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Spatial dependence of weed seed banks and strategies for sampling

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Weed management could be more efficient and require less herbicide if growers could afford to estimate the composition, density, and distribution of weed seed banks. Spatial distribution of a weed seed bank will affect the accuracy of both mean estimates and interpolated maps of density. Consequently, information about the general characteristics of spatial distributions of seeds in a seed bank is needed to identify the most efficient strategies for sampling. Seed banks were sampled on 8.4-m square grids in eight irrigated corn fields to identify the common features of distributions of seed banks of annual weeds. Spatial dependence was described with correlograms for four to eight species in each field. Spatial dependence was detected for 36 of 45 distributions, and seed counts were correlated to an average distance of 25 to 150 m for a distribution. Seed banks of different species and fields had common features of spatial correlation: spatial pattern accounted for less than half of the total variability of seed counts, spatial correlation decreased rapidly over short distances, and ranges of spatial dependence varied with direction. For half of the distributions, the maximum range of spatial dependence was at least twice as long as the minimum range. Seed counts were correlated for the longest distances in the direction of the crop row for 16 distributions, and the distance was longer in the direction of the crop row than across rows for 26 of the 36 samples. Researchers should be able to design more efficient sampling plans for growers if the common features of spatial dependence are considered. For seed banks like these, the accuracy of maps and estimates of seed bank density may be improved by collecting multiple cores around each sampling location to mitigate the effect of short-scale spatial variability. In addition, sampling may be more efficient with grids and interpolation methods that account for ranges that are 1.5 to 2 times longer in the direction of the crop row than perpendicular to the row. With a 55- by 30-m sampling grid, adjacent observations would be correlated, and maps could be made for 80% of these seed banks. More closely spaced observations would be needed to describe the rapid decline in spatial correlation with distance for a more accurate or finer-scale map. Whether sampling seed banks for making management decisions will be cost-effective is not clear. However, potential methods to sample and map seed bank distributions more efficiently have not been exhausted.

Nomenclature: Corn, *Zea mays* L.

Key words: Geostatistics, map, spatial distribution, spatial correlation, redroot pigweed, *Amaranthus retroflexus* L. AMARE, hairy nightshade, *Solanum sarrachoides* Sendtner, SOLSA, barnyardgrass, *Echinochloa crus-galli* (L.) Beauv., ECHCG, green foxtail, *Setaria viridis* L., SETVI.

Weed seed banks can indicate future weed problems. Consequently, weed management may be more efficient and may require less herbicide when the density and distribution of major species in a seed bank can be estimated by sampling. Some bioeconomic weed management models identify the best management option from an estimate of the composition of the seed bank in a field (Lybecker et al. 1991; Swinton and King 1994; Wiles et al. 1996b). In several trials, management according to model recommendations has achieved control of weeds with less total herbicide compared with a standard practice (Buhler et al. 1997; Forcella et al. 1996; VanGessel et al. 1996). Describing the spatial distribution of the seed bank in a field requires more intensive and costly sampling than estimating the composition does, but the time and effort may be justified by the potential benefits of site-specific weed management. Seed banks, like weed populations, often have patchy distributions (Benoit et al. 1992; Cardina et al. 1996; Dessaint et al. 1991; Wiles and Westra 1999), and soil-applied herbicides could be varied within a field to match the variation in the seed bank. A seed bank map could also be used to plan postemergence treatments, or sampling of the seedling population could be targeted to areas where uncertainty about optimal postemergence management is greatest. As a result, fewer observations of the seedling population may be needed (Cardina et al. 1996). Moreover, a seedling map may be more accurate or may require fewer observations if both seed bank and seedling data are used for interpolation. With the observed persistence of some weed patches, a seed bank map may be useful for making management decisions for several years.

Identifying and counting weed seeds is expensive and time-consuming (Benoit et al. 1992; Gross and Renner 1989; Wiles and Schweizer 1999); therefore, researchers must develop efficient sampling plans if growers are going to use information about seed banks to enhance weed man-

agement. These plans must achieve the appropriate balance between cost of sampling and value of information obtained. Spatial distribution of a seed bank will affect the accuracy of both global mean density estimates (Ambrosia et al. 1997) and interpolated maps (Gotway et al. 1996). For example, the number of observations needed to estimate density at some level of precision increases with the degree of aggregation (Ambrosia et al. 1997). Also, spatial distribution determines the appropriate distances between sampling locations to obtain the correlated observations needed to make a map (Weisz et al. 1995). Accordingly, knowledge of spatial dependence of seed banks can lead to the development of guidelines for efficient sampling and mapping (Burrough 1991). The nature of spatial correlation affects the best choice of sample unit, the distances between sampling locations, the placement of sampling locations (type of grid and orientation), and the interpolation method (Burrough 1991; Flatman et al. 1988; Gotway et al. 1996; Oliver et al. 1997; Weisz et al. 1995). Sampling plans may be efficient even when based on generalizations about spatial distribution. For example, entomologists recommend sampling plans that have been based on assumed values of dispersion of infestations (Davis 1994). For soil properties, information about the common features of spatial distributions has led to savings in the cost of sampling and improvement in the quality of the information (Burrough 1991).

Too little is known about the spatial distribution of weed seed banks to recommend any aspect of a sampling plan for making weed management decisions. Further, there is not even a consensus on how to sample research plots in order to estimate the composition of a seed bank (Jones 1998). In the first studies about sampling seed banks, seed counts were analyzed without considering the relative locations of the observations, and spatial distributions were not described (Ambrosia et al. 1997; Benoit et al. 1989; Bigwood and Inouye 1988; Dessaint et al. 1996). Relative locations of observations are needed to analyze spatial correlation and provide a basis for designing sampling plans (Benoit et al. 1992; Cardina et al. 1997; Dessaint et al. 1991; Wiles and Westra 1999). Common features of the spatial distributions of weed seed banks must be identified in order to design efficient sampling plans, but spatial data are scarce because sampling is so expensive. The objective of this study was to describe the spatial distributions of weed seed banks in irrigated corn fields and identify the characteristics of distributions that are consistent across fields and species.

Materials and Methods

Sampling Procedure

Seed banks were sampled in an 8.1-ha block of four corn fields in 1993 and in four additional fields in 1994. These fields were in eastern Colorado, where the typical rotation is corn, dry beans (*Phaseolus vulgaris* L.), and sugar beets (*Beta vulgaris* L.). Soil texture varied from sandy to clay loam. Seed banks were sampled immediately after planting, using an 8.4-m square grid aligned with the crop row. Soil cores were 5 cm in diameter and 10 cm deep and were placed in plastic bags in the field and stored at 6 C for 7 to 14 d until the soil could be air-dried in a greenhouse. The air-dried samples were weighed and then processed in an elutriator that uses water to separate seeds from the soil (Wiles et al. 1996a). The elutriated samples were transferred to fabric bags, dried overnight in an oven at 38 to 49 C, and then stored at room temperature until analysis. Seeds that were firm when squeezed slightly with a forceps were counted and identified.

Spatial Analysis

Spatial dependence was described with correlograms (Rossi et al. 1992). Correlograms were used because a standardized measure of spatial dependence was needed for comparisons among seed banks with disparate levels of spatial variability (Rossi et al. 1992). Also, a correlogram can provide a better summary of spatial pattern when compared with a variogram when local means and variances change within a sample area. Spatial correlation can be modeled even when a trend is present in the data (Rossi et al. 1992).

A correlogram describes similarity of seed counts with correlation. A value of a correlogram ($\rho(h)$) is the correlation coefficient for all pairs of observations separated by a particular distance h (Isaaks and Srivastava 1989). Values can range from -1 (perfect negative correlation) to $+1$ (perfect positive correlation), but most are between 0 and 1. Correlation usually decreases with increasing distance between observations. For a directional correlogram, h represents distance in a particular direction, and the correlation coefficient is calculated only from pairs of observations separated by distance h in the specified direction. The general process of describing spatial dependence with a correlogram involves calculating the correlation coefficients by distance, using the sample data, and then fitting an equation to a plot of the correlation coefficients by distance. A plot of correlation coefficients by distance and direction is called a directional sample correlogram, whereas the equation fit to sample correlogram is a correlogram model.

Species in a field were analyzed individually, and only samples with seeds in at least 17 cores were analyzed. Seed counts were transformed ($\ln(x + 1)$) to reduce the effect of skewed frequency distributions of seed counts on the analysis because skewness statistics were greater than 2 for all samples (data not shown). Sample correlograms were calculated for the direction of the crop row (0°), and 45, -45, and 90° from the crop row. Sample correlogram values were calculated at 8.4-m intervals for 0 and 90° and at 11.8-m intervals for -45 and 45°. The length of the interval is called the lag spacing. Which observations were included in the calculation of a sample correlogram value was specified by tolerances for both direction (angular tolerance and bandwidth) and distance (lag tolerance) for pairing counts (Isaaks and Srivastava 1989). Because the number of observations was large, the tolerances used were small in order to describe the nature of spatial correlation as specifically in a direction as possible. That is, the tolerances were specified to have sufficient pairs for each lag to obtain a clear directional correlogram yet only use observations separated by directions that would lead to a correlogram that was representative of the specified direction (Isaaks and Srivastava 1989). The lag tolerance was one-half the lag spacing, the angular tolerance was 22.5°, and the bandwidth was 18 m. With these tolerances, each observation was paired only with observations that were within an area that was approximately an 18-m band centered on and extending about one-half of the lag spacing on either side of the point

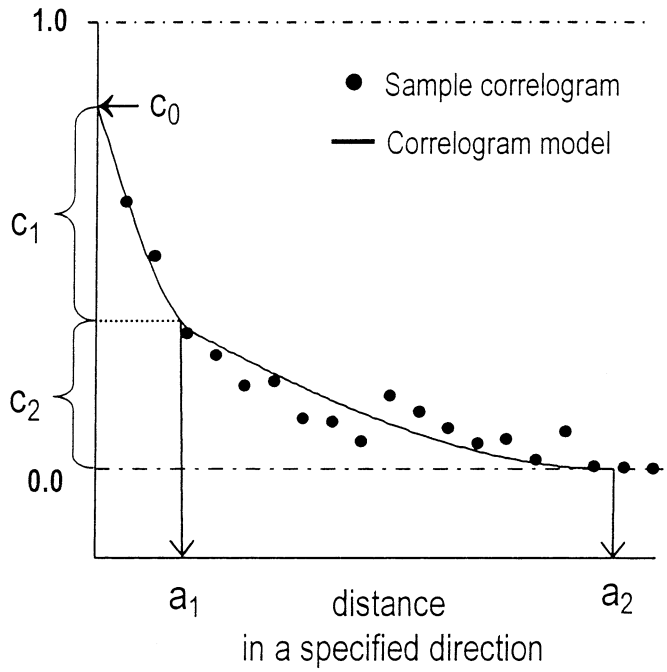

FIGURE 1. Example of a directional sample correlogram with the directional correlogram model.

representing the specified distance and direction of the correlogram. For some short distances, the area was limited by the angular tolerance rather than by the bandwidth and was smaller. Each correlogram value was calculated from at least 730 pairs of seed counts, and the number of pairs for a lag was similar in all directions.

Theoretically, a correlogram should have a value of one for a distance of 0 (perfect correlation) and then decline to a sill of 0 (no correlation). In reality, the value of the correlogram at $h = 0$ is less than 1 as a result of experimental error and variability between observations separated by very short distances (Rossi et al. 1992). The value of the correlogram at $h = 0$ is the parameter c_0 of a correlogram model, and it is the proportion of variability in seed counts that can be explained by the spatial pattern. The proportion of variability due to experimental error and short-scale variability is $1 - c_0$ (Rossi et al. 1992). The distance at which the correlogram reaches the sill is called the range of spatial dependence (a). Typically, the sill is zero (no correlation), and the range of spatial dependence is the average distance over which observations are correlated. The range represents the transition from distances over which spatial correlation exists ($h < a$) to distances for which there is no correlation ($h > a$) (Rossi et al. 1992).

The decline of spatial correlation between c_0 ($h = 0$) and the sill ($h = a$) can be described with an exponential, gaussian, or spherical model, or a combination of these models (Isaaks and Srivastava 1989). More than one model may be used if a single model will not adequately describe the decline of spatial correlation with distance. A correlogram with nested models can describe possibly disparate features of the spatial correlation that may represent the independent influences of different factors on the spatial pattern (Isaaks and Srivastava 1989). For weed seed banks, a correlogram with two nested models could represent both the natural dispersal of seed over short distances and equally in all directions from the parent plant and the movement of seed by machinery for longer distances and primarily in the direction of the crop row.

All sample correlograms were modeled with the same functional form so that parameters of the model could be compared to identify the similarities and differences observed in spatial correlation of the seed banks. Spatial dependence of weed populations has been described with spherical models (Cardina et al. 1995, 1996; Colbach et al. 2000; Johnson et al. 1996). Spherical models are linear over short distances but then flatten out and eventually plateau (Isaaks and Srivastava 1989). Two nested spherical models were used to model the spatial correlation of the seed banks:

$$\rho(h) = \begin{cases} c_0 & \text{if } h = 0 \\ c_0 - c_1 \cdot \left(1.5 \cdot \left(\frac{h}{a_1}\right) - 0.5 \cdot \left(\frac{h}{a_1}\right)^3\right) & \\ \quad - c_2 \cdot \left(1.5 \cdot \left(\frac{h}{a_2}\right) - 0.5 \cdot \left(\frac{h}{a_2}\right)^3\right) & \text{if } 0 < h < a_1 \\ c_0 - c_1 - c_2 \cdot \left(1.5 \cdot \left(\frac{h}{a_2}\right) - 0.5 \cdot \left(\frac{h}{a_2}\right)^3\right) & \text{if } a_1 \le h < a_2 \\ 0 & \text{if } h \ge a_2 \end{cases} \quad [1]$$

Values of a_1 and a_2 are the distances at which each spherical model reaches a plateau, and the range of spatial dependence (a) is the maximum of a_1 and a_2 (Figure 1). Values of c_1 and c_2 are the proportions of the variability of seed counts explained by each spherical model. With $c_2 = 0$, the correlogram is modeled with a single spherical model.

Both sample and theoretical correlograms were calculated using SAGE2001[1,2] software, which fits a correlogram model using regression. A single model of spatial correlation is estimated simultaneously from all the directional sample correlograms calculated for a distribution (SAGE2001 1999). The resulting model can be used to determine the correlogram for any direction (SAGE2001 1999). With this model, values of c_0, c_1, and c_2 are the same for all directions, but values of a_1 and a_2 can vary independently with the direction. Variation in a_i is modeled with an ellipse that is described with the minimum ($a_{i\,\min}$) and maximum ($a_{i\,\max}$) values of a_i and the direction of the maximum value of a_i (Deutsch and Journel 1992):

$$\frac{x^2}{(a_{i\,\min})^2} + \frac{y^2}{(a_{i\,\max})^2} = 1 \quad [2]$$

The y-axis represents the distance in the direction of the maximum value of a_i. A line from the center of the ellipse to a point on the ellipse indicates the distance of a_i for the direction of the line. Including the parameters of the ellipse, eight parameters must be estimated for a single model of spatial correlation of a seed bank. These are c_1 and c_2 ($c_0 = c_1 + c_2$), the maximum and minimum values of a_1 and a_2, and the directions of the maximum values of a_1 and a_2.

Correlograms were modeled using the four directional sample correlograms. To assess the fit of the model, directional correlogram models were calculated and graphed for the directions of the sample correlograms. The values of a_1

and a_2 were calculated for every degree from 0 to 179° to determine the mean value of the range of spatial dependence of each sample.

Results and Discussion

Seed Counts: Frequency Distributions

The relative abundance of weed species in the seed banks was typical for corn production in eastern Colorado (Schweizer et al. 1998). Twelve species were sufficiently abundant for analysis, with four to eight species in a field for a total of 45 sample data sets (Table 1). Grasses were less common than broadleaves. Pigweed (primarily redroot pigweed [*Amaranthus retroflexus* L.]) was found in all fields, and nightshade (primarily hairy nightshade [*Solanum sarrachoides* Sendtner]), barnyardgrass [*Echinochloa crus-galli* (L.) Beauv.], and foxtails (primarily green foxtail [*Setaria viridis* L.]) were found in at least six fields. Five other species were observed in just one field (Table 1).

Frequency distributions of seed counts were usual for seed banks (Ambrosia et al. 1997; Benoit et al. 1989; Bigwood and Inouye 1988; Chauvel et al. 1989; Dessaint et al. 1996; Jones 1998). That is, counts were highly variable, and distributions were skewed, with many zero counts. Two samples had extreme density or variability (31AMA, 42ECH). Excluding those samples, the average coefficient of variability of seed counts was 582%, mean density ranged from 0.01 to 2.55 seeds core^{-1} (5 to 1,257 seeds m^{-2}), and half of the samples had a mean density of less than 0.13 seeds core^{-1} (64 seeds m^{-2}). Seeds were found in only 1 to 10% of the cores of 28 samples (Table 1), and at most, 65% of the cores of a sample contained seeds. Maximum counts ranged from 1 to 108 seeds core^{-1} (493 to 53,244 seeds m^{-2}) and were 10 to 300 times larger than the mean count of a sample (Table 1). The median count was zero for all samples except for pigweed in Field 42 and foxtail in Field 31. These samples had a median count of 1 seed core^{-1}.

The coefficient of variability of the extreme barnyardgrass sample (42ECH) was twice as large as that of any other sample (Table 1). Barnyardgrass seed were found in only 17 cores, and 70% of the seeds were in one core. The pigweed seed bank in Field 31 was over three times larger than any other seed bank (Table 1). Manure was a major contributor to this seed bank. The field was located next to a feedlot, and manure was regularly applied for several years. Abundant pigweed seed and some foxtail seed were found in samples of manure.

Sample Correlograms

No spatial dependence was detected for 9 of the 45 seed bank samples (Table 2). That is, seed bank density was either not spatially correlated or was correlated only for distances shorter than the scale of sampling (i.e., 8.4 m for 0 and 90° clockwise from the crop row and 11.8 m for − 45 and 45°). These seed banks were small (0.01 to 0.06 seeds core^{-1}), and no seeds were found in 95 to 99% of the cores of a sample (Table 1), but spatial dependence was detected for eight seed banks of similar size (31CCH, 31SIN, 33EPH, 34POR, 41ECH, 42ECH, 42POR, 44SOL). For those eight samples, 24 to 48% of the variability in seed counts was explained by the spatial pattern (Table 2).

TABLE 1. Summary statistics for weed seed banks sampled in eight irrigated corn fields in Colorado.

Sample	Field	Species[a,b]	Number of cores	Mean	Maximum	Coefficient of variability	Cores with no seeds
				seeds core^{-1}		%	
31AMA	31	AMARE	1,049	8.24	318	171	4
31CCH	31	CCHPA	1,224	0.03	6	1,072	99
31CHE	31	CHEAL	1,224	0.28	45	686	91
31ECH	31	ECHCG	1,224	0.28	72	794	89
31SET	31	SETVI	1,224	2.01	23	140	35
31SIN	31	SINAR	1,224	0.06	6	575	96
31SOL	31	SOLSA	1,224	0.49	19	307	79
32AMA	32	AMARE	1,260	0.15	3	294	88
32CHE	32	CHEAL	1,260	0.08	4	445	94
32ECH	32	ECHCG	1,260	0.14	7	308	88
32SET	32	SETVI	1,260	0.01	1	855	99
32SOL	32	SOLSA	1,260	0.17	4	292	87
33AMA	33	AMARE	1,225	0.05	3	492	95
33CHE	33	CHEAL	1,225	0.02	1	819	99
33EPH	33	EPHDE	1,225	0.03	2	614	97
33SOL	33	SOLSA	1,225	0.20	14	349	86
34AMA	34	AMARE	1,225	0.41	19	258	73
34CHE	34	CHEAL	1,225	0.10	18	797	96
34ERA	34	ERACN	1,225	0.04	3	586	97
34POR	34	POROL	1,225	0.06	5	597	96
34SOL	34	SOLSA	1,225	0.80	46	357	72
41AMA	41	AMARE	1,224	0.16	10	327	88
41CHE	41	CHEAL	1,224	0.02	3	947	99
41ECH	41	ECHCG	1,224	0.03	4	670	97
41POR	41	POROL	1,224	0.29	53	894	94
41SET	41	SETVI	1,224	0.07	3	424	94
41SOL	41	SOLSA	1,224	0.07	5	519	95
42AMA	42	AMARE	1,223	2.55	83	200	37
42ECH	42	ECHCG	1,223	0.06	55	2,512	99
42EPH	42	EPHDE	1,223	0.15	21	473	88
42PAN	42	PANCA	1,223	0.13	9	400	91
42POL	42	POLCO	1,223	0.66	23	261	73
42POR	42	POROL	1,223	0.02	3	878	98
42SET	42	SETVI	1,223	0.11	4	334	90
42SOL	42	SOLSA	1,223	0.94	29	268	65
43AMA	43	AMARE	1,224	0.20	69	1,119	93
43ECH	43	ECHCG	1,224	0.01	1	898	99
43EPH	43	EPHDE	1,224	0.02	2	947	99
43POR	43	POROL	1,224	0.32	108	1,269	91
43SET	43	SETVI	1,224	0.03	5	752	98
44AMA	44	AMARE	943	0.33	10	229	76
44ECH	44	ECHCG	943	0.13	5	361	90
44EPH	44	EPHDE	1,223	0.22	3	228	82
44SET	44	SETVI	1,223	0.06	10	801	97
44SOL	44	SOLSA	1,223	0.06	23	1,155	96

[a] Letter codes for weed names are WSSA-approved codes from the *Composite List of Weeds of Weeds*, revised 1989. Available only on computer disk from WSSA, 810 East 10th Street, Lawrence, KS 66044–8897.

[b] Scientific names for plants and their respective codes: redroot pigweed, *Amaranthus retroflexus* AMARE; longspine sandbur, *Cenchrus longspinus* (Hack) Fern. CCHPA; common lambsquarters, *Chenopodium album* L. CHEAL; barnyardgrass, *Echinochloa crus-galli* (L.) Beauv. ECHCG; green foxtail, *Setaria viridis* L. SETVI; wild mustard, *Brassica kaber* (DC.) L.C. wheeler SINAR; hairy nightshade, *Solanum sarrachoides* Sendtner SOLSA; toothed spurge, *Euphorbia dentata* Michx. EPHDE; stinkgrass, *Eragrostis cilianensis* (All.) E. Mosher ERACN; common purslane, *Portulaca oleracea* L. POROL; wild buckwheat, *Polygonum convolvus* L. POLCO.

TABLE 2. Directional correlogram models for weed seed banks in irrigated corn fields. Models are for the direction of the crop rows (0°) and perpendicular to the crop rows (90°). Correlograms for other directions can be calculated using the parameters in Appendix.

				Direction from crop row (deg.)			
				0°		90°	
Sample	c_0	c_1	c_2	a_1	a_2	a_1	a_2
				m			
31AMA	0.31	0.16	0.15	14	170	64	85
31CCH	0.35	0.17	0.18	7	70	8	84
31CHE	0.37	0.14	0.23	39	89	64	55
31ECH	0.32	0.13	0.19	59	120	16	109
31SET	0.41	0.20	0.21	14	143	28	148
31SIN	0.47	0.32	0.15	12	60	45	40
31SOL	0.28	0.22	0.06	12	62	12	99
32AMA	0.14	0.01	0.13	9	152	5	46
32CHE	0.42	0.27	0.15	34	125	10	15
32ECH	0.18	0.14	0.04	51	51	8	15
32SET	—[a]	—	—	—	—	—	—
32SOL	0.22	0.05	0.17	10	120	8	42
33AMA	—	—	—	—	—	—	—
33CHE	—	—	—	—	—	—	—
33EPH	0.48	0.14	0.34	10	129	40	39
33SOL	0.27	0.18	0.09	8	45	7	49
34AMA	0.21	0.14	0.07	53	16	11	11
34CHE	0.33	0.21	0.12	7	44	8	11
34ERA	—	—	—	—	—	—	—
34POR	0.33	0.17	0.16	37	51	12	83
34SOL	0.14	0.08	0.06	7	63	5	74
41AMA	0.18	0.04	0.14	7	60	24	18
41CHE	—	—	—	—	—	—	—
41ECH	0.26	0.13	0.13	6	80	15	18
41POR	0.43	0.26	0.17	51	95	13	93
41SET	0.24	0.15	0.09	7	60	8	19
41SOL	0.14	0.04	0.10	25	32	10	25
42AMA	0.50	0.38	0.12	15	72	15	77
42ECH	0.48	0.22	0.26	7	37	25	17
42EPH	0.30	0.11	0.19	17	60	8	100
42PAN	0.33	0.15	0.18	28	95	7	75
42POL	0.35	0.07	0.28	12	118	11	127
42POR	0.44	0.32	0.12	15	41	20	13
42SET	0.27	0.15	0.12	14	75	11	66
42SOL	0.32	0.11	0.21	18	100	19	51
43AMA	0.33	0.06	0.27	6	80	31	14
43ECH	—	—	—	—	—	—	—
43EPH	—	—	—	—	—	—	—
43POR	0.71	0.65	0.06	42	36	7	23
43SET	—	—	—	—	—	—	—
44AMA	0.19	0.12	0.07	12	80	17	60
44ECH	0.29	0.21	0.08	22	56	15	67
44EPH	0.13	0.06	0.07	6	83	6	46
44SET	—	—	—	—	—	—	—
44SOL	0.24	0.16	0.08	54	29	8	38

[a] "—" indicates that no spatial dependence was detected.

Sample correlograms of most seed banks with spatial dependence decreased monotonically to a sill that was approximately zero in all directions. However, hole effects and zonal anisotropy were also observed. If the size, shape, and arrangement of patches of a seed bank create a periodic pattern in a direction, then the decrease in the directional sample correlogram will not be monotonic but will exhibit a hole effect. Correlogram values will increase over some separation distances because counts at these distances will be more strongly correlated than counts at some shorter separation distances (Isaaks and Srivastava 1989). Because processes that create the periodicity rarely act in all directions, a hole effect is usually present in a limited number of directions for a distribution (Trangmar et al. 1985). Three samples exhibited a hole effect for one of the sample correlograms. The hole effect of wild buckwheat (*Polygonum convolvus* L.) in Field 42 was in the direction of − 45° from the crop row as a result of two patches aligned in that direction. Wild mustard [*Brassica kaber* (DC.) L.C. Wheeler] and common lambsquarters (*Chenopodium album* L.) in Field 31 exhibited similar hole effects for the direction perpendicular to the crop row (Figure 2). Patches of those species were similar in size, shape, and alignment, but the patches did not coincide. Hole effects were not modeled because the distance at which the correlogram first reaches the sill is the range of spatial dependence (a). A correlogram model up to the distance a was sufficient for comparisons of spatial dependence among all samples. Spatial correlation of samples exhibiting a hole effect was modeled by visually estimating a in the direction of the hole effect from the sample correlogram and then fitting a correlogram model with the parameter a specified rather than estimated as part of fitting the model.

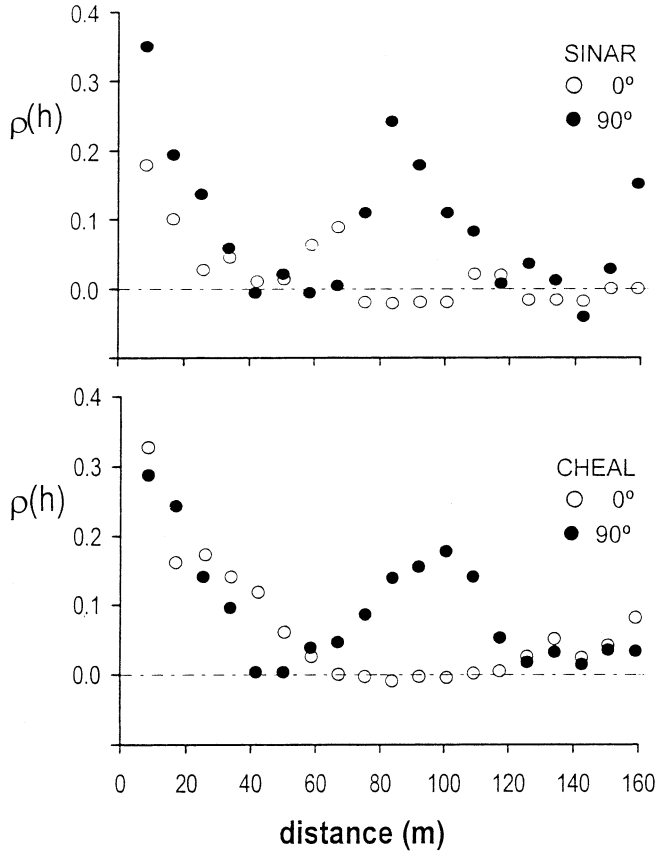

FIGURE 2. Sample and modeled correlograms (0 and 90° from the crop row) for common lambsquarters (31CHE) and wild mustard (31SIN) seed banks in Field 31. These seed banks had patches that created a periodic spatial pattern in the direction perpendicular to the crop row.

Sills of sample correlograms varied with direction for three seed banks (31AMA, 44AMA, 44ECH) because total variability of seed counts varied with direction. This varia-

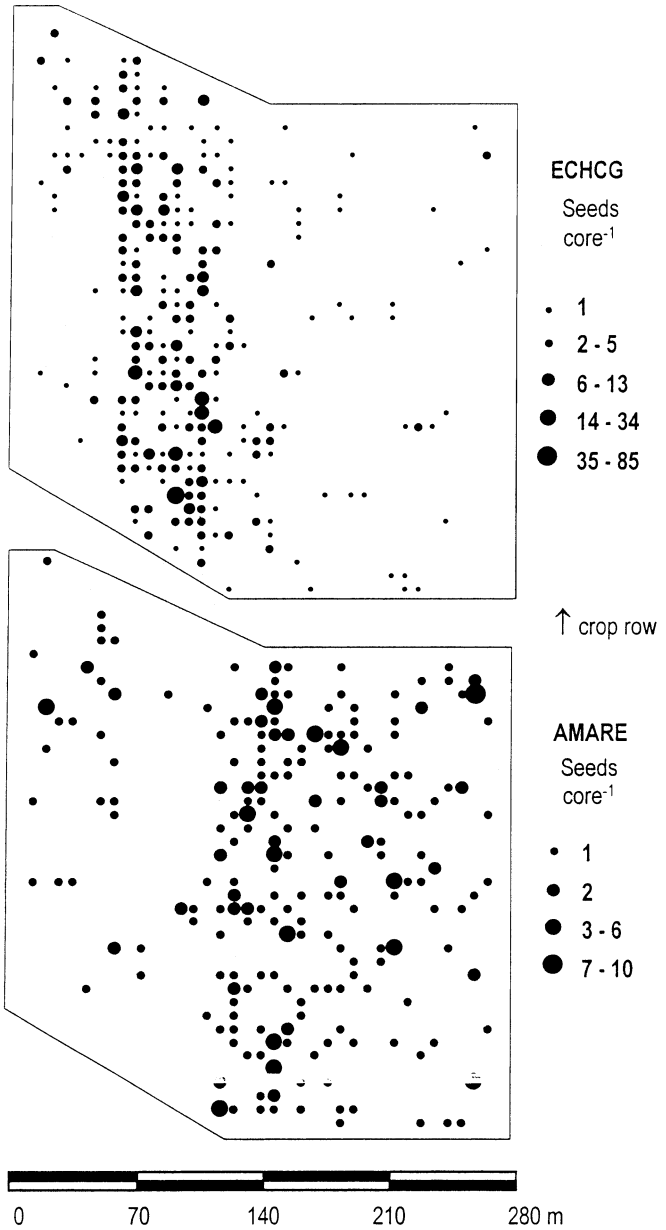

FIGURE 3. Seed banks of pigweed (44AMA) and barnyardgrass (44ECH) that had zonal anisotropy with a lower variability of seed counts in the direction of the crop row than in other directions.

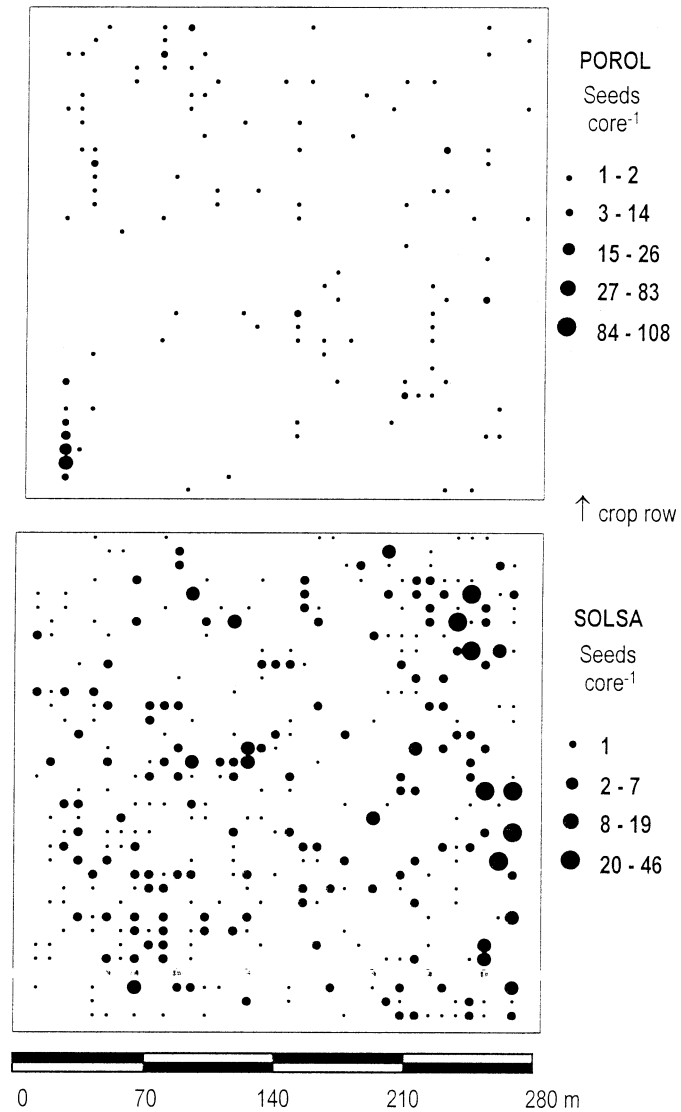

FIGURE 4. Seed banks with 71 (43POR) and 14% (34SOL) of the variability of seed counts explained by spatial pattern.

tion in the sill, called zonal anisotropy (Isaaks and Srivastava 1989), has been observed for weed seedling distributions (Colbach et al. 2000). For these seed banks, zonal anisotropy indicated the presence of two distinct spatial distributions that were created by nonuniform management within the field. With distinct distributions, variability in seed counts is higher when a sample correlogram includes pairs with points from both distributions instead of primarily pairs with points from a single distribution. For pigweed in Field 31, the sill was − 0.15 for 45, − 45, and 90° from the crop row but 0.30 for the direction of the crop row. The first four sample rows of Field 31 were adjacent to a feedlot, and the pigweed seed bank in those rows was four times larger (38.66 seeds core^{-1}) and more uniform (CV = 100%) than in the remainder of the field (data not shown). The different distributions in Field 44 were likely the result of soil compaction from a road that crossed the field at one time. The road was oriented in the direction of the crop row, and the sill in the row direction was 0.20 for barnyardgrass, 0.10 for pigweed, and slightly less than zero for the other directions (data not shown). Barnyardgrass seed bank density was 16 times greater (2.18 seeds core^{-1}) and about 20% less variable (CV = 279%) where the road had been compared with the rest of the field (Figure 3). In contrast, pigweed density was lowest where the road had been (Figure 3). Because pooling data across distinct spatial distributions can mask the spatial structure (Deutsch and Journel 1992), spatial analysis was done only for the more extensive of the two distributions of each seed bank (Table 1).

Correlogram Models

Variability Explained by Spatial Pattern

Spatial pattern accounted for less than half of the total variability of seed counts for 34 of the 36 samples with spatial dependence. That is, c_0 was greater than or equal to 0.50 for just pigweed in Field 42 and common purslane

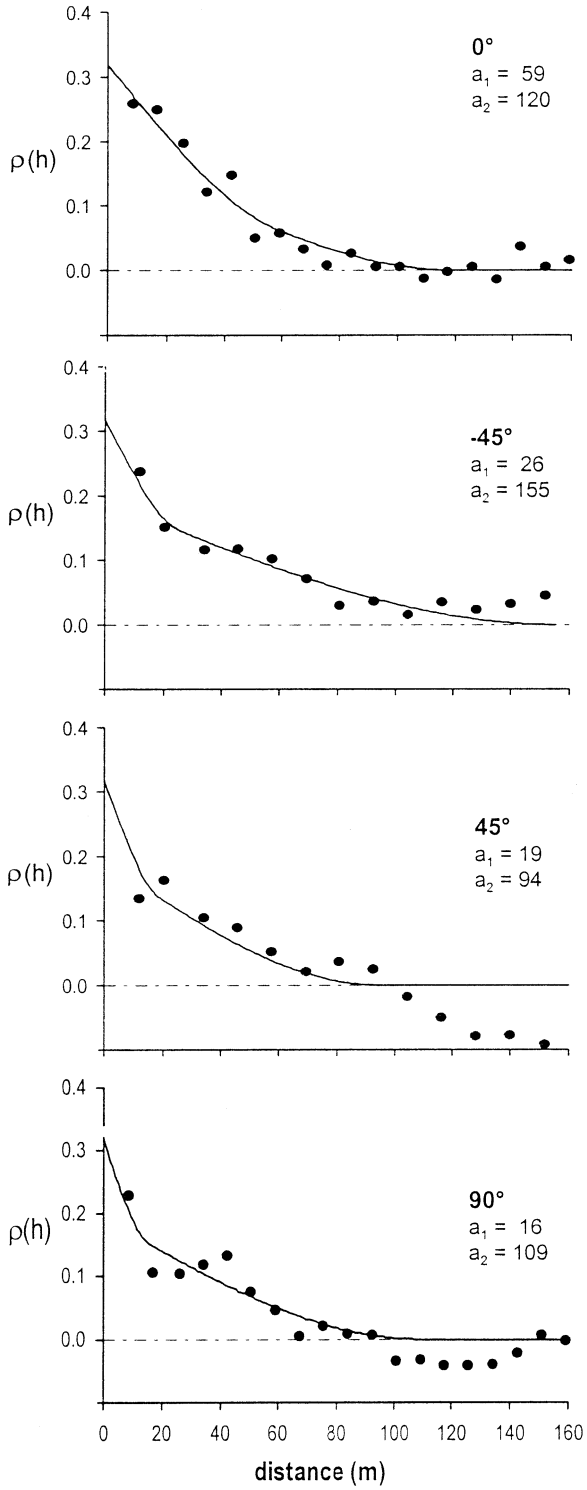

FIGURE 5. Sample and modeled correlograms for a barnyardgrass seed bank (31ECH). Directions are relative to the crop row, and directional correlogram models were derived from a model of spatial dependence estimated from all four sample correlograms.

(*Portulaca oleracea* L.) in Field 43 (Table 2). The average value of c_0 was 0.32, and c_0 did not vary much among seed banks (CV = 18%). The largest value of c_0 was 0.71 for common purslane in Field 43. Seed banks of common purslane and common lambsquarters exhibited the most spatial correlation. The average value of c_0 was only 0.48 for common purslane and 0.37 for common lambsquarters (Table

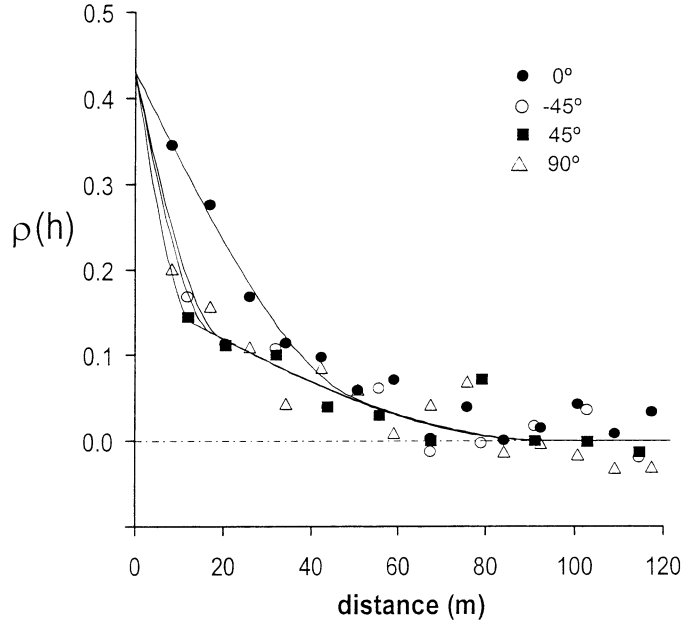

FIGURE 6. Sample and modeled correlograms for a common purslane seed bank (41POR) that had variation in spatial correlation with direction, yet ranges of spatial dependence did not vary with direction.

2), however, and two of the five common lambsquarters seed banks showed no spatial correlation. Seed banks of common purslane and common lambsquarters had small, distinct patches or seeds distributed along isolated sample rows with a smooth gradient from high to low seed counts in a row (Figure 4).

The smallest value of c_0 was 0.13 for a seed bank with little variability in counts (44EPH; Table 2). Seeds of toothed spurge (*Euphorbia dentata* Michx.) were found in 220 cores collected throughout the field, but just one seed was found in 82% of the cores, and the maximum count was only three seeds (Table 1). Seed banks of nightshade consistently had low spatial correlation with spatial pattern, explaining about 23% of the variability of counts across all seed banks (Table 2). For nightshade seed banks in Fields 31, 33, and 34, the largest seed counts were scattered throughout the field rather than being clustered (Figure 4). Dispersal of seed in berries may contribute to the low spatial correlation of nightshade seed banks. Spatial correlation of seed banks may be masked by both spatial variability in seed counts below the scale of sampling and errors arising from the tedious task of counting and identifying seeds. Limited spatial dependence and spatial correlation to only 3.2 to 6.9 m has been observed for seed banks of common lambsquarters and annual grasses (Cardina et al. 1996).

Spherical Models

Two spherical models were needed to describe a more rapid decline in spatial correlation over short distances than could be described with a single spherical model. Usually, spatial correlation decreased with distance more rapidly up to a distance of a_1 than for a_1 to a_2. Correlograms for barnyardgrass in Field 31 illustrate this decline in spatial correlation and variation in the decline with direction (Figure 5). Values of a_1 were small compared with the range of spatial dependence, and values varied with direction. The initial,

TABLE 3. Variation in the range of spatial dependence with direction of weed seed bank distributions in irrigated corn for seed banks showing spatial correlation.

Sample	Direction of maximum range	Anisotropy ratio[b]	Range of spatial dependence	
			Maximum	Mean
	deg.[b]		m	
31AMA	1	2.1	186	125
31CCH	−79	1.2	85	77
31CHE	60	2.7	154	94
31ECH	−40	1.5	156	118
31SET	51	1.1	160	150
31SIN	0	1.5	60	49
31SOL	−79	1.7	99	74
32AMA	−1	3.3	152	77
32CHE	0	8.3	125	34
32ECH	−2	3.4	51	25
32SOL	0	2.9	120	66
33EPH	2	3.2	130	69
33SOL	90	1.1	51	48
34AMA	10	10.9	110	32
34CHE	13	10.2	112	29
34POR	−65	2.4	115	71
34SOL	−62	1.3	80	69
41AMA	−1	3.5	60	30
41ECH	−1	4.7	80	32
41POR	90	1.1	100	97
41SET	0	3.2	60	31
41SOL	0	1.3	32	28
42AMA	−53	1.3	82	72
42ECH	−1	2.2	37	26
42EPH	−89	1.7	100	76
42PAN	3	1.3	95	84
42POL	63	1.1	144	135
42POR	−15	4.6	76	29
42SET	−7	1.2	75	69
42SOL	3	1.8	100	73
43AMA	−1	5.6	80	30
43POR	26	2.5	49	30
44AMA	0	1.3	80	69
44ECH	13	1.5	80	64
44EPH	−14	1.9	90	64
44SOL	56	2.4	60	39

[a] Ratio of the maximum range over the minimum range.
[b] Direction of the crop row is 0°, and − 90 and 90° are the directions perpendicular to the crop row. Positive values are degrees clockwise from the crop row, and negative values are degrees counterclockwise.

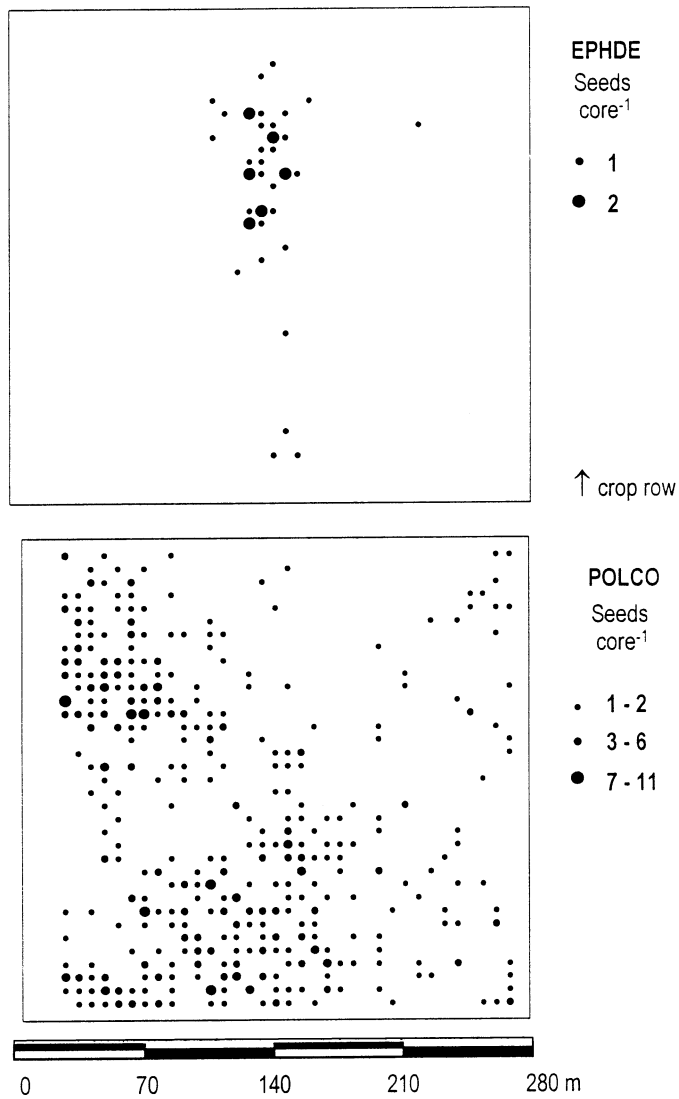

FIGURE 7. Examples of isotropic (42POL) and anisotropic (33EPH) seed bank distributions.

rapid decline accounted for 13% of the total variability in barnyardgrass seed counts (c_1 = 0.13) and 41% of the variability caused by spatial pattern ($c_1/(c_1 + c_2)$ = 0.41) (Table 2). In the direction of the crop row, a_1 was 59 m, which was 50% of the range of spatial dependence. Spatial correlation declined more rapidly in the other directions. The value of a_1 was 16 to 26 m and just 15 to 20% of the range of spatial dependence in the other directions. Values of a_1 (and a_2) in each direction were influenced by sample correlogram values in all four directions because the directional correlogram models come from a single model of correlation.

One of the two spherical models of a correlogram explained 92 to 93% of the variability in seed counts as spatial pattern for two samples (32AMA and 43POR). A single spherical model would have been sufficient for these samples. Across all samples, the first spherical structure accounted for 50% of the variability caused by spatial pattern (calculated from Table 2), and for the directions of 0, − 45, 45, and 90° from the crop row, the average value of a_1 was 17 m, and the average value of a_2 was 63 m (data not shown). Spatial correlation over short distances varied with direction even when the range of spatial dependence did not vary with direction. For example, the range of spatial dependence of common purslane in Field 41 was 93 to 95 m in the directions of 0, − 45, 45, and 90°, but a_1 ranged from 13 to 51 m (Figure 6).

Some values of a_1 were less than the distance between sampling locations (Table 2). With a_1 modeled as an ellipse, small values of a_1 were possible if spatial correlation was evident for several times the scale of sampling in some directional sample correlograms but was not evident or was limited to the scale of sampling in other directions. These values only indicate that the range of spatial dependence was less than the scale of sampling in that direction. Exact values are not meaningful. Data on a finer scale or knowledge of c_0 would be needed to confirm the small values. Currently, the error rate of enumerating seeds is unknown,

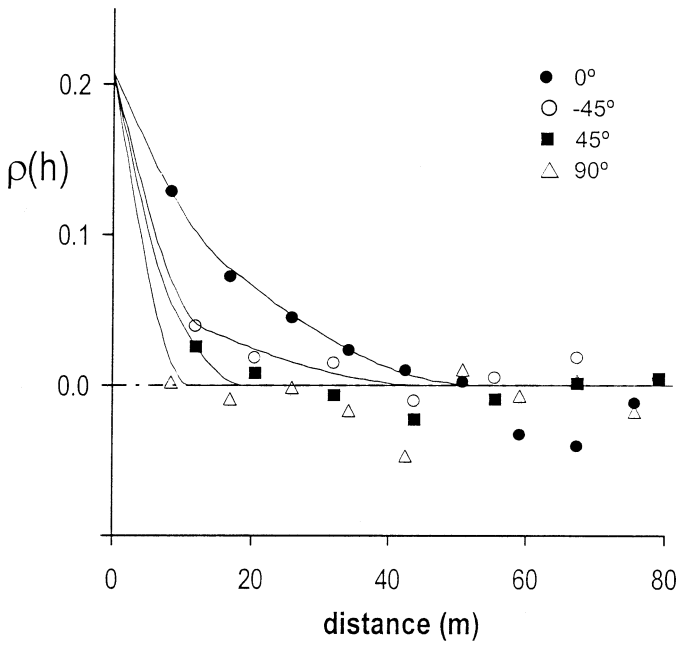

FIGURE 8. Sample and modeled correlograms for a pigweed seed bank (34AMA) that had a range of spatial dependence shorter than the scale of sampling in the direction perpendicular to the crop row but several times longer than the scale of sampling in the direction of the crop row.

and information about the short-scale variability of seed banks is minimal.

Range of Spatial Dependence

Seed bank density of some samples was correlated to longer distances than has been observed in previous studies. Mean range of spatial dependence of a seed bank was as small as 25 m (32ECH) and as large as 150 m (31SET), with a median value of 68 m (Table 3). The minimum range of spatial dependence was between 10 (34AMA) and 141 m (31SET), with a median value of 47 m, whereas the maximum range was 32 (41SOL) to 186 m (31AMA), with a median value of 88 m. Ranges of 5 to 42 m and 3 to 41 m have been observed for common lambsquarters and annual grass seed banks (Cardina et al. 1996). The range was approximately 69 m for total seed counts in another study (Halstead and Gross 1990).

Range of spatial dependence varied with direction, and many seed banks had elongated patches with the range of spatial dependence longest in the direction of the crop row (i.e., 33EPH; Figure 7). Patches like these have been observed for seedling and seed bank populations (Benoit et al. 1989; Colbach et al. 2000; Johnson et al. 1996; Wyse-Pester et al. 1999) and are consistent with the movement of seeds within a field during harvesting, tillage, and cultivation (Cousens and Mortimer 1995; Rew and Cussans 1997). Variation in the range of spatial dependence with direction is called geometric anisotropy, and the magnitude of anisotropy can be described by the ratio of the maximum range over the minimum range. The direction of the maximum range of spatial dependence of a distribution is called the direction of maximum continuity. For example, the ratio of anisotropy was 3.2 for the elongated patch of toothed spurge seeds in Field 33, and the direction of maximum continuity was 2°, with a range of 130 m (Figure 7; Table 2).

The range of spatial dependence was similar (i.e., within 20% of the maximum range) in all directions for just six samples (Table 3). For example, the range of spatial dependence varied only from 126 to 144 m for wild buckwheat in Field 42 (Figure 7). In contrast, the maximum range was at least twice the minimum range for 50% of the samples. The ratio of anisotropy was 4.6 to 10.9 for six samples, and maximum ranges were 59 to 110 m longer than the minimum ranges (Table 3). The largest ratios reflected the apparent movement of seeds primarily in the direction of the crop row (Table 3). For some seed banks, spatial dependence was not detected in the direction perpendicular to the crop row, although density was correlated for several times the scale of sampling in the direction of the crop row (Figure 8). For the 24 other samples with anisotropy, the average ratio was 2.2 ± 0.8. Distributions of common lambsquarters had the strongest anisotropy of the species found in more than one field, as well as the most spatial correlation (Tables 2 and 3). Nightshade and foxtail seed banks had the most isotropic distributions, with average ratios of less than 2. However, anisotropy is influenced by factors besides the dispersal characteristics of a species. Common purslane in Field 41 had the least variation in the range of spatial dependence with direction (ratio of 1.1), but other distributions of common purslane were anisotropic, with ratios of 2.4, 2.5, and 4.5 (Table 3; Figure 4).

Corresponding to the movement of seeds in the direction of the crop row, the direction of maximum continuity was within 3° of the direction of the crop row for 16 of the 36 seed banks showing spatial correlation (Table 3). In addition, seed counts were correlated to longer distances in the direction of the crop row than across rows for 26 samples (Table 2). The direction of maximum continuity was perpendicular to the crop row (90 ± 3°) for just three samples (33SOL, 41POR, 42EPH). However, the maximum range was just 5 m longer than the minimum range for common purslane in Field 41 and 6 m longer for nightshade in Field 33 (Table 3). For the seed banks without maximum continuity in the directions of 0 or 90°, the direction of maximum continuity was 45 ± 25° relative to the crop row. Actual directions were − 79 to − 7° and 10 to 63°.

Implications for Sampling Seed Banks

These results highlight the need to maximize the efficiency of sampling seed banks. A single core may not be representative of the seed bank in the immediate area, and closely spaced observations may be needed to make a map. However, the time and expense of sampling and analysis limits the feasibility of collecting numerous cores to improve the accuracy of estimates or maps of seed bank density. However, the observed spatial dependence should be interpreted in the context of the sampling plan. Detection of spatial dependence depends on both the sampling plan and the spatial distribution, and modifying a sampling plan may change the observed spatial dependence (Rossi et al. 1992).

Spatial pattern accounted for an average of only 32% of the variability of seed counts of the samples. Limited spatial correlation constrains the accuracy of seed bank maps. Reducing experimental error and the observed variability caused by short-scale spatial pattern may increase the spatial

dependence detected and improve the accuracy of a map or minimize the sampling needed. Mistakes in counting and identifying seeds may be the principal cause of experimental error, and reducing these errors could be a productive strategy to increase the efficiency of sampling and the accuracy of maps. The best approach will likely be using image analysis and other advanced technology for counting and identifying seeds (Buhler and Maxwell 1993). Increasing the size of the sample unit can mitigate variability from short-scale pattern (Burrough 1991; Weisz et al. 1995). Experimental error was reduced, and more spatial dependence was detected for infestations of Colorado potato beetle (*Leptinotarsa decemlineata* Say) when the size of the sampling unit was increased (Weisz et al. 1995). For soil properties, collecting and compositing cores from a larger area at each sampling location has effectively increased the size of the sample unit (Burrough 1991). This technique is worth considering for sampling weed seed banks.

A rectangular sampling grid should be more efficient for sampling weed seed banks than a square grid. Uncorrelated observations are needed to estimate the density of a seed bank, and correlated observations are needed to make a map. Compared with a square grid, the placement of sampling locations relative to the range of spatial dependence would be more appropriate with a sampling grid that is sized and oriented for expected anisotropy (Flatman et al. 1988). For the observed spatial dependence, a rectangular grid should have observations separated by distances that are 1.5 to 2.0 times greater in the direction of the crop row than across rows. With the variability of the range of spatial dependence among the seed banks, the actual grid size is more difficult to suggest than the relative spacing of observations. However, with a 130- by 95-m grid oriented in the direction of the crop row, adjacent observations would have been farther apart than the range of spatial dependence for 80% of the seed banks. That is, 80% of the seed banks had a range that was less than 130 m in the direction of the crop row and less than 95 m in the perpendicular direction (Table 2), and density would have been estimated only from uncorrelated observations. With a 55- by 30-m grid, adjacent observations would have been closer together than the range of spatial dependence for 80% of the seed banks. Ranges were greater than 55 m in the direction of the crop row and greater than 30 m for 90° from the crop row for 80% of the seed banks. However, spatial correlation declined rapidly over short distances. Consequently, more closely spaced observations would be needed for a more accurate or finer-scale map. Management practices and demographic characteristics of a weed species influence spatial distributions (Cousens and Mortimer 1995). These considerations for sampling may be useful only for seed banks in irrigated corn–bean–sugar beet rotations in the area of this study.

Interpolation for maps could be more accurate if common features of the spatial correlation of seed banks are modeled. Anisotropy varied between seed banks. Still, maps may be more accurate if spatial correlation is modeled using general assumptions about the nature of anisotropy rather than be modeled from limited sample data or using the implicit assumptions about anisotropy of some interpolation methods. Anisotropy and features of the decline in spatial correlation with distance can be specified by geostatistical methods for making maps like kriging and stochastic simulation (Isaaks and Srivastava 1989). The resulting maps will reflect both actual observations and the model of anisotropy (Deutsch and Journel 1992). Also, anisotropy can be indirectly modeled with interpolation methods like inverse distance weighting by selecting a search neighborhood that will estimate a value from more observations in the direction of maximum continuity than in other directions (Isaaks and Srivastava 1989).

A sampling plan based on the typical spatial correlation of weed seed banks will be a universal plan. That is, the plan will be most efficient, on average, for sampling many different types of seed bank distributions. The efficiency of sampling a particular field may be increased, at very little cost, by modifying a universal sampling plan for what is known about the spatial variability of the weed seed bank in that field. Growers and agricultural consultants can often describe the variability of the seed bank within a field based on knowledge of past weed populations and management. Modifications will depend on the intended management. Sampling without knowledge of multiple distributions may not lead to the best choice of uniform management, and the presence of the distinct spatial distributions may warrant variable management within a field. With multiple distributions in a field, sampling of a distribution might be reduced or eliminated if the area is small or if the information from the area would be irrelevant or misleading when mapping or estimating density. Sampling could be increased to delineate and describe the distributions within a field that will be managed independently. More than one sampling grid might be useful in a field if large areas have contrasting spatial distributions.

This research indicates that weed seed banks of different species and fields share common features of spatial correlation and that knowledge of these features could be valuable for researchers designing sampling plans for growers or research. In addition, a grower's or agricultural consultant's knowledge of the variability of a seed bank within a field may be valuable for choosing a more efficient sampling plan. We have provided a basis for beginning to develop sampling plans for seed banks in irrigated corn. Many of the features we observed are consistent with the spatial distributions of seed banks found in other studies, but only tentative, broad guidelines for sampling can be suggested until more comparative studies of the spatial correlation of seed banks are done. Whether sampling seed banks will be cost-effective for making management decisions is unclear, but potential methods to sample and map seed bank distributions more efficiently have not been exhausted.

Sources of Materials

[1] Reference to a trade or company name is for specific information only and does not imply approval or recommendation of the company by the USDA to the exclusion of others that may be suitable.

[2] SAGE2001: Spatial and Geostatistical Environment for Variography, Isaaks & Co.,1042 Wilmington Way, Rewood City, CA 94062.

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Appendix. Models of anisotropy for the spherical models of the correlograms (Equation 2) for seed banks showing spatial correlation.

Sample	First spherical model			Second spherical model		
	Minimum a_1	Maximum a_1	Direction of maximum a_1	Minimum a_2	Maximum a_2	Direction of maximum a_2
	m		deg.[a]	m		deg.
31AMA	15	63	86	90	186	1
31CCH	6	10	50	70	85	−79
31CHE	34	154	60	50	130	−26
31ECH	16	76	−10	97	156	−40
31SET	15	28	88	141	160	51
31SIN	12	50	88	40	60	0
31SOL	12	12	−77	58	99	−79
32AMA	5	20	26	46	152	−1
32CHE	10	37	2	15	125	0
32ECH	8	51	0	15	51	−2
32SOL	6	25	−38	42	120	0
33EPH	11	62	79	41	130	2
33SOL	7	9	42	45	51	90
34AMA	10	110	10	8	91	−35
34CHE	6	48	50	11	112	13
34POR	11	45	−10	48	115	−65
34SOL	4	20	31	60	80	−62
41AMA	7	25	−82	17	60	−1
41ECH	6	20	75	17	80	−1
41POR	12	53	−3	95	100	90
41SET	5	20	49	19	60	0
41SOL	10	25	4	25	32	0
42AMA	14	16	−35	64	82	−53
42ECH	7	29	81	17	37	−1
42EPH	7	16	2	60	100	−89
42PAN	6	27	5	75	95	3
42POL	8	59	−43	126	144	63
42POR	14	22	83	13	76	−15
42SET	10	25	35	64	75	−7
42SOL	17	20	56	55	100	3
43AMA	7	35	87	13	80	−1
43POR	7	45	−1	20	49	26
44AMA	10	41	56	60	80	0
44ECH	14	28	−21	53	80	13
44EPH	5	42	46	48	90	−14
44SOL	8	52	1	25	60	56

[a] Direction of the crop row is 0°, and the direction perpendicular to the crop row is 90°. Positive values are degrees clockwise from the crop row, and negative values are degrees counterclockwise.