Vertical movement of weed seed surrogates by tillage implements and natural processes

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Abstract

Vertical position of weed seeds in the soil column is one of the critical factors governing the density of emerged seedlings, but data on movement of subsurface seeds and seed surrogates by tillage are limited. In this experiment ceramic beads were seeded at 0, 4, 8, 12, 16 and 20 cm using specially constructed equipment. Plots were then tilled at right angles to the bead slots with either a moldboard plow, a chisel plow with curved blades, a chisel plow with straight blades, heavy tandem disks, a rotary tiller, or left untilled. Soil was sampled to determine bead positions. The probability matrix describing movement of beads from each soil layer to any other was estimated for each tillage regimen by maximum likelihood. Movement patterns for moldboard plow, the two chisel plow treatments, and disk and rotary tillage differed significantly. The difference between disking and rotary tillage was only marginally significant ($0.05 < P < 0.10$), as was the difference between the two chisel treatments. The chisel, disk and rotary tillage treatments all buried at least 70% of surface beads to below 2 cm but they showed little vertical displacement of beads below 10 cm. For example, beads below 14 cm in the chisel treatments had a $>80\%$ probability of remaining in at their original depth. Tillage by moldboard plow showed the expected soil inversion, but burial of surface beads was greater than return of buried beads to the surface. For example, the probability of a surface bead ending up below 10 cm was over 77\% whereas the probability of a bead originally in the 14–18 cm layer moving to the top 10 cm was only 44\%. Sampling of the no tillage and moldboard plow treatments the following spring showed an upward movement of beads by natural causes for beads below 14 cm. To allow flexibility in vertically structured population models, the movement probability matrices were fitted with a continuous model based on the beta distribution. The model showed that for a hypothetical uniformly distributed seed bank, 97\% of seeds in the top 4 cm following moldboard plowing had arrived there from greater depths. In contrast, only about one third of seeds in the top 4 cm of soil after tillage by chisel, disk or rotary tiller arrived from deeper layers.

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1. Introduction

Understanding the movement of weed seeds in the soil profile is critical to modeling the response of weed populations to tillage (Cousens and Moss, 1990; Mohler, 1993; Gonzalez-Andujar, 1997). Several studies have examined the incorporation of surface sown seeds and seed surrogates into the soil by tillage implements (Pawlowski and Malicki, 1968; Van Esso et al., 1986; Staricka et al., 1990; Moss, 1988; Yenish et al., 1996). Such studies are useful and realistic since the input of seeds to the soil occurs at the surface. Nevertheless, seeds of most species of agricultural weeds remain viable in the soil for several years (Roberts and Feast, 1972; Lewis, 1973; Chancellor, 1986), and study of the movement of surface seeds provides little useful information on the movement of seeds already in deeper layers of the soil. In particular, if good weed management practices deplete the surface seed bank, then knowing the probability that a seed will return to the surface by various tillage methods would facilitate further management of the seed bank.

Two previous studies have examined the probability of seed surrogates moving between multiple soil layers. Cousens and Moss (1990) excavated 1.5 m by 1.5 m by 0.2 m deep holes and filled them with alternating layers of soil and plastic beads. Each level received a different color of bead. They then plowed the plots with either a rigid tine implement or a moldboard plow, and smoothed the surface with a spring tine harrow and crumbler before sampling. They used their results to model the vertical distribution of seeds in the soil over multiple years under various scenarios that affect seed input. Limitations of this pioneering study included a small number of tillage regimens and severe disturbance of the soil profile during set-up of the experiment. The latter may have affected soil movement by the implements. Results from this study were used to parameterize a model analyzing the effects of crop rotation on seed banks (Jordan et al., 1995).

In the second study, colored plastic beads were placed at seven different depths in a trench, and several tillage implements were taken through the plots at right angles to the trench (Mead et al., 1998; Grundy et al., 1999). This allowed assessment of both the vertical and horizontal movement of the beads. The tillage implements they investigated are primarily used in vegetable cropping systems and included a spading machine, rotary tiller, spring tine harrow, and power harrow. The authors also combined results of their seed movement study with earlier work on depth of seedling emergence for nine weed species (Grundy and Mead, 1998) to predict relative density of seedlings following various tillage sequences.

The purpose of the study reported here was to determine (i) the probability of seed-like beads moving between various layers in the soil during tillage by several types of implements used in large-scale production of field crops, and (ii) the probability of movement by natural processes during intervals between tillage events. The usefulness of movement probability matrices for modeling is limited, however, because other processes included in depth stratified population models (e.g., seedling emergence, seed survival) will not usually be measured on the same intervals as movement. Consequently, an important goal of this study was the development of continuous movement probability models from the movement matrices.

2. Materials and methods

2.1. Bead placement, tillage and sampling

The experiment used a randomized complete block design with six treatments and six replications, and was run in both 1996 and 1997 at sites near Aurora, New York. Soil in both years was a moderately well drained Lima silt-loam (fine-loamy, mixed, mesic Glossoboric hapludalf) with a moderate density of irregular stones. The field used in 1996 had been in soybean the year before. The field used in 1997 had been in winter wheat the year before. To insure an exceptionally flat soil surface for the 1997 experiment, the field was chisel plowed, disked and worked diagonally with a springtooth harrow after wheat harvest. It was then planted with a cover crop of spring barley and the soil surface smoothed with a roller harrow. In both years, weeds were killed with glyphosate prior to planting seed surrogates. Additional applications of glyphosate were used to keep late-planted replications vegetation free, and rate varied depending on the target weeds. The boom
sprayer reached to the center of the plots without wheel tracking in the plots.

Brightly colored ceramic beads of approximately neutral density were drilled at depths of 0, 4, 8, 12, 16 and 20 cm using specially developed equipment that created minimal soil disturbance. The beads were Macroline ceramic spheres, ML1430, screened to a 0.50–0.85 mm diameter class in 1996 and to a 0.5–1.0 mm diameter class in 1997. Beads were dyed with acrylic ink. Each color was seeded at a rate of 6900 beads m\(^{-2}\) in 1996 and 6100 beads m\(^{-2}\) in 1997.

Because of the great depth of planting and the desire to minimize soil disturbance, planting was a two-step process in which slots were opened, and then beads were seeded into the slots with a separate piece of equipment. Slots were opened with 1 cm wide worn anhydrous ammonia knives spaced at 35.6 cm in two ranks on a double toolbar. To minimize heaving of the soil, the device was pulled slowly (2.5 km h\(^{-1}\)) and the entire frame and knife assembly was vibrated using a vibrator from a gravel tamper welded to the frame (5600 RPM in 1996 and 1400 RPM in 1997). A roller behind the slot opener pressed clods lifted by the knives back into position.

A special seed drill was constructed using three forage seeder boxes, which were each divided into multiple compartments by vertical partitions. Feeds on the boxes were individually adjusted to deliver at the desired rate. Each color of bead was placed at a different depth. The 4, 12 and 20 cm depths were sown in one set of slots, the 8 and 16 cm depths in a second set, and the 0 cm depth was dropped on the surface. Small horizontal wings below the delivery points for each bead color sealed the slots to prevent beads from dropping into deeper positions. The planter laid three pairs of rows per pass. Slow operating speed (0.7 km h\(^{-1}\) in 1996 and 1.0 km h\(^{-1}\) in 1997) and an observer stationed on the drill insured that the bead drops stayed in the previously formed slots to minimize soil disturbance. A roller behind the bead drill pressed clods lifted by the delivery knives back into position.

Tillage was applied at 90° relative to the planter tracks. Bead-sown areas of the plots were 6.4 m long in 1996 (three seeder passes) and 8.5 m long in 1997 (four seeder passes), but the tillage implement was run for several additional meters at both ends of each plot to ensure constant speed through the plot. Plots were nominally 4.9 m wide but actual tillage width varied with the implement. Tillage treatments were (1) no-till (two plots per replication), (2) heavy tandem disk only (Sunflower model 1211), (3) tractor mounted rotary tiller (Long model 1537 with L-shaped blades), (4) chisel plow (Brillion model CPP) with straight 5.2 cm wide shares followed by the same disk, (5) the same chisel plow but with curved 7.6 cm wide shares followed by the disk, and (6) moldboard plow (4-bottom International Harvester model 710) followed by the disk. Plots were tilled once. In 1997 the soil surface following disking was excessively rough, and all disked plots were roller harrowed (John Deere model 950).

To minimize time between tillage and soil sampling, one to three replications of the experiment were sown and tilled at a time. Beads were sown on 3 June, 28 June and 5 July 1996, and 25 June, 16 July and 4 August 1997. Tillage was completed within 2 days of sowing.

Depth of tillage was assessed on the day of tillage by shoving a meter stick vertically into the soil as far as it would easily go. Two to four such measurements were made near the end of each plot. After tillage, a heavy steel box was driven into the soil and soil was removed in layers. Boxes were 71 cm long to span both types of bead rows and the width was sized to the spacing of the tillage implement: 40.6 cm for moldboard plow, 30.5 cm for the chisel plows and 20.3 cm for the other implements. Sample layers were 0–2, 2–6, 6–10, 10–14, 14–18, 18–22 and 22–26 cm. The box was driven to the bottom of each successive layer, with the appropriate stopping position indicated by removable pins in the ends of the side plates (Fig. 1). The soil was then carefully removed to the bottom of the box using small trowels and a scraper/depth gauge that hung from the top of the box. When placing the boxes, the pair of bead rows was centered on the box using tapes stretched from flagged bead row positions in no-till plots and other untilled ground. Two samples were taken in each plot, and bulked by layer. Foot traffic was avoided outside the immediate vicinity of sample locations. An additional set of samples was taken the following spring (late April to mid-May) in undisturbed plot areas of the no tillage and moldboard plow treatments to assess bead movement by natural processes between tillage events.
Soil from each layer was crumbled by screening through 1.2 cm mesh, thoroughly mixed, and subsampled by weight. The subsamples were dried for storage. To separate the beads, the samples were wet screened with a dipping basket to remove silt and clay (Fay and Olson, 1978), and the coarse sand and gravel removed by screening with a 1.0 mm sieve. The beads were floated away from the remaining sand with a 20% (by weight) magnesium sulfate solution, dried, sorted by color and counted.

2.2. Supplemental controlled experiments

Anomalous results in the movement of beads between the summer post-tillage sampling and the following spring prompted two controlled experiments to explore the effects of floatation and frost heaving on bead movement.

Due to variation in the amount of air entrained into the ceramic beads, some floated in water. To test whether beads could float upward through macropores in the soil column during periods of soil saturation, four 5 cm diameter by 25 cm tall PVC tubes were filled with field soil that had been screened through a 1.2 cm mesh to remove stones. Beads of various colors were placed at 4 cm increments as the tubes were filled, with 100 beads placed at each level. The soil was then frozen solid at $-20^\circ$C. The sides of the tubes were warmed with warm water, the column slid out in slightly less than 4 cm increments (adjusted to compensate for settling in each tube) and increments were cut off with a warmed knife. The increments were thawed, wet screened to remove silt and clay, and the beads were sorted by color and counted.

To test for possible movement of beads by frost heaving, the same tubes used in the previous experiment were filled with soil and beads as in the experiment just described. The soil was saturated with the rain simulator, and the tubes were placed outside, above ground, and out of direct sunlight from 15 to 29 March 2002. The soil went through at least three freeze-thaw cycles, and ice needles were observed in the tubes. After removal from the field, the soil was frozen at $-20^\circ$C and beads were recovered as in the previously described experiment.

2.3. Data analysis

Multivariate analysis of variance (MANOVA) (SAS, 1996, proc GLM) of bead counts in the bead color by recovery depth matrices assessed differences in the movement patterns of the tillage regimens. Data were transformed to square roots first to stabilize variance. Non-independence between recovery depths was accounted for by using a repeated measures design with recovery depth as an analogue to sampling time. Each bead color (sowing depth) was analyzed separately. Differences between tillage treatments were considered significant if any bead color differed at $P < 0.05$. Since seeding rate differed in the 2 years, separate MANOVAs were used each year.

Since depth placement of the beads was not perfect, the probability of a bead moving from one soil layer to another could not be read directly from the color by recovery depth matrices. Instead, movement probabilities were estimated by maximizing the log of the likelihood given by

$$
\log L_T = \sum_i \sum_k o_{ik} \log \sum_j (m_{ij} \cdot n_{jk})
$$

where $L_T$ is the likelihood of beads in tillage regimen $T$ occurring at the observed recovery depths;
\( o_{ik} \) is the observed number of beads of starting position (color) \( k \) found in level \( i \); \( m_{ij} \) is the probability of a bead moving from level \( j \) to level \( i \) in the soil column, and \( n_{jk} \) is the number of beads of color \( k \) that started in position \( j \), as observed in the no-till treatment. The maximization algorithm was programmed in MATLAB (MathWorks, 1999) with the constraint that elements of \( M_T \) (i.e., \( m_{ij} \)) were positive and columns of \( M_T \) summed to 1, as required for a matrix of probabilities. The maximum likelihood analysis was performed both for individual plots and for treatments summed over replications within a year. The latter provided a best estimate of the movement probabilities for a given year, whereas the former were used to compute standard errors for the elements of \( M_T \).

Repeated measures MANOVA (SAS, 1996) was used to compare the movement matrices for the 2 years after arcsine square root transformation of the matrix elements to stabilize variance. Since year by movement interaction terms were not significant for any treatment, means over year of the matrix elements and of their standard errors are reported. Since only a few beads occurred in the 22–26 cm layer by accident, estimates of probability-of-movement from this layer were unreliable, and the 7 by 7 probability-of-movement matrices were reduced to 7 by 6 for reporting.

To allow computation of the probability-of-movement between soil layers divided differently than in the field experiments, a probability model was fitted to the probability-of-movement matrices. The process was analogous to fitting a regression surface to data, except that in this case, the data were the movement probabilities. Individual columns of each of the movement matrices were fitted to a beta distribution. Since the beta distribution is defined on the range 0–1, depths were rescaled from the original 0–26 cm range by dividing by 26. The beta distribution has the form

\[
P(a, b) = \frac{\Gamma(\alpha_1 + \alpha_2)}{\Gamma(\alpha_1)\Gamma(\alpha_2)} \int_a^b x^{(\alpha_1-1)}(1-x)^{(\alpha_2-1)} \, dx,
\]

\( 0 \leq x \leq 1 \)

where \( P \) is the probability of a bead moving to a soil layer between depths \( a \) and \( b \) (rescaled), \( \Gamma \) is the gamma function, and \( \alpha_1 \) and \( \alpha_2 \) are fitted parameters (Hoel et al., 1971, p. 148). This function was chosen for its ability to describe the data rather than for theoretical reasons. Computations were performed in MATLAB (MathWorks, 1999). The analysis produced a least squares fit in which the sum of the difference between probabilities in Table 2 and the integral of the beta distribution over the corresponding depth intervals were minimized.

To calculate beta distribution functions for particular starting locations, computed beta distribution parameter values for the sampled starting intervals were assumed to characterize the beta distributions at the center of those intervals. Parameter values for depths between adjacent interval center points were calculated by straight-line interpolation. Parameter values for starting positions from 0 to 1 cm and from 20 to 22 cm depths were set equal to those for 1 and 20 cm respectively. The resulting models were programmed into spreadsheets, and the probability-of-movement from any specified depth interval to any other specified interval was then calculated by (i) integrating the beta distribution over the specified arrival interval and (ii) averaging the resulting values for those starting positions that lay within the specified starting interval.

Several column vectors for movement from summer to spring in the moldboard plow treatment could not be fit with a beta distribution. For this probability-of-movement matrix, the spreadsheet was divided into 0.2 cm increments, and the probability of a bead moving to any particular 0.2 cm increment was assumed to be 1/20 of the probability of moving to the 4 cm increment within which the smaller increment lay. All columns of the summer to spring no-till matrix could be fit with the beta distribution and were treated as in the movement by tillage models except for the 0–2 cm column which was treated as for columns of the summer to spring moldboard plow matrix. Microsoft Excel spreadsheets implementing the probability models are available at cost from the corresponding author.

Whether a particular weed infestation derives primarily from seeds that were deep in the soil prior to tillage depends in practice on the vertical distribution of the seed bank as well as the movement probabilities. The depth distribution after tillage can be derived from the distribution before tillage by...
matrix multiplication (Cousens and Moss, 1990; Grundy et al., 1999):

\[
\begin{bmatrix}
  n_{1,i+1} \\
  n_{2,i+1} \\
  \vdots \\
  n_{m,i+1}
\end{bmatrix}
= 
\begin{bmatrix}
  P_{11} & P_{12} & \cdots & P_{1m} \\
  P_{21} & P_{22} & \cdots & P_{2m} \\
  \vdots & \vdots & \ddots & \vdots \\
  P_{m1} & P_{m2} & \cdots & P_{mm}
\end{bmatrix}
\times
\begin{bmatrix}
  n_{1,i} \\
  n_{2,i} \\
  \vdots \\
  n_{m,i}
\end{bmatrix}
\]

where \( n_{i,i} \) is the number in layer \( i \) before tillage, \( n_{i,i+1} \) is the number in that layer after tillage, \( p_{ij} \) is the probability of a seed moving from layer \( j \) to layer \( i \), and \( m \) is the number of layers. To illustrate the use of the movement probability models, seeds were assumed to be uniformly distributed between 0 and 26 cm and the movement probabilities were aggregated in two soil layers: 0–4 cm and 4–26 cm. The soil profile was divided into these two layers for the illustration since most weed seedlings arise from the top 4 cm of soil (Chancellor, 1964; Grundy and Mead, 1998).

3. Results

Excavation of bead tracks before tillage showed that the surface soil was cracked to a depth of 5–10 cm, but that few surface clods were inverted. Disturbance deeper in the profile was confined to the slot. For all tillage implements, soil following tillage in the bead-sown areas appeared indistinguishable from that in adjacent unseeded ground.

Measurements of the depth of loosened soil indicated that the plows penetrated roughly to the depth of the customary plow layer (20 cm) whereas tillage by disk and rotary tiller was shallower (Table 1). Tillage depth varied by a few centimeters between years and among tillage operations within a year.

3.1. Bead movement by tillage implements

MANOVAs comparing the bead color by recovery depth data between tillage regimens indicated that all of the tilled treatments differed significantly from the no-till treatment in both years. Moldboard plow differed from other tilled treatments, and the chisel plow treatments differed from shallower tillage by disk or rotary tiller. However, only a marginally significant difference (\( P < 0.1 \)) between the two chisel plow treatments was detected in 1 year, 1997. Similarly, rotary tillage and disking only differed marginally in 1 year, 1996.

Probability-of-movement matrices showed that the disk and rotary tiller mixed the surface 10 cm but produced less disturbance below 10 cm (Table 2). The effect of both of these implements was to bury the surface 0–2 cm layer but move the 6–10 cm layer upward in the profile. Thus, these implements perform a partial inversion of the surface soil. Nevertheless, the probability of a bead remaining roughly in its original position was substantial with these implements, and it

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Mean depth (cm)</th>
<th>S.D. within operations&lt;sup&gt;a&lt;/sup&gt; (cm)</th>
<th>S.D. of operation means&lt;sup&gt;b&lt;/sup&gt; (cm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1996</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Disk only</td>
<td>10.4</td>
<td>1.9</td>
<td>1.5</td>
</tr>
<tr>
<td>Straight chisel</td>
<td>21.5</td>
<td>0.3</td>
<td>0.4</td>
</tr>
<tr>
<td>Curved chisel</td>
<td>20.3</td>
<td>1.7</td>
<td>0.8</td>
</tr>
<tr>
<td>Rotary tillage</td>
<td>14.2</td>
<td>1.8</td>
<td>1.7</td>
</tr>
<tr>
<td>Moldboard plow</td>
<td>22.0</td>
<td>1.9</td>
<td>1.4</td>
</tr>
<tr>
<td>1997</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Disk only</td>
<td>12.0</td>
<td>2.0</td>
<td>0.9</td>
</tr>
<tr>
<td>Straight chisel</td>
<td>23.1</td>
<td>1.4</td>
<td>0.6</td>
</tr>
<tr>
<td>Curved chisel</td>
<td>24.6</td>
<td>1.6</td>
<td>2.1</td>
</tr>
<tr>
<td>Rotary tillage</td>
<td>14.5</td>
<td>1.7</td>
<td>0.7</td>
</tr>
<tr>
<td>Moldboard plow</td>
<td>21.4</td>
<td>1.3</td>
<td>0.5</td>
</tr>
</tbody>
</table>

<sup>a</sup> Mean standard deviations of depth measurements taken in replications tilled on a particular date. This is a measure of spot-to-spot variation in tillage depth.

<sup>b</sup> Standard deviation of depth measurements means computed from replications tilled on various dates. This is a measure of variation in tillage depth among tillage events.
The chisel treatments produced a relatively symmetrical displacement of beads away from their original depth. A small but consistent net downward displacement, however, occurred at all depths. The chisel treatments were effective at burying surface beads into the 2–6 and 6–10 cm layers. The probability of a bead remaining in its original position increased with depth in the chisel treatments.

As expected, the moldboard plow treatment showed pronounced inversion of the soil profile.
To this depth Movement from this depth

<table>
<thead>
<tr>
<th>To this depth</th>
<th>0–2 cm</th>
<th>2–6 cm</th>
<th>6 to cm10</th>
<th>10–14 cm</th>
<th>14–18 cm</th>
<th>18–22 cm</th>
</tr>
</thead>
<tbody>
<tr>
<td>0–2 cm</td>
<td>0.957 ± 0.062</td>
<td>0.034 ± 0.050</td>
<td>0.006 ± 0.015</td>
<td>0.001 ± 0.003</td>
<td>0.000 ± 0.002</td>
<td>0.008 ± 0.018</td>
</tr>
<tr>
<td>2–6 cm</td>
<td>0.000 ± 0.055</td>
<td>0.950 ± 0.070</td>
<td>0.106 ± 0.102</td>
<td>0.000 ± 0.002</td>
<td>0.001 ± 0.005</td>
<td>0.005 ± 0.013</td>
</tr>
<tr>
<td>6–10 cm</td>
<td>0.019 ± 0.008</td>
<td>0.000 ± 0.059</td>
<td>0.861 ± 0.115</td>
<td>0.109 ± 0.063</td>
<td>0.000 ± 0.006</td>
<td>0.005 ± 0.018</td>
</tr>
<tr>
<td>10–14 cm</td>
<td>0.011 ± 0.003</td>
<td>0.000 ± 0.006</td>
<td>0.013 ± 0.041</td>
<td>0.825 ± 0.079</td>
<td>0.593 ± 0.139</td>
<td>0.000 ± 0.084</td>
</tr>
<tr>
<td>14–18 cm</td>
<td>0.004 ± 0.005</td>
<td>0.004 ± 0.000</td>
<td>0.000 ± 0.012</td>
<td>0.060 ± 0.020</td>
<td>0.395 ± 0.137</td>
<td>0.446 ± 0.143</td>
</tr>
<tr>
<td>18–22 cm</td>
<td>0.009 ± 0.005</td>
<td>0.007 ± 0.003</td>
<td>0.013 ± 0.014</td>
<td>0.000 ± 0.007</td>
<td>0.002 ± 0.003</td>
<td>0.530 ± 0.143</td>
</tr>
<tr>
<td>22–26 cm</td>
<td>0.000 ± 0.002</td>
<td>0.006 ± 0.002</td>
<td>0.001 ± 0.013</td>
<td>0.003 ± 0.001</td>
<td>0.008 ± 0.005</td>
<td>0.006 ± 0.015</td>
</tr>
</tbody>
</table>

Thus, the most likely resting position for a bead initially between 0 and 6 cm was 14–18 cm, whereas many beads initially at 14–18 cm moved nearer to the soil surface. Beads initially in the 18–22 cm layer appeared to move downward.

3.2. Bead movement between tillage events

MANOVAs comparing recovery depths in the summer shortly after tillage to recovery depths the following spring indicated some movement of beads by natural processes occurred in both the no-till and moldboard plow treatments. The most significant movements occurred below 10 cm depth. This movement consisted primarily of an upward drift of beads in the 14–18 cm and 18–22 cm layers (Table 3). Overall, beads in the surface layers of the no-till treatment moved little by natural processes whereas beads in the surface and middle layers of the moldboard plow treatment showed substantial upward and downward scatter from their initial post-tillage positions.

3.3. Bead movement in supplemental controlled experiments

In 4 replicate trials of 100 beads placed in water and stirred, 67.9% floated (S.E. of 2.3%). Of 2000 beads in the saturation and tapping experiment (4 replicate tubes, 5 colors/levels, 100 beads of each color) only 30 were found outside of their original placement layer. Of these 10 moved down, 3 moved up and 22 were in residual soil that clung to a tube and could not be assigned to a position. Thus, only 0.66% of the beads could be shown to have moved, and most of these moved downward.

Results for the freeze-thaw experiment were similar. Nine beads moved upward, 22 moved downward, and 17 were left on a tube. Thus, only 1.6% of the beads could be shown to move and most of these moved downward. Neither experiment gave any indication that depth affected the likelihood of a bead moving from its original position.

3.4. Statistical modeling of movement probabilities

Fits of the beta distribution to columns of the tillage movement matrices were good. In most cases, the proportion of variance accounted for by the beta distribution exceeded 0.95 and some values approached 1.0 (Table 4). Values of the beta distribution parameters showed systematic change with starting depth (Table 4). This justifies the interpolation between starting depths used in constructing the spreadsheet probability models.
The utility of modeling movement probabilities can be illustrated by computing the probability of a bead moving from below 4 cm to the surface 0–4 cm layer from which most weed seedlings emerge. For all tillage regimens other than moldboard plow, the probability of beads in the surface 4 cm layer remaining in place during tillage was roughly an order of magnitude greater than the probability that a bead deep in the soil will be carried to the surface (Table 5). The pattern was reversed for moldboard plow tillage. Note that such probabilities could not be deduced from the matrices in Table 2 without a probability model.

4. Discussion

4.1. Bead movement by tillage

Beads were used in this study rather than actual seeds for several reasons. First, coloring actual seeds intensely enough that several colors could be identified after burial would be extremely laborious and would inevitably require significant seedling loss due to extraneous factors. A second, related, reason is that the movement of the beads from one soil stratum to another that we observed is qualitatively similar to the movement of dyes with which we have studied the movement of soil aggregates in our laboratory. Thus, we can assume that the movement of the beads is representative of the movement of actual seedling roots. The model used to describe the movement of the beads is based on the beta distribution. The beta distribution is given by

\[ P(a, b) = \frac{\Gamma(a_1 + a_2)}{\Gamma(a_1)\Gamma(a_2)} \int_0^b x^{(a_1-1)}(1-x)^{(a_2-1)} \, dx \]

and describes the probability of a bead’s moving to the strata lying between depths \(a\) and \(b\). In the equation \(x\) (and hence \(a\) and \(b\)) are rescaled from the original interval of 0–26 cm to the interval 0–1 for mathematical reasons (see text).

\(a\) Strata are represented by their mid-points since that is how the equations are used (see text).

\(b\) Variance explained was rounded to two decimal places, which resulted in some very good fits appearing to be perfect fits.

### Table 4

Parameters of the beta distribution and proportion of variance explained by the equation for starting depths corresponding to the mid-points of sample increments for each of the five tillage regimens

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Parameter</th>
<th>Movement froma</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>1 cm</td>
</tr>
<tr>
<td>Disk only</td>
<td>(a_1)</td>
<td>0.960</td>
</tr>
<tr>
<td></td>
<td>(a_2)</td>
<td>4.192</td>
</tr>
<tr>
<td></td>
<td>Variance explainedb</td>
<td>0.99</td>
</tr>
<tr>
<td>Rotary tiller</td>
<td>(a_1)</td>
<td>1.597</td>
</tr>
<tr>
<td></td>
<td>(a_2)</td>
<td>5.213</td>
</tr>
<tr>
<td></td>
<td>Variance explained</td>
<td>0.95</td>
</tr>
<tr>
<td>Straight chisel</td>
<td>(a_1)</td>
<td>1.616</td>
</tr>
<tr>
<td></td>
<td>(a_2)</td>
<td>4.682</td>
</tr>
<tr>
<td></td>
<td>Variance explained</td>
<td>0.89</td>
</tr>
<tr>
<td>Curved chisel</td>
<td>(a_1)</td>
<td>1.367</td>
</tr>
<tr>
<td></td>
<td>(a_2)</td>
<td>4.490</td>
</tr>
<tr>
<td></td>
<td>Variance explained</td>
<td>0.96</td>
</tr>
<tr>
<td>Moldboard plow</td>
<td>(a_1)</td>
<td>2.897</td>
</tr>
<tr>
<td></td>
<td>(a_2)</td>
<td>2.734</td>
</tr>
<tr>
<td></td>
<td>Variance explained</td>
<td>0.83</td>
</tr>
</tbody>
</table>

The beta distribution is given by

\[ P(a, b) = \frac{\Gamma(a_1 + a_2)}{\Gamma(a_1)\Gamma(a_2)} \int_0^b x^{(a_1-1)}(1-x)^{(a_2-1)} \, dx \]

and describes the probability of a bead’s moving to the strata lying between depths \(a\) and \(b\). In the equation \(x\) (and hence \(a\) and \(b\)) are rescaled from the original interval of 0–26 cm to the interval 0–1 for mathematical reasons (see text).

\(a\) Strata are represented by their mid-points since that is how the equations are used (see text).

\(b\) Variance explained was rounded to two decimal places, which resulted in some very good fits appearing to be perfect fits.

### Table 5

Probabilities of a bead moving between the surface 0–4 cm layer of the soil and a deeper 4–26 cm layer as computed from the spreadsheet models (probabilities associated with staying at a given depth are shown in bold)

<table>
<thead>
<tr>
<th>To this depth</th>
<th>Movement from this depth</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>0-4 cm</td>
</tr>
<tr>
<td>Disk only</td>
<td>0.482</td>
</tr>
<tr>
<td></td>
<td>0.518</td>
</tr>
<tr>
<td>Rotary tiller</td>
<td>0.342</td>
</tr>
<tr>
<td></td>
<td>0.658</td>
</tr>
<tr>
<td>Straight chisel</td>
<td>0.341</td>
</tr>
<tr>
<td></td>
<td>0.659</td>
</tr>
<tr>
<td>Curved chisel</td>
<td>0.409</td>
</tr>
<tr>
<td></td>
<td>0.591</td>
</tr>
<tr>
<td>Moldboard plow</td>
<td>0.013</td>
</tr>
<tr>
<td></td>
<td>0.987</td>
</tr>
</tbody>
</table>

The utility of modeling movement probabilities can be illustrated by computing the probability of a bead moving from below 4 cm to the surface 0–4 cm layer from which most weed seedlings emerge. For all tillage regimens other than moldboard plow, the probability of beads in the surface 4 cm layer remaining in place during tillage was roughly an order of magnitude greater than the probability that a bead deep in the soil will be carried to the surface (Table 5). The pattern was reversed for moldboard plow tillage. Note that such probabilities could not be deduced from the matrices in Table 2 without a probability model.
distinguished after the seeds were recovered from the soil would be difficult. Second, if the seeds were alive, some would have germinated before recovery. Since germination would be more likely for seeds near the soil surface, germination would distort the depth distribution of the remaining seeds. Conversely, if the seeds were killed (e.g., by heat treatment) prior to planting, seeds in the deeper, moister layers of soil would likely have decomposed faster, again distorting the depth distribution. Most studies that have compared the movement of surface sown seeds and beads have shown that the movement patterns of beads and seeds by tillage implements were indistinguishable (Moss, 1988; Staricka et al., 1990; Starika et al., unpublished). Similarly, Soriano et al. (1968) found no appreciable difference in the distribution of surface sown seeds of alfalfa and linseed even though the two species differ in seed shape and seed coat characteristics. Rötele and Koch (1981) found a slightly shallower distribution of plastic beads relative to Galium aparine seeds after one plowing; the difference became more pronounced after a second plowing. The two studies by Staricka et al. (1990, unpublished) used the same type of ceramic spheres used in the study reported here. Unlike plastic beads, the ceramic beads had a density similar to that of real seeds due to entrained air bubbles.

No statistical difference was detected between years in the movement pattern for any tillage regimen. This may seem surprising in that a roller harrow was used on all but the rotary tilled treatment in 1997 but not in 1996. Penetration of the roller harrow was shallow (<5 cm), and this was the most mixed layer of the soil for all implements anyway. Probably the harrow had some effect on seed distribution, but given the statistical power of the comparison (N = 30), the effect must have been small.

The disk, rotary tiller and chisel plow all mixed the surface 0–10 cm of soil in a roughly similar way, and produced progressively less disturbance of deeper beads (Table 2). For all of these tillage regimens, the probability of finding a bead that was initially on the soil surface peaked between 2 and 10 cm.

In contrast, the moldboard plow produced the skewed bell shaped distribution of surface sown beads found by other investigators (Pawlowski and Malicki, 1968; Rötele and Koch, 1981; Van Esso et al., 1986; Moss, 1988), with the peak probability at 14–18 cm. The movement by the moldboard plow was, however, not a simple inversion of the soil column. For example, the probability that a surface bead moved downward more than 10 cm was 0.70 whereas the probability that a bead in the 14–18 cm layer moved upward more than 8 cm was only 0.30. Overall, the moldboard plow was more effective at burying beads than at bringing them to the surface. Nevertheless, it produced a higher probability of moving deeply buried beads upward in the soil profile than other implements.

Apparently, the moldboard plow only occasionally penetrated to the 20 cm depth, and consequently, most beads planted at 20 cm remained in place. Because the moldboard plow incorporated much air into the soil, however, the soil surface raised, leading to the apparent downward movement of beads in the 18–22 cm layer. This effect probably also contributed to the overall tendency toward net downward movement noted above. Similar loosening of the soil probably accounted for the apparently greater probability of bead movement downward than upward in the chisel plow treatments (Table 2), and likely affected the movement matrices for disk and rotary tillage as well.

The apparent downward movement of beads at 20 cm by the moldboard plow indicates that field measurements of the depth of tilled soil (Table 1) did not reflect actual tillage depth. The field measurements do probably reflect relative depths of tillage among primary tillage implements and provide some indication of variability in tillage depth within a given regimen. The within operation standard deviation in Table 1 represents an upper estimate of the actual spot-to-spot variation in tillage depth since the measuring stick probably sometimes struck a rock before reaching the bottom of the tilled layer. Although the plows were adjusted for depth with each use, tillage depth still varied by a few centimeters between periods of operation, largely due to variation in soil moisture. The disk and rotary tiller were always run at maximum depth and so their penetration necessarily varied with soil moisture. Such variation is normal and expected. It implies, however, that any given movement probability matrix in Table 2 should be interpreted as the average behavior of beads subjected to that tillage regimen rather than the expected behavior of beads on a particular day or in a particular field.

All implements tended to bury surface beads to a substantial extent, with least incorporation by disk
only and most by moldboard plow (Table 2). The lesser incorporation of surface beads by disk only relative to the chisel plow treatments is reasonable since the latter were also disked after chiseling.

The greater incorporation of surface beads by rotary tillage relative to disk (Table 2) accords with results of Hulburt and Menzel (1953), who found that whereas 49% of surface sown P32 was incorporated to below 5 cm by one pass with a rotary tiller, only 22% was incorporated that deeply by a disk. Apart from the slightly greater movement of surface beads, the overall pattern of bead movement by rotary tillage and disking in the present study was similar. Both implements move soil in an arc, and the diameter of rotation of the two types of blade was similar. The shallower working depth of these implements relative to the plows (Table 1) may explain their tendency to move deeply buried beads upward. If the blades occasionally grazed into the top of a band of beads, the only possible direction of movement would have been upward.

The marginally significant (0.05 < P < 0.10) difference between the two types of chisel plow was due to a slightly greater downward movement of beads in the 6–10 cm layer with the curved chisel (Table 2). The greater tendency of the curved chisel to bury surface crop residue (Mohler and Frisch, personal observation) was not reflected in the bead data, but particles of crop residue differ greatly from beads and weed seeds in size, shape and density. Similar to the results reported here, Staricka et al. (1990) found that most surface sown seeds and seed surrogates moved to between 2 and 8 cm depth with chisel tillage.

4.2. Movement of beads between tillage events

The upward movement of beads in the 14–18 and 18–22 cm layers between summer tillage and the following spring is a mystery (Table 3). Such movement in the moldboard plow treatment might be expected since the soil there was greatly loosened and then presumably settled again over the winter. Greater upward movement in the deeper layers than in shallow layers due to settling would be expected, since the effect is cumulative with distance from the soil surface. Upward movement was equally great in the no-till treatment, however, and occurred to some extent in all layers. The soil surface in the no-till treatment was raised by 1–2 cm due to soil cracking during the seeding process, and then settled during the winter. This small amount of loosening can scarcely account for the substantial upward movement of beads in the no-till, and in any case, the degree of loosening was far less in the no-till than in the moldboard plow treatment. The fields, including the no-till treatment, were plowed the year before initiation of each experiment, and some of the upward movement may have been due to residual settling during the period of observation.

Another possible explanation for the upward movement of beads relates to their specific gravity. Individual spheres varied in density, and most could float. Conceivably, spheres may have migrated upward through macropores by floatation during periods of soil saturation in the spring. Greater upward migration would be expected from deeper layers where the soil remains saturated for longer periods. If this is the explanation for the upward movement of beads from summer to spring, then it would apply to propagules of many weed species also, since many float (Kelley and Bruns, 1975; Wilson, 1980). Floatation would not have affected measurement of bead movement by tillage implements since the soil was never saturated between tillage and sampling. The supplemental laboratory experiment to determine whether beads can float upward in soil indicated that they did not. Macropores were probably larger in the field soil than in the soil in the experimental tubes, which may make upward floatation more likely in the field. The vibration applied by tapping the tubes, however, would have favored floatation in the laboratory experiment relative to field conditions.

Conceivably, frost heaving could have caused some upward movement of beads in the field. The lack of net upward movement in the small controlled experiment on frost heaving makes this possibility appear unlikely.

The substantial non-directional scatter of beads from their original post-tillage position in the moldboard plow treatment (Table 3) may relate to a lower degree of certainty regarding their starting position. Since beads of all colors were distributed throughout the soil column after tillage by moldboard plow (Table 2), accurately assessing movement between layers was more difficult for moldboard plow than for no-till. This is reflected in the larger standard errors for moldboard plow relative to no-till (Table 3).
4.3. Modeling movement probabilities

Since most weed seedlings emerge from the top few centimeters of soil it is worthwhile determining whether the seed bank near the surface is composed primarily of seeds that remained in place during tillage or whether many seeds were carried up from deeper layers of the soil. If a tillage regimen brings many seeds to the surface, then avoiding that form of tillage would be wise following a year in which the surface seed bank had been depleted by good weed management.

Moldboard plow tillage had about twice the probability of bringing deeply buried beads into the surface 4 cm of soil relative to other tillage regimens (Table 5). The other regimens were all roughly equivalent. Conversely, however, moldboard plow tillage was 26–37 times more effective at removing beads from the surface 4 cm than the other types of tillage. In principal, deep burial of species with short survival times in the soil can effectively limit weed populations (Mohler, 2001).

Assuming that a seed bank was uniformly distributed within the top 26 cm of soil and that the seeds moved like the beads in this study, then the origin of seeds in the surface 4 cm layer is given in Table 6. For most tillage regimens about 2/3 of the seeds were already in the surface layer prior to tillage, but only 3% of the post-tillage seeds were already near the surface with moldboard plowing. Based on these calculations, moldboard plowing should be avoided if the surface seed bank has been successfully depleted during the previous season, and the other tillage regimens are about equally good at preventing seed return to the soil surface.

This result only indicates a general tendency. The effect of a tillage regimen on the subsequent weed density of a field will depend on the actual depth distribution of seeds prior to tillage and the probability of seedlings emerging from seeds at various depths. Use of movement probabilities in dynamic models that take these and other factors into account should provide a powerful tool for understanding the population dynamics of weeds in agricultural systems.

5. Conclusions

The disk, rotary tiller and chisel plows all mixed the surface soil but displaced relatively few beads below 10 cm. Upward and downward displacement of beads below 10 cm tended to be symmetrical for these implements. In contrast, the moldboard plow inverted the soil, burying surface beads and raising beads from deeper layers of the profile. The probability of a near surface bead moving downward with moldboard plowing was greater than the probability of a deeply buried bead moving upward, however, probably because the moldboard plow entrained much air into the soil, thereby raising the soil surface.

Movement of beads by tillage implements was much greater than movement by natural causes between tillage events. The most notable pattern of movement of beads between tillage events was upward movement of deeply buried beads, possibly due to settling of soil.

Conversion of the probability-of-movement matrices into probability models allowed calculation of bead movement between soil layers that was not observed directly. Movement probability models for the several tillage regimens will facilitate development of depth stratified models of weed seed banks.

Table 6
Percentage of hypothetical seeds in the surface 0–4 cm that prior to tillage were either in the 0–4 cm layer or in the 4–26 cm layer, assuming a uniform distribution of seeds prior to tillage

<table>
<thead>
<tr>
<th>Tillage type</th>
<th>Seeds in the surface 0–4 cm that prior to tillage were</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Above 4 cm (%)</td>
</tr>
<tr>
<td>Disk only</td>
<td>72</td>
</tr>
<tr>
<td>Rotary tillage</td>
<td>64</td>
</tr>
<tr>
<td>Straight chisel</td>
<td>63</td>
</tr>
<tr>
<td>Curved chisel</td>
<td>63</td>
</tr>
<tr>
<td>Moldboard plow</td>
<td>3</td>
</tr>
</tbody>
</table>

References
