

# Anthropogenic forcing on the spatial dynamics of an agricultural weed: the case of the common sunflower

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## Summary

1. Establishment and spread are central in weed invasion. In this study we quantified the impact of harvest and weed management practices on these processes in row-crop agriculture. Quantifying the dynamics of patch expansion can direct management aimed at containment of weed populations.
2. We assessed annual patterns of common sunflower *Helianthus annuus* seedling recruitment to determine the influence of management on seed dispersal and patch expansion. Weed seed banks were sowed at three initial densities and exposed to either high or low intensity weed management. Fields were maintained in a maize–soybean crop rotation, with cultivation and harvest orientated in a single direction. We analysed spatial pattern in annual seedling recruitment using geostatistics and an integro-difference model to determine treatment effects on spatial dynamics.
3. The two spatial analyses allowed us to separate and quantify the contributions of natural and anthropogenic dispersal to seedling emergence and patch expansion. Expansion was predominantly isotropic, and estimated rates of isotropic spread (i.e. diffusion) were consistent between analysis methods.
4. We also confirmed that directional management practices can effect significant anisotropy on dispersal and expansion. Crop rotation had the greatest impact on expansion; anisotropy in patch expansion was more pronounced in maize compared with soybean. However, the scale of weed seed dispersal by machine (combine harvester) was greater following harvest of soybean. Simulation of patch dynamics indicated that harvest can increase expansion rate nearly fourfold.
5. *Synthesis and applications.* Patches of *H. annuus* originating from intermediate and high seed bank densities had the potential to spread rapidly from the source population. Patches with a low initial seed bank experienced extinction when subjected to high levels of chemical weed management. The combined approach of spatial modelling and geostatistics was particularly effective for quantifying admixed modes of dispersal from sequential data of population distribution. Independence of the two methods provided a system for cross-validating model assumptions and estimated parameters. The scales of spatial dynamics we assessed were well suited to these methods. The results of the analysis underscore the importance of managing populations in order to keep local populations at low densities. *Helianthus annuus* is difficult to manage and once intermediate or high local densities are reached, the rate of spread is accelerated, distributing this weed widely across fields. A targeted site-specific approach to maintaining populations at low levels would reduce the necessity for more costly field-wide management.

*Key-words:* anisotropy, cross-correlation, geostatistics, integro-difference, seed dispersal, weed management

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## Introduction

The within-field spread of weeds depends on the dispersal characteristics of seeds and the subsequent site-dependent success of emergence and growth. Within agricultural fields, weed spread and establishment result from the interaction between the innate dynamics of the weed, as determined by its spatial life-history characteristics and density-dependent survival/growth of seedlings, and the anthropogenic vectoring and facilitation/inhibition that result from management. Emergence and growth are dictated by underlying spatial heterogeneities in environmental characteristics (e.g. local nitrogen and potassium availability; Dieleman *et al.* 2000), imposed disturbance regimes (e.g. tillage; Rew & Cussans 1997), and herbicide application (Mortensen & Dieleman 1998). Seed dispersal is likewise a combined function of natural and management-related process (Cousens & Mortimer 1995). When seed set coincides with crop harvest, mechanical vectoring may dominate dispersal. The influence of cultivation and harvest on horizontal movement of the seed bank has been assessed in various agricultural settings using direct observation and simulation models (Ballaré *et al.* 1987a,b; Howard *et al.* 1991; Rew, Froud-Williams & Boatman 1996; Rew & Cussans 1997; Paice *et al.* 1998; Woolcock & Cousens 2000; Gonzáles-Andújar, Plant & Fernández-Quintanilla 2001). Most studies conclude that redistribution of the seed bank following cultivation is generally of the order of  $\leq 1$  m (Rew & Cussans 1997). Dispersal of weed seed during mechanical harvest (combine harvester) has been found to be more significant, although the exact shape of the resultant 'dispersal kernel' varies (Woolcock & Cousens 2000). Few studies have quantified the influence of mechanical practices on rates of patch spread, although Woolcock & Cousens (2000) demonstrated through simulation that combine-aided seed dispersal can increase rate of spread by an order of magnitude.

Seed dispersal is an integral process in weed patch expansion, but realization of the dispersal kernel is the combination of dispersal and establishment. The transition from 'seed kernel' to 'seedling kernel' is therefore filtered by habitat suitability, density-dependent self-thinning during emergence and management intended for weed control. Patch expansion, then, is a function of dispersal and reproductive success.

We used common sunflower *Helianthus annuus* L. as our study species to quantify its dispersal kernel and the role anthropogenic vectoring plays in weed patch expansion. This species was chosen for several reasons. First, it is an important summer annual weed of crops. Secondly, a body of knowledge regarding life-history transitions and density-dependent mortality has developed over the past decade (Dieleman, Mortensen & Martin 1999; Burton *et al.* 2004; Humston, Mortensen & Wyse-Pester, in press). Finally, because

this species drives management decisions in western maize production, its spread within and between fields is of great practical concern.

Our statistical analysis had two facets. First, we quantified the degree of anisotropy in seed dispersal relative to the direction of management. This provided a direct test for whether anthropogenic vectoring is a significant force in the weed patch expansion. Secondly, we studied the consequences of such vectoring on the rate of weed-patch expansion. In order to pursue these interrelated topics we used two complementary sets of statistical methods. We first used an anisotropic geostatistical analysis to test for anisotropy. Secondly, we developed a stochastic integro-difference model (Kot & Schaffer 1986; Kot, Lewis & van den Driessche 1996; Latore, Gould & Mortimer 1998), incorporating both innate and anthropogenic dispersal, to make predictions about rate of spread. We estimated the parameters in this model from successive snapshots of weed distribution and abundance using maximum likelihood.

## Materials and methods

### THE SPECIES: *HELIANTHUS ANNUUS*

The common sunflower, *Helianthus annuus* (Asteraceae) is a native annual of North America and is widespread across the high plains and mid-western region of the continent. It is considered one of the most competitive broadleaf weeds of maize (Bauer *et al.* 1991) and has a moderately persistent seed bank (5–10 years). Common sunflower seeds are large, measuring 7–12 mm in length, and buoyant (Burton 2000; Burton *et al.* 2004). In level fields like those in this study (and representative of those in the region), distribution of shed seeds is largely driven by natural dispersal, dispersal facilitated by the combine harvester, and post-dispersal redistribution aided by anthropogenic activities including soil tillage. The degree to which seed is dispersed by combine harvester is determined largely by time of seed shed relative to time of harvest. In early harvested crops such as soybean, a greater proportion of seed may be dispersed by the combine harvester than in a later harvested crop such as maize.

Common sunflower establishment is influenced by soil heterogeneity (Dieleman *et al.* 2000), with plant fitness greatest in low lying moist sites. However, the dominant force governing the probability of transition from seed to seedling is management practices aimed at weed control. Cultivation performed prior to crop planting results in high mortality of early cohorts. Many herbicides have only marginal activity on common sunflower; the low efficacy is further reduced at high common sunflower densities, where plants effectively 'compete' for the herbicide (Dieleman, Mortensen & Martin 1999). As seedlings grow to a larger size, inter- and intraspecific thinning may also limit plant success (Teo-Sherrel 1996).

## FIELD METHODS

Common sunflower seed banks were introduced in a field known to be free of that species. During the patch initiation phase (1994, year 0) seed banks of common sunflower were established by sowing 250, 1250 or 2500 seeds (seeds per 1.3 m<sup>2</sup>) in a 0.61 × 2.13-m area, with a common sunflower seed-free buffer of 9.9 × 15.8 m surrounding each seed bank. Patch growth was monitored in 1994 (year 0), 1995, 1996 and 1997 by characterizing seedling density within each of 3750.46-m<sup>2</sup> cells in the 9.9 × 15.8-m plot. Seedlings were censused approximately 30 days after the crop was planted (between late May and mid-June) and all other weed species were removed by hand. During the sampling period all tillage and harvest practices were orientated in a single direction so that seed movement as a result of mechanical redistribution was unidirectional. All fields were tilled or harvested on the same day regardless of crop species cultivated. Common sunflower density was determined 2–4 days before the post-emergence herbicide application and 1 week after inter-row cultivation.

Common sunflower densities were replicated four times within each weed management treatment. The experiment was conducted in a maize–soybean rotation, where each phase of the rotation was represented in each year; seed banks were established in both maize and soybean crops in year 0. Data from the first 3 years of the experiment are presented. Experiments were conducted at the Agricultural Research and Development Center near Mead, Nebraska, located 60 km north of Lincoln, Nebraska, USA, in a Sharpsburg silty clay loam soil (fine, montmorillonitic, mesic Typic Arguidolls). In addition to the range in seed bank densities, the experiment included two weed management intensities: (i) high herbicide, intended to overcome the effect of reduced efficacy under high weed densities; and (ii) low herbicide, where *per capita* mortality was likely to be reduced at high weed densities because of herbicide shading. For a detailed discussion of the treatments and experimental design see Dieleman, Mortensen & Martin (1999).

## STATISTICAL ANALYSES

The statistical analyses were applied separately to the replicates of the different treatment factors (crop type, herbicide rate and initial seed density) and the different years. We generally present the results as averages over the replicates of the same treatment. We denote the three annual surveys as T<sub>0</sub>, T<sub>1</sub> and T<sub>2</sub> and use this notation to indicate sampling periods in which annual spatial seedling density data were collected. Dispersal and recruitment processes occurred in the intervals between the annual samplings; we denote the two annual transitions as Tr1 (i.e. T<sub>0</sub>–T<sub>1</sub>) and Tr2 (i.e. T<sub>1</sub>–T<sub>2</sub>) when describing patch dynamics.

## GEOSTATISTICS

The spatial correlogram (or related methods) is a common way to describe spatial patterns in plant ecology (Donald 1994; Legendre & Legendre 1998; Jurado-Expósito *et al.* 2004). When applied to quadrat-count data, this method quantifies how correlation in abundance is a function of the distance separating different quadrats. Weed patches have high correlations over small distances that decay to zero at the distance representing the extent of the patch (Legendre & Legendre 1998). Cross-correlograms can be used to quantify changes in patch extent and location over time, i.e. patch expansion or patch movement. This is done by correlating the abundances in 1 year with the abundances in the next year (again as a function of the distance). Because the cross-correlation is derived from maps from different years, these are sometimes called time-lagged cross-correlograms (Bjørnstad *et al.* 2002). For expanding patches, the between-year cross-correlograms will extend further out than the within-year standard correlograms. For moving patches, peak correlation in the cross-correlograms will be offset from zero distance. The distance of offset is linked to the speed of patch movement (Bjørnstad *et al.* 2002).

To study directional bias in weed patch spread, we can examine directional (anisotropic) correlograms (Oden & Sokal 1986). If spread is directional, cross-correlation will extend further out in the associated directions. To study the influence of the directionally orientated management practices on weed seedling distribution, we used anisotropic cross-correlograms in 9 cardinal directions (0°, 22.5°, 45°, 67.5°, 90°, 112.5°, 135°, 157.5° and 180°). Here 0° corresponds with the direction of harvest and cultivation. If anthropogenic vectoring by weed seeds is important, we expect the cross-correlation to extend furthest in the 0° direction (parallel to cultivation).

We used spline (cross-)correlograms in both directional and non-directional calculations. All correlograms were estimated using 19 d.f., using the NCF package (available from the authors at <http://onb.ent.psu.edu>) for R software (available at [www.R-project.org](http://www.R-project.org)). For further technical details on the methods see Bjørnstad & Bascompte (2001), Bjørnstad & Falck (2001) and Bjørnstad *et al.* (2002).

## A SPATIAL MODEL

We denote the number of weed plants in quadrat *i* at location (*x<sub>i</sub>*, *y<sub>i</sub>*), in year *t*, by *N<sub>i,t</sub>*. In year T<sub>0</sub>, those plants arose from the experimental seeding in target quadrats (see Field Methods). However, in the succeeding years (years T<sub>1</sub> and T<sub>2</sub>), the weeds arose from seed production and seed dispersal by individuals in the previous year. If the *per capita* reproductive rate is *r*, then the number of seeds produced in the preceding year by weeds in quadrat *i* would be *rN<sub>i,t-1</sub>*.

If we assume that natural seed dispersal is equally likely in all directions, then the probability that a seed

**Table 1.** Definitions of letters and symbols used in text

Symbol	Definition
$T_0$	Initial year of experiment, during which weed seed banks were artificially established and weed emergence quantified
$T_1$	Second year of experiment and census of weed patches
$T_2$	Third year of experiment and census of weed patches
Tr1	First annual transition, between patch censuses in $T_0$ and $T_1$
Tr2	Second annual transition, between patch censuses in $T_1$ and $T_2$
$N$	Weed density
$r$	<i>Per capita</i> annual increase in weed density
$\rho_{ij}$	Distance between two quadrats $i$ and $j$
$\theta_{ij}$	Angle of separation between two quadrats $i$ and $j$ relative to direction of management [= $\tan^{-1}(y_j - y_i)/(x_j - x_i)$ ]
$\kappa$	Admixed dispersal kernel as a function of $\rho$ and $\theta$
$H$	Anthropogenic (advected) dispersal kernel function
$K$	Natural (non-directional) dispersal kernel function
$P$	Relative contribution of natural vs. anthropogenic dispersal in the admixed kernel $\kappa$
$\lambda_i$	Expected number of recruits in quadrat $i$ at time $t$ , summing potential contributions from all quadrats
$D$	Diffusion coefficient in Gaussian (non-directional) kernel $K$
$h$	Scale of dispersal in anthropogenic (advected) dispersal kernel $H$
$c$	Normalization constant for discrete kernel distribution in two dimensions

produced in quadrat  $i$  will end up in quadrat  $j$  will depend on the distance,  $\rho_{ij}$ . The function ( $K$ ) describing how probability depends on distance is the natural dispersal kernel. In contrast, a seed that is caught in a combine harvester during crop harvest is more likely to disperse downstream than sideways or upstream. Thus the probability that a seed produced in quadrat  $i$  will end up in quadrat  $j$  will depend on the distance,  $\rho_{ij}$ , and their angle relative to the direction of management,  $\theta_{ij}$  ( $= \tan^{-1}(y_j - y_i)/(x_j - x_i)$ ). The function ( $H$ ) that governs how this probability depends on distance is the anthropogenic dispersal kernel. Note the asymmetry between  $0^\circ$  (where  $i$  may be a donor to  $j$ ) and  $180^\circ$  (where their potential roles are reversed).

The probability that a seed will disperse according to its natural kernel depends on the relative timing of the weed life cycle and the crop harvest. Therefore, the probability of dispersing from  $i$  to  $j$  will be a weighted average:

$$\kappa(\rho, \theta) = P \times K(\rho) + (1 - P) \times H(\rho, \theta) \quad \text{eqn 1}$$

where  $P$  is the relative contribution of natural vs. anthropogenic dispersal in the admixed kernel. We merge the local reproduction together with the dispersal kernel to predict the number of recruits in location  $i$  in a given year from the summed contribution of the individuals in the previous year:

$$\lambda_{i,t} = \sum_{j=1}^J r N_{j,t-1} \kappa(\rho_{ji}, \theta_{ji}) \quad \text{eqn 2}$$

where  $\lambda_{i,t}$  is the expected number of recruits, and the sum is across all the  $J$  quadrats in the field. In a finite world, any actual realization around this expectation will be clouded by demographic stochasticity. Assuming independence between seeds, we may assume:

$$N_{i,t} \sim \text{Poisson}(\lambda_{i,t}) \quad \text{eqn 3}$$

where  $\sim$  means 'is distributed as'.

To complete the model we need to specify the shape of the two dispersal kernels. The literature on dispersal kernels is voluminous (Kot, Lewis & van den Driessche 1996). For simplicity we assume that natural dispersal represents a simple diffusion process (Okubo 1980). This leads to a Gaussian dispersal kernel of the form:

$$K(\rho) = \exp(-\rho^2/D^2)/c \quad \text{eqn 4}$$

where  $D$  is the diffusion coefficient (and the standard deviation of the kernel) and  $c$  is the normalization constant for a discretized Gaussian distribution in two dimensions. Patterns of seed dispersal by combine harvester are poorly characterized by comparison, and reports from empirical studies vary (Cousens & Mortimer 1995; Woolcock & Cousens 2000). Assuming (i) a constant rate of release of seeds trapped in the combine harvester, and (ii) that the combine harvester travels along fixed transects, first principles (e.g. Bjørnstad & Bolker 2000) suggest that the anthropogenic dispersal should follow a directional exponential kernel, with deposition limited to cells in the same crop row as the parental source. That is:

$$H(\rho, \theta) = \exp(-\rho/h)/c' \quad \text{eqn 5}$$

for  $\theta=0$  and 0 otherwise. Here  $h$  is the scale of the exponential kernel, and  $c'$  is the normalization constant for the directional 'discrete exponential' (i.e. geometric) distribution. All symbol definitions are listed in Table 1 for reference.

We estimate all parameters in the model (equations 1–5) from the successive annual surveys of the experimental plots using maximum likelihood (Ribbens, Silander & Pacala 1994). In particular, we assume the observed abundance  $N_t$  follows a Poisson distribution (equation 3) around its expectation (equation 2) and use Poisson likelihoods to estimate the parameters (McCullagh & Nelder 1989). The likelihoods are maximized using the Nelder-Mead algorithm as implemented in the

'optim' functions in R. Standard errors are subsequently calculated from basic likelihood theory (McCullagh & Nelder 1989) and the numerically estimated Hessian matrix (R Development Core Team 2004). Standard errors are used to weight ANOVA models examining the influence of experimental factors on parameter estimates. We summarize the effect of the experimental treatment levels on dispersal first by specifying a simple additive ANOVA model. We subsequently use stepwise selection to remove individual factors or add significant interaction terms, assessing the change in model fit using the Akaike Information Criterion (AIC). Once the final, most appropriate, model is determined, we then evaluate pairwise comparisons of significant treatment means using weighted *t*-tests. We parameterize models for each replicate data set characterizing spatial seedling recruitment patterns occurring in years 1 and 2.

Finally, we use a deterministic version of the model (equation 2) to quantify how management affects the rate of patch expansion. By varying the parameter *P*, the measure of relative importance of anthropogenic vs. natural dispersal, we also predict how timing of crop harvest relative to the life-cycle of the weed affects weed spread.

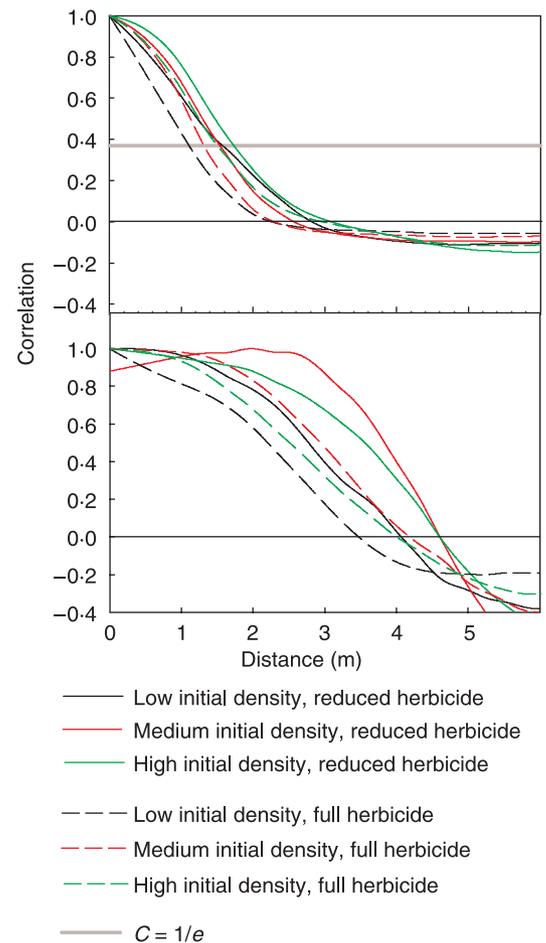
## Results

### NON-DIRECTIONAL CROSS-CORRELATION

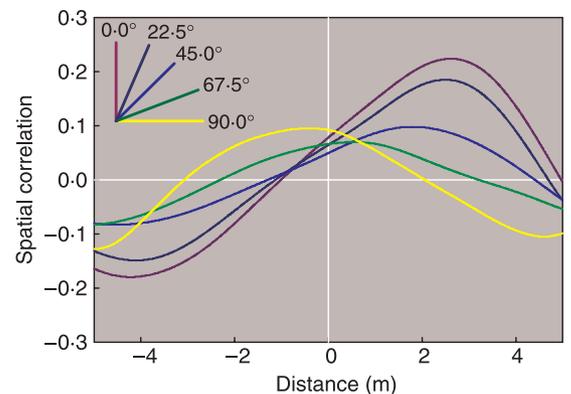
Spline correlograms representing the time-lagged cross-correlation analysis (correlating abundances in year *t* with abundances in year *t* - 1) revealed the patterns of patch expansion. The cross-correlation functions depicted in Fig. 1 represent treatment means from patches sown in soybean. During the first transition (Tr1), cross-correlations were positive to around 2–3 m, reflecting the extent of the patches following seed dispersal from artificially sown patches. The extent of positive spatial cross-correlation increased during the subsequent year, illustrating expansion of the experimental weed patches. Treatment differences between cross-correlation functions indicated the influence of management on spatial dynamics. In all cases, initial low density patches exposed to high intensity herbicide displayed the shortest extent of positive correlation. The longest extents were associated with mid- and high initial density patches exposed to low intensity herbicide, reflecting a greater rate of spread of *H. annuus* for these treatments. The shape of the non-directional correlation functions resembled Gaussian correlation functions, with locally high values, a 'shoulder' and then decay with distance.

### DIRECTIONAL CROSS-CORRELATION

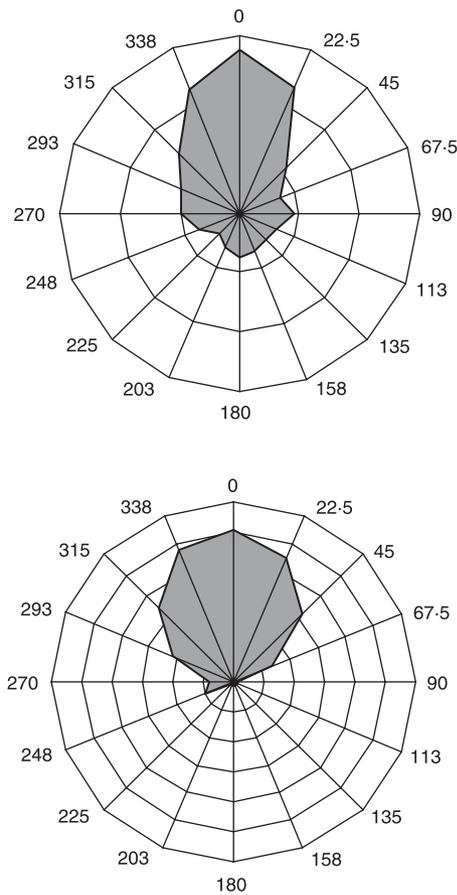
We used directional cross-correlation analysis to test for anisotropy in the weed spread. Figure 2 illustrates the directional cross-correlation functions from year 1 to 2 (Tr2) for a single treatment group (maize harvest in T<sub>1</sub>, high initial seed bank density, half rate herbicide



**Fig. 1.** Spline correlograms from non-directional cross-correlation analysis of data from intervals 0–1 (top) and 1–2 (bottom); all patches represented were sown in soybean in year 0. Correlation values are means across treatment replicates, with treatment separation by line style as indicated. Splines are scaled to  $C_{(\max)} = 1$  and the grey horizontal line in the top panel indicates the value  $C = 1/e$ .



**Fig. 2.** Directional cross-correlation functions of patches within a single treatment group during from year 1 to 2 transition (Tr2). The particular experimental treatment was high seed bank density, reduced rate herbicide, following harvest of maize in T<sub>1</sub>. Lines are colour-coded according to angle of direction ( $\theta$ ) of spatial correlation, covering an arc from  $\theta = 0^\circ$  (direction of harvest) to  $\theta = 90^\circ$  (perpendicular to direction of harvest).

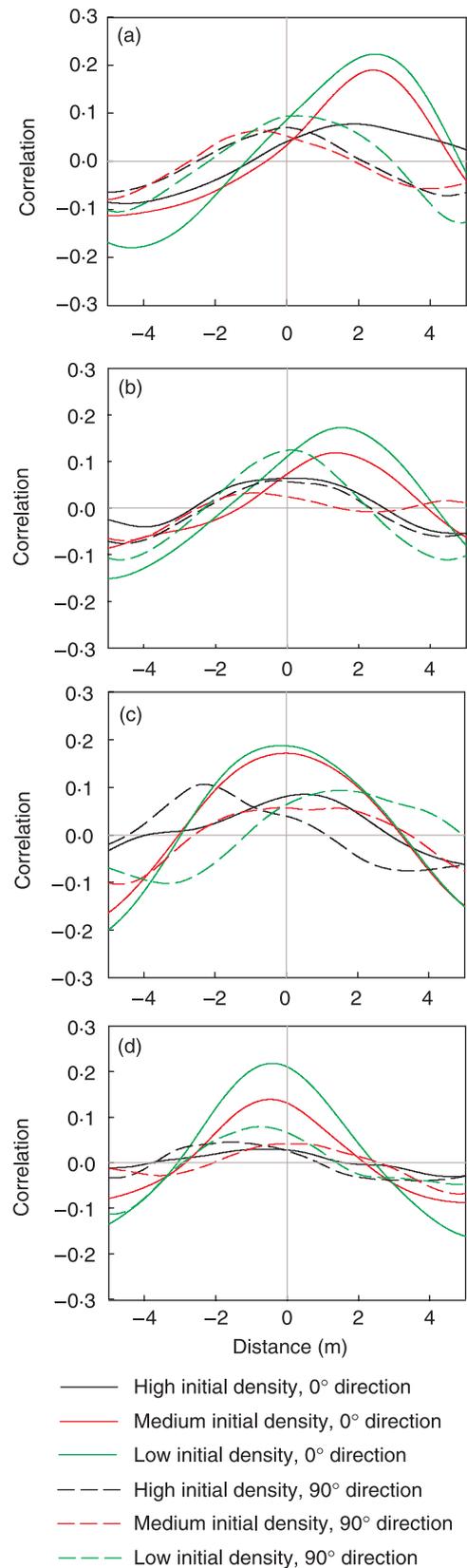


**Fig. 3.** Radial plots illustrating directional patterns in spatial correlation (top) and offset distance from zero of maximum correlation (bottom). Contour intervals are 0.1 in correlation plot, 0.5 m in offset distance plot.

application). The functions depicted represent the average across the replicates. In the direction of management ( $\theta = 0^\circ$ ), the peak in correlation was offset from the origin by approximately 2.5 m. This demonstrated how spatial expansion of the weed patch is biased in the direction of harvest. In contrast, the correlation function perpendicular to the direction of management ( $\theta = 90^\circ$ ) had a shorter spatial extent that was not significantly offset from zero, indicating non-directional expansion in this plane. The directional analyses in the arc between  $0^\circ$  and  $90^\circ$  revealed the progression from directional (advected) to non-directional spread in the directions parallel and perpendicular to the direction of harvest.

Radial plots (Fig. 3) of the peak in spatial cross-correlation further characterize the directional bias. Figure 3a illustrates directional bias in the magnitude of spatial correlation, indicating that density at  $T_2$  was most highly correlated with  $T_1$  densities in the  $0^\circ$  direction. This reveals that in the interval  $Tr_2$ , the centre of weed patches shifted in the direction of harvest as a result of the dispersal of seed by the combine. The distance of this offset is shown in Fig. 3b.

In Fig. 4 we present the parallel results for the different treatment combinations of crop type and



**Fig. 4.** Spline cross-correlograms from directional cross-correlation analysis of data from annual interval  $Tr_2$  in the  $0^\circ$  and  $90^\circ$  directions. Experimental treatments as follows: (a) reduced rate herbicide application, transition following harvest of soybean; (b) full rate herbicide, harvest of soybean; (c) reduced rate herbicide, harvest of maize; and (d) full rate herbicide, harvest of maize.

**Table 2.** Significant factors in fitted linear models for maximum likelihood parameters of the spatial model. Significance indicated as \*\* $P < 0.001$ , \* $P < 0.01$  and † $P < 0.05$ . Note that annual transition is evaluated as an experimental factor

Parameter	Form of GLM
$D$	~ Transition** + crop* + herbicide** + seed bank† + herbicide:seed bank**
$h$	~ Transition** + crop** + herbicide** + crop:herbicide* + transition:seed bank†
$P$	~ Crop** + herbicide** + seed bank** + herbicide:seed bank†
$r$	~ Transition** + herbicide** + transition:herbicide*

**Table 3.** Global means of integro-difference model parameters and means of factors with significant (or notable) pairwise comparisons ( $P < 0.05$ , except where noted). Note that annual transition is evaluated as an experimental factor. Coefficient of variation (CV) is expressed as a percentage of global mean and provides a general measure of parameter dispersion among all treatments

Parameter	Global mean (SD)	CV (%)	Pairwise comparison factor	Treatment values	Treatment mean	SE
$D$	3.65 (2.53)	69.3	Annual transition	Tr1	2.04	0.99
				Tr2	5.59	2.46
$h$	3.28 (3.38)	103.0	Crop at seed set	Maize	2.43	1.53
				Soybean	4.21	4.48
$P$	0.91 (0.15)	16.5	Crop at seed set	Maize	0.87	0.16
				Soybean	0.95	0.12
$r$	8.95 (11.37)	127.0	Crop at seed set*	Maize	6.99	9.25
				Soybean	11.73	13.51
			Management intensity**	Full	7.77	9.40
				Half	10.16	13.11

\* $P = 0.076$ , \*\* $P = 0.37$ .

herbicide treatment. The directional cross-correlations highlight significant and consistent anisotropy in the direction of harvest ( $\theta = 0^\circ$ ) following cultivation and harvest of maize (Fig. 4a,b). In contrast, weed spread in soybean appears to be much less affected by management (Fig. 4c,d), indicating a possible crop influence on the dynamics of seed dispersal.

#### PARAMETERIZATION OF THE INTEGRO-DIFFERENCE MODEL

Maximum likelihood parameter values showed significant variability, with some variation attributable to experimental factors. While different combinations of treatment factors were identified as significant in linear models (Table 2), few significant differences between treatment means emerged in pairwise comparisons (Table 3). Crop species present during the period of seed set and dispersal had a consistent influence on parameter values, affecting all parameters except the distance of natural dispersal (Table 3). Crop species particularly influenced the dynamics of seed dispersal by harvester. Crop species significantly influenced the value of parameter  $P$ , suggesting a greater proportion of weed seed is distributed by the combine when *H. annuus* sets seed in maize crops than in soybean. Crop species also influenced the mean distance of dispersal by combine harvester, with seeds dispersed a greater distance during harvest of soybeans. This result paralleled the much stronger (anisotropic) signature of weed vectoring revealed by the directional correlation functions (Fig. 4). Natural dispersal distances ( $D$ ) were significantly greater in the second transition Tr2 (Table 2).

Pairwise comparisons of estimates of *per capita* population increase ( $r$ ) between treatments did not indicate significant differences ( $P < 0.05$ ). *Per capita* population increase was greater following cultivation and harvest of soybean ( $r = 11.73$ ) than maize ( $r = 6.99$ ), and this difference was borderline significant ( $P = 0.076$ ). Maximum likelihood estimates of *per capita* increase showed a great deal of variability (CV; Table 3).

#### Discussion

Agricultural ecosystems are characterized by high levels of disturbance, relatively rich resource supply and, in fields where disturbance includes tillage, limited interspecific competition early in the life of annual plants. A limited seed supply coupled with high levels of seedling-targeted mortality result in weed populations that are often recruitment limited. Therefore, factors influencing the size of weed seed banks are likely to strongly influence the persistence and spread of weedy populations (Westerman *et al.* 2003). The temporal trajectory of seed bank density is regulated by seed bank persistence, fecundity, immigration and emigration.

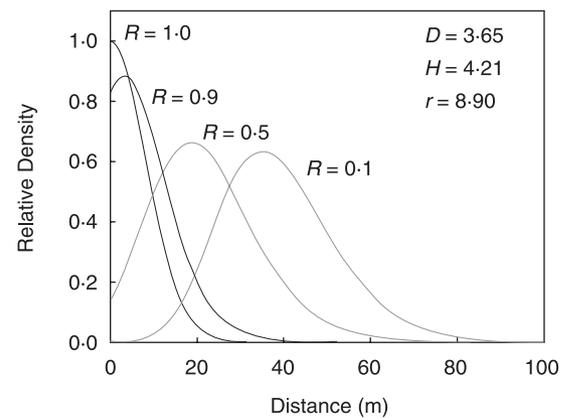
This study set out to assess the importance of initial seed bank pool size on the persistence and spread of populations over a period of 4 years. The study species, *H. annuus*, is a summer annual weed with a persistent seed bank. Previous work in this study system revealed an interesting density-dependent dynamic influencing the survivorship probabilities in seed to seedling transitions. High densities of seedlings shortly following emergence resulted in reduced mortality when herbicides were applied for control (C. Neeser, J.A. Dille &

D.A. Mortensen, unpublished data). With such controls as the overwhelming source of mortality in annual cropping systems, it is clear that one important way in which initial seed bank pool size influences the fate of populations is through seedling mortality. This study expands on previous work by following populations through time. With small initial seed banks, the likelihood of patch extinction was high and the rate of patch spread greatly constrained. Because of its large seed, innate dispersal of *H. annuus* seed is limited to several metres in distance (Teo-Sherrel 1996), with the largest proportion of seed falling within 1–2 m of the parent. This study used the spatial extent of seedling patches arising from seed banks established in 1994 to quantify the relative roles of natural and management-aided dispersal on weed patch expansion.

In the experiment we intentionally carried out all management-related traffic in a unidirectional fashion. This uniquely allowed us to characterize and separate the two dispersal processes. Directionality in spread is the signature of anthropogenic vectoring, while radial symmetry reflects natural dispersal. The significant anisotropy in our geostatistical analysis (Figs 2–4) testifies to considerable management-related dispersal. Management-influenced weed-patch expansion was highest in maize (Table 2 and Fig. 4). The crop type, thus, significantly influenced the proportion of weed seeds dispersed during harvest relative to those dispersed by natural means (i.e.  $P$ ). Harvest of all fields occurred on the same day; therefore this may be attributable to differential weed–crop competition dynamics effected by tall maize plants vs. low-lying soybean plants.

*Helianthus annuus* recruitment is seed limited (Neeser, Dille & Mortensen, unpublished), where small seed banks are less likely to yield reproductive adult plants. While evidence suggests that seeds of the common sunflower are naturally long-lived in the seed bank with a small proportion germinating each year (Burnside *et al.* 1981, 1996), the seeds are favoured by many granivores (Pilson 2000; Alexander *et al.* 2001; Cummings & Alexander 2002) and experience high rates of post-dispersal mortality from seed predators (Teo-Sherrel 1996). Seed bank persistence (beyond 1 year) appeared to play a minor role in patch dynamics in our experiment. In this study, as in others, we found that *H. annuus* patches with small initial seed banks and high herbicide treatments declined to extinction.

The empirically parameterized integro-difference model allowed us to (i) measure the spatial scales of the two modes of dispersal (natural and management-aided), (ii) estimate their relative importance and (iii) calculate how the within-field rate of weed patch expansion is enhanced by manage-aided dispersal. Based on these calculations, we found that weed patch expansion may increase by as much as a factor of 3–4 with heavy management traffic (compare the length of the tails in Fig. 5). However, the actual traffic in our experiment resulted in somewhat less extreme effects. Woolcock & Cousens (2000) suggested a potential 16-fold increase in weed grass (*Bromus* sp.) patch expansion rate from



**Fig. 5.** Effect of varying the contribution of natural vs. harvest dispersal ( $P$ ) on patch expansion in one dimension parallel to direction of harvest. Density curves show results of 10 years of simulations projecting the integro-difference model using mean maximum likelihood parameter values. All populations were initiated at 0 m, with direction of combine harvest orientated from left to right. All densities are scaled relative to weed density at origin when  $P = 1.0$  (i.e. no seed dispersal by harvest).

seed dispersal by combine harvester. Their more extreme effect results from the assumption that anthropogenic dispersal distances were orders of magnitude greater than natural dispersal. This may be unrealistically great for large-seeded weeds such as *H. annuus*. Nevertheless, our experiment and analysis lend qualitative credibility to Woolcock & Cousens' (2000) theoretical results, in that we confirm that management-related traffic results in considerable vectoring of seeds and affects patch expansion of an annual weed. In practice, such anisotropic dispersal may significantly influence field-scale population dynamics of *H. annuus*. Moderate and high density patches would serve as source populations from which local infestations would spread. In time, patches would coalesce, minimizing the effectiveness of site-specific management.

To gain insights into scales of dispersal, and the relative importance of anthropogenic vs. natural dispersal, we made several assumptions. First, we assumed negligible density-dependence in emergence and survival of weeds. It is realistic that density-dependence effects are negligible in this early post-invasion time frame (Buckley, Briese & Rees 2003). Secondly, we made assumptions about the shape of the dispersal kernels. For instance, we assumed that the kernel of natural dispersal is predominantly shaped by diffusive movement of seeds, predicting the dispersal distance distribution to be proportional to  $\exp(-d^2)$ : a Gaussian kernel. Although previous studies have considered the plausibility of alternative kernel forms (Kot, Lewis & van den Driessche 1996; Latore, Gould & Mortimer 1998), we made this assumption by appealing to first principles. In considering patch expansion in a single agricultural field immediately following weed invasion, recruitment is probably dominant in near-source 'shoulders' of the dispersal kernel (where seed rain

is highest). Using leptokurtic or 'heavy-tailed' kernels would probably increase the predicted expansion rate. However, we suggest such dispersion is probably of lesser relevance at these scales. Interestingly, our geostatistical analysis renders critical evidence on the validity of this assumption: Bjørnstad & Bolker (2000) show that the spatial correlation function (e.g. Fig. 1) inherits its shape from the dispersal kernel, and Bjørnstad & Falck (2001) show that the spline correlogram is a non-parametric estimate (in the sense of not assuming any specific functional form) of this correlation function. A visual inspection of the non-directional spline correlograms from Tr1 (Fig. 1a), reveals distinct Gaussian features: there is a 'Gaussian shoulder' near the origin and a seemingly exponentially decaying tail. Furthermore, we can use the result in Bjørnstad & Bolker (2000) to validate our likelihood estimates of the scale of the natural dispersal kernel; specifically the distance at which the scaled spline correlograms drops to  $1/e$  ( $\approx 0.37$ ), the so-called  $L_c$ -correlation length is equivalent to the scale  $D$  of the Gaussian kernel (equation 4) or the scale  $h$  of the exponential kernel (equation 5). Across the treatments, the average correlation length is 1.80 m (SE = 0.51). This compares well with the averaged likelihood estimate of  $D$  in Tr1 (2.04 m, SE = 0.68).

Ribbens, Silander & Pacala (1994) pioneered the use of likelihood methods to parameterize integro-difference equations from sequential spatial mappings of plant distributions. We extended their approach for applicability in the agro-ecological setting, and to parameterize mixtures of dispersal kernels (natural and anthropogenic) from differences in the anisotropy of the signatures of the two. Admixed modes of dispersal are likely to be common. Invasions, for instance, are often argued to result from rare (e.g. long-distance) dispersal events. One may speculate that this is the admixed signature of the kernel of a rarer, more distant, dispersal mode. We believe that our protocol of combining geostatistical analysis of sequential mappings with parameterization of spatial population models facilitates characterization and separation of distinct modes of dispersal. Independence of the two methods provides a system for cross-validating model assumptions and estimated parameters.

Our focus is on how localized seed limitation and local dispersal are the keys to weed control. We found that a critical minimum seed bank density was needed for patch persistence and spread. Once that minimum density was met, patches became a seed source to move propagules rapidly about the field. The relatively rapid anisotropic spread of populations observed in the study provides compelling evidence that once a critical minimum density in a local population is exceeded, increased management is needed to contain the spread of this weed. Study of these local dynamics is a different perspective from the many important past studies on how rare long-distance events determine long-term colonization and range expansion (Clark *et al.* 1999; Clark, Lewis & Horvath 2001; Nathan & Muller-Landau

2000). However, for precision agriculture and ecological recommendations that are relevant to individual farms, rare long-distance processes are of lesser concern. For precision agriculture, finer spatiotemporal scales and the methodology presented here may be more relevant.

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