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Fractal analysis of seed dispersal and spatial pattern in wild oats

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Abstract: This study investigates the relationship between seed dispersal and spatial pattern in a population of wild oats (*Avena fatua* L.), a common annual weed of arable fields in western Canada. Fractal analysis revealed that wild oats has an aggregated spatial pattern with statistically self-similar properties. Wild oats seed dispersal was successfully modelled using the fractal inverse power law. The estimated fractal dimension of the seed dispersal curve (D = 1.912) is strikingly similar to that of the population's spatial pattern (D = 1.881), indicating that the observed spatial pattern is characteristic of the dispersal distribution. This result suggests that the dispersal curve of a given weed species may be used to successfully predict its pattern of invasion.

Introduction

Intensively managed agricultural ecosystems are regularly and frequently disturbed. Annual disturbances such as soil tillage and fertilizer addition produce homogeneous edaphic conditions compared to the variability of natural ecosystems. Given this edaphic uniformity, one might intuitively expect invading weed species to evenly cover an arable field over time. However, numerous empirical studies have demonstrated that weed populations of intensively managed fields show highly under-dispersed (aggregated) spatial patterns (e.g., Marshall 1988, Wiles et al. 1992, Cardina et al. 1995, Johnson et al. 1995, Wallinga 1995). Such observations suggest that processes other than environmental heterogeneity determine spatial patterning in weed populations. For example, Wallinga (1995) argues that herbicide use in arable fields keeps weed populations at such low densities that "critical phenomena" (Grassberger 1983) drive the process. By adjusting the removal rate of weeds in a population model to maintain a constant density, he produced self-similar aggregated spatial patterns that mimicked well the observed pattern of the weed cleavers (*Galium aparine* L.) in a winter wheat field in the Netherlands.

Aggregated spatial patterns in weed populations may also arise naturally from the self-similar characteristics of species dispersal curves. Kenkel and Irwin (1994) simulated seed dispersal using a Lévy flight model (Mandelbrot 1983), in which dispersal distances are selected from an inverse power law probability distribution. The model produces statistically self-similar spatial patterns in which the degree of spatial aggregation is determined by the exponent of the inverse power law function. They proposed a theoretical relationship between dispersal characteristics and spatial aggregation. Specifically, species with the capacity for long-distance seed dispersal (long-tailed dispersal curves) expand by continuously establishing new colonies well beyond the original parental patches. By contrast, species that shed their seed close to the parent plant expand as a slowly advancing front. Numerous other researchers have suggested that patterns of biological invasion are a function of species dispersal curves (van der Plank 1960, Harper 1977, Shaw 1995). However, we are not aware of any empirical studies that have specifically linked the process of dispersal to the resulting spatial pattern.

The objective of this study is to examine the relationship between seed dispersal and spatial patchiness in a population of wild oats (*Avena fatua* L.), a common annual weed of arable fields in southern Manitoba. Agroecosystems are well-suited to examining this relationship; because edaphic conditions are relatively uniform, the spatial pattern of a population is not confounded by environmental heterogeneity.

Study area

Two sites in southern Manitoba were used in this study. Wild oats seed dispersal was examined at the University of Manitoba Agricultural Field Station at Carman (49°26'N, 98°09'W), while the mapped wild oats patch was located at the Glenlea Agricultural Field Station near Winnipeg (49°50'N, 97°10'W). Black chernozemic soils occur at both sites, but the soils at Glenlea contain more clay. The climate of south-east Manitoba is continental, with a mean annual temperature of 1.8°C and ranging from 19.5°C in July to –19.5°C in January. Approximately two-thirds of the 54 cm annual precipitation falls as rain from May through August (Environment Canada 1993).

Wild oats (*Avena fatua* L.)

Wild oats is an annual plant that produces flowering stems 0.6 to 1.2 m in height (Sharma and Vanden Born 1978). The species is native to Eurasia but has become a troublesome weed of grain fields throughout western Canada. It is the second most common weed in Manitoba, infesting 65% of all arable fields. Wild oats is self-pollinated, and an individual plant may produce up to 500 seeds. The seeds mature early and shatter readily, and are usually shed in late summer prior to crop harvest (Shirtliffe et al. 2000). Recently shed seeds are dormant, which allows the species to survive the winter. Seeds generally germinate the following spring, but may enter secondary dormancy if conditions are not favourable (Kropac et al. 1986). Like most graminoid weeds, the seeds of wild oats are relatively heavy (20-40 mg) and have no specific adaptations for long-distance dispersal. As a result, graminoid weeds in a grain crop rarely disperse their seed at distances greater than the height of the plant (O'Toole and Cavers 1983). Wild oats generally has a patchy (spatially underdispersed) spatial distribution in cultivated fields (e.g., Thornton et al. 1990). The spatial dispersion of plants within a single patch has not been previously investigated, however.

Materials and methods

Seed dispersal

At the Carman site, six experimental plots were sown in 1996 to spring wheat (*Triticum aestivum* L. cv. Katepawa) at 75 kg ha^{-1}, resulting in an emerged density of 100 plants m^{-2}. The wheat crop averaged 1.1 m in height at maturity. In addition, a short row of wild oats was hand-seeded into each plot. Following emergence, a single plant of wild oats was randomly selected from each plot to study seed dispersal, and the other plants terminated. At maturity, the six wild oats plants ranged from 1.2 to 1.4 m in height. Thirty-six seed traps were arranged around each wild oats plant in a hexagonal grid to produce three concentric rings or distance classes:

Distance class	Mean (Range) Distance (m)	No. seed traps per plant
1	0.68 (0.5 - 0.9)	10
2	1.06 (1.0 – 1.12)	8
3	1.49 (1.35 to 1.68)	18

The seed traps were 15 cm diameter petri dishes containing filter paper sprayed with Tanglefoot (Tanglefoot Co., Grand Rapids, Michigan) to ensure seeds adherence in the traps. Six small holes were drilled around the periphery of each petri dish to allow for drainage of rainwater. Seeds were collected from the traps on a regular basis from seed shed initiation to termination.

For analytical purposes, data from the six plants were pooled. A weighted mean dispersal distance was computed for each of the three distance classes. Total capture area (the sum petri dish area for each distance class) was determined and expressed as a proportion of the total area of each distance class. The number of seeds captured within each distance class was then divided by the proportion of capture area to obtain an estimate of the expected number of seeds shed in each distance class. These data were used to model seed dispersal in wild oats using the inverse power law:

$$Y = \alpha\, S^{-(D+1)}$$

where Y is the expected number of seeds shed in a distance class, S is the weighted mean dispersal distance, α is a constant, and D is the fractal dimension of the dispersal curve (Kenkel and Irwin 1994). Plotting log Y against log S linearizes the inverse power law and so provides an estimate of the fractal dimension of the wild oats dispersal curve.

Spatial pattern

A wild oats patch located within a large experimental plot sown to wheat was mapped in 1997. The plot is part of a crop rotation experiment initiated in 1992, and had a rotation of wheat, pea, flax, wheat and flax. The experimental area receives inorganic fertilizer, but herbicides have not been applied since the experiment was initiated. Beginning in 1994, the crops were harvested with a New

Holland conventional combine and the chaff collected using a Redekop chaff collection system.

The wild oats patch was first noted in 1994, and has been expanding since. A 10 x 10 m plot was randomly positioned within the patch and divided into one hundred 1 x 1 m grid units. Each grid unit was in turn divided into sixteen squares, and the spatial coordinates of wild oats plants in each square were carefully mapped. A total of 6896 individual plants were enumerated in this way.

A fractal analysis of the wild oats spatial pattern was undertaken using the box counting method to estimate the fractal dimension D (Hastings and Sugihara 1993). In box counting, a δ covering of the point pattern is obtained by centering a square box of side length δ on each point, and counting the number of boxes N_δ required to cover the pattern. This procedure is repeated for various integer multiples of δ. A simpler approach involves superimposing a grid of non-overlapping boxes on the pattern, and counting the number of boxes occupied. In this study, we began with a 60 x 60 grid of boxes (δ = 1, or box size of 16.7 x 16.7 cm) and sequentially combined adjacent boxes to obtain counts at δ = 1, 2, 3, 4, 5 and 6. The fractal dimension of the pattern is given by the limit:

$$D = -\lim_{\delta \to 0} [\log N_\delta \,/\, \log \delta]$$

where N_δ is the number of boxes of side length δ containing at least one point (Appleby 1996). In practical applications the defining power law relationship is:

$$N_\delta \propto \delta^{-D}$$

The point pattern is statistically self-similar if the log-log plot is linear over a specified range of δ values. The negative gradient of the fitted line is the fractal dimension.

The fractal dimension describes the space-filling properties of a point pattern (Mandelbrot 1983). A random point pattern is completely space-filling since all regions of the plane have an equal chance of being occupied, giving $D = 2$. Values of $D < 2$ imply some degree of self-similar spatial aggregation, with smaller values of D indicating greater aggregation (less space-filling). The fractal dimension is thus interpretable as a scale-invariant measure of the degree of spatial aggregation.

The method described above determines the cluster dimension (Hastings and Sugihara 1993: 44). In computing the cluster dimension, the number of occupied boxes is counted but the frequency distribution of point counts within occupied boxes is not considered. By considering the frequency distribution of point counts, a continuum of q dimensions is defined that more fully characterizes a fractal pattern. Specifically, the number of points n_i in each of N_δ occupied boxes is determined and expressed as proportions of the sample size n ($p_i = n_i/n$). These proportions are used to determine the generalized entropy (Rényi 1970), expressed as:

$$I_q(\delta) = 1/(1-q) \log \sum_{i=1}^{N_\delta} p_i^q$$

The generalized entropy defines a continuum of functions referenced by the parameter q. The generalized dimension D_q for the qth fractal moment is given by the limit:

$$D_q = -\lim_{\delta \to 0} [I_q(\delta) \,/\, \log \delta]$$

The plot of generalized entropy $I_q(\delta)$ against log δ is used to estimate D_q (Hentschel and Procaccia 1983). By varying q an entire family of generalized dimensions is obtained, the most common of which are:

q	$I_q(\delta)$	Dimension
0	$\log N_\delta$	cluster
1	$-\sum p_i \log p_i$	information
2	$-\log \sum p_i^2$	correlation

When estimating the fractal dimension of a finite number of points n, the log-log plot will necessarily deviate from linear at small values of δ, since N_δ approaches n as δ decreases. Indeed, the maximum number of occupied boxes is $N_\delta = n$, and is thus independent of δ when fine-scaled grids are used (Hagen et al. 2001). Failure to recognize this problem will result in under-estimation of the fractal dimension of the original pattern (Hall 1995). We therefore followed Hall's (1995) recommendation and used a relatively coarse-scaled grid to estimate D.

A statistically random spatial pattern has a theoretical fractal dimension $D = 2$, but this value is only achieved as n approaches infinity (Hagen et al. 2001). The smaller the sample size n, the greater the deviation from a theoretical $D = 2$. An empirically determined D value should therefore be compared against values obtained from random simulations of the same sample size, to determine whether the observed pattern deviates significantly from random (Hastings and Sugihara 1993: 106). We generated 100 random point patterns at $n = 6896$ to determine expected random D values. An observed pattern is deemed to be significantly different from random if its fractal dimension D is less than the smallest D value from the100 random simulations.

Results

Seed dispersal

A total of 159 seeds (mean = 26.5 seeds per plant) were captured by the 216 seed traps. Of these, 105 (66%) occurred in the first distance class (< 90 cm), 40 (25%) in the second distance class (90 – 125 cm), and only 14 (9%) in the third distance class (125 to 175 cm). These results indicate that long-distance dispersal in wild oats is very infrequent. In fact, no seeds were recovered from the 24 traps placed at a distance of 168 cm. The vast majority of seeds were shed within 120 cm of the plant, which corresponds closely to the mean plant height. A simple inverse power law model fit the seed dispersal data very well (R^2 = 96.4%; Figure 1). The data suggest that each plant produces approximately 400 seeds. The slope of the plot gives a fractal dimension for dispersal of $D = 1.912$, indicating that long-distance dispersal events are very rare (Kenkel and Irwin 1994).

Spatial pattern

The mapped wild oat patch produced a linear $I_1(\delta)$ vs. ln (δ) plot, indicating that its spatial pattern is statistically self-similar (Figure 2). Statistical self-similarity implies that the degree of aggregation is invariant across spatial scales. Over the complete range of box sizes (δ = 1 to 6), the estimated information dimension $D_1 = 1.812$ (R^2 = 99.8%). However, careful examination of the plot reveals non-linearity at the two smallest grid sizes. Following Hall (1995), we removed the smaller grid sizes (δ = 1 and 2) and recalculated the regression. The resulting plot is almost perfectly linear (R^2 = 100%, inset of Figure 2), increasing the estimated information dimension to D_1 = 1.881. Estimates of generalized fractal dimensions D_q from q = 0 to 3 (in increments of 0.5, again with the two smallest grid sizes excluded) are summarized in Table 1.

Table 1. Fractal dimension as a function of I_q. Estimates of fractal dimension D_q were obtained from the slope of I_q vs. ln(box size) plots, using the four largest box sizes (range 50 to 100 cm). R^2 = 100% for all regressions.

q	D_q
0.0	1.807
0.5	1.866
1.0	1.881
1.5	1.871
2.0	1.851
2.5	1.826
3.0	1.794

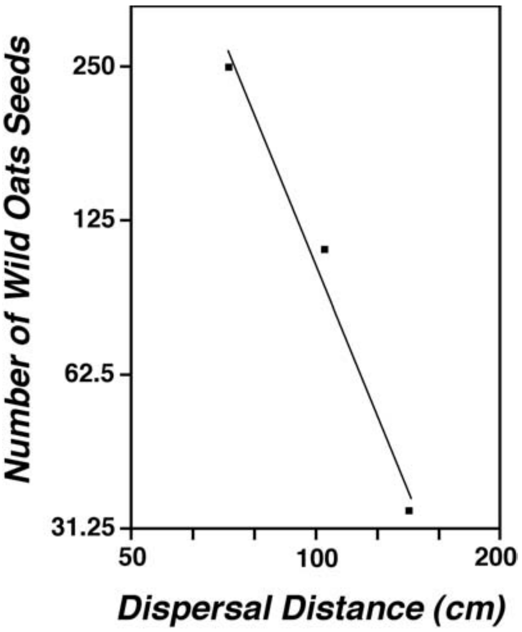

Figure 1. Seed dispersal of wild oats fitted to the inverse power law (R^2 = 96.4%, P < 0.001). The slope of the fitted regression line is –2.912, giving a fractal dimension D = 1.912.

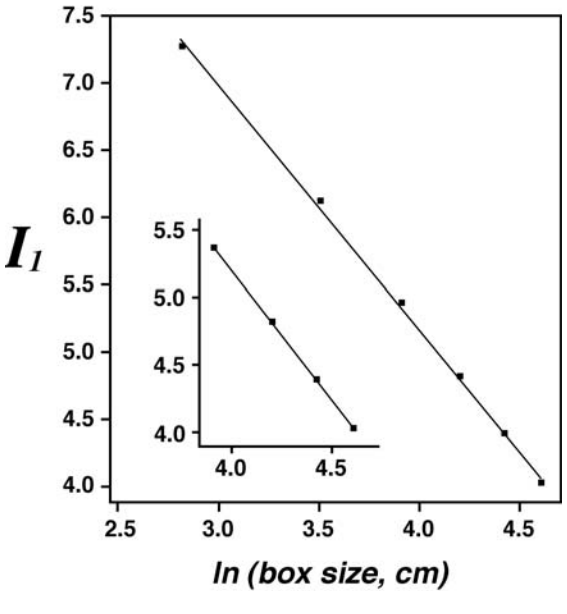

Figure 2. Power law relationship between $I_1 = - \Sigma p_i \log p_i$ and box size δ. In the main graph δ ranges from 1 (16.7 cm) to 6 (100 cm); the estimated information dimension D_1 = 1.812 (R^2 = 99.8%, P < 0.001). The inset graph shows the same data over the range δ = 3 to 6; the estimated information dimension D_1 = 1.881 (R^2 = 100%, P < 0.001).

The detection of spatial aggregation is greatest at $q = 0$ ($D_0 = 1.807$) and $q = 3$ ($D_3 = 1.794$), and lowest at $q = 1$ ($D_1 = 1.881$). In theory, D_q should decline monotonically with increasing q (Schroeder 1991: 222). Our results, which indicate a non-monotonic relationship, are likely attributable to sampling error (finite sample size).

Estimated fractal information dimensions for the 100 simulated random point patterns ($n = 6896$) averaged $D_1 = 1.992$; the lowest value was $D_1 = 1.983$. The spatial pattern of the wild oats patch is therefore significantly underdispersed, since the observed $D_1 = 1.881 < 1.983$. Note, however, that the theoretical range of the fractal dimension is from $D = 1$ (highly aggregated) to $D = 2$ (statistically random). The observed value of $D_1 = 1.881$ therefore suggests that the degree of spatial aggregation is not particularly strong.

Discussion

Our study demonstrates that wild oats has a spatially aggregated pattern with self-similar properties. Furthermore, wild oats seed dispersal is successfully modelled by the inverse power law. The estimated fractal dimension of the dispersal curve ($D = 1.912$) is very near that of the population's spatial pattern ($D = 1.881$), indicating that the observed spatial pattern is characteristic of the dispersal distribution (Shaw 1995). This is an important finding, as it suggests that the dispersal curve of a given weed species may be used to successfully predict its pattern of invasion. This finding is in keeping with Kenkel and Irwin's (1994) proposed functional relationship between dispersal characteristics and the observed degree of spatial aggregation (see also Shaw 1995, Wallinga 1995).

Kenkel and Irwin (1994) showed that by varying species dispersal characteristics (the power law exponent) different degrees of spatial aggregation are produced. Their Lévy flight inverse power law model predicts that species with limited capacity for long-distance dispersal ($D =2$) will be randomly distributed. Values of $D < 2$ produce spatially aggregated patterns; the greater the capacity for long-distance dispersal (lesser values of D), the higher the degree of spatial aggregation at all scales. In general, dispersal models that consider long-distance dispersal (so-called "fat-tailed" curves), such as the inverse power law, result in spread rates that accelerate with time (Kot et al. 1996). Shaw (1995) demonstrated that dispersal curves with exponential tails (log-linear distributions) result in models of species invasion as an expanding front. The negative exponential probability distribution assumes that long-distance dispersal events are "completely negligible", so that all moments of the dispersal distribution are defined (Shaw 1995). By contrast, dispersal curves that decline at less than an exponential rate (log-log distributions, including the power law, Cauchy and Pareto) have infinite first and higher moments, and are therefore dimensionless and scale-free (Okubo and Levin 1989). Models based on non-exponential dispersal curves produce invasion patterns characterized by the continuous formation of new daughter patches (Minougue 1987, Mollison 1986, Kot et al. 1996). Such models result in what appear to be more "natural" dispersal patterns (Shaw 1995). The greater realism of non-exponential models is supported by pollen evidence from the late Pleistocene, which demonstrates that tree species with "fat-tailed" dispersal curves underwent very rapid post-glacial spread even though their mean dispersal distances are short (Clark 1998).

It is noteworthy that the empirical pattern of wild oats proved to be statistically self-similar. Wallinga (1995) demonstrated statistical self-similarity in cleavers (*Galium aparine* L.), an annual weed of cultivated crops in Europe. However, the degree of spatial aggregation in cleavers was much greater ($D = 1.51$, vs. $D = 1.88$ in wild oats). Unlike wild oats, cleavers has small barbs on the seeds and foliage that assist in long-distance dispersal (Malik and Vanden Born 1988). The lower fractal dimension (greater degree of spatial aggregation) in cleavers is entirely consistent with its increased capacity for long-distance dispersal (Kenkel and Irwin 1994). By contrast, wild oats seeds are comparatively heavy and have no special adaptations to assist in their natural dispersal. While wild oats seeds are dispersed at various distances from the parent plant, the vast majority fall only a short distance away. As a result, new daughter patches are very rarely formed and the degree of spatial aggregation is therefore low (higher D). By contrast, greater capacity for long-distance dispersal in cleavers increases the likelihood of new daughter patches establishing at some distance from their parents, thereby increasing the degree of spatial aggregation (lower D).

Under uniform environmental conditions, a close relationship is expected between weed dispersal and spatial pattern (Kenkel and Irwin 1994, Shaw 1995). However, in practice the spatial pattern of a weed population may be affected by other factors such as edaphic and micro-environmental variation, interspecific competition, combine harvesting, and soil tillage. In this study, the striking similarity between the fractal dimensions of dispersal and spatial pattern suggests that natural seed dispersal is of overwhelming importance in determining wild oats spatial pattern. While seed germination and establishment of weeds may be affected by natural edaphic variability (Andreasen et al. 1991), repeated soil tillage of intensively managed fields produces highly uniform edaphic conditions (Wallinga 1995). Interspecific competition can also affect the spatial distribution of weeds (Lehman and Tilman 1997, Bergelson 1996), but in most crop monocultures the intensity of competition is probably spatially invariant. Mechanical transport of weed seeds during combine harvesting may be an important vector of dispersal (McCanny and Cavers 1988, Cousens and Mortimer 1995). However, in this study chaff collection was performed, and virtually all wild oats seeds present at harvest were removed with the chaff (Shirtliffe 1999). Furthermore, most wild oats seeds are naturally shed prior to crop harvest (Shirtliffe et al. 2000). Soil tillage equipment may disperse weed seeds over short distances (< 1 m, see Rew and Cussans 1997) and may therefore reduce spatial aggregation at scales comparable to the mean dispersal distance of wild oat seeds.

While a self-similar spatial pattern in wild oats was detected over the spatial scales assessed, the 10 x 10 m plot used in our study was far too small to permit examination of interpatch spatial relationships over the entire cropped field. Empirical observations suggest that wild oats has a spatially aggregated distribution in cultivated fields (e.g., Thornton et al. 1990), but whether the spatial pattern is statistically self-similar at these larger scales remains to be demonstrated. Further research should be directed toward determining the specific mechanisms by which weed spatial patterns develop in arable fields. Investigation of the invasion dynamics of weed species under controlled experimental conditions (no initial seed bank, homogeneous substrate, no interspecific competition) would be particularly useful in determining the link between seed dispersal and spatial aggregation.

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References

Andreasen, C., J.C. Streibig and H. Hass. 1991. Soil properties affecting the distribution of 37 weed species in Danish fields. *Weed Res.* 31: 181-187.

Appleby, S. 1996. Multifractal characterization of the distribution pattern of the human population. *Geogr. Anal.* 28: 147-160.

Bergelson, J. 1996. Competition between two weeds. *Biosci.* 84: 579-584.

Cardina, J., D.H. Sparrow and E. L. McCoy. 1995. Analysis of spatial distribution or common lambsquarters (*Chenopodium album*) in No-Till Soybean (*Glycine max*). *Weed Sci.* 43: 258-268.

Clark, J.S. 1998. Why trees migrate so fast: confronting theory with dispersal biology and the paleorecord. *Am. Nat.* 152: 204-224.

Cousens, R. and M. Mortimer. 1995. *Dynamics of Weed Populations.* Cambridge University Press, Cambridge.

Environment Canada. 1993. *Canadian Climate Normals: 1961-1990. Vol. 2. Prairie Provinces.* Environment Canada, Ottawa.

Grassberger, P. 1983. On the critical behaviour of the general epidemic process and dynamic percolation. *Math. Biosci.* 63: 157-162.

Hagen, C.A., N.C. Kenkel, D.J. Walker, R.K. Baydack and C.E. Braun. 2001. Fractal-based spatial analysis of radiotelemetry data. In: J.J. Millspaugh and J.M. Marzluff (eds.), *Radio Tracking and Animal Populations.* Academic Press, San Diego. pp. 167-187.

Hall, P. 1995. On the effect of measuring a self-similar process. *SIAM J. Appl. Math.* 55: 800-808.

Harper, J.L. 1977. *The Population Biology of Plants.* Academic Press, London.

Hastings, H.M. and G. Sugihara. 1993. *Fractals: A User's Guide for the Natural Sciences.* Oxford University Press. Oxford.

Hentschel, H.G.E. and I. Procaccia.1983. The infinite number of generalized dimensions of fractals and strange attractors. *Physica 8D*: 435-444.

Johnson, G.A., D.A. Mortensen and A.R. Martin. 1995. A simulation of herbicide use based on weed spatial distribution. *Weed Res.* 35: 197-205.

Kenkel, N.C. and A.J. Irwin. 1994. Fractal analysis of dispersal. *Abst. Bot.* 18: 79-84.

Kot, M., M.A. Lewis and P. van den Driessche. 1996. Dispersal data and the spread of invading organisms. *Ecology* 77: 2027-2042.

Kropac, Z., T. Havranek and J. Dobry. 1986. Effect of duration and depth of burial on seed survival of *Avena fatua* in arable soil. *Folia Geobot. Phytotax.* 21: 249-262.

Lehman, L. and D. Tilman. 1997. Competition in spatial habitats. In: D. Tilman and P. Kareiva (eds.), *Spatial Ecology*. Princeton Univ. Press, Princeton. pp. 185-203.

Malik, N and W.H. Vanden Born. 1988. The biology of Canadian weeds. 86. *Galium aperine L.* and *Galium spurium* L. *Can. J. Plant Sci.* 68: 481-499.

Mandelbrot, B.B. 1983. *The Fractal Geometry of Nature.* W.H. Freeman, New York.

Marshall, E.J.P. 1988. Field scale estimates of grass weed populations in arable land. *Weed Res.* 28: 191-198.

McCanny, S.J. and P.B. Cavers. 1988. Spread of proso millet (*Panicum miliaceum* L.) in Ontario, Canada. II. Dispersal by combines. *Weed Res.* 28: 67-72.

Minogue, K. P. 1987. Disease gradients and the spread of disease. In: K.J. Leonard and W. E. Fry (eds.), *Plant Disease Epidemiology Vol. 1: Population Dynamics and Management.* Mcmillan, New York. pp. 285-310.

Mollison, D. 1986. Modelling biological invasions: chance, explanation, prediction. *Phil. Trans. R. Soc. Lond. B* 314: 675-693.

Okubo, A. and S.A. Levin. 1989. A theoretical framework for data analysis of wind dispersal of seeds and pollen. *Ecology* 70: 329-338.

O'Toole, J.J. and P.B. Cavers. 1983. Input to seed banks of proso millet (*Panicum miliaceum*) in southern Ontario. *Can. J. Plant Sci.* 63: 1023-1030.

Rényi, A. 1970. *Probability Theory*. North-Holland, Amsterdam.

Rew, L.J. and G.W. Cussans. 1997. Horizontal movement of seeds following tine and plough cultivation: implications for spatial dynamics of weed infestations. *Weed Res.* 37: 247-256.

Schroeder, M. 1991. *Fractals, Chaos, Power Laws: Minutes from an Infinite Paradise*. W.H. Freeman, New York.

Sharma, M.P. and W.H. Vanden Born. 1978. The biology of Canadian weeds. 27. *Avena fatua* L. *Can. J. Plant Sci.* 58: 141-157.

Shaw, M.W. 1995. Simulation of population expansion and spatial pattern when individual dispersal distributions do not decline exponentially with distance. *Proc. Royal Soc. London Series B* 259: 253-248.

Shirtliffe, S.J. 1999. The effect of chaff collection on the combine harvester dispersal of wild oat (*Avena fatua* L.). Doctorate of Philosophy Dissertation, University of Manitoba.

Shirtliffe, S.J., M.H. Entz and R.D. Van Acker. 2000. The development and seed shatter of *Avena fatua*. *Weed Sci.* 48: 555-560.

Thornton, P.K., R.H. Fawcett, J.B. Dent and T.J. Perkins. 1990. Spatial weed distribution and economic thresholds for weed control. *Crop Prot.* 9: 337-342.

Van der Plank, J.E. 1960. Analysis of epidemics. In: J. G. Horsfall and A.E. Dimond (eds.), *Plant Pathology, Vol 3*. Academic Press, New York. pp. 229-289.

Wallinga, J. 1995. The role of space in plant population dynamics: annual weeds as an example. *Oikos* 74: 377-383.

Wiles, L.J., G.W. Olive, A.C. York, H.J. Gold and G.G. Wilkerson. 1992. Spatial distribution of broadleaf weeds in North Carolina soybean (*Glycine max*) fields. *Weed Sci.* 40: 554-557.