or 'passive dispersal' will be used here in the same sense for dispersal of seeds, stems or fruits that fall to the ground and are not transported by animals. The term 'active diffusion' or 'active dispersal' will be used when transport of the seeds, stems or fruits may be attributed to animals. The actual movements of animals in the dispersal of a plant away from a source will not be considered, only the consequences of that movement. Active dispersal may play a more significant role than passive dispersal in rangeland conditions due to the presence of cattle.

The spatial distribution of plants away from a source depends on a multitude of factors (intrinsic and extrinsic) which affect the dispersal of disseminules and their germination success. As noted by Harper (1977, p. 112), it is almost impossible after seedling growth to discover what were the direct causes of density, pattern and

composition of a plant population. More-detailed models must account for each part of the dispersal process over much smaller time scales (e.g. seed dispersal; Liddle, Parlange & Bulow-Olsen 1987; Okubo & Levin 1989) and these individual factors must be determined via detailed quantitative investigations into distribution, emergence and mortality of seedlings (e.g. Friedman & Orshan 1975). We consider the total impact of these factors on the dispersal process, and make the assumption that the contributing factors may be grouped into one or more mechanisms of dispersal (e.g. active and passive dispersal) and then test this assumption.

Differing dispersal mechanisms have been used to explain species invasions and their subsequent spread. Although the mechanisms are defined differently, Hengeveld (1988, 1989) showed that two different dispersal mechanisms may be responsible for the invasion of *Streptopelia decaocto* (collared dove) into Europe. According to Hengeveld (1988), the biota arising from species or individuals having different dispersal mechanisms with specific efficiencies may be the rule rather than the exception.

We begin with a simplistic model, based on the diffusion equation, in which factors influencing the spatial pattern are grouped into a single parameter, the diffusion coefficient. An initial value problem can be formulated for $S(x,y,t)$, the probability density distribution for the number of plants per unit area at position (x,y) and time t . The governing differential equation for the dispersal of these plants is given by the diffusion equation:

$$\frac{\partial S}{\partial t} = K \left(\frac{\partial^2 S}{\partial x^2} + \frac{\partial^2 S}{\partial y^2} \right),$$

with the corresponding initial condition,

$$S(x,y,0) = \delta(x) \delta(y),$$

where K is the diffusion coefficient and δ is the Dirac delta function. The initial condition is a point source which represents an isolated parent plant at which all of the disseminules are located (with probability one). We consider only the diffusion process and not the growth of the population, because the model is applied to the dispersal of second-generation plants which arise from a parent plant (point source) and not successive generations which arise from these plants.

The solution to the above system is well known (Pielou 1977) and is given by

$$S(x,y,t) = \frac{1}{4\pi Kt} \exp\left(-\frac{x^2 + y^2}{2Kt}\right).$$

If we let $D = 4Kt$, where t is a sufficiently long time period during which the plants become established, and consider S in terms of polar coordinates, r and θ , then the distribution for S becomes

$$S(r,\theta,D) = \frac{e^{-r^2/D}}{\pi D}.$$

As $S(r,\theta,D)$ is independent of θ , the probability density distribution can be written as a function of distance r from the source (parent plant) as follows (Pielou 1977):

$$f(r,D) = 2\pi r S(r,\theta,D) = \frac{2r}{D} e^{-r^2/D}, \quad (1)$$

where f is the probability density distribution of plants per unit distance. (Note that f has the form of a particular exponential distribution, i.e. Rayleigh distribution.) In other words, f is the probability of finding offspring plants per unit distance from the source or parent plant. The above distribution has mean, $\bar{r} = \sqrt{(D\pi)}/2$, mode, $r_m = \sqrt{(D/2)}$, and variance, $\sigma_r^2 = D(1 - \frac{\pi}{4})$. We shall refer to D , rather than to K , as the diffusion coefficient in the following analysis. The units of D are the square of distance.

If dispersal is primarily due to one mechanism, for example either passive or active dispersal, then we should expect the data to fit an equation of the form (1), a unimodal distribution. However, if the observed distribution is bimodal, there are probably at least two methods of dispersal which significantly affect the form of the distribution. In this case, a proportion, p_1 , of the distribution of plants is due to one method and the remaining proportion, p_2 , is due to a second method ($p_1 + p_2 = 1$). Therefore, a distribution of the following form is appropriate:

$$F(r, p_1, p_2, D_1, D_2) = p_1 f(r, D_1) + p_2 f(r, D_2), \quad (2)$$

where F is the probability density distribution of plants per unit distance. The distributions $f(r, D_1)$ and $f(r, D_2)$, given by eqn 1, are the probability density distributions for each method of dispersal with diffusion coefficients D_1 and D_2 , respectively. We assume $D_1 \leq D_2$; therefore, the first method of dispersal (e.g. passive dispersal) locates plants closer to the source than the second method (e.g. active dispersal). Obviously, if $D_1 = D_2 = D$, eqn 2 is the same as eqn 1. Although not considered in the remainder of this paper, more than two methods of dispersal could be considered. Clearly, eqn 2 can be generalized to n methods of dispersal, and if $D_i = D$, then the model reduces to eqn 1. However, as n goes to infinity, the form of the distribution F is hard to predict unless relations between the parameters p_i and D_i are known.

It is important to remember that the basic underlying assumption is that dispersal is by a random diffusion process and it is this assumption which provides the motivation for using eqns 1 or 2 (rather than some other distribution) in the following analysis.

The distribution given in eqn 2 is a finite mixture distribution with known component distribution function f , but where the mixing weights or proportions, p_1 and p_2 , and the component parameters, D_1 and D_2 , are unknown (Titterington, Smith & Makov 1985). In the following section we use a minimum distance estimation procedure based on the χ^2 distance measure (which we refer to as the χ^2 method) to estimate the unknown weights and parameters. This proves to be a practical method for our application. The method of moments estimation procedure was also considered but, in some cases, it did not provide feasible solutions. Some other estimation procedures of the unknown weights and parameters are discussed by Titterington, Smith & Makov (1985).

The χ^2 method was also used to test if eqn 1 provides a reasonably good fit to the data, i.e. to test if there exists a parameter D such that the resulting χ^2 value is suitably small. Titterington, Smith & Makov (1985) discuss some procedures designed to directly test eqn 1 vs. eqn 2 when the function f has a particular form such as the normal form. However, these procedures are complicated and depend very heavily on the functional form f . Therefore, we did not test eqn 1 against eqn 2, but tested if eqn 1 provides a reasonably good fit. If this hypothesis is rejected, we cannot conclude that eqn 2 is the alternative, but that eqn 2 is one among many alternatives

that may provide a better fit. However, because our basic assumption is that dispersal by random diffusion is the underlying mechanism, eqn 2 is the reasonable alternative.

Goodness of fit of the model

The χ^2 goodness-of-fit test was used to determine if field data from *O. imbricata* could be explained by a probability density distribution that assumes either one dispersal mechanism (distribution f , eqn 1) or two dispersal mechanisms (distribution F , eqn 2). The same test was used to estimate the model parameters.

To apply the χ^2 goodness-of-fit test to field data, the location of plants must be recorded according to distance from a source. The data are then grouped according to the frequency of occurrence in n radial intervals. The endpoints of the radial intervals, denoted as $0 = R_0 < R_1 < R_2 < \dots < R_n = \infty$, are determined by the expected proportion of plants within each annular region. For a specified D or p_1, p_2, D_1 , and D_2 , the radii are determined as follows:

$$\int_0^{R_1} g(r) dr = \frac{5}{N} = \int_{R_{n-1}}^{\infty} g(r) dr, \quad (3)$$

$$\int_{R_{i-1}}^{R_i} g(r) dr = \frac{N-10}{(n-2)N} \quad i = 2, \dots, n-1, \quad (4)$$

where $g(r)$ is either the distribution $f(r)$ or $F(r)$, given by eqn 1 or eqn 2, respectively, and N is the total number of plants. Because the value of N is known and the distribution $g(r)$ (either $f(r)$ or $F(r)$) is specified by the model parameters, the endpoints R_i are determined uniquely from the formulas given in eqns 3 and 4. The expected frequency in each of the tail regions is 5, whilst the expected frequency in each of the central regions is $\frac{N-10}{n-2}$. For $\frac{N-10}{n-2} > 5$, the χ^2 goodness-of-fit test can be applied (Wetherill 1967; Dudewicz & Mishra 1988). Thus, for a given N the number of annular regions n is fixed so that $\frac{N-10}{n-2} > 5$. (The expected frequencies for each of the tail regions is set = 5, thereby according finer intervals to these regions as differences between the actual and hypothesized distributions are more likely to show up in the tail regions.)

To test if one dispersal mechanism is adequate to explain the spatial distribution, distribution f , eqn 1 is considered first. The data are tested against many distributions of the form (1) by selecting many different values for the diffusion coefficient. It is clear that the goodness of fit of the theoretical model and the field data hinges on the choice of D , the diffusion coefficient. An initial approximation for this parameter can be obtained from an estimate of the mean. The mean of the distribution f is $\bar{r} = \sqrt{(D\pi)}/2$. An estimate of the mean is the sample mean, \hat{r} :

$$\bar{r} = \int_0^{\infty} rf(r) dr \approx \sum_{i=1}^N \frac{r_i}{N} = \hat{r}.$$

Therefore, the diffusion coefficient approximation, $D \approx \hat{D}$, is given by $\hat{D} = 4\hat{r}^2/\pi$. Different values of the diffusion coefficient are chosen based on this approximation, in order to test a wide range of possible values. (In the application section we choose twenty different values of D , $D = 0.1\hat{D}, 0.2\hat{D}, \dots, 2\hat{D}$.) The range of distributions

with acceptably low χ^2 gives a corresponding range of acceptable values for the diffusion coefficient, D . If the χ^2 values for all of the different distributions tested against the data are greater than a specified χ^2 of low probability, then it is assumed that more than one dispersal mechanism is influential.

To determine the parameters in the distribution of the form (2), the χ^2 goodness-of-fit test can again be applied. The diffusion coefficients, D_1 and D_2 , and the proportions, p_1 and p_2 , can be varied over many combinations to obtain distributions which give acceptably low χ^2 values. The values of the parameters corresponding to these distributions are used as parameter estimations. (Best estimates of parameter values correspond to minimum χ^2 values.)

The range of parameters limits the number of combinations to be chosen. Because $D_1 \leq D_2$, $p_1 + p_2 = 1$, and the mean of the distribution F is given by

$$\bar{R} = \int_0^{\infty} rF(r)dr = p_1\sqrt{(D_1\pi)}/2 + p_2\sqrt{(D_2\pi)}/2,$$

it follows that $D_1 \leq 4\bar{R}^2/\pi \leq D_2$. The sample mean, \hat{r} , can be used to estimate the mean, \bar{R} , of the distribution F ,

$$\bar{R} \approx \hat{r} = \sqrt{(\hat{D}\pi)}/2.$$

Therefore, it is reasonable to expect that $D_1 \leq \hat{D} \leq D_2$.

The method of moments was also used to estimate the parameters p_1 , p_2 , D_1 and D_2 and provided a check on the χ^2 method. The method is more fully explained in the Appendix. The first four moments of the distribution F ($\int_0^{\infty} r^k F(r)dr$, $k = 0, 1, 2, 3$) can be expressed in terms of the parameters. Approximations to the moments can be obtained from the data ($\sum_{i=1}^N r_i^k/N$, $k = 0, 1, 2, 3$). In this manner, four non-linear equations are obtained which can be solved for the unknown parameters, p_1 , p_2 , D_1 and D_2 . If the solutions are feasible, they may serve as estimates for p_1 , p_2 , D_1 and D_2 and may be used to check the estimates obtained via the χ^2 method.

APPLICATION OF THE MODEL

Four pastures with different densities of *Opuntia imbricata* were selected for the collection of field data. Pastures were located in private ranches and were grazed by livestock and wildlife. They are identified by the name of the city closest to the ranch. Three pastures were located in south-west Texas: Alpine, Amarillo and Post. The fourth, Lovington, was located in eastern New Mexico. The approximate locations of the four pastures are 30°22'N, 103°34'W (Alpine), 35°21'N, 101°50'W (Amarillo), 33°05'N, 103°21'W (Lovington) and 33°08'N, 101°18'W (Post). Broadly speaking, they represent variations of climate (arid to semi-arid) and management due to different ownership. At a more detailed scale, they varied in size, form, soil types, range sites (vegetation) and landscape features such as slope, grass cover, etc. Sampling was stratified according to soil types and/or range sites, as defined and drawn in Soil Conservation Survey (SCS) maps and Soil Surveys for the pasture (Turner *et al.* 1974; Richardson, Grice & Putnam 1975; Pringle, Geiger & Burns 1980; U.S. Department of Agriculture, unpublished data).

In each range site parent plants of *O. imbricata* were located. Parent plants were considered sources of dispersal for the species, and defined as the oldest plants that

could be found. Relative isolation, height and number of nodes were the primary variables used to identify and distinguish between the oldest plants and the individuals belonging to the next generation (second generation) of the species. Offspring of later generations were identified using additional variables (percentage of green tissue, number of branches and diameter). The oldest plants were easily located due to their large size and relative isolation from other plants (Fig. 1).

In a circular plot with a radius of 20 m centred on each parent plant, the individuals belonging to the next generation (second generation) of the species were identified. Distance in metres (± 0.1 m) from the centre of each second generation plant to the centre of each parent plant was recorded. The underlying assumption was that the second-generation plants were originally seeds or joints arising from the parent plant. Therefore, no two circular plots intersected (any two parent plants within 40 m of each other were rejected). Plants of later generations could have originated from the parent plant, its offspring, or some other generation; therefore, only the parent plant and its presumed offspring (second-generation plants) were included in the analysis. In this study there were sixteen, twelve, twenty-four and thirty-three parent plants identified at the Alpine, Amarillo, Lovington and Post pastures, respectively. The mean number of second-generation plants within a circular plot for all pastures was 2.7 ± 1.2 plants. In the Amarillo and Lovington pastures the mean number of second-generation plants within a circular plot was 3 plants, whereas, in the Alpine and Post pastures there was a mean of 2.4 and 2.5 plants, respectively. The average height and number of nodes for individual plants varied between pastures, although within a pasture the variation was small. For example, in the Post pasture the mean (\pm S.D.) height of a parent plant was 2.4 ± 0.4 m, whereas the mean height of a second-generation plant was 1.9 ± 0.4 m. Also, in the Post pasture the mean number of nodes of a parent plant was 20.9 ± 2.6 , whereas the mean

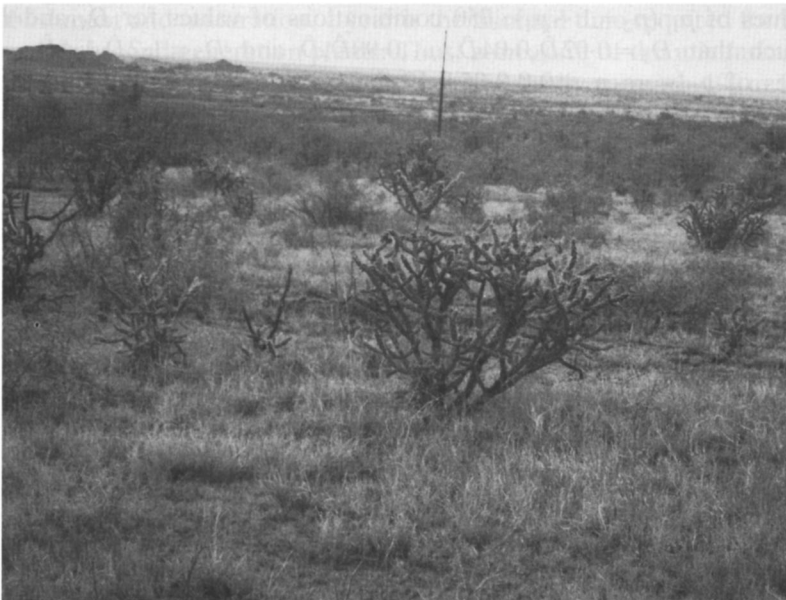


FIG. 1. Infestation by *Opuntia imbricata* (cholla) in pasture at Post, Texas.

number of nodes of a second-generation plant was 15.9 ± 2.5 . Further details are given by Kunst (1990).

The data for each pasture, analysed separately, were divided into six radial regions ($n=6$), because the total number of second-generation plants ranged from a minimum of 36 (Amarillo) to a maximum of 84 (Post). (Application of the χ^2 -test requires $\frac{N-10}{n-2} > 5$.) For the unimodal distribution, f , the lowest χ^2 and the corresponding value of the diffusion coefficient, D (in m^2) were calculated from a range of twenty values, $D=0.1\hat{D}, 0.2\hat{D}, \dots, 2\hat{D}$ (with \hat{D} given in Table 1). The null hypothesis was that a parameter D exists such that $\chi^2 < 9.24$, i.e. the data can be explained by one dispersal mechanism. Therefore, the range of values for D that produced $\chi^2 < 9.24$ was also calculated (Table 1). The null hypothesis is rejected if $\chi^2 > 9.24$. The probability of $\chi^2 > 9.24$ is < 0.10 , assuming the sample is from the theoretical distribution with 5 degrees of freedom. Therefore, the probability of rejecting a true null hypothesis is < 0.10 (i.e. the probability of making a Type II error is $\beta = 0.10$ and the power of the test is 0.90). Therefore, it is unlikely (less than 10% probability) that the value of the diffusion coefficient D is outside the range of values.

Based on Table 1, the data from Alpine and Amarillo pastures can be fitted quite well to the distribution f , assuming only one dispersal mechanism. The Lovington data were borderline as the probability of obtaining $\chi^2 > 7.29$ is < 0.20 (with 5 degrees of freedom). However, the Post data clearly cannot be explained by a distribution of the form (1); the probability of obtaining $\chi^2 > 20.5$ is < 0.001 (with 5 degrees of freedom). Thus, for the Post data, assuming dispersal by diffusion, we are forced to consider more than one dispersal mechanism (i.e. more than one diffusion coefficient).

To test if two dispersal mechanisms are operative, distribution F (eqn 2) was used. The diffusion coefficients, D_1 and D_2 (in m^2), and the proportions, p_1 and p_2 , were varied over 15 000 combinations and the χ^2 values computed. For twenty different values of p_1 ($p_2 = 1 - p_1$), 750 combinations of values for D_1 and D_2 were chosen such that $D_1 = 0.02\hat{D}, 0.04\hat{D}, \dots, 0.98\hat{D}, \hat{D}$ and $D_2 = 1.2\hat{D}, 1.4\hat{D}, \dots, 4.0\hat{D}$. The values of p_1 were $p_1 = 0.0, 0.05, 0.10, \dots, 1.0$. Again, the null hypothesis was that there exist parameter values p_i and D_i , $i=1,2$ such that $\chi^2 < 9.24$. The null hypothesis is rejected if $\chi^2 > 9.24$ (which occurs with probability $\beta = 0.10$).

Data for all four pastures were tested for two dispersal mechanisms. In all four cases the null hypothesis was not rejected; i.e. dispersal by two mechanisms cannot

TABLE 1. Dispersal of *Opuntia imbricata* on four pastures in Texas and New Mexico. One dispersal mechanism is assumed for each pasture. Parameter \hat{D} is an approximation to the diffusion coefficient D , and D corresponds to the minimum χ^2 . Values outside the range of the diffusion coefficient D occur with probability < 0.10 . Index T is an estimation of the minimum number of years for plants to eventually reach 100 m from the parent plant.

Pasture	\hat{D}	D	Range of diffusion coefficient D	T	χ^2
Alpine	97.6	126.8	87.8–156.0	4.14	2.29
Amarillo	116.7	140.0	81.7–163.4	3.94	0.969
Lovington	68.6	75.4	75.4 (one value)	5.37	8.29
Post	103.5	103.5	None	4.58	34.0

be rejected. A range of values for each of the parameters can be given (similar to Table 1), where the range of the χ^2 values is <9.24 . The minimum χ^2 values for distribution F and their corresponding parameters were estimated (Table 2).

Probability frequency histograms clearly show a bimodality of the data for the Alpine and Post pastures (Fig. 2). The χ^2 values (Tables 1 and 2) indicate that distribution F with two dispersal mechanisms provides a better fit to the data than distribution f with only one dispersal mechanism. The fit is significantly better for Lovington and Post data (Fig. 2).

The parameters p_1 , p_2 , D_1 and D_2 were also estimated using the method of moments. For three of the pastures, the parameter estimations gave solutions that were not feasible (the value of $\sqrt{D_1}$ or $\sqrt{D_2}$ was negative). The probable cause of this was due to the small data sets ($N = 38, 36, 72$ and 84 in each of the four pastures, respectively). However, for the Lovington pasture, feasible solutions were obtained and were given by $p_1 = 0.094$, $p_2 = 0.906$, $D_1 = 0.442$, and $D_2 = 82.4$. These estimations are comparable to those given by the χ^2 method (Table 2).

In addition to the diffusion coefficients (D or D_1 and D_2), it is useful to define a parameter which provides a rough estimate for the rate of spread of cholla. We consider the value of the radial distance within which 99% ($r_{0.99}$) of the offspring are located. From a practical standpoint, $r_{0.99}$ ($= \sqrt{D \ln 100}$) is a measure of the potential length of the step at which *O. imbricata* disperses in a particular range environment. We define an index T , an estimate of the minimum time required for offspring eventually to reach 100 m from the parent plant. An estimate of T requires information about plant establishment, growth and maturation.

The development of joints and fruits and their dispersal, including plant establishment, may occur each year from spring to late autumn. Plants may be established in 1 year (assuming no allowances or delays due to bad seasons, unavailability of gaps, or other deleterious factors); but there is an additional period of time required for seeds or plants to mature. Therefore, considering the period of time required for plant establishment and maturation, 1 year is the minimal time required for dispersal to commence in second-generation plants. Thus, a measure of the minimum number of time steps (years) for successive generations eventually to reach 100 m from the original parent plant is $T = 100/r_{0.99}$ (Tables 1 and 2).

The diffusion equation with population growth,

$$\frac{\partial S}{\partial t} = K \left(\frac{\partial^2 S}{\partial x^2} + \frac{\partial^2 S}{\partial y^2} \right) + rS,$$

TABLE 2. Dispersal of *Opuntia imbricata* on four pastures in Texas and New Mexico. Two dispersal mechanisms are assumed for each pasture. The proportions of the two dispersal mechanisms p_1 and p_2 and diffusion coefficients D_1 and D_2 correspond to the minimum χ^2 . Indices T_1 and T_2 are estimations of the minimum number of years for plants eventually to reach 100 m from the parent plant with respect to each of the dispersal mechanisms.

Pasture	p_1	p_2	D_1	T_1	D_2	T_2	χ^2
Alpine	0.10	0.90	3.90	23.6	136.6	3.99	0.343
Amarillo	0.15	0.85	116.7	4.31	140.0	3.94	0.662
Lovington	0.10	0.90	1.37	39.8	82.3	5.14	1.87
Post	0.15	0.85	2.07	32.4	124.2	4.18	2.65

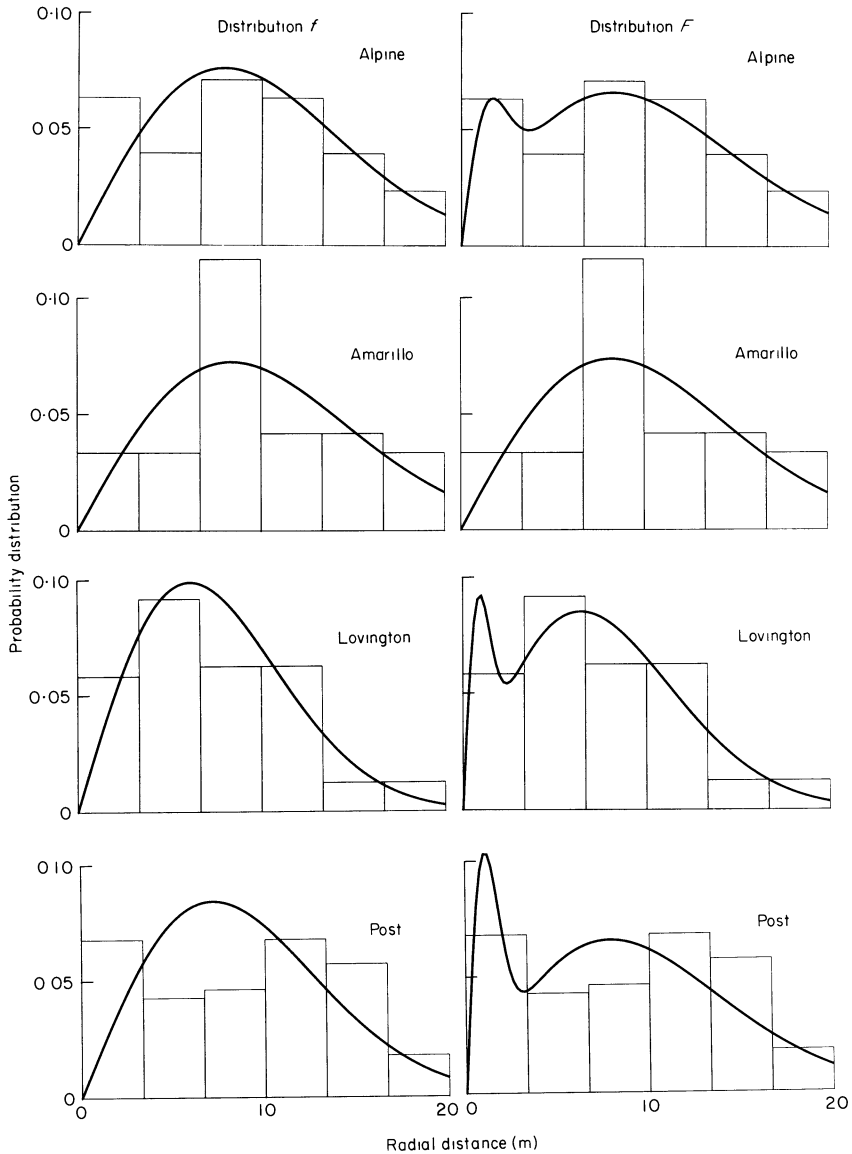


FIG. 2. Dispersal of *Opuntia imbricata* on pastures in Texas and New Mexico. Probability frequency histograms and probability distributions corresponding to one dispersal mechanism (distribution f with diffusion coefficient given in Table 1) and to two dispersal mechanisms (distribution F with proportions and diffusion coefficients given in Table 2) are given as a function of radial distance from the parent plant.

has been used to estimate the asymptotic rate of spread for invading population ($=\sqrt{4rK}$) (Mollison 1986; Andow *et al.* 1990). However, this model cannot be applied to our population data, because there is insufficient information on the history of cholla invasion within each pasture. Therefore, using model (2), the index T provides an approximate estimate for the spread of cholla within each pasture.

DISCUSSION

The result of the χ^2 -tests for Post (Tables 1 and 2) suggest that the dispersal of cholla is due to two dispersal mechanisms (distribution F , Fig. 2). Diffusion through passive dispersal (joints and fruits free-falling to the ground) locates the offspring close to the parent plant. It will take a minimum of 30 years for *O. imbricata* to spread 100 m (T_1 , Table 2) with only the passive component. Active dispersal locates the offspring further from the parent plant; it will take a minimum of 4 years for cholla to spread 100 m by active dispersal.

The ranch owner (J. Kirkpatrick, personal communication 1990) reported that the Post pasture was root-ploughed during the late 1950s, with the consequent elimination of almost all standing woody vegetation. He observed that beginning with a few plants, *O. imbricata* invaded the pasture. Based on this information, cholla attained its current density in 30–35 years, indicating that passive dispersal alone did not account for the current spread.

In the Lovington pasture, the χ^2 -test for the single dispersal mechanism (distribution f) was not as conclusive as for the Post data (Table 1). However, the management history of the pasture and landscape features support the choice of the distribution F (Fig. 2). The owner (L. Monteith, personal communication 1986) reported that *O. imbricata* was present in low densities in a small spot close to the watering point and was not a problem. The high infestation currently observed was due to overgrazing in the last 10–15 years. As in the case of Post, and given the even shorter time span, a passive dispersal mechanism alone does not explain the sudden increase in the species density (Table 2).

The significance of the χ^2 tests for the Alpine pasture was inconclusive as far as selecting the distribution (f or F) that better explains the data. The species may disperse by either one or two mechanisms. There was no information available about the previous history of the pasture or the behaviour of the cholla population to help in the decision.

The results of the χ^2 tests for the Amarillo pasture were similar to that of Alpine. Both mechanisms of dispersal locate the offspring plants approximately the same distance (Table 2) from the source. The field data show only one maximum, a unimodal distribution (Fig. 2). It is not clear, however, which mechanism was primarily responsible for the peak in the probability distribution. Unlike the other pastures, however, the Amarillo pasture has a broken topography, resulting in a mixture of range sites. The only areas available for sampling were smooth hilltops and slopes surrounding the main watering point, where cholla plants were mechanically cut off at ground level and left in the pasture, and where parent plants were not present. Although the range was in good condition, it was reported that severe overgrazing had occurred sometime in the past. The previous history of overgrazing and rough topography were assumed to be responsible for the results obtained.

As can be seen from Table 2, at least for the Post and Lovington pastures, about 10–15% of the plants disperse close to the parent plant (passive dispersal), whilst 85–90% disperse further away (active dispersal). If the dispersal mechanism responsible for the large diffusion coefficient D_2 is truly active dispersal, then it may be inferred that the sudden invasions of *O. imbricata* would not be possible without the help of livestock and wildlife grazing.

A basic assumption of our model was that dispersal of cholla can be explained

by a model based on the diffusion equation, with multiple diffusion coefficients. This appears to be a plausible assumption; however, if evidence suggests that other dispersal processes are significant, such as convection or long-range jump processes, then it is necessary to consider other model formulations (e.g. Okubo 1980; Banks, Kareiva & Zia 1988; Othmer, Dunbar & Alt 1988; van den Bosch *et al.* 1988; van den Bosch, Zadoks & Metz 1988a,b; Hengeveld 1989).

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REFERENCES

- Andow, D. A., Kareiva, P. M., Levin, S. A. & Okubo, A. (1990). Spread of invading organisms. *Landscape Ecology*, **4**, 177–188.
- Banks, H. T., Kareiva, P. M. & Zia, L. (1988). Analyzing field studies of insect dispersal using two-dimensional transport equations. *Environmental Entomology*, **17**, 815–820.
- van den Bosch, F., Frinking, H. D., Metz, J. A. J. & Zadoks, J. C. (1988). Focus expansion in plant disease. III. Two experimental examples. *Phytopathology*, **78**, 919–925.
- van den Bosch, F., Zadoks, J. C. & Metz, J. A. J. (1988a). Focus expansion in plant disease. I. The constant rate of focus expansion. *Phytopathology*, **78**, 54–58.
- van den Bosch, F., Zadoks, J. C. & Metz, J. A. J. (1988b). Focus expansion in plant disease. II. Realistic parameter-sparse models. *Phytopathology*, **78**, 59–64.
- Brown, A. L. (1950). Shrub invasion of southern Arizona desert grassland. *Journal of Range Management*, **38**, 172–177.
- Dudewicz, E. J. & Mishra, S. N. (1988). *Modern Mathematical Statistics*. Wiley-Interscience, New York.
- Edelstein-Keshet, L. (1988). *Mathematical Models in Biology*. Random House, New York.
- Friedman, J. & Orshan, G. (1975). The distribution, emergence and survival of seedlings of *Artemisia herba-alba* Asso in the Negev desert of Israel in relation to distance from the adult plants. *Journal of Ecology*, **63**, 627–632.
- Glendening, G. (1952). Some quantitative data on the increases of mesquite and cactus on a desert grassland range in southern Arizona. *Ecology*, **33**, 319–328.
- Harper, J. L. (1977). *Population Biology of Plants*. Academic Press, London.
- Hengeveld, R. (1988). Mechanisms of biological invasions. *Journal of Biogeography*, **15**, 819–828.
- Hengeveld, R. (1989). *Dynamics of Biological Invasions*. Chapman and Hall, London.
- Humphrey, R. R. & Mehikoff, L. A. (1958). Vegetation changes in a southern Arizona grassland range. *Ecology*, **39**, 720–726.
- Kunst, C. R. G. (1988). *Carbohydrate trends in Opuntia imbricata (Haw.) D. C. (Cholla)*. M. S. thesis, Texas Tech University.
- Kunst, C. R. G. (1990). *Some autoecological aspects of Opuntia imbricata (Haw.) D. C. (Cholla)*. Ph. D. thesis, Texas Tech University.
- Laycock, W. A. & Mihlbacher, B. S. (1987). Ecology and management of prickly pear cactus in the Great Plains. *Integrated Pest Management On Rangeland: A Short Grass Prairie Perspective* (Ed by J. L. Capinera), pp. 81–99. Westview Press, Boulder, CO.
- Little, M. J., Parlange, J. -Y. & Bulow-Olsen, A. (1987). A simple method for measuring diffusion rates and predation of seed on the soil surface. *Journal of Ecology*, **75**, 1–8.
- Mollison, D. (1986). Modelling biological invasions: chance, explanation, prediction. *Philosophical Transactions of the Royal Society of London*, **B314**, 675–693.
- Moody, M. E. & Mack, R. N. (1988). Controlling the spread of plant invasions: the importance of nascent foci. *Journal of Applied Ecology*, **25**, 1009–1021.
- Murray, J. D. 1989. *Mathematical Biology*. Springer, Berlin.
- Okubo, A. (1980). *Diffusion and Ecological Problems: Mathematical Models*. Springer, Berlin.
- Okubo, A. & Levin, S. A. (1989). A theoretical framework for data analysis of wind dispersal of seeds and pollen. *Ecology*, **70**, 329–338.

- Othmer, H. G., Dunbar, S. R. & Alt, W. (1988). Models of dispersal in biological systems. *Journal of Mathematical Biology*, **26**, 263–298.
- Pielou, E. C. (1977). *Mathematical Ecology*. Wiley-Interscience, New York.
- Pieper, R. K., Rea, H. & Fraser, J. (1974). Ecological characteristics of walkingstick cholla. *New Mexico Agriculture Experiment Station Bulletin* **623**.
- Pringle, F., Geiger, L. & Burns, H. E. (1980). *Soil Survey of Potter Co., Texas*. Soil Conservation Service, U.S. Dept. of Agriculture, Washington, DC.
- Richardson, W. E., Grice, D. G. & Putnam, L. (1975). *Soil Survey of Garza County, Texas*. Soil Conservation Service, U.S. Dept. of Agriculture, Washington, DC.
- Skellam, J. G. (1951). Random dispersal in theoretical populations. *Biometrika*, **38**, 196–218.
- Titterton, D. M., Smith, A. F. M. & Makov, U. E. (1985). *Statistical Analysis of Finite Mixture Distributions*. John Wiley, New York.
- Turner, M. T., Cox, D., Mickelson, B. C., Roath, A. & Wilson, C. D. (1974). *Soil Survey of Lea Co., New Mexico*. Soil Conservation Service, U.S. Dept. of Agriculture, Washington, DC.
- Wetherill, G. B. (1967). *Elementary Statistical Methods*. Methuen, London.

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APPENDIX

Another way to estimate the parameters p_1 , p_2 , D_1 and D_2 in the distribution F (eqn 2) is to use the first four moments of the distribution. These moments can be expressed in terms of the parameters as follows:

$$\int_0^{\infty} F(r) dr = p_1 + p_2 = 1;$$

$$\int_0^{\infty} rF(r) dr = \frac{\sqrt{\pi}}{2} (p_1\sqrt{D_1} + p_2\sqrt{D_2}) = \frac{\sqrt{\pi}}{2} \alpha;$$

$$\int_0^{\infty} r^2 F(r) dr = p_1 D_1 + p_2 D_2 = \beta;$$

$$\int_0^{\infty} r^3 F(r) dr = \frac{3\sqrt{\pi}}{4} (p_1 D_1^{3/2} + p_2 D_2^{3/2}) = \frac{3\sqrt{\pi}}{4} \delta.$$

The approximations to the integrals in the equations above are calculated from sample data,

$$\sum_{i=1}^N \frac{r_i^k}{N r_i^k}, \quad k = 0, 1, 2, 3,$$

and used in place of the integrals to obtain four (approximate) equations with four unknowns (p_1 , p_2 , $\sqrt{D_1}$, $\sqrt{D_2}$). It can be shown, by algebraic manipulation, that $\sqrt{D_1}$ and $\sqrt{D_2}$ are the two roots of the quadratic equation:

$$(\alpha^2 - \beta)x^2 + (\delta - \alpha\beta)x + (\beta^2 - \alpha\delta) = 0.$$

The solutions are not feasible if either of the roots is negative or complex. The value of p_2 is given by

$$p_2 = \frac{\beta - D_1}{D_2 - D_1}$$

and $p_1 = 1 - p_2$. The value of p_1 or p_2 may be negative which again yields infeasible solutions.