Spatial analysis of weed patterns

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Proefschrift

ter verkrijging van de graad van doctor
op gezag van de rector magnificus
van Wageningen Universiteit,
Prof. dr. M.J. Kropff
in het openbaar te verdedigen
op dinsdag 13 november 2007
des ochtends te elf uur in de Aula

Abstract

Heijting, S., 2007. *Spatial analysis of weed patterns*. PhD thesis, Wageningen University, Wageningen, The Netherlands. With summaries in English and Dutch, 146 pp.

Weeds in agriculture occur in patches. This thesis is a contribution to the characterization of this patchiness, to its analysis, and to its prediction, and some of its results may be useful for weed management.

Spatial patterns of six weed species monitored in contiguous quadrats are characterized, using Mead's test. Five of the six analysed weed species showed aggregation at several levels of scale. The only wind dispersing species, *Taraxacum officinale* was random at all scales. Next, 2-D correlograms were used to analyse spatio-temporal behaviour of weed patterns for 15 weed species groups throughout three years. *Chenopodium album*, *C. polyspermum*, *E. crus-galli* and *S. nigrum* were strongly aggregated and also exhibited the largest incidence and highest maximum weed density of the species studied. 2-D correlograms showed that patterns of *C. polyspermum* and *S. nigrum* were stable in location. Patches of one species, *E. crus-galli* appeared to shift from year to year.

The four patchy weed species, *C. album*, *C. polyspermum*, *E. crus-galli* and *S. nigrum*, showed consistent relations of moderate strength with soil variables (pH, texture fraction or organic matter) over the three years of study using Generalized Linear Models with a Poisson log link. Models with spatially uncorrelated and spatially correlated error terms were compared, using Taylor's power law (TPL) as a link function, resulting in modest decreases in model significance when the spatial correlation in errors was accounted for, and in a few cases, there were big differences in model significance. Spatial correlation remained in the residuals of the regression, demonstrating that factors other than the selected soil variables also contributed to the spatial correlation in the weeds.

Dispersal of weed seeds in fields by harvest and rigid-tine cultivator was studied in continuous maize using a range of plant species as model weeds. The rigid-tine cultivator significantly contributed to the dispersal in the driving direction, most likely by dragging plant material with seeds through the field. Irregularities were found in the tail of the dispersal kernels, probably as a result of deposition of plant debris in the headlands by machinery.

Taylor's power law was used to predict the weed free fraction in the field using spatially implicit weed count data. The general model gave accurate predictions for most weed species, but for some, e.g. *E. crus-galli*, a species specific model was required to achieve adequate accuracy.

Keywords: Spatial analysis, weed patterns, Mead's test, space-time correlograms, 2-D correlograms, dispersal, Generalized Linear Models, heterogeneity, soil, Taylor's power law.

Voorwoord

Voordat ik aan mijn promotie begon dacht ik dat het wel eens een eenzame aangelegenheid zou kunnen worden. Gelukkig bleek niets minder waar. Dankzij de inzet, hulp, en aanwezigheid van vele mensen is het niet alleen een leerzame maar bovendien ook gezellige en gevarieerde tijd geworden. In iedere fase van het onderzoek waren er weer andere mensen die mij hebben geholpen. Ik wil ze graag bedanken voor al hun hulp bij de totstandkoming van dit proefschrift.

Allereerst wil ik mijn promotoren Martin Kropff en Alfred Stein, en co-promotor Wopke van der Werf bedanken voor al hun steun, hulp en geduld bij het maken van dit proefschrift. Jullie hebben me de ruimte en tijd gegeven om mijn eigen weg te vinden, dat waardeer ik enorm. Martin, hartelijk dank voor al je positieve input. Het was altijd inspirerend om je te spreken. Alfred, dank voor je inzet, het heeft mooie resultaten gegeven. Wopke, ik heb veel van je geleerd en bewonder je geduld.

Aan het begin van mijn onderzoek, hebben verschillende mensen mij geholpen bij de verkenning van het onderwerp ruimte en onkruiden. Hoe moest ik de plantjes in kaart brengen? Ik begon met high-tech apparatuur. Ik wil Jan Hein Loedeman bedanken voor zijn hulp en het uitlenen van de RTK-DGPS. Uiteindelijk heb ik voor een kleinschaligere en non-tech methode gekozen bij het in kaart brengen van onkruid-patronen. Dat kostte ook de nodige inspanning, want het veld bleek soortenrijk. Bij het bepalen van de soorten hebben de volgende mensen geholpen: Ton Elzenbroek, Koop Wind, Henk Naber, Karle Sykora, Roel Groeneveld en Marijn Verbeek bedankt voor jullie hulp.

Om de koers van het onderzoek te bepalen ben ik op bezoek geweest bij twee onkruid ecologen in de VS. Dave Mortensen, thanks very much for your hospitality, help and time in getting me acquainted with the topic of spatial aspects of weed ecology. Anita Dille thanks for your time and showing me your work. The visits to you two were very inspiring and interesting and greatly helped me to set my aims for this thesis.

I would also like to thank Roland Gerhards and Markus Sökefeld for the great day we had in Bonn. It was very impressive to see the possible high-tech solution to weed mapping.

Gedurende de zoektocht naar ruimtelijke onkruidpatronen heb ik ook de expertise van twee akkerbouwers, Gerard Jurrius en Dirk Dorrestein genoten. Fijn dat ik op jullie bedrijven mocht rond kijken en bedankt voor de interessante verhalen.

Ten slotte wil ik graag mijn familie bedanken. Lieve papa en mama, hartelijk dank voor al jullie hulp en het oppassen. Dorien, Joris, Mirjam, Pake en Beppe, dank voor jullie steun.

Lieve Jan, je hebt zo ontzettend veel gedaan…een simpel dankjewel is niet voldoende. Van programmeren en mooie plaatjes maken tot het aanhoren van al mijn verhalen…. jij promoveert stiekem ook vandaag!

Gedurende de AIO-tijd kwamen er ook nog drie kleine rekels bij, wat een geluk dat jullie er zijn, lieve Hugo, Oscar en Vivian. Deze trekker is voor jullie:

Contents

CHAPTER 1

General introduction

BACKGROUND

Agriculture, weeds and herbicides

Weeds interfere in several ways with agricultural cropping systems. The main problem they cause is yield reduction by competing with the crop for light, water and nutrients. They can hamper harvest by getting entangled in machinery, or contaminate the harvested product by their presence. Some weed species can act as a host plant for pests and diseases (Mortimer, 1990).

Chemical control with herbicides is a quick, cheap and effective way to eradicate or control weeds. In The Netherlands, herbicides are generally applied uniformly over the field. Following application, herbicides and their by-products enter the environment and they can enter the food chain as residues on the harvested crop. The policy on registration of pesticides has become more stringent during the past decades in an attempt to minimize the effect of these chemicals on the environment and humans. Pesticides with the greatest (eco-)toxicological impact are banned. The newer herbicides such as sulfonylurea compounds require less active ingredient leading to less environmental burden. Still, the presence of herbicides in the environment, drinking water and food is unwanted and reducing the input is desirable.

Reducing herbicide input

Spatial variation in density of weedy plants on arable fields offers a possibility to reduce chemical input as weed plants often occur aggregated or patchy in the field (Marshall, 1988). Site-Specific Weed Management (SSWM) takes this spatial aggregation into account and herbicides are applied only where weed plants are present. The possible reduction depends on the precision of the monitoring and the spraying equipment (Rew *et al*., 1996a, 1997; Wallinga *et al*., 1998). Calculations on actual weed populations in arable fields showed reductions beyond 90% can be achieved if the herbicide is only applied where a weed is present (Johnson *et al*., 1995a). With advancing technological developments, increasing precision in weed control is likely to be achieved. Stability of weed patches will facilitate SSWM as weed maps made in one year can be used in subsequent years for targeting weeds effectively (Goudy *et al*., 2001).

PROBLEM STATEMENT

Types of weed spatial patterns
In this study, we will use the word 'pattern' to indicate the two-dimensional configuration of specimens of a weed species in the field. Three types of spatial pattern can broadly be discerned: regular, random and aggregated (Figure 1). A random pattern indicates each unit of equal size has an equal chance of being occupied by a set number of individuals. If individuals are more evenly distributed than in a random pattern, the pattern is addressed as regular (Upton & Fingleton, 1985). If an individual tends to occur near others, the pattern is termed aggregated. In an aggregated pattern, areas of higher density are alternated with areas with lower density.

Mapping weed patterns
In most weed studies on the spatial ecology of weeds, weed patterns have been mapped by sampling weed densities according to a regular grid with interspersed unsampled space. Weed densities at unsampled locations are calculated using geostatistical interpolation methods (e.g. Colbach *et al*., 2000; Goudy *et al*., 2001). These techniques are likely to miss weed patches that are smaller than the distance between sampling points (Rew & Cousens, 2001; Wyse-Pester *et al*., 2002). Although labour intensive, mapping weeds with contiguous quadrats will yield more reliable information on weed spatial and temporal behaviour. This method has been applied only in a few studies (Cousens *et al*., 2004; Dieleman & Mortensen, 1999), and statistical tests to analyse such data need to be explored.
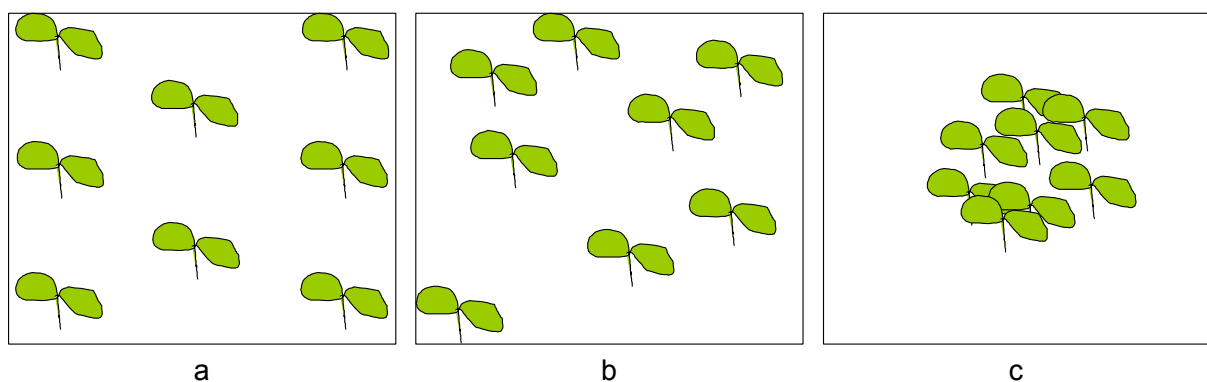
Figure 1. Three types of spatial pattern: Regular (a), random (b) and aggregated (c).

Scale

The level of scale that is used to monitor a pattern can influence the nature of the pattern observed. Variation in the data can be reduced by clustering units in spatial analysis. As such, a clearer diagnosis of species patterns may be obtained, as shown for example in tropical forest trees (Bellehumeur *et al.*, 1997). However, patterns can be obscured if the size of the aggregated units exceeds the scale of the pattern (Rew & Cousens, 2001).

Effect of soil on weed patterns

Weed populations in an arable field are subjected to various forces which can affect their spatial and temporal behaviour. Spatial heterogeneity of the soil has been found to be related to variation in weed densities (Dammer *et al.*, 1998; Dunker & Nordmeyer, 2000). Very few studies have looked at the actual contribution of spatial correlation of the soil to spatial correlation of weed patterns and thus their temporal stability. Techniques need to be investigated to assess the role of heterogeneity of underlying soil properties on spatial correlation of weed patterns.

Effect of machinery and weed biology on weed dispersal

Although machinery is known to contribute to weed spatial dynamics (see Blanco-Moreno *et al.*, 2004) by dispersing weed seeds, the interaction with weed biology needs further examination. It is expected on the basis of a model study that timing of seed shedding will affect dispersal distance of weed seeds (Woolcock & Cousens, 2000). Actual data on this process will improve insight in spatial aspects of the ecology of weeds.

Potential for SSWM

A simple tool to assess the potential savings by applying herbicides site-specifically would be very valuable for arable practice. At present such tool is not available.

OBJECTIVES OF THIS THESIS

The objective of this thesis is to increase insight in the causes and behaviour of weed spatial patterns using detailed information on count data. Furthermore statistical tools to analyse this data are explored. A way to assess the potential savings for SSWM is determined. To reach this goal, the following sub-objectives were defined:

1. Obtain detailed information on species specific weed spatio-temporal behaviour by mapping patterns using contiguous quadrats.
2. Develop and test statistical tools to analyse weed spatial and temporal behaviour.

3. Asses the role of spatial heterogeneity of underlying soil properties on weed spatial patterns.
4. Investigate the effect of timing of seed shed on dispersal by harvest combiner and rigid-tine cultivator.
5. Determine the relation between frequency distributions of weed densities and spatial aggregation and examine consequences for SSWM species specifically.

METHODOLOGY

Observational studies were used to gather spatial count data for objective 1, 2 and 3. Controlled experiments were performed to obtain data for objective 4. Data of objective 1, 2, 3 and 4 were gathered in fields cropped with continuous maize. As such, no rotational effect was present on the spatial behaviour of weed species. Maize is an important crop in The Netherlands covering approximately 10% of the total agricultural area. Maize as a silage fodder is often cropped continuously. Post emergence weed control is still mainly performed by full field application of herbicides in combination with mechanical weeding.

To be able to assess the potential for SSWM in a range of crops and cropping situations (objective 5), data gathered in various crops under a wide range of circumstances throughout The Netherlands were used.

OUTLINE OF THESIS

In Chapter 2, species specific patterns observed in contiguous quadrats in the first year of the study are analysed with a randomization test to assess the level of aggregation of the weed patterns. This test is named after its inventor, R. Mead (1974). It is the first application of this test to two-dimensional weed data.

The weed data of Chapter 2 were observed during a total of three consecutive years on a maize field near Wageningen (clay soil). Due to the collection of data in three years, the spatio-temporal behaviour of weed species can be studied. This is dealt with in Chapter 3. Two-dimensional (2-D) correlograms are used to characterize the patterns and their evolution over time. The direction of greatest auto- and cross-correlation is derived from explicit 2-D analyses. The effect of the size of quadrats on the outcomes of spatial analysis is also investigated.

Regression analysis was used to examine the relations between soil properties and weed patterns (Chapter 4). Soil samples were taken on the observation plot of the weed patterns (Chapters 2, 3). After an initial selection of covariates (soil) to explain species specific plant density, the covariance structure of the response data (weed counts) was incorporated in the regression analysis to account for the spatial correlation of the data.

The effect of timing of seed shedding of weed species on the dispersal by harvest combiner and rigid-tine cultivator was determined in a separate experiment on sandy soil (Chapter 5). Plots with introduced plant species which served as model weeds were sown and grown in the field. During harvest the selected species carried ripe seeds. As a contrast, weed seeds of other species were placed on the soil shortly before harvest. A few weeks after harvesting and cultivating the soil (rigid-tine), the entire field (2 ha) was mapped to investigate the dispersal of the plants by the machinery.

The potential for herbicide saving using SSWM is assessed using data collected in The Netherlands at various sites and in different years in a range of crops (Chapter 6). An equation is derived, and tested, to predict the non-occupied fraction of the land based on mean density. The equation is derived by combining models for the frequency distribution of weeds and the relationship between spatial variance and the mean. The relationship between scale and weed free fraction is explored using the spatially explicit data set collected for studies in Chapters 2, 3 and 4.

Chapter 7 is the General Discussion and results of the preceding chapters are integrated. Important determinants for weed spatial dynamics are discussed and implications for SSWM are addressed.

CHAPTER 2

Testing the spatial significance of weed patterns in arable land using Mead's test[*]

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Summary

There is a need in weed science for statistical tests for patchiness and spatial pattern. The objective of this study is to investigate the performance of Mead's test for detecting patterns in synthetic data and in real weed counts made in maize, and making a first assessment of its applicability in ecological studies on weeds. In an extension to Mead's test, made here for the first time, we merge original quadrat count data into rectangular cells of m by n quadrats. Care was taken to rule out the effect of starting point on the test result. Using the synthetic data, we demonstrate ability of the test to detect both patchiness and homogeneity as deviations from randomness. The first deviation results in right-sided significance, and the second in left-sided significance of the test. Analysis of the real weed patterns demonstrated patchiness at many scales for five of the six investigated species, and lack of any deviation from randomness in the sixth: *Taraxacum officinale*. The latter was the only wind dispersing species in the data set. No deviation towards homogeneity was found in any of the real weed species at any scale. All patchy patterns showed anisotropy, being elongated in the direction of field traffic. As it turns out, Mead's test is well suited to detect departures from randomness in observed weed patterns and enhances the suite of diagnostic tools that can be employed by weed ecologists.

Keywords*:* Mead's test, weeds, spatial pattern, patchiness, scale, anisotropy.

INTRODUCTION

The distribution of weeds on arable land is spatially heterogeneous (Dieleman & Mortensen, 1999). As farming practices contributing to seed dispersal are often performed in a specific direction within the field, it is unlikely that weeds are randomly dispersed. Indeed, besides patchiness, Dieleman & Mortensen (1999) and Colbach *et al.* (2000) reported directionality of weed patterns, observing elongated weed patterns in the driving direction. The extent to which patterns differ between weed species, may be linked to differences in life cycle and ecology such as the time of seed shed (Colbach *et al.*, 2000). Hence, both precision agriculture and weed spatial ecology may benefit from the observation and analysis of weed patterns.

The term pattern has been interpreted as departure from spatial randomness (Mead, 1974), or containing a certain amount of predictability (Dale, 1999). We use the term 'pattern' to indicate the spatial configuration of specimens of a weed species in a field. Three categories of spatial patterns are often distinguished: aggregated, random and regular. The existence of an aggregated, or patchy, weed pattern indicates that some areas in the field have a higher weed density than their surroundings. Conversely, the lower weed density areas can be called gaps (Perry *et al.*, 1999). Random patterns are patterns where all areas of equal size have an equal chance of being occupied by a certain number of individuals. A Poisson distribution describes the frequency distribution underlying such a pattern. Regular patterns are patterns where individuals are more evenly spread than in a random pattern (Upton & Fingleton, 1985).

To obtain detailed and reliable information on weed patterns, the use of contiguous quadrats has been advocated (Rew & Cousens, 2001; Cousens *et al.*, 2002). This classical method has been used for monitoring vegetation, and was only recently applied in weed science (Dieleman & Mortensen, 1999; Cousens *et al.*, 2002). The space to be sampled is then divided into a grid of contiguous quadrats of equal size and the number of plants in each quadrat is counted. For data thus collected, Mead's test (Mead, 1974; Manly, 1991; Diggle, 2003) has been suggested to detect deviation from randomness. This test can be applied at several subsequent levels of scale independently, as the position of sub-units within a unit at one scale does not influence the test result at higher scales.

So far, the testing of spatial indices and measures for statistical significance in spatial ecology is not strongly developed (Fortin & Dale, 2005). Significance of the autocorrelation values using *t*-values borrowed from the correlation coefficient is not convincing, as these are based on independence, where the dependence is precisely the topic studied. In that sense, randomization test serve as an interesting opportunity.

The objective of the work is to carry out a test of spatial significance for counts of weeds in contiguous quadrats. To do so, we focus on detection and characterization of

non-randomness. As an application, we consider observational data on weed patterns in maize in The Netherlands. Detection of scale in pattern has a general applicability, and therefore the study well extends beyond the scope of a single case study.

MATERIALS AND METHODS

Field observations

Observations were made within an arable field on clay soil near Wageningen, The Netherlands. The field was 1.8 ha in size, 64 m wide and 281 m long. In the six years preceding the study, the field was planted with winter wheat, corn, potatoes, winter wheat, fodder beets and summer barley. In May 2001, maize (*Zea mays* L.) was sown in 0.75 m wide rows. The spatial pattern of weeds was determined before herbicide spraying, from 18 until 21 June 2001.

Patterns of six weeds species were subjected to further analysis: *Chenopodium album* L. (fat hen), *Chenopodium polyspermum* L. (many-seeded goosefoot), *Echinochloa crus-galli* (L.) Beauv. (barnyard grass), *Polygonum aviculare* L. (knotweed), *Solanum nigrum* L. (black nightshade) and *Taraxacum officinale* Wiggers (dandelion). The first five species were abundant in the field, and their patterns looked patchy upon visual inspection. *T. officinale* occurred at low densities, and its pattern looked random upon visual inspection.

Observations were made on a 50.25 m long and 12 m wide rectangular plot with the long side parallel to the direction of field traffic. The plot was situated just south of the northern headland of the field, with the northern edge of the plot 17.5 m from the field edge and the long side 13 m from the western border of the field. Square quadrats with sides of 0.75 m were used to count weeds, resulting in a total of 16 × 67 = 1072 quadrats being counted. Quadrats were placed between crop rows. The position of quadrats in the within-row direction was secured by using a tape measure. In each quadrat, the number of individual specimens for each weed species was determined. The quadrat counts are the input into the analyses.

Mead's test

Mead's test (Mead, 1974; Ripley, 1981; Manly, 1991) is a statistical test for identification of spatial pattern. It tests the null hypothesis H_0: 'the weed pattern is random', against deviation from randomness. The test was originally developed to quantify non-randomness for count data on specimens in both transects and for 2-D data at subsequent levels of scale (Mead, 1974).

The test is constructed as follows. Let $X_0(i)$ denote the number of weed counts for the ith quadrat (Figure 1). Then $X_0(i) = \mu_0 + \varepsilon_0(i)$, where the means of the $X_0(i)$ are

taken to be equal to μ_0, and the random variables $\varepsilon_0(i)$ have zero mean and variance equal to σ^2. To illustrate, we consider the basic quadrat counts, $X_0(i)$, consisting of sixteen quadrats (Figure 1). We examined the following combination of pairs:

$$TSS = \sum_{i=1}^{16} X_0^2(i) - 16\overline{X}_0^{\,2} \tag{1}$$

where $\overline{X}_0$ is the mean of counts. The sum of squares between the four sub-units of the unit is given by

$$BSS = \sum_{i=1}^{4} \frac{1}{4}\left(\sum_{j=1}^{4} X_0(4\cdot(i-1)+j)\right)^2 - 16\overline{X}_0^{\,2} \tag{2}$$

and the appropriate test statistic is $Q = BSS/TSS$. The distribution of Q under H_0 can be readily assessed by randomization (Besag & Diggle, 1977).

In our application we used levels of spatial scale that both acknowledge the size of units and their length to width ratio. As an addition to Manly (1991), the scale issue is dealt with by combining neighbouring quadrat counts into cells measuring m quadrats in the row (y) direction and n quadrats in the cross-row (x) direction. By adding, for instance, the counts of two cells that are aligned cross-row, new cells are formed that are aggregated in the cross-row direction, but not in the within-row direction ($m = 1$, $n = 2$). Using these new cells, a test for pattern can be done at a scale level that is one higher than the original one into the cross-row direction. Similarly, the counts of two within-row aligned cells can be added, leading to aggregation in the within-row direction and hence to a test for pattern at a scale that is one higher than the original

Cross-row direction

$X_0(1)$	$X_0(2)$	$X_0(5)$	$X_0(6)$
$X_0(3)$	$X_0(4)$	$X_0(7)$	$X_0(8)$
$X_0(9)$	$X_0(10)$	$X_0(13)$	$X_0(14)$
$X_0(11)$	$X_0(12)$	$X_0(15)$	$X_0(16)$

Within-row direction
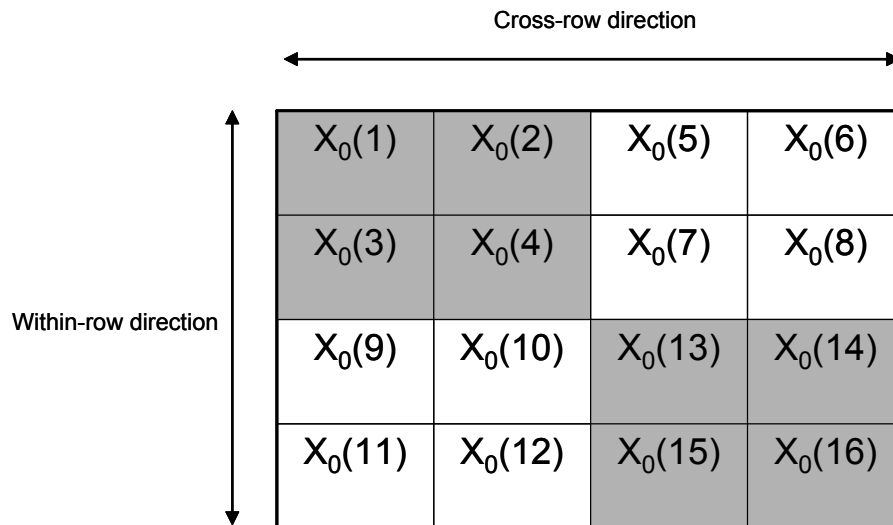
Figure 1. Configuration of 16 quadrats within a unit.

Table 1. Scale levels used in Mead's test for observed weed patterns.

Scale	Size sub-unit	Number of units
1	0.75 m × 0.75 m	64
2	1.50 m × 0.75 m	32
	0.75 m × 1.50 m	32
	1.50 m × 1.50 m	16
3	2.25 m × 0.75 m	16
	2.25 m × 1.50 m	8
	2.25 m × 2.25 m	5
	1.50 m × 2.25 m	10
	0.75 m × 2.25 m	20
4	…	…

one in the within-row direction. This procedure is then repeated, as far as the available data permit. As our field consists of 16 by 67 quadrats, we could pursue this procedure up to four levels into the cross-row direction and up to 16 levels into the within-row direction (Table 1).

Upton (1984) mentions the sensitivity of the test results to the starting point. In initial calculations, we experienced lack of robustness of the test result in relation to starting point, even if 50 random starting points were chosen to minimize the effect of starting point. In the final implementation of Mead's test, we conduct at each level of scale the test a fixed number of times for each possible starting point, such that the total number of randomizations is at least 10,000. For each scale level s_x, the number of starting points in the x-direction, n_x, is determined as $n_x = \min(4s_x, n-4s_x-1)$. The starting point is expressed as index number for a quadrat, and runs from 1 though n_x. The rationale behind this formula is that the number of starting points should be $4s_x$, to allow all different possible combinations of $4s_x$ adjacent quadrat counts within one unit to be generated during the calculations. The number of starting points is bounded by the size of the dataset, and cannot exceed $n-4s_x-1$. An analogous formula applies for the starting position in the y-direction: $n_y = \min(4s_y, m-4s_y-1)$.

To carry out the test, we determined the overall number of starting points as $N_{stp} = n_x \cdot n_y$. Then we calculated how many randomizations were needed for each starting point to generate at least 10,000 realizations of the test statistic overall, i.e. $10,000/N_{stp}$, rounded up to the nearest integer. Then, the test statistic Q was calculated for each starting point, and a corresponding P-value was calculated by making random permutations of the cell values within units, followed again by calculation of the value of the test statistic. The rank of the original value of the test statistic among the

10,000/N_{stp} values of the randomized data was determined. Finally, the obtained *P*-values were averaged over all the starting points.

Synthetic data

To assess the performance of Mead's test in a simple situation, we analysed six artificial patterns presented in Fortin & Dale (2005, pp. 128-129). Each pattern occurs on a 20 × 20 grid (Figure 2).

- Pattern 1 ('trend') is a gradient into the cross-row direction, with constant within-row values; the width of the strips is equal to four quadrats.
- Pattern 2 ('random') consists of 400 random values.
- Pattern 3 ('one patch') consists of a single large patch.
- Pattern 4 ('16 patches') consists of 16 patches of nine cells each, regularly spaced in the grid.
- Pattern 5 ('same patch') consists of 9 identical patches, irregularly spaced in the grid.
- Pattern 6 ('same distance') consists of 12 unequal patches, spaced at an inter-patch distance of 2 quadrats in the grid.
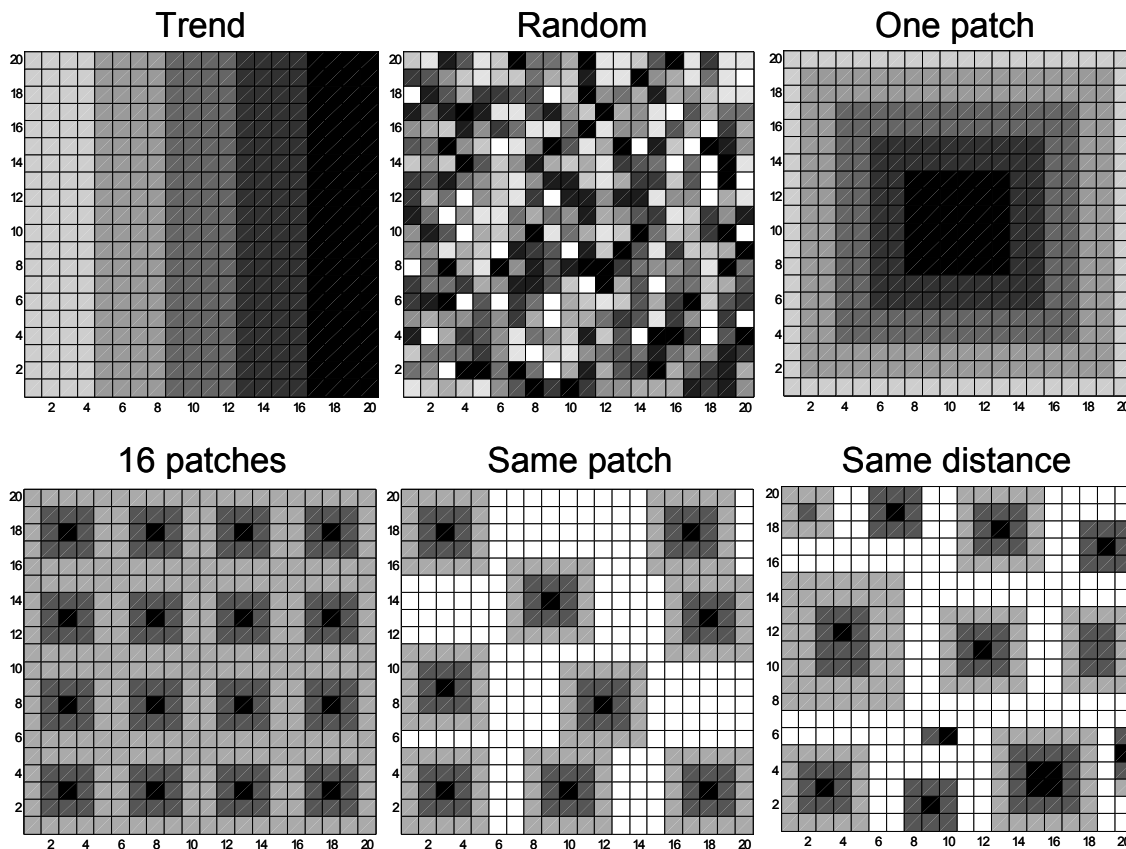
Figure 2. Six synthetic patches analysed with Mead's test. Each set contains 400 cells, after Fortin & Dale (2005).

Table 2. Number of starting points at 5 × 5 levels of scale in the synthetic patterns (Figure 2). According to the formula given in the text, the number of starting position in either direction is 4 at scale 1, 8 at scale 2, 9 at scale 3, 5 at scale 4 and 1 at scale 5. The total number of starting points is the product of the number of starting positions in *x*- and *y*-direction.

Scale in *y*-direction	Scale in *x*-direction				
	1	2	3	4	5
1	16	32	36	20	4
2	32	64	72	40	8
3	36	72	81	45	9
4	20	40	45	25	5
5	4	8	9	5	1

We analysed the full combination of scale levels, i.e. 5 levels in the *x*-direction times 5 levels in the *y*-direction, resulting in a 5 × 5 matrix of scales. The number of starting positions at each level of scale is given in Table 2. The resulting *P*-values of Mead's test are presented as a matrix plot, where the *x*-coordinate is the scale level in the *x*-direction, the *y*-coordinate is the scale level in the *y*-direction, and the grey scale indicates significance of the test. Right-sided significance indicates a large value of the test statistic, and a large difference between the sub-units within units, hence, clustering at sub-unit level. Left-sided significance indicates a small value of the test statistic and similarity among sub-units, i.e. homogeneity at sub-unit level.

RESULTS

Mead's test applied to artificial patterns
Pattern 1 ('trend') yields significance at all scale levels in the *x*-direction, except the first (Figure 3). The test thus correctly identifies clustering at the 4-quadrat level and above. (Note that significance at scale level 2 indicates that the clustering occurs at a sub-unit size of four quadrats, *cf*. Figure 1). The random pattern is correctly not recognized as a pattern at any scale. In the case of the single patch, clustering is detected at scales of 1×1, 2×1, 3×1, 1×2 and 1×3. Not shown in the figure is borderline significance at level 2×2, 3×2 and 2×3 (*P*=0.06) and 3×3 (*P*=0.08). The test result is symmetric, as is the pattern. Contrary to the pattern 'trend', no significance at higher levels of scale was found. This may be related to the narrowness of the bands of equal density. These bands are only two quadrats wide, thus the basic data becomes already
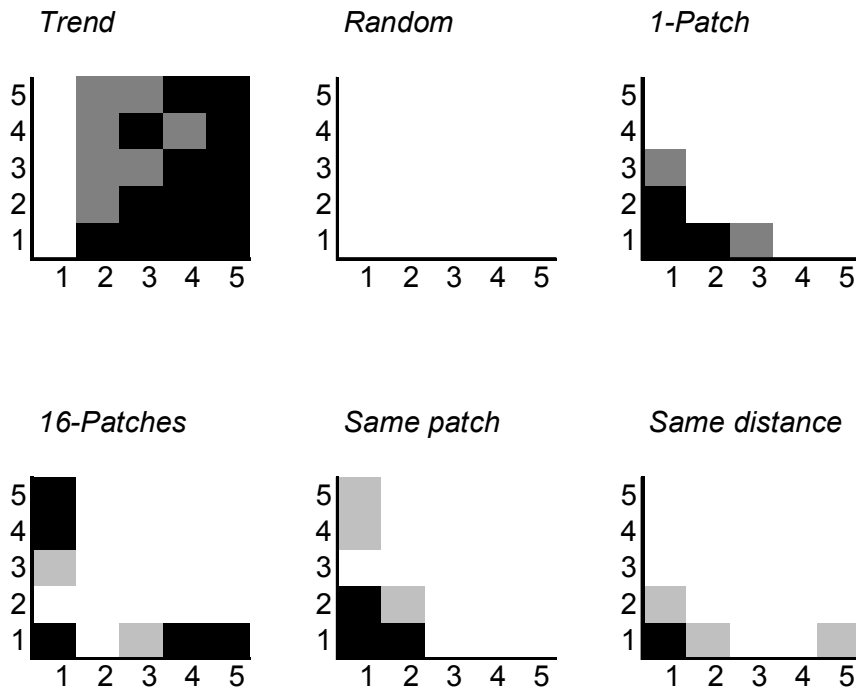
Figure 3. Results of Mead's test (*P*-values, right-sided significance) for six synthetic patterns at five levels of scale in the *x*- and *y*-direction. Grey shades indicate *P*-value at each joint scale level: black: $P \leq 0.001$; dark grey: $P \leq 0.01$; light grey: $P \leq 0.05$; white: $P > 0.05$.
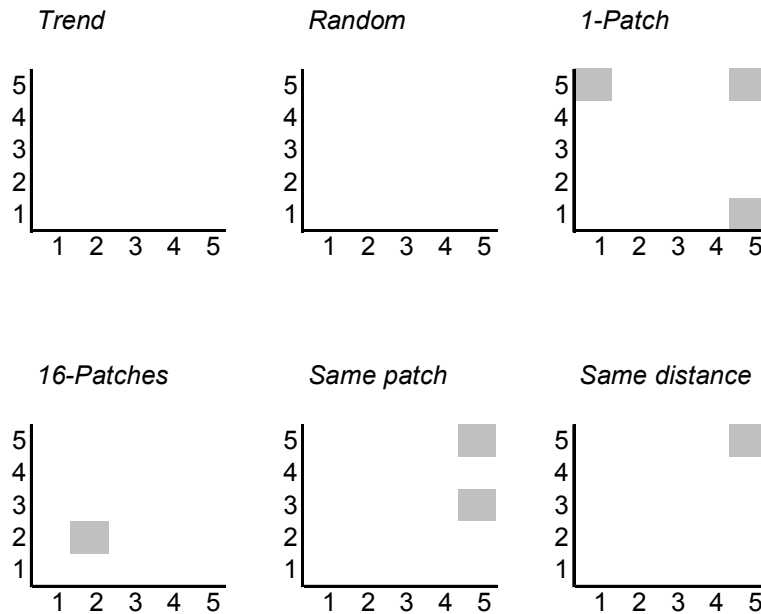
Figure 4. Results of Mead's test (*P*-values, left-sided significance) for six synthetic patterns at five levels of scale in the *x*- and *y*-direction. Grey shades indicate *P*-value at each joint scale level: black: $P \leq 0.001$; dark grey: $P \leq 0.01$; light grey: $P \leq 0.05$; white: $P > 0.05$.

very diverse at the within sub-unit level if higher scales are analysed. In the case of 16 patches, significance is found at all levels of scale for cells that are one quadrat wide or long, except at scale level 2 where the pattern is somewhat less significant (*P*=0.10). The lack of significance upon simultaneously upscaling in the *x*- and *y*-direction indicates that doing so enters so much variability within the sub-units, that the variability between sub-units is no longer significant. Patterns of significance for the 'same patch' and 'same distance' patterns resemble those of the '16 patches' pattern. Left-sided significance, which occurred in 1-patch, 16-patches, same patch and same distance pattern (Figure 4), reflects the homogeneity present at certain levels of scale in these four patterns. The synthetic data show that most patterns can be recognized, but interpretation of the test result is not directly intuitive or straightforward.

Descriptive statistics and visualization of weed patterns

The spatial patterns of the most abundant weed species and of *T. officinale* are presented in Figure 5 and descriptive statistics in Table 3. *Chenopodium album*, *E. crus-galli* and *S. nigrum* all displayed a gradient, with weed density decreasing with distance from the northern headland. *Chenopodium polyspermum* had a higher density in the eastern than in the western half of the plot. *E. crus-galli* had the highest mean density (8.86) and maximum number of weed plants per quadrat (158) of all weeds, and its density decreased steeply with increasing distance from the headland. *Chenopodium album* had the highest level of occupancy of all weeds present (nearly 80%). Counts for *P. aviculare* and *T. officinale* yield variance/mean ratios of 1.22 and 1.02, respectively, indicating little or no clustering of plants within quadrats. Nevertheless, upon visual inspection the pattern of *P. aviculare* bears no resemblance to a random pattern, whereas the pattern of *T. officinale* does (Hurlbert, 1990).

Mead's test applied to observed patterns

Mead's test yielded many right-sided significance for most of the weed data (Figure 6), but with the notable exception of *T. officinale.* The pattern of *T. officinale* was not significantly different from randomness at any scale. For the other five species, clustering was present at many scales (Figure 6). Not a single instance of left-sided significance was found in any of the six species (data not shown), thus the observed patterns did not display a trace of homogeneity at any scale. The five species that give significant clustering displayed the greatest significance at the *x*-scales of 1 and 4, indicating that clustering is strongest at the cross-row level of 2 quadrats, and 8 quadrats, respectively. Thus, the test indicates significant clustering at the smallest cross-row scale and also at the largest cross-row scale that can be analysed with the data. The large scale effect can be interpreted as a difference between the western and
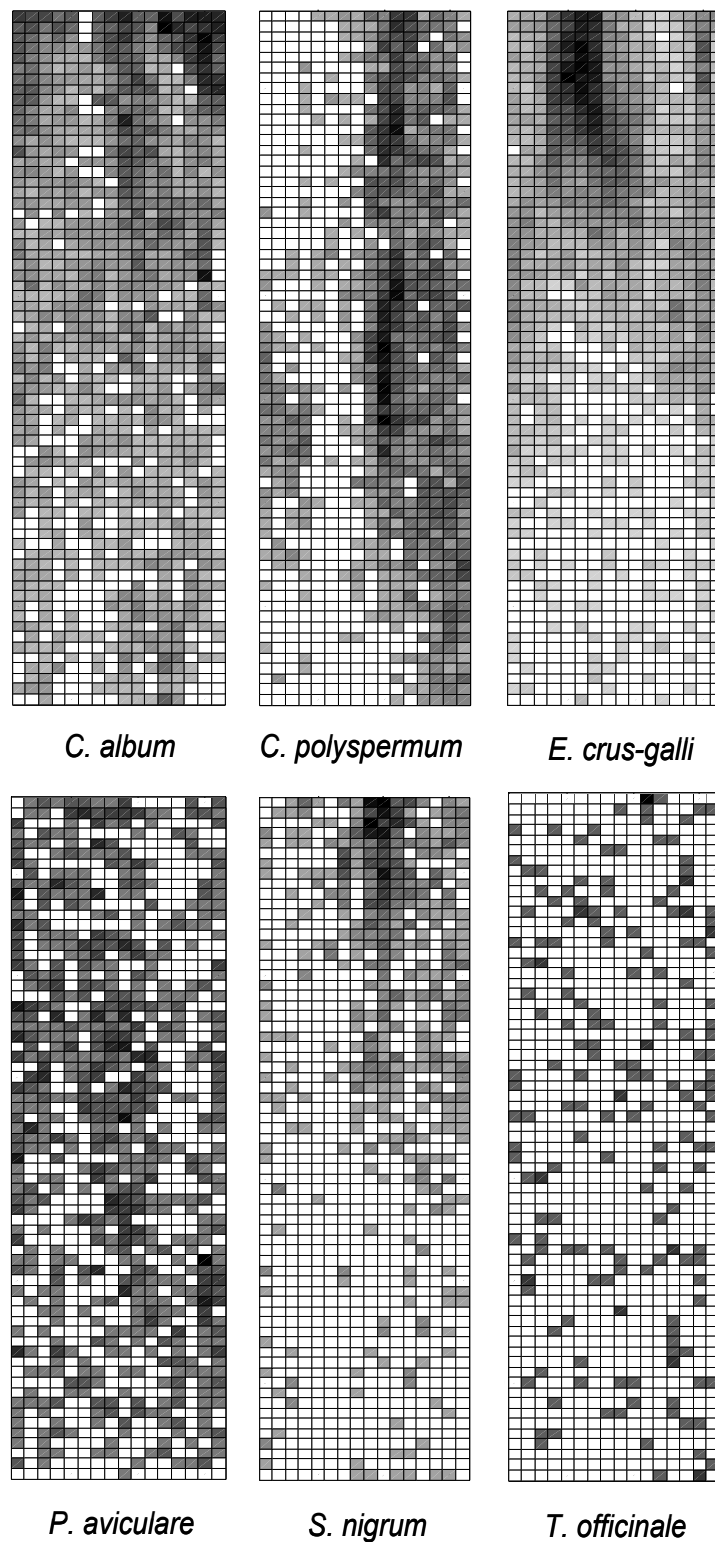
Figure 5. Spatial patterns of six weed species in a maize field before spraying. Each quadrat is 75 × 75 cm. The north side of the plot borders on the head land of the field, the left and right sides of the plots are more than 10 m away from the field edge. Densities are visualized using a linear scale of grey tones representing the cubic root of the single quadrat counts.

Table 3. Mean, standard deviation (s.d.), variance and percentage
of quadrats occupied by the six different weed species in 2001.

Weed species	mean	s.d.	variance	occupancy (%)
C. album	3.51	5.05	25.5	80
C. polyspermum	2.48	3.63	13.2	59
E. crus-galli	8.86	19.90	395.8	69
P. aviculare	0.90	1.05	1.10	56
S. nigrum	0.75	1.83	3.33	33
T. officinale	0.18	0.43	0.18	16
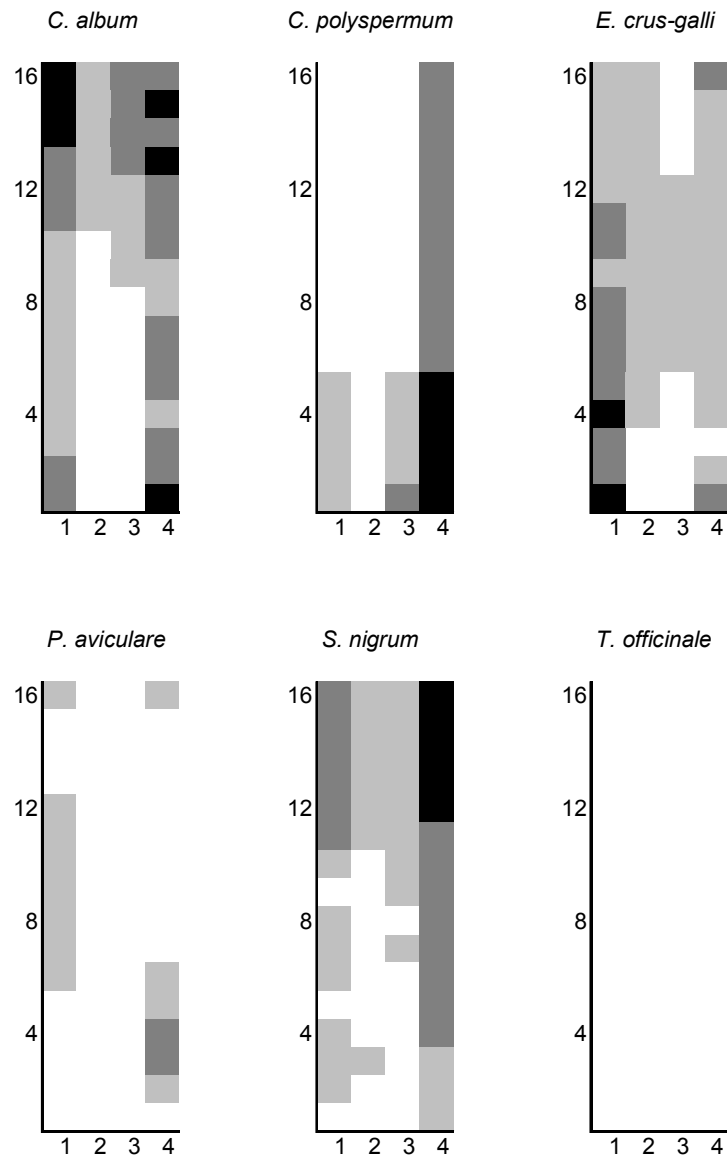
Figure 6. Results of Mead's test (*P*-values; right-sided) for six weed species at different scale levels in the cross-row (*x*) and within-row (*y*) directions. Grey shades indicate *P*-value at each scale level: black: $P \leq 0.001$; dark grey: $P \leq 0.01$; light grey: $P \leq 0.05$; white: $P > 0.05$.

the eastern half of the field. Significant clustering is found at *x*-scale 3 in four species (*C. album*, *C. polyspermum*, *E. crus-galli* and *S. nigrum*) and at *x*-scale 2 in three species (*C. album*, *E. crus-galli* and *S. nigrum*). In *C. album*, the effects at *x*-scales 2 and 3 were significant when the *y*-scale parameter had large values, at least 11 and 9 quadrats for the two scales, respectively. In *S. nigrum* a similar effect was found. However, in *E. crus-galli,* significance of clustering at *x*-scale 2 occurred over a wide range of *y*-scales (4 or more), while at *x*-scale 2, significance was found when *y*-scale varied between 6 and 12. Of the five species that showed clustering, the weakest evidence for clustering was found in *P. aviculare,* both in the level of significance (never below 0.001), and in the number of levels at which clustering was significantly demonstrated. The results indicate that Mead's test reflects both directionality and aggregation (patchiness) of the pattern, with patch direction aligning with the driving direction.

Moran's *I*

As reference for the outcomes of Mead's test, we calculated Moran's *I* (Moran, 1950; Fortin & Dale, 2005) both for the within-row and cross-row directions. Moran's *I* statistic expresses the strength of spatial autocorrelation of a pattern as the correlation between counts at a distance *d*. The value of Moran's *I* as a function of distance, is shown in a correlogram. To facilitate comparison with Mead's test, distance is expressed in number of quadrats (i.e. multiples of 0.75 m). Significance of Moran's *I* was determined using Pearson's product moment correlation coefficient, because of the analogy between the two. Plots of Moran's *I* versus distance (Figure 7) showed that spatial dependence differed between the cross-row and the within-row directions. The strongest anisotropy was detected for *C. polyspermum* where spatial autocorrelation was significant in the within-row direction up to a distance of 29 quadrats, compared to a distance of only 2 quadrats in the cross-row direction. Also for the species *E. crus-galli* and *S. nigrum*, spatial dependence extended further in the within-row direction than in the cross-row direction. Correlation decreased with distance in all weed species, except in *C. album* in the cross-row direction. No spatial dependence was present in either the cross-row or within-row direction for *T. officinale* and *P. aviculare*. The result for *P. aviculare* is different from the result of Mead's test in as far as that Mead's test does detect deviations from randomness, whereas Moran's *I* does not detect spatial correlation.

DISCUSSION

Our results confirm that Mead's test can be used for detecting departures from randomness in two-dimensional data sets, such as weed counts in contiguous quadrats.
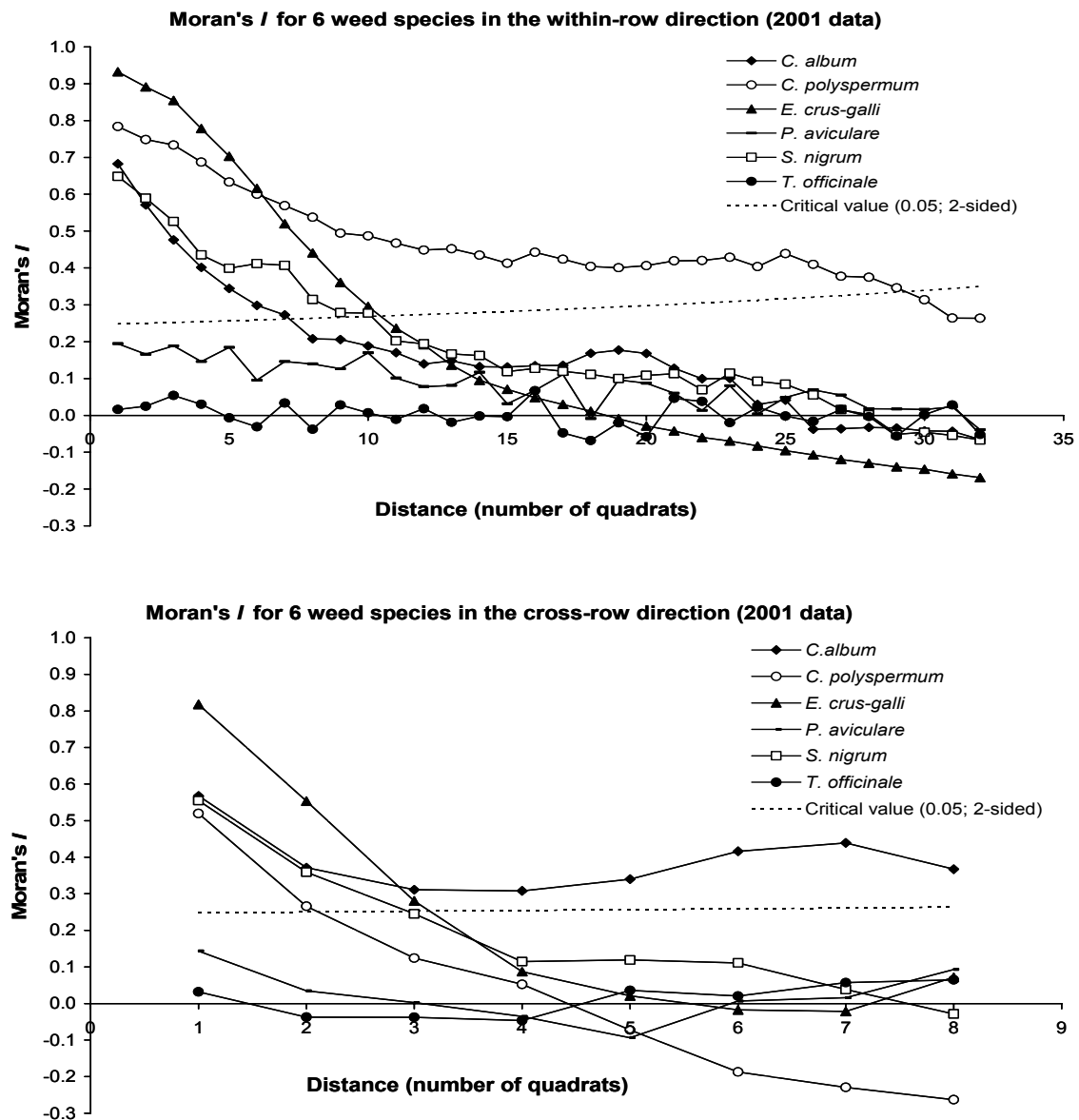
Figure 7. Moran's *I* for six weed species in the within-row direction (top) and in the cross-row direction (bottom).

One particular strong point of Mead's test is that it provides a two-sided test and two alternative hypotheses for randomness, *viz.* clustering and homogeneity. As such, it seems ideally suited to help establish to which of the three basic categories *random, clustered* and *homogeneous* an observed pattern belongs. Our investigation of artificial patterns demonstrates how the test can provide significance either way. However, we also found that the test result is not always easy to interpret, and more work will be needed to ascertain the application of the test in weed research.

Mead's test was originally designed for square grids, where independence between significance tests at subsequent levels of scale was obtained by using the units of one scale as the sub-units for the next scale up. Thus, the upscaling results in a 'lineage' of cells that first consist of one quadrat, then 2×2 quadrats, next 4×4 quadrats, and so forth. Our extension of Mead's test shows that multiple scales can also be studied on the basis of flexible basic shapes that are not restricted to squares, and which are created by aggregating the observation quadrats. This extension makes the test more flexible, and extends the potential applications. Thereby, however, the dependency of *P*-values that make use of the same data is a caveat. That is not to say that the test result is not correct. The *P*-values themselves are not compromised by their inter-dependency. The caveat is that *P*-values will be somehow dependent between different 'lineages' of scale levels, based on given basic shapes. Each lineage itself, still maintains the basic property of Mead's test of independence of the test result in subsequent levels of upscaling. The dependency of *P*-values among alternative lineages implies that they should be interpreted with caution, as in experiments with multiple comparisons in *post hoc* tests, or in interpreting the significance of values of Moran's *I* at different lags. In our opinion, this is an acceptable cost for an important gain: a greater flexibility of the basic shape enabling greater versatility of the test.

Upton (1984) found that Mead's test is sensitive to the choice of starting point. We observed the same, and solved this by conducting the test the same number of times for every possible starting point, and averaging the *P*-value. As a comparison, Moran's *I* (Moran, 1950) was applied. A major benefit of Mead's test is that it is a randomization test, and hence well-equipped to deal with spatial dependence. Testing for significance with Moran's *I* is hampered by the absence of appropriate analogies to *t*-values. For descriptive purposes, however, Moran's *I* still appears to be useful. Alternatively, Syrjala's method (Syrjala, 1996) or 2-D correlograms (Heijting *et al.*, 2007) may be applied.

Mead's test was applied to six selected weed species. It revealed that patterns of *C. album, C. polyspermum, E. crus-galli, S. nigrum* and *P. aviculare* differed significantly from a random pattern at various levels of scale and in various directions. The apparent randomness of the pattern of *T. officinale* may be caused by its mode of dispersal, being the only wind dispersing species that was analysed. Hence seeds may have been introduced from adjacent flowering fields. Alternatively, it may be a relict from historic land-use. In any case, this species did not appear to reproduce within the field, thereby an important cause for spatial clustering was removed. The striking elongated shape of the pattern of *C. polyspermum* could be caused by spatial heterogeneity of soil factors as differences in soil colour were present, but explaining the abrupt transition; competition with other weeds may also be the cause. Mead's test

confirmed that some significant patterns were elongated (those for *C. polyspermum* and *P. aviculare*), stretching out in the prevailing cultivation direction. Mead's test also gives an indication of the patch sizes. Moreover, the test is flexible in the choice of shapes of (sub)units. This feature might be further explored to get a better understanding of the size of the patches.

Left-sided exceedance was studied as well. It occurred a few times in the synthetic data but not in the actual weed patterns. Left-sided exceedance indicates that the sub-units within units are more similar than could be expected on the basis of the variability of the cell counts if the cell counts were spatially distributed at random. When left-sided exceedance is demonstrated, the cells counts are distributed in such a way over the sub-units that the sub-unit means within a unit become similar to each other. This means that in one way or another, the cells within a sub-unit have 'compensatory' counts, i.e. high values for one cell are compensated by one or more low values for other cells. Such compensatory behaviour could occur when the density is periodic over space as in a checker board of high and low values. Some of the artificial patterns provide examples of this phenomenon of left-sided exceedance. It is not wholly unthinkable in practice either, with tracks of machinery providing a spatially periodic signal, with potential consequences for weeds.

What emerges from this study is that crop management is a likely cause for the formation of anisotropic patterns by dispersing weed seeds further into the driving direction of equipment than perpendicular to this. The majority of weed seeds, however, is not dispersed further than 1–2 m from the source, whereas after five successive operations they may move to distances up to 15 m (Rew & Cussans, 1997; Marshall & Brain, 1999). In addition, each equipment pass it likely to make the seed distribution in the soil less uniform, resulting in the elongated shape of weed patterns. Mead's test confirmed that patterns of *C. polyspermum* and *P. aviculare* have elongated patterns, in the direction of cultivation and harvest equipment. Such anisotropy has been reported as well by Rew *et al*. (1996a), Johnson *et al*. (1996b), Dieleman & Mortensen (1999) and Colbach *et al*. (2000).

Presence of weeds may reduce the yield. Therefore, scope is provided for site-specific weed management, being a form of precision agriculture (Stein & Goudriaan, 2001). Identification and quantification of anisotropy in weed patterns may have an influence on weed spraying for site-specific weed management and hence on the quality of the environment (Gerhards *et al*., 1997a, b). The dispersal of weed seeds in a tall crop like maize is affected by the 'wall-like' structure of the crop before harvest (Colbach *et al*., 2000). For herbicide spraying, clogging of a nozzle of a spray boom could facilitate a striped weed pattern, with a width of approximately one row. Aggregation at the level of single rows is probably too fine a scale to be detectable

with the implementation of Mead's test. Cross-row patchiness due to the effects of ploughing or cultivation could be detectable using Mead's test depending upon the working width of the machinery. However, relations between patch width and agricultural machinery are speculative, as many other factors could also contribute. For example, seed removal of *C. album* by vertebrates in a maize field was also found to be patchy (Marino *et al*., 1997). Further, chemical control of *E. crus-galli* with several high-density foci in 2001, was not successful that year (unpubl. results). Herbicides had been applied uniformly throughout the field. A specific application of dosage to varying weed densities may result in a better control of *E. crus-galli*. An understanding of weed patch behaviour, to which the Mead's test can contribute, should aid weed management in the future.

CHAPTER 3

Are weed patches stable in location? Application of an explicitly two-dimensional methodology[*]

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Summary

Field observations were made in three years continuous corn cultivation in The Netherlands to study spatial pattern and stability of spatial pattern over time in agricultural weeds. Two-dimensional correlograms were made, using data from single years, to characterize spatial correlation and pattern, while data from two different years were used to calculate correlation over space *and* time, to characterize the *stability* of pattern. Weeds that were able to attain high recruitment exhibited also the strongest spatial correlations. These weeds were *Echinochloa crus-galli, Chenopodium album, Chenopodium polyspermum,* and *Solanum nigrum.* Weeds that were less successful in attaining high densities in the maize rotation also showed less spatial correlation. Wind dispersing Compositae, e.g. *Taraxacum officinale*, had spatially uncorrelated patterns. All weeds that showed spatial correlation also showed stability in space, except *E. crus-galli*. The latter species showed marked population increase, and the locations and extent of its patches changed over the years. Statistical interpretation of the data is discussed, as are potential consequences for site-specific management and optimal sampling of weeds.

Keywords: Spatial pattern, space-time correlogram, cross-correlogram, *Chenopodium album*, *Chenopodium polyspermum, Echinochloa crus-galli, Solanum nigrum, Taraxacum officinale.*

INTRODUCTION

It has been extensively documented that the distribution of weeds on arable land is spatially heterogeneous (e.g. Marshall, 1988; Rew *et al.*, 1996a; Gerhards *et al.*, 1997a, b; Dieleman & Mortensen, 1999). The patchy nature of weed patterns provides scope for site-specific weed management through adjustments of herbicide dosage to the presence and density of weeds (see references in Christensen *et al.*, 1999). Reductions in herbicide use, greater than 90%, might thereby be possible (Johnson *et al.*, 1995a). Site-specific management is facilitated if weed patches are stable in location from one year to the next, such that maps of weed patterns made in one year can be used for site-specific control in subsequent years (Goudy *et al.*, 2001). Information on patterns can also assist in the interpolation of sensor-derived real time data on the presence or density of weeds during control. There is a clear need to characterize weed patterns. This requires good data over a wide range of conditions, as well as suitable methods.

In most studies on spatial patterns of weeds, samples are taken according to a regular grid with interspersed unsampled space. Geostatistical interpolation methods are then used to calculate the weed density at unsampled locations (e.g. Johnson *et al.*, 1995a, 1996b; Cardina *et al.*, 1996; Gerhards *et al.*, 1997b; Colbach *et al.*, 2000; Goudy *et al.*, 2001). Interpolation methods may fail to detect patches if these are smaller than the distance between sample locations (Rew & Cousens, 2001; Wyse-Pester *et al.*, 2002). Observations on contiguous quadrats therefore give more reliable information on weed patterns. This method has been applied little in weed science because it is laborious. With respect to patch stability, which requires data in subsequent years, there are only two data sets resulting from samples in contiguous quadrats, one from a diverse crop rotation in Victoria, Australia (Cousens *et al.*, 2002, 2004, 2006) and another from continuous corn cultivation in Nebraska, USA (Dieleman & Mortensen, 1999). The first study included fourteen species present in the samples, whereas the latter study focused on a single weed species (*Abutilon theophrasti* Medik.). Most other published studies are based on spatially interpolated data. It can, therefore, be safely concluded that there still is a paucity of detailed data on the stability of weed patterns.

When analysing and characterizing spatial dynamics of weed patterns, a methodology should be chosen that can detect and quantify several possible patch behaviours. Patches could expand radially as a result of population increase and dispersal, or they could shrink. Moreover, they could *intensify* or *extensify*, as a result of local population change without clear spatial expansion or shrinkage, or patches could shift in space, e.g. as a result of harvest or tillage operations (Humston *et al.,* 2005). In this chapter, we choose for the analysis of spatial processes a methodology that is based on calculating two-dimensional (2-D) empirical correlograms across space and time.

Calculated correlations across space are used to characterize the shape and extent of patches for all possible directions (Oden & Sokal, 1986; Legendre & Fortin, 1989; Rossi *et al.*, 1992). Correlations are calculated over a matrix of lag distances in-row and cross-row direction that agree in spatial grain with the observational grid. All possible compass directions are accounted for because all combinations of different row and cross-row distances are taken into account. The advantage of such a method over one that merely tests whether two patterns are the same or not (Syrjala, 1996) is that the 2-D correlograms provide clues as to the ways in which two pattern are similar or dissimilar, contrary to a method that only gives a yes/no answer.

In diagnosing potential patch movement, we calculate correlation between weed densities in one year with weed densities the next year, again using a matrix of lag distances in-row and cross-row direction. This approach enables detection of spatial correlation structure and patch movement without making prior assumptions about isotropy, or anisotropy according to a presupposed shape, e.g. an ellipse (e.g. Wiles & Brodahl, 2004) or about the boundaries of the patch (e.g. Krohmann *et al.*, 2006). When calculating correlations we use Spearman's non-parametric coefficient of rank correlation (Gibbons, 1997). At a small loss of power (Lehmann, 1998) compared to the commonly used product moment correlation coefficient of Pearson, this coefficient provides robustness against deviations from linearity in relationships, skewed distributions, non-normal error structure (the rule with weeds) and outliers (Isaaks & Shrivastava, 1989).

This chapter has the following objectives: (1) to add a new substantial data set to the scarce data on the development of weed patches over time, derived from samples with continuous quadrats; (2) to explore and demonstrate the application of 2-D correlograms and cross-correlograms for the characterization of weed patterns and the locational stability of patches; (3) to characterize weed patterns over three years of continuous maize and determine whether weed patches are stable in location or not. The direction of greatest auto- and cross-correlation is derived from explicit 2-D analyses. The effect of the size of quadrats on the outcomes of spatial analysis is also investigated.

MATERIALS AND METHODS

Field
Observations were made in 2001, 2002 and 2003 on a 1.8 ha arable clay field (Kortenoord II) near Wageningen, The Netherlands. In the six years preceding the study, the field had been planted with winter wheat (1995), maize (1996), potatoes (1997), winter wheat (1998), fodder beets (1999) and summer barley (2000). The field

was tilled with a rigid-tine cultivator in early October and with a mouldboard plough plus skim-coulter in November. Fertilizer (450 kg N ha^{-1}, 240 kg K ha^{-1}, 150 kg P ha^{-1}) was applied in the spring of each year before seedbed preparation with a rotary harrow. Maize (*Zea mays* L. cv. '*Limatop*') was sown at 0.75 m row distance in May 2001, 2002 and 2003 at a density of 100 000 seeds ha^{-1}. Herbicide was sprayed broad field post-emergence ca. 5 weeks after sowing. Only post-emergence herbicides were used (details are available on request). Maize was harvested in late September. The entire field was cultivated and sown in the north-south direction, with the exception of the headlands where field traffic was east-west.

Observations

The spatial pattern of weeds was determined each year, before the first herbicide application, in an observation area of 12 m (16 rows) by 50.25 m row length. The counts were made from 18–21 June 2001, from 17–19 June 2002, and from 10–12 June 2003. The observation area was situated just south of the northern headland and was divided into $16 \times 67 = 1072$ quadrats of 0.75×0.75 m. Two of the sides of the quadrats coincided with the crop rows. The exact locations of the corners of the observation plot were indicated with permanent poles in the edges of the field. All weed plants in the plot were identified to species or species group and their number in each quadrat enumerated.

Weed species

Seventeen weed species were present in more than five percent of the quadrats in one or more of the three observation years. Records were taken of fifteen groups of species because the seedlings of some species were hard to distinguish in the field. These 15 species groups were: (1) *Capsella bursa-pastoris* L. (shepherd's purse), (2) *Chenopodium album* L. (fat hen), (3) *Chenopodium polyspermum* L. (many-seeded goosefoot), (4) *Echinochloa crus-galli* (L.) Beauv. (barnyard grass), (5) *Lamium purpureum* L. (purple deadnettle), (6) *Poa annua* L. (annual meadow grass), (7) *Polygonum aviculare* L. (knotweed), (8) *P. persicaria* L. + *P. lapathifolium* ssp. *lapathifolium* L. + *P. lapathifolium* ssp. *pallidum* (With.) Fries) (lady's thumb and pale smart weed), (9) *Ranunculus sceleratus* L. (celery-leaved buttercup), (10) *Senecio vulgaris* L. (common groundsel), (11) *Solanum nigrum* L. (black nightshade), (12) *Sonchus* spp. (*S. asper* L. Hill and *S. oleraceus* L.) (prickly and common sow thistle), (13) *Stellaria media* L. (chickweed), (14) *Taraxacum officinale* Weber (dandelion), and (15) *Trifolium repens* L. (white clover). The set of species, thus, comprised 13 annual dicots, two annual grasses (*P. annua* and *E. crus-galli*) and two perennial dicots (*T. repens* and *T. officinale*). Most of these species depend on agricultural implements

for seed dispersal; however, the seeds of *T. officinale*, *S. vulgaris* and *Sonchus* spp. (all Asteraceae) are mainly dispersed by wind.

Initial data analysis

Descriptive statistics were calculated for 2001, 2002 and 2003 data: mean number per quadrat, variance, standard deviation, median and other quartiles, coefficient of variation, and incidence (percentage of quadrats occupied). An estimate for the parameter *k* of the negative binomial distribution (NBD) was obtained by the method of moments (Binns *et al.*, 2000, p. 77): $k = \mu^2 / (\sigma^2 - \mu)$ where μ is the mean and σ^2 the variance of the counts per quadrat. The parameter *k* serves as a guide towards gauging the variance of the sampling distribution compared to a Poisson distribution. For large *k* ($>> \mu$), the NBD tends towards a Poisson, whereas for small *k*, the variance of the distribution is notably larger than that of the Poisson distribution, resulting in more quadrats with extreme counts (small as well as large).

Spatial autocorrelation *within* years

Spatial structure of the weed patterns within each year was characterized by calculating Spearman's rank correlation coefficient (*r*) between counts in all possible combinations of quadrats at a given *within-row* and *cross-row* distance within the sampled support $\{(x_i \in \{1, N_x\}, y_i \in \{1, N_y\})$, where *x* denotes distance (measured in numbers of quadrats) cross-row and *y* denotes distance within-row, and $N_x = 16$ and $N_y = 67$ are the number of sample locations in *x*- and *y*-direction. Let a weed count at location (x_i, y_i) be denoted as $u(x_i, y_i)$. Then the coefficient of rank correlation is calculated between all matching data pairs $\{u(x_i, y_i), u(x_i + h_x, y_i + h_y)\}$ at a cross-row distance h_x and a within-row distance h_y, where x_i and y_i are part of the set $(x_i \in \{1, N_x - h_x\}, y_i \in \{1, N_y - h_y\})$. The total number of point pairs involved in the calculation of the correlation coefficient at a given combination of lag distances h_x and h_y equals $(N_x - h_x)(N_y - h_y)$ (Figure 1). Thus, at greater lag distances, there are fewer point pairs available to calculate the statistic, and the significance of calculated coefficients changes accordingly. Spearman's *r* was then determined by calculating a Pearson product moment correlation coefficient on the ranks (e.g. Gibbons, 1997). Ties in the data were handled by the mid-rank method (Gibbons, 1997; p. 305). As the calculation uses an overall population mean rank for calculating correlation, the resulting correlogram is ergodic (Rossi *et al.*, 1992). The result is represented as a 2-D 'checker board' plot with grey scales in which the data value at a 2-D lag (h_x, h_y) indicates the rank correlation pertaining to a lag in cross-row direction of h_x and a simultaneous lag in-row direction of h_y. The centre of the correlogram indicates a lag distance of 0, and per definition, the correlation coefficient at this point equals 1.
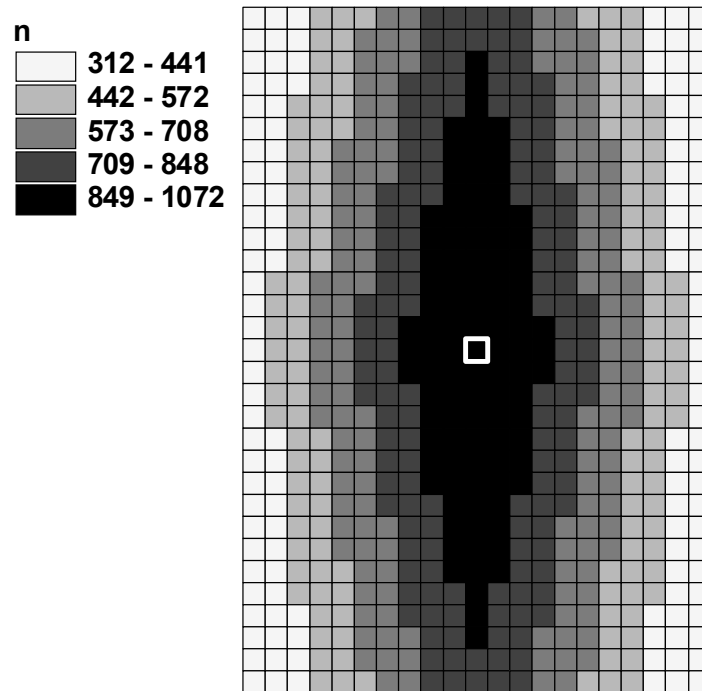
Figure 1. Number of quadrat pairs (*n*) that can be used for calculation of the correlation coefficient *r* as a function of the lag distance across rows (horizontal axis) and within rows (vertical axis). The centre of the plot indicates lags of $h_x = h_y = 0$.

Values of h_x were taken between -10 and $+10$ quadrat distances, while the chosen range of values for h_y was greater (-15 to $+15$) to account for a greater spatial extent of the observation plot in the *row* direction (*y*) than in the *cross-row* direction (*x*). In total, therefore, $21 \times 31 = 651$ values of *r* were calculated to characterize the two-dimensional correlogram. Calculated *r*-values were classified into six categories for presentation: $[-0.4, -0.2]$, $[-0.2, +0.2]$, $[+0.2, +0.4]$, $[+0.4, +0.6]$, $[+0.6, +0.8]$, $[+0.8, +1.0]$. Calculations of spatial correlation within years were made for each of the 15 selected weed species, in each of the three years.

Temporal behaviour: spatial cross-correlation *between* years
Spatial correlation between weed patterns of two years was calculated in a similar way as within years, the only difference being that the data of the quadrat pairs now originated from two different years instead of the same year: $\{u(x_i, y_i, t_1), u(x_i + h_x, y_i + h_y, t_2)\}$ where t_1 and t_2 indicate different years. The Spearman rank correlation coefficient was calculated between patterns of 2001–02, 2002–03 and 2001–03. This was done for each weed species separately. Results were again visualized in 2-D correlograms using six class intervals for *r*.

Effect of scale on spatial autocorrelation *within* years: clustering of observation quadrats

To examine the effect of the spatial resolution of observations on correlogram outcomes, data were aggregated by merging four contiguous observation quadrats into one large quadrat (1.5 m × 1.5 m) and summing the four counts. Values of *r* were calculated for all $11 \times 15 = 165$ combinations of $h_x \in [-5,+5]$ and $h_y \in [-7,+7]$. Results were again visualized in correlograms.

Modelling the correlograms

Empirical correlogram data were fitted to an analytical function (Eq. 1), in which spatial coordinates are expressed in polar form (angle *θ* and distance *h*), to quantify anisotropy and orientation of the main correlogram axis with respect to the direction of field traffic:

$$\rho(h,\theta) = s \qquad\qquad\qquad\qquad\qquad h = 0$$

$$\rho(h,\theta) = s \, \frac{\sin\left(h\sqrt{a^2 \cos^2(\theta-\varphi) + b^2 \sin^2(\theta-\varphi)}\right)}{h\sqrt{a^2 \cos^2(\theta-\varphi) + b^2 \sin^2(\theta-\varphi)}} \quad h > 0 \qquad (1)$$

This model contains four parameters: *φ*, *a*, *b*, and *s*, where *φ* is the direction of largest anisotropy, *a* characterizes dependence in the direction of largest correlation (*φ*), *b* characterizes dependence in the direction of smallest correlation, and *s* is a parameter indicating the correlation for distance 0 (Journel & Huijbregts, 1978; Webster & Oliver, 2000). Parameters of this model were estimated using a weighted non-linear regression fit, with the number of point pairs in each distance class (h_x, h_y) as weights. The analysis focused on the *within year* correlograms of a selection of species with high levels of spatial correlation. To determine the goodness of fit it is not meaningful to calculate an ordinary R^2 when using weighted regression. Instead, following Eq. 8 in Willett & Singer (1988), a pseudo R^2_{WLS} coefficient was calculated. This coefficient can be interpreted like an ordinary coefficient of determination, i.e. as the proportion of variance accounted for by the regression.

Software

Descriptive statistics were calculated with S-Plus. Calculations of correlations were programmed and run in Compaq Visual Fortran v. 6.6. ArcView GIS 3.3 (ESRI, Redlands, Ca, USA) was used to visualize observed weed patterns and two-dimensional correlograms. Parameter fitting was done with SAS procedure NLIN.

Table 1. Descriptive statistics of weed counts in 1072 75 cm × 75 cm quadrats in a 12 m × 50.25 m observation plot in continuous corn in 2001, 2002 and 2003. The minimum count was 0 in all species in all years.

Species	year	mean	1st quartile	median	3rd quartile	maximum	variance	s.d.	CV (%)	k	incidence (%)
C. bursa-pastoris	2001	0.31	0	0	1	4	0.33	0.57	187	3.98	26
	2002	0.01	0	0	0	2	0.02	0.13	895	0.12	1.3
	2003	0.17	0	0	0	4	0.19	0.43	254	1.65	15
C. album	2001	3.51	1	2	4	44	25.50	5.05	144	0.56	80
	2002	0.57	0	0	1	30	2.30	1.52	264	0.19	33
	2003	1.32	0	1	2	16	2.86	1.69	128	1.14	62
C. polyspermum	2001	2.48	0	1	4	26	13.20	3.63	146	0.58	59
	2002	0.97	0	0	1	41	4.54	2.13	220	0.26	40
	2003	3.53	0	1	5	65	28.50	5.34	151	0.50	66
E. crus-galli	2001	8.86	0	2	8	158	396.00	19.90	225	0.20	69
	2002	4.48	0	2	6	49	42.30	6.50	145	0.53	70
	2003	28.43	6	15	33	282	1458.00	38.18	134	0.57	98
L. purpureum	2001	0.10	0	0	0	2	0.11	0.33	342	0.72	8.6
	2002	0.05	0	0	0	3	0.06	0.24	500	0.25	4.3
	2003	0.10	0	0	0	4	0.14	0.38	370	0.25	8.4
P. annua	2001	0.35	0	0	1	4	0.43	0.66	186	1.57	27
	2002	0.66	0	0	1	5	0.85	0.92	139	2.32	44
	2003	0.71	0	0	1	8	1.01	1.01	142	1.64	43
P. aviculare	2001	0.90	0	1	1	7	1.10	1.05	116	4.11	56
	2002	0.05	0	0	0	1	0.05	0.21	443	N.E.	5
	2003	1.13	0	1	2	8	1.68	1.30	114	2.34	61

Table 1. Continued.

Species	year	mean	1st quartile	median	3rd quartile	maximum	variance	s.d.	CV (%)	k	incidence (%)
P. persicaria and P. lapathifolium	2001	0.44	0	0	1	5	0.51	0.72	165	2.39	33
	2002	0.27	0	0	0	9	0.46	0.68	254	0.37	20
	2003	1.79	0	1	3	14	3.28	1.81	101	2.15	75
R. sceleratus	2001	0.00	0	0	0	1	0.00	0.03	3274	N.E.	0.09
	2002	0.05	0	0	0	2	0.06	0.25	496	0.23	4.3
	2003	0.10	0	0	0	3	0.13	0.37	368	0.29	8.0
S. vulgaris	2001	0.08	0	0	0	3	0.09	0.30	389	0.42	7.0
	2002	0.01	0	0	0	1	0.01	0.08	1234	N.E.	0.7
	2003	0.02	0	0	0	3	0.03	0.17	723	0.11	2.2
S. nigrum	2001	0.75	0	0	1	19	3.33	1.83	243	0.22	33
	2002	0.43	0	0	0	13	1.18	1.09	250	0.25	24
	2003	1.05	0	0	1	25	6.08	2.47	234	0.22	39
S. asper + S. oleraceus	2001	0.04	0	0	0	2	0.04	0.19	528	2.30	3.5
	2002	0.03	0	0	0	1	0.03	0.17	561	N.E.	3.1
	2003	0.07	0	0	0	3	0.07	0.27	403	0.88	6.3
S. media	2001	0.09	0	0	0	4	0.10	0.32	358	0.57	8.2
	2002	0.01	0	0	0	2	0.02	0.13	863	0.13	1.4
	2003	0.05	0	0	0	8	0.13	0.36	763	0.03	3.5
T. officinale	2001	0.18	0	0	0	4	0.18	0.43	239	8.20	16
	2002	0.04	0	0	0	2	0.04	0.20	501	5.47	3.9
	2003	1.27	0	1	2	9	1.44	1.20	95	9.29	68
T. repens	2001	0.18	0	0	0	3	0.17	0.41	227	N.E.	17
	2002	0.05	0	0	0	2	0.05	0.23	433	3.42	5.2
	2003	0.31	0	0	1	5	0.34	0.58	189	3.22	26

RESULTS

All weed species varied in density and incidence over the three years of survey (Table 1). Density and incidence were intermediate in 2001, low in 2002, and high in 2003. The 15 weed species groups differed with regard to their pattern. Four species (*E. crus-galli, C. polyspermum, C. album* and *S. nigrum*) showed substantial spatial aggregation as indicated by the estimated values of *r* (Table 2). These weed species also had a high maximum weed density per quadrat. The remaining 11 weed species groups showed weak correlation or no spatial correlation at all (Table 2). Strong spatio-temporal dependency between years was shown by three weed species (*E. crus-galli, C. polyspermum,* and *S. nigrum*) whereas two weed species (*C. album, L. purpureum*) showed weak spatial dependency between years. The remaining 10 weed species groups showed no spatial dependency between years (*r* interval [–0.2, +0.2]) (Table 2).

Table 2. Strength of spatial structure of weed patterns as expressed by correlograms within and between years. Strength is divided in five classes and is based on the values of the interval of *r* in the three survey years (2001, 2002 and 2003).

Correlation strength	Interval *r*	Within years	Between years
Very strong	[–0.2, +1.0]	*E. crus-galli*	*E. crus-galli*
Strong	[–0.4, +0.8]	*C. polyspermum*	*C. polyspermum*
Moderate	[–0.2, +0.6]	*C. album, S. nigrum*	*S. nigrum*
Weak	[–0.2, +0.4]	*L. purpureum, P. aviculare, P. persicaria + P. lapathifolium, R. sceleratus*	*C. album, L. purpureum*
None to very weak	[–0.2, +0.2][*]	*C. bursa-pastoris, P. annua, S. media, S. asper + S. oleraceus, S. vulgaris, T. officinale, T. repens*	*C. bursa-pastoris, P. annua, P. aviculare, P. persicaria + P. lapathifolium, R. sceleratus, S. media, S. asper + S. oleraceus, S. vulgaris, T. officinale, T. repens*

[*] If one or two lag distances yielded an *r*-value > 0.2, but the far majority of *r*-value was < 0.2, the correlogram was classified in the lowest category of spatial correlation (cf. Figure 4e).

Weed maps and descriptive statistics

Maps of *C. album, C. polyspermum, E. crus-galli*, *S. nigrum* and *T. officinale* in 2001, 2002 and 2003 are presented in Figure 2. The first four exemplify species whose patterns were correlated in space and time. *Taraxacum officinale* exemplifies a weed species with a spatially and spatio-temporally uncorrelated random pattern. The other species, not shown in Figure 2 but included in Table 2, show intermediate degrees of spatial correlation, that vary from virtually uncorrelated (*C. bursa-pastoris, P. annua, S. media, S. asper + S. oleracea, S. vulgaris* and *T. repens*) to weakly correlated (*L. purpureum, P. aviculare, P. persicaria + P. lapathifolium*, and *R. sceleratus*). In all three years, *E. crus-galli* reached the highest mean and maximum densities per quadrat of all weeds (Table 1); it also had the highest incidence in two of the three years: 2002 (70%) and 2003 (98%). *Chenopodium album, S. nigrum* and *E. crus-galli* had higher densities in the northern half of the observation area, near the headland, than in the southern part of the sample area. The patches of *C. polyspermum* and *S. nigrum* were stable in location, but the high-density areas of *E. crus-galli* shifted a few meters south-east-ward in the course of the study (Figures 2c, 2h and 2m). High densities of *C. polyspermum* were limited to the eastern half of the sample area (Figures 2b, 2g and 2l). The pattern of *T. officinale* exhibited no spatial structure (Figures 2e, 2j and 2o).

Spatial autocorrelation within years

Chenopodium album, C. polyspermum, E. crus-galli and *S. nigrum* showed spatial dependence in the 2-D correlograms, as indicated by dark grey shades at short distance lags in Figure 3. In contrast, *T. officinale* showed no correlation at any distance lag. In the first four species, the extent of spatial correlation was greater in the direction of crop rows than across (Figure 3). Spatial properties differed for each species. For instance, the pattern of *E. crus-galli* showed the greatest range of correlation in a direction that was slanted with respect to the crop rows, a feature that was not observed in any other species. The pattern of *E. crus-galli* also showed the highest overall spatial correlation with values of *r* at short distance exceeding 0.8 in 2001 and 2003 (Figure 3c; Table 2). The elongated shape of the spatial pattern of *C. polyspermum* (Figure 2b, g and l) was reflected in correlograms that were elongated in the row direction (Figure 3b; Table 2). Comparison of the correlograms of *S. nigrum* in the three years suggests that its patches had shrunk in 2002, and expanded in 2003. However, this apparent shrinkage might also be due to the generally lower counts of this species in the second year of the study, as a result of which correlations at greater distances may not have exceeded the detection threshold (see also *Discussion*). The correlogram of *T. officinale* represents a spatially uncorrelated random pattern (Figure 3e; Table 2). Note that all 2-D correlograms are radially symmetric in the origin
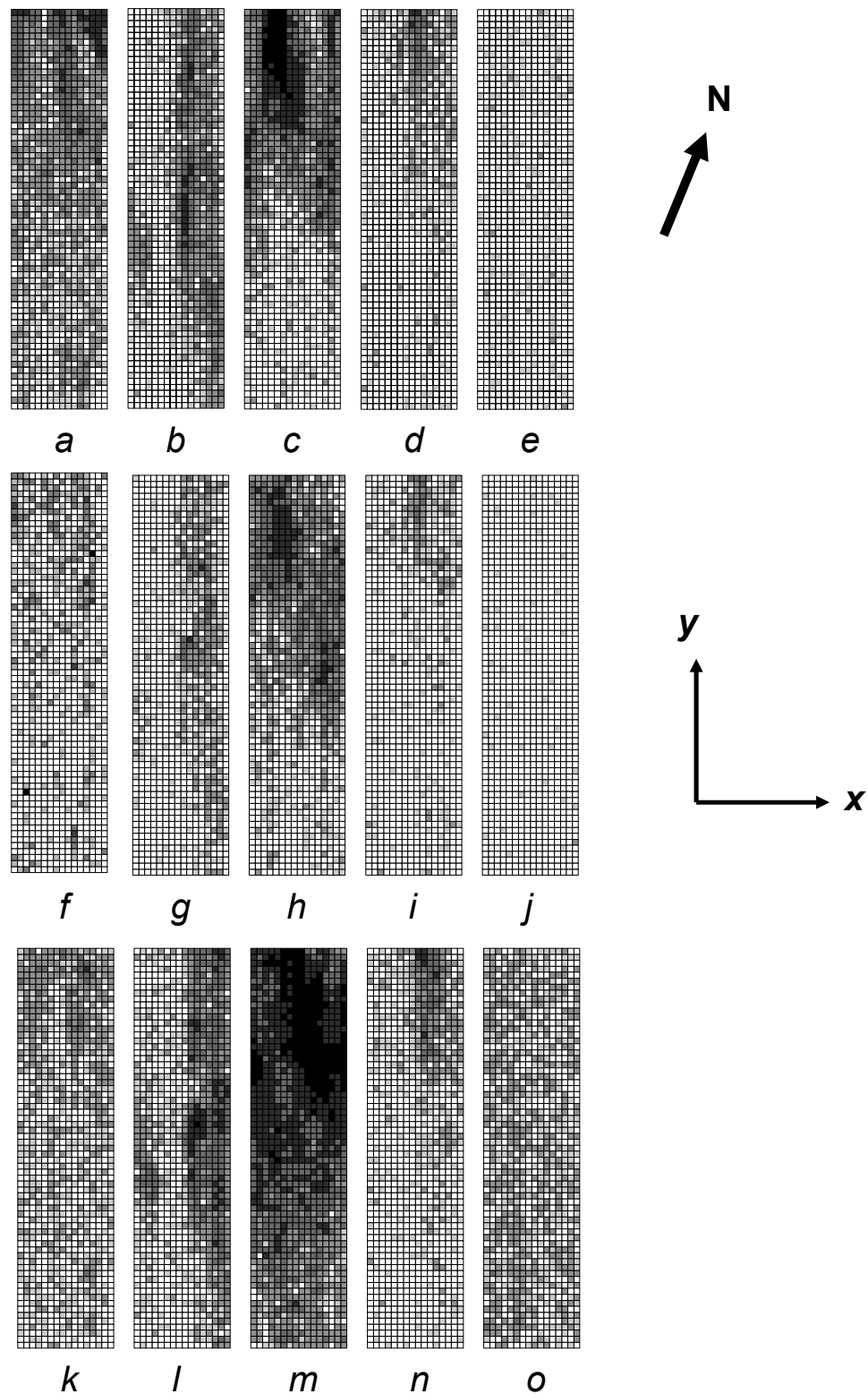
Figure 2. Spatial patterns of *C. album* (a, f, k), *C. polyspermum* (b, g, l), *E. crus-galli* (c, h, m), *S. nigrum* (d, i, n) and *T. officinale* (e, j, o) in 2001 (a–e), 2002 (f–j) and 2003 (k–o). Each quadrat is 0.75 m × 0.75 m. Number of plants per quadrat is indicated by grey tones: ▢=0, ▢ =1, ▩ =2–5, ▨ = 6–15, ▦ = 16–50, ■ = > 51.
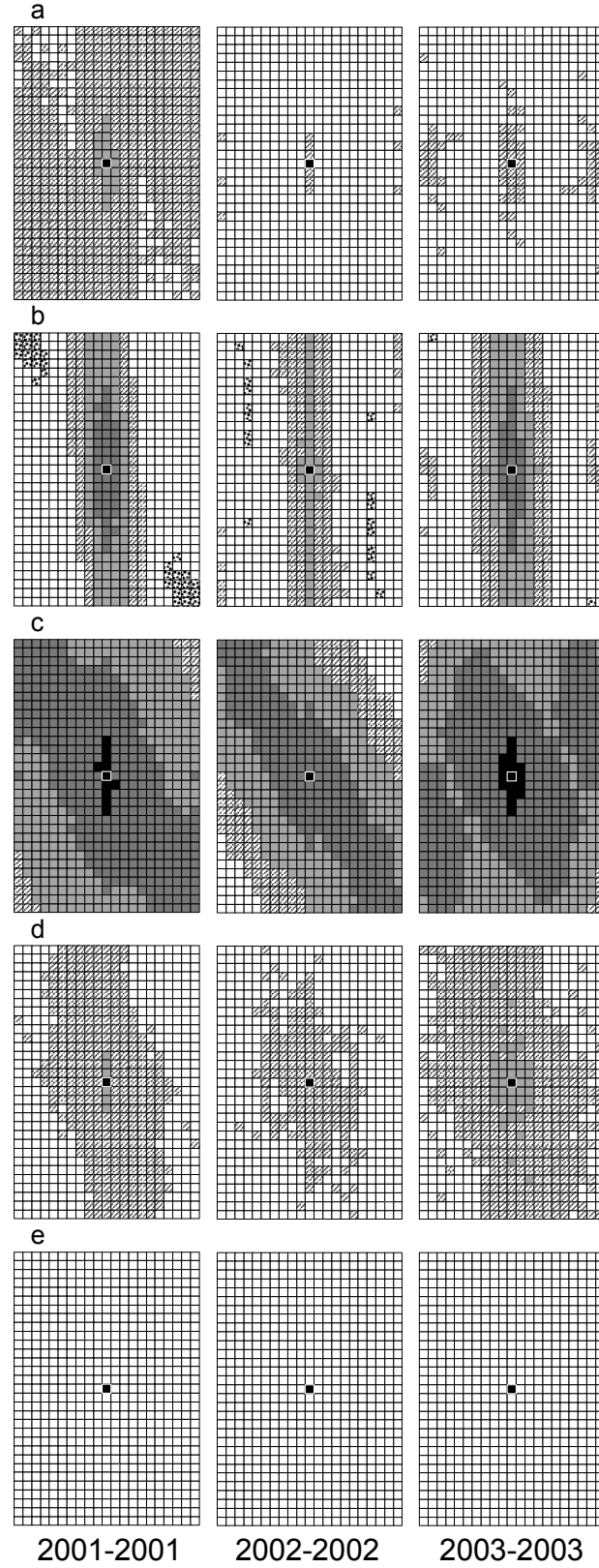
Figure 3. Correlograms within years of *C. album* (a), *C. polyspermum* (b), *E. crus-galli* (c), *S. nigrum* (d) and *T. officinale* (e). Horizontal axis is h_x [–10, +10] and vertical axis is h_y [–15, +15]. Values of correlation coefficient are indicated by grey tones: ▦ (–0.4) – (–0.2); ☐ (–0.2) – 0.2; ▨ 0.2 – 0.4; ▧ 0.4 – 0.6; ▩ 0.6 – 0.8; ■ 0.8 – 1.0.
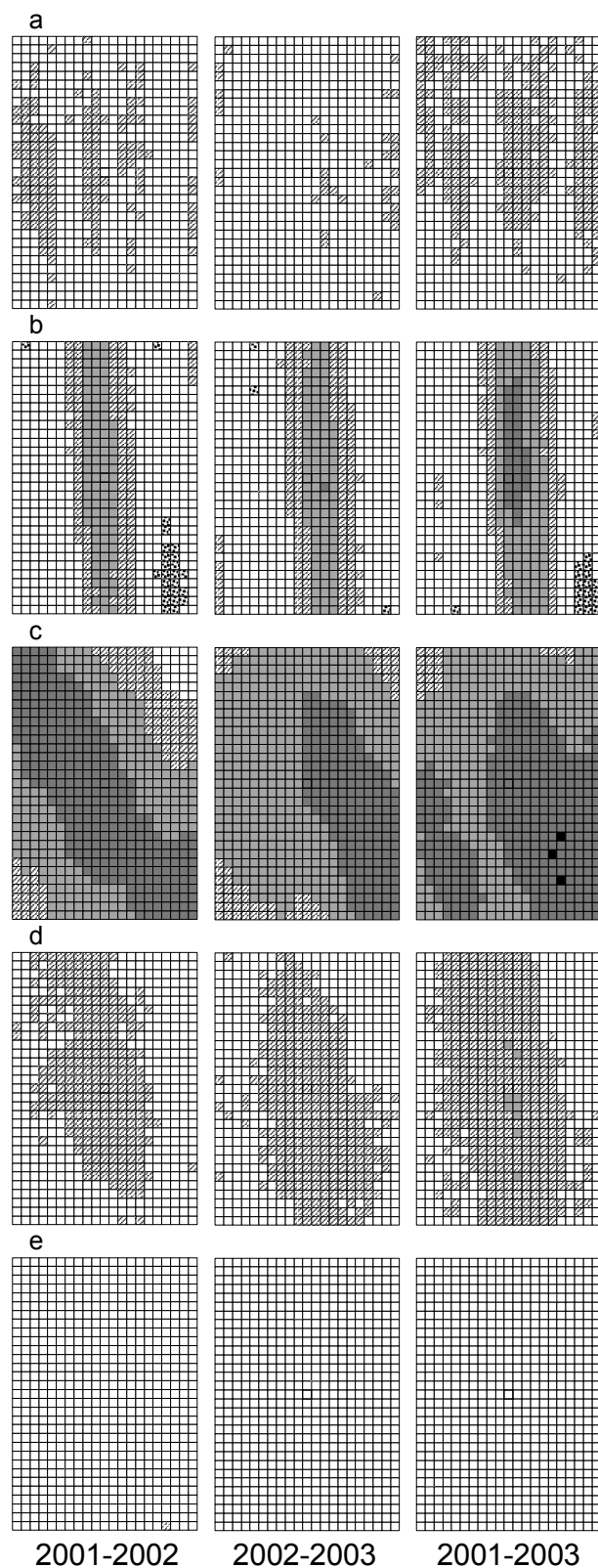
Figure 4. Correlograms between years of *C. album* (a), *C. polyspermum* (b), *E. crus-galli* (c), *S. nigrum* (d) and *T. officinale* (e). Horizontal axis is h_x [–10, +10] and vertical axis is h_y [–15, +15]. Values of correlation coefficient are indicated by grey tones: (–0.4) – (–0.2); (–0.2) – 0.2; 0.2 – 0.4; 0.4 – 0.6; 0.6 – 0.8; 0.8 – 1.0.

as the same point pairs are formed whether the lags are applied to the first or second data value.

Spatial cross-correlation between years

Three of the 15 weed species groups showed consistent spatio-temporal dependency: *C. polyspermum*, *E. crus-galli* and *S. nigrum* (Figures 4b, c and d; Table 2). The strongest correlation between years occurred for *E. crus-galli* but its pattern was not stable in location (Figure 4c). The spatial displacement of *E. crus-galli* is evidenced by the 'off-centre' peak in the 2-D cross-correlogram between years (Figure 4c). Spatial patterns of *C. polyspermum,* by comparison, were comparatively consistent in space and time as evidenced by the similarity of the between year cross correlograms of this species to the within year correlograms. Nevertheless, a slight displacement in the *x*-direction is indicated for this species from the first year (2001) and the second year (2002) to the third year (2003), because the greatest correlation is found for $h_x > 0$ in the cross correlograms for 2001–2003 and 2002–2003, but not for 2001–2002 (Figure 4b). *S. nigrum* was spatially consistent from 2001 to 2002 and from 2002 to 2003 (Figure 4d) but had moderate *r* values not exceeding 0.4. Spatial patterns of *T. officinale* (Figure 4e) were spatio-temporally uncorrelated. Spatio-temporal correlation in *C. album* was weak (Figure 4a), indicating weak location consistency of its patches. Note that the correlograms in Figure 4, contrary to those in Figure 3, are *not* radially symmetric. This is because the data values for each data pair are from two different years, i.e. $r\{u(x_i, y_i, t_1), u(x_i+h_x, y_i+h_y, t_2)\} \neq r\{u(x_i+h_x, y_i+h_y, t_1), u(x_i, y_i, t_2)\}$.

Aggregation of quadrats to larger scale and spatial autocorrelation

For most species, correlograms were basically the same when observations on aggregated units of 1.5 m by 1.5 m were analysed within years. Exceptions to this general finding are *C. album* (Figure 5a) and *P. annua* (not shown here), for which spatial correlations became more distinct, and *C. polyspermum*, for which the correlogram virtually vanished (Figure 5b). Possible reasons are addressed in the discussion.

Quantification of correlograms

The anisotropic correlogram model (Eq. 1) gave a good description for *C. polyspermum* (2001) and *S. nigrum* (2001) (Figure 6). Both weeds showed distinct anisotropy. Other weed species either showed a noisy correlation without any apparent structure, or a behaviour that could not be fitted with the model. The direction of the largest anisotropy varied between $\varphi = -0.0698$ radians (–4°) with respect to the direction of field traffic for *C. polyspermum* to $\varphi = -0.212$ (–12°) for *S. nigrum*. In

2001-2001   2002-2002   2003-2003
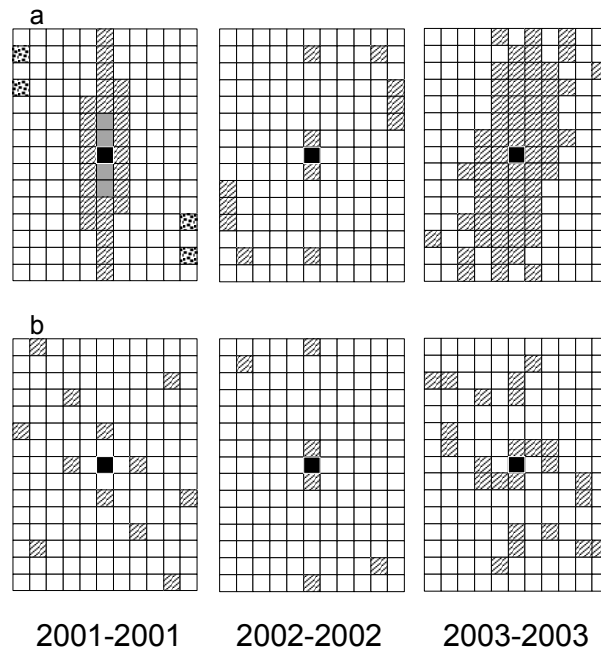
Figure 5. Correlograms within years for aggregated quadrats of *C. album* (a) and *C. polyspermum* (b). Horizontal axis is h_x [–5, +5] and vertical axis is h_y [–7, +7]. Values of correlation coefficient are indicated by grey tones: (–0.4) – (–0.2); (–0.2) – 0.2; 0.2 – 0.4; 0.4 – 0.6; 0.6 – 0.8; 0.8 – 1.0.

both species, the value of *a* (0.088 for *C. polyspermum* and 0.125 for *S. nigrum*) was considerably smaller than that of *b* (0.821 and 0.312, respectively), indicating substantial patch elongation in the direction closest to the direction of field traffic. The parameter *s,* specifying the strength of the correlation, was 0.33 for *S. nigrum* and 0.59 for *C. polyspermum.* Pseudo R^2_{WLS} were 0.65 for *S. nigrum* and 0.73 for *C. album,* indicating that the fitted anisotropic correlogram models satisfactorily described the empirical correlograms of these two species.

DISCUSSION

The objectives of the research described here were to characterize spatial pattern and pattern dynamics of weeds in an area of 12 m by 50.25 m in a continuous maize rotation. Data were collected over three years, using contiguous quadrats to obtain spatially continuous data and avoid artefacts from spatial interpolation. Two-dimensional empirical correlograms were developed to interpret the results. The main findings are: (1) a minority of weed species showed distinct spatial aggregation and

Empirical correlogram   Modeled correlogram
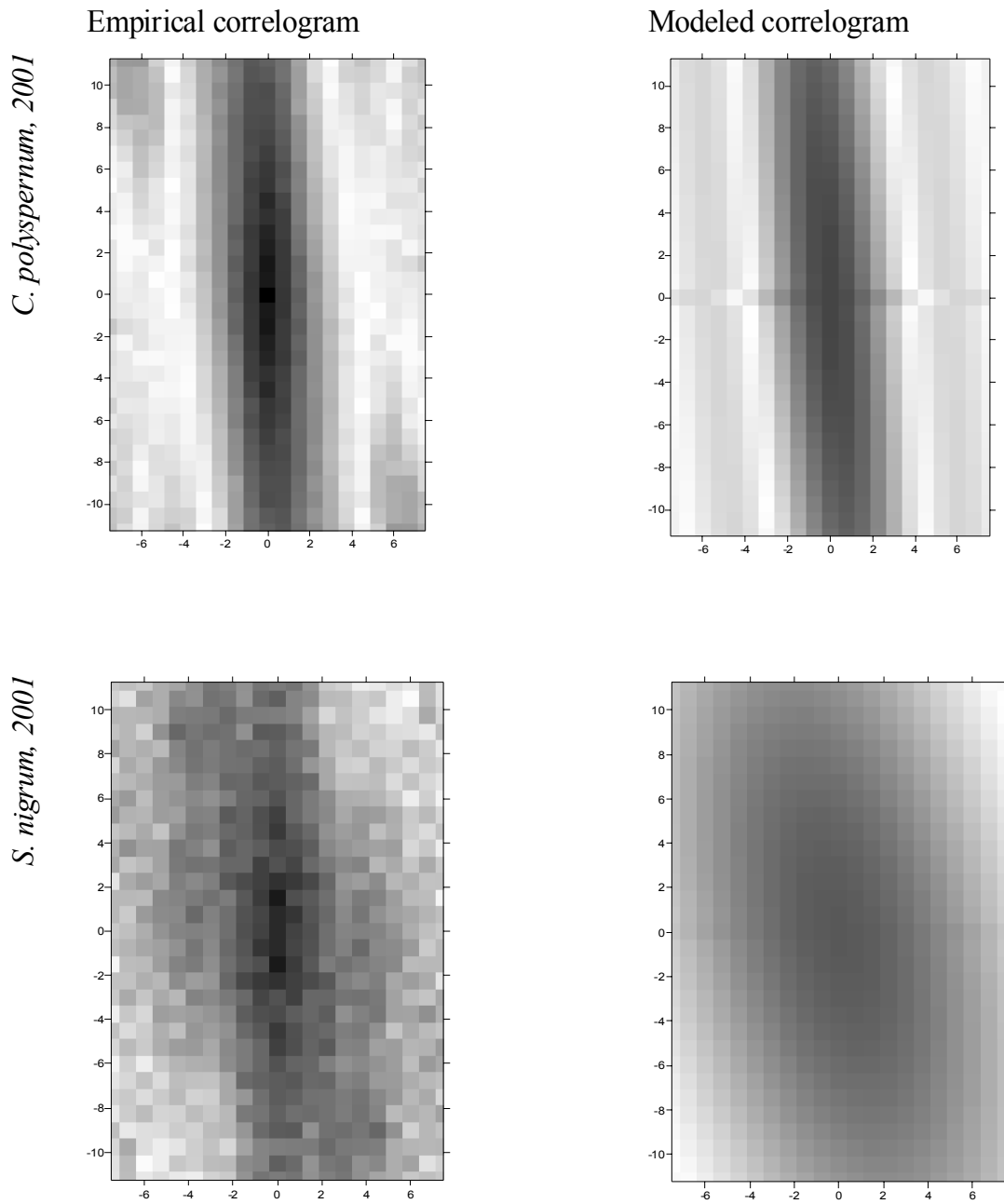
Figure 6. Empirical and modelled anisotropic correlograms within years for *C. polyspermum* (2001) *and S. nigrum* (2001). Grey tones vary from −0.4 to 0.8 (*C. polyspermum*) and from 0.25 to 0.50 (*S. nigrum*).

these were the species that occurred in the highest densities; (2) one species (*E. crus-galli*) showed patch displacement; (3) wind dispersing weed species in the Compositae, such as *Taraxacum officinale*, exhibited spatially uncorrelated patterns; and (4) 2-D correlograms provided a helpful tool to characterize spatial pattern as well as spatial pattern dynamics. These issues are further discussed below.

The results indicate that only those weeds that were abundant exhibited strong spatial correlation. The abundant species were *C. polyspermum*, *C. album*, *S. nigrum* and *E. crus-galli*, all of which are summer annuals (Zanin *et al*., 1997). These species are able to reach high densities in maize, due to germination after the completion of weed control operations, in combination with good competitive ability. The other weed species synchronize less well with the maize crop, being either spring annuals or seasonally indifferent as to their germination (Zanin *et al*., 1997). Such species established lower densities, and exhibited weak or no spatial correlation at all. This suggests that adaptive phenology and substantial reproduction within the field are requirements for the formation of spatially aggregated patterns in annual weeds. A question is, however, whether the lack of distinct spatial correlation in those weeds that did *not* reach high densities could – in part – also be due to insufficient statistical power to detect it.

A simple mathematical analysis can demonstrate that a relationship between spatial correlation and density may indeed be expected on the basis of the statistical properties of count data. In general, the negative binomial distribution provides an adequate model to describe variability of count data (Wiles *et al*., 1992; Johnson *et al*., 1995b). For this model, given k, the variance of the count per quadrat equals

$$\sigma^2 = \mu\left(1 + \frac{\mu}{k}\right)$$

Where σ^2 is variance, μ is the mean count per quadrat and k is the dispersion parameter. The coefficient of variation of the count per quadrat (σ/μ) is then

$$CV = \frac{\sigma}{\mu} = \frac{1}{\mu}\sqrt{\mu\left(1 + \frac{\mu}{k}\right)} = \sqrt{\frac{1}{\mu} + \frac{1}{k}}$$

The coefficient of variation thus increases as μ decreases, or – in other words – the proportion of the data value that is due to random variation increases compared to the proportion of the data value that represents the underlying structure as μ decreases, irrespective of the value of k. A similar analysis may be conducted using a power relationship between variance and mean as a starting point (Taylor, 1961). As the exponent in the equation $\sigma^2 = a\mu^b$ is generally below 2 for weeds (Clark *et al.,* 1996; Heijting, unpubl. obs.), the coefficient of variation is greatest at small μ:

$$CV = \frac{\sigma}{\mu} = a^{\frac{1}{2}}\mu^{\frac{b-2}{2}}$$

As a result of an increasing relative error in the data, correlations will become more difficult to detect at a lower mean density of weeds. Our findings with *S. nigrum* are

consistent with this principle. We found high and spatially far reaching correlations in 2001 and 2003 with high densities, *versus* lower and less far reaching correlations in 2002 with lower densities of this weed. This principle may hold in any data set in which count data with Poisson or negative binomial distributions are analysed.

The question is whether greater relative variability in the counts can be regarded as the only reason why weeds that occur at lower density showed less spatial structure. The results for *C. album* in comparison to those for *C. polyspermum* and *S. nigrum* suggest that it may not be the only factor. *Chenopodium album* occurred at high densities, similar to those of *C. polyspermum*, and greater than those of *S. nigrum* (Table 1). Its coefficient of variation was of the same order of magnitude as those of the other two species or smaller. Nevertheless, in the correlograms, *C. album* shows less spatial correlation than the other two species. This difference probably reflects a true difference in spatial pattern, which is apparently less correlated in space in *C. album* than in the other two species. Whether the same holds for the species that occurred at lower densities is difficult to ascertain. Correlograms thus can be used to describe patterns, but they do not provide an unequivocal identification of the mechanism causing a pattern. The range over which significant correlation occurs may not only depend on the biological characteristics of the pattern itself, but also on the statistical properties of the weed count data, in particular the signal-to-noise ratio, which is likely to be related to density of the seed bank and recruitment success, as affected by weather.

Two patchy weed species, *C. polyspermum* and *S. nigrum*, showed strong locational stability throughout the three years of observation. Field studies by Wilson & Brain (1991), Dieleman & Mortensen (1999) and Gerhards *et al*. (1997b) showed that pre-harvest dispersal was essential for patch stability of annual weed species, since it will result in compact and dense seed shadows. Heavy seeds are likely to favour dense seed shadows. *Solanum nigrum* fits the profile of a species with heavy propagules (berries) that are predominantly shed before the harvest of maize. These characteristics and the longevity of its seeds will have favoured the locational stability of this weed species. In contrast, most of the seeds of *E. crus-galli* stay on the plant until harvest. Thus, these seeds could be readily dispersed during harvest and subsequent tilling as a result of dragging of plant debris by machinery (Heijting & Van der Werf, 2005). Such dragging of plant material would enlarge the seed shadow and may have contributed to the patch displacement observed in *E. crus-galli*. Whereas dispersal of seeds has been carefully studied, resulting in quantitative characterization of dispersal kernels (e.g. Marshall & Brain, 1999), the spread of weed seeds due to dispersal of seed-bearing parent plant material has so far received comparatively little attention. This topic warrants further study. Adult specimens of *C. polyspermum* were very rare and seed

production by this species during the years of the study has therefore been minimal; the locational stability of the patch of this species can likely be attributed to recruitment from a spatially unmoving seed bank. The location of this patch could be related to a historic event such as a failure in crop establishment or weed control in a year before the study was started. Spatial correlations can also result from spatially correlated variability in soil (Heisel *et al.*, 1999; Walter *et al.*, 2002; Heijting *et al.*, 2005).

Patterns of the wind dispersing species *T. officinale*, *S. vulgaris* and *Sonchus* spp. did not show spatial dependence or spatial stability. The observed randomness of *T. officinale* matches results of Goudy *et al.* (2001). No reproducing adults of *T. officinale* were found in our field throughout the 3-year study, indicating that the seedlings had resulted from an old seed bank or from aerial seed dispersal from nearby pastures. The latter explanation is plausible as the experimental field was surrounded by pastures with moderately abundant *T. officinale*. The same explanation may apply to the other two composite species, but in those cases, failure to detect spatial correlation may also be due to the lower densities in these species.

The observed patterns were mostly elongated in the direction of field traffic, in accordance with most reports in the literature (Johnson *et al.*, 1996b; Gerhards *et al.*, 1997b; Dieleman & Mortensen, 1999; Colbach *et al.*, 2000), but the pattern of *E. crus-galli* showed a marked deviation. Its direction of greatest correlation made a substantial angle with the direction of field traffic. A possible explanation for this finding is that there may have been multiple patches in the observation plot (see e.g. Figure 2h), and thus the direction of greatest correlation for this species may be related to correlation *between* rather than *within* patches. A four parameter model (Journel & Huijbregts, 1978; Webster & Oliver, 2000) was found to be suitable to characterize anisotropy, the angle of greatest correlation and scale in the 2-D correlogram for a selection of observed weed patterns. The function did not fit all data sets in our study, however, and further study is needed to explore suitable correlogram functions and their application to weed patterns.

Aggregation of units in spatial analysis may be used to reduce variability in the data and obtain a clearer diagnosis of species patterns, as shown for example in tropical forest trees (Bellehumeur *et al.*, 1997). However, aggregation of units can obscure patterns if the size of the aggregated units exceeds the scale of the pattern (Rew & Cousens, 2001). Both effects were seen in our analyses: the spatial correlation in the pattern of *C. polyspermum* virtually disappeared after aggregation of units, whereas the patterns of *C. album* and *P. annua* became more distinct. Chance effects become more dominant in counts as the size of sample units is reduced. Therefore, the degree of spatial resolution can only be increased at the expense of intrinsic accuracy of the

population estimate per quadrat, and *vice versa*. Thus, the size of sample units should reflect an optimal compromise between spatial resolution and intrinsic accuracy of the population estimate per quadrat. When a single quadrat size is used in field studies on patterns for multiple weed species, using contiguous quadrats, the unit of scale for the quadrats should be determined by the species with the smallest spatial scale for the pattern. Data can always be aggregated to larger units for species that occur at low densities and require a larger quadrat size to obtain sufficiently accurate data.

Automatic detection techniques for individual weed plants, developed originally for site-specific weed management, provide an emerging alternative technology for mapping weed patterns (Gerhards & Christensen, 2003). An advantage of mapping individual plants is that all processes on all scales can be studied as no particular quadrat size is imposed on the study area (Bellehumeur *et al.*, 1997; Rew & Cousens, 2001).

This study used 2-D correlograms to characterize spatial pattern of weeds and the dynamics of spatial patterns. The novelty of this approach is the combination of an explicit 2-D spatial representation of spatial correlation structure byway of 2-D maps and the usage of a non-parametric statistic for expressing correlation. By presenting the correlation structure of the data on the whole of a checkerboard of lag distance in *x*- and *y*-directions, errors resulting from assuming isotropy or spatial stability are avoided. The advantages of an exhaustive 2-D representation of correlation in all compass directions were recognized by Rossi *et al.* (1992), but there are alternative methods that achieve the same goal. For instance, Wiles & Brodahl (2004) and Humston *et al.* (2005) use directional correlation functions to investigate anisotropy in correlation structure of weeds. The latter paper uses cross-correlation between years to address patch displacement, using the direction and offset distance of greatest correlation, as calculated from those directional correlation functions, to assess spatial patch displacement. Rossi *et al.* (1992) likewise allude to the possibility of using cross correlograms to compare two distributions in space, and a comparable methodology (but with variograms instead of correlograms) was used by Stein *et al.* (1994) to study spatial dynamics of a plant disease. The methodology of Humston et al. (2005) is more heavily parametric than ours, with attendant advantages and disadvantages. The advantage of the more parametric approach of Humston *et al.* (2005) is that direction and lag distance of greatest correlation are derived explicitly and quantitatively from the data; the disadvantage is that details in the spatial correlation structure are aggregated into more simple quantitative terms, which can potentially result in smoothing and loss of information. Yet another method to quantify patch displacement is to calculate displacement of the centre of gravity of the patch (Krohmann *et al.*, 2006). This straightforward and easy to understand method requires that the existence

and spatial delineation of the patches is determined first. The method of Syrjala (1996), applied to weeds by Barroso *et al.* (2004), can be used to test whether patterns observed in two years are similar or not. As this method provides only a yes/no answer, further exploration of the type of similarity or dissimilarity would seem useful to characterize the data more fully after this test has produced an outcome. Thus, different methods should be seen as complementary options, and whether one is more suitable than another depends on the study objectives and the data at hand.

In calculating correlograms, we chose a non-parametric coefficient of correlation to protect against problems frequently encountered in weed data sets, such as non-linear relations between variables, skewed sampling distributions, non-normal errors and outliers. Non-parametric statistics provide robustness against these problems (Gibbons, 1997; Lehmann, 1998). In calculating non-parametric correlations it must be accepted that the statistical power of resulting test (if any test is made) is somewhat (but not greatly) reduced if the data would be coming from a normal distribution (Lehmann, 1998). However, we consider this disadvantage rather theoretical, because weed count data are seldom normally distributed. It has in general been found that the negative binomial distribution is a good model for sampling distributions of weeds (Marshall, 1988; Wiles *et al*., 1992; Johnson *et al*., 1995b) and there is no *a priori* guarantee that transformation, such as the logarithm of $x + 1$, can normalize such data. Moreover, the ordinary coefficient of correlation, the Pearson product moment estimator, is only useful and appropriate if a linear relationship between variables may be assumed (e.g. Isaaks & Shrivastava, 1989, p. 31). As far as we know, there is no theoretical underpinning for the validity of this linear assumption in weeds; thus we consider our choice for a non-parametric coefficient of correlation for the spatial analysis of weed data to be well-justified. While calculating coefficients of correlation, we have used the mid rank method to treat ties in the data (especially zero counts), which is the recommended way (Gibbons, 1997; p. 305). A more precise estimation of correlation can be obtained by more sophisticated methods of dealing with ties (Gibbons, 1997; p. 305), but this was not necessary for the current analysis. It should be noted that the problem of zero counts does not only affect non-parametric coefficients of correlation, but also the 'ordinary' Pearson correlation. We note from Conover (1980, p. 252) that Spearman's coefficient of rank correlation can be used in the presence of a moderate number of ties, although no sharp definition is given for what is 'moderate'. Zeros in weed data sets are indicators of 'gaps' (i.e. spatial clusters of weed absence) as opposed to patches. They are not an artefact but intrinsic information-carrying numbers that contribute to the value of a population statistic like the coefficient of spatial correlation at a given lag distance. The topic of non-parametric statistics for characterizing spatial correlations in weeds may be further explored. Thereby, it

appears promising to explore the use of different coefficients, e.g. Kendall's τ or Goodman-Kruskal Gamma (Siegel & Castellan, 1988). These test statistics measure strength of relationship in a different way than Pearson's and Spearman's *r,* i.e. they quantify the probability that the elements of two observed vectors are in the same rank order (coefficient value tends to one, if this probability is high) or in the opposite rank order (coefficient value tends to –1, if this probability is high). In the absence of a relationship these coefficients tend to 0, while intermediate values represent intermediate tendencies towards the same or opposite ordering of the elements in the two data vectors. The gamma statistic corrects for ties, which could be an advantage in weed datasets with many zeros.

The finding that the weeds with the highest densities showed the strongest correlations, offers scope for site-specific management. Spatial correlatedness indicates that weeds are clumped in space, and this provides the option of focusing control at clusters of units with the higher densities. This study does not elucidate whether the comparatively lower spatial auto- and cross-correlation in species that occur at low to intermediate densities is entirely due to a statistical effect. The data are congruent with the hypothesis that one and the same demographic process (i.e. local population growth and spread) could result *both* in high densities *and* in high spatial correlation. Simulation studies could demonstrate whether a relationship between spatial correlation and population density, as observed in this study, is indeed an emerging property of a population process with stochastic short range dispersal and recruitment.

CONCLUSIONS

- Data on weed patterns were collected by sampling with contiguous quadrats during three years in continuous maize cultivation. Two-dimensional (2-D) correlograms were then used to characterize spatial pattern of weeds while space-time correlograms were used to assess stability of spatial pattern between years. Correlograms are developed on the basis of the parameter-free correlation coefficient of Spearman which is robust against problems frequently encountered in weed data sets, such as non-linear relations between variables, non-normal errors and outliers.

- Four weed species occurred at high numbers in the field samples: *C. album, C. polyspermum*, *E. crus-galli* and *S. nigrum*, and each of these species showed patchy patterns. Patches of *C. polyspermum* and *S. nigrum* were stable in location over time whereas patches of *E. crus-galli* shifted in location from year to year. The patches of *C. album* were less clearly defined than those of the other three species and this species showed no locational stability over time.

- Weeds that occurred at lower densities than the four dominant weeds (e.g. *L. purpureum*, *C. bursa-pastoris*, *Polygonum* spp. and *R. sceleratus*) were less correlated in space, as indicated by lower values of the correlation coefficient in the 2-D correlogram, and there was no well defined locational stability of the pattern. The lower correlation can in part be ascribed to a statistical effect with smaller numbers per quadrat resulting in a higher expected coefficient of variation and lower spatial autocorrelation.

- The patterns of three wind dispersing composite species, e.g. *T. officinale,* showed no spatial correlation. Ancillary observations suggest that the lack of correlation in those species is related to a combination of absence of reproduction within the field and the potential for long distance dispersal of their seeds between fields.

- The size of observation units affected the correlograms. For *C. album* and *P. annua*, observations on larger units resulted in more distinct correlograms. On the other hand for *C. polyspermum*, correlations at short distance were lost when larger units were used. The choice of quadrat size hinges on the trade-off between sufficient spatial resolution (many small quadrats) in order to detect steep gradients in density, and sufficient numbers per quadrat (fewer and larger quadrats) to reduce as much as possible the coefficient of variation of counts and ascertain statistical significance.

- The results show that four weed species that occur in agronomically significant high densities have spatially aggregated patterns that can be characterized with correlogram functions that could be used to help guide site-specific weed management. Correlograms were less clearly defined in those species that occurred in lower densities. 2-D correlograms, based on Spearman's parameter free *r*, provide a convenient statistical methodology to visualize spatial correlation at a single point in time, as well as between two points in time, in order to characterize – respectively – the *state* and *dynamics* of weed patches.

- Alternative parameter-free statistics of correlation are worth exploring.

CHAPTER 4

Does soil spatial heterogeneity explain patchiness in weeds?
A regression approach accounting for spatial correlation[*]

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Summary

We examined the extent to which weed dispersion patterns within cultivated maize fields depended on soil heterogeneity. Seedling density of four patchy weed species (*Chenopodium album*, *Chenopodium polyspermum*, *Echinochloa crus-galli*, and *Solanum nigrum*) showed a consistent association with soil variables, notably texture, OM and pH, throughout the three years of study. Statistical significance of the regressions typically decreased markedly after accounting for spatial correlation, but all models remained significant ($P < 0.05$). After fitting, some residual correlation remained indicating that spatial variability in the soil parameters did not completely account for spatial aggregation in the weeds. Spatial patterning may have also been influenced by other, unobserved environmental variables (e.g., light, soil toxins, moisture, temperature, herbivory, historical land management practices etc.) as well as by processes intrinsic to the population (e.g. dispersal, competition). Implications for the ecology and management of weeds are discussed.

Keywords: Spatial patterns, weed, soil properties, regression analysis, Taylor's power law.

INTRODUCTION

Weed population densities vary greatly within arable fields (see Christensen *et al*., 1999). Soil properties also often exhibit spatial heterogeneity (Cambardella *et al*., 1994; Cambardella & Karlen, 1999; López-Granados *et al*., 2002). Variation in presence and abundance of weeds has been found to be related to heterogeneity of soil characteristics in several studies. For example, density of *Veronica hederafolia* L. was related to nitrogen content (Dammer *et al*., 1998), and a relation between the density of *Viola arvensis* Murray and clay content was established by Walter *et al*. (2002). Weed species distribution has also been linked to soil organic carbon (e.g. Andreasen *et al*., 1991; Gaston *et al*., 2001; Burton *et al*., 2005) and soil pH (e.g. Andreasen *et al*., 1991; Dunker & Nordmeyer, 2000; Gaston *et al*., 2001; Walter *et al*., 2002; Nordmeyer & Häusler, 2004).

Information about soil heterogeneity and its relation with weed spatial patterns could be used to improve weed management techniques. If consistent spatial relations between weed species and soil properties can be established, the presence of weeds can be predicted on the basis of information on spatial variation of soil properties. Heisel *et al*. (1999) used spatial information on silt content in a field for co-kriging *Lamium* spp., improving the prediction variance. Probabilities of *Setaria* spp. and *Solanum ptycanthum* Dun. *ex* DC. were adequately predicted using local predictor variables and presence of these weeds in a previous year (Dille *et al*., 2002).

Various techniques have been used to analyse soil-weed relations. As the occurrence of weed species is often related to one or more soil variables, stepwise regression techniques can be used to select for explanatory variables (soil) (Andreasen *et al*., 1991; Walter *et al*., 2002). Such regression models, however, do not account for the spatial dependency of the data, which could result in an overestimation of the significance of the regression parameters (Walter *et al*., 2002). Dalthorp (2004) addressed the issue of spatial dependency of data in regression analysis specifically in a study on the spatial relation between densities of the Japanese beetle grub (*Popillia japonica* Newman) and soil organic matter in turf grass, comparing models with spatially correlated errors and models with spatially uncorrelated errors. He accounted for spatial dependence by incorporating the covariance structure of the residuals into generalized linear regression models (GLM), and showed that model significance can be substantially overestimated when spatial dependency is neglected. Such overestimation of model significance could easily occur in analyses of the relationship between weed densities and soil variables, as weed counts show strong spatial correlations (e.g. Heijting *et al*., 2007).

We apply the technique proposed by Dalthorp (2004) to weed counts. In this study, we explore the dependence of weed abundance on soil properties in a 12 m × 48 m

field plot over 3 years of continuous corn cultivation. The consistency of parameters in regression equations was investigated by fitting regression models to weed data collected in three years. The essential question is whether weed patterns occur independently from soil patterns, or – alternatively – whether these patterns in weeds and soil properties are correlated, so that weed dispersion patterns can be predicted from soil properties.

MATERIALS AND METHODS

Data collection

Weed data
Weed counts in contiguous quadrats of 0.75 m × 0.75 m in a 12 m × 48 m plot (16 × 64 quadrats) on a 1.8 ha maize field near Wageningen were recorded for several species prior to herbicide application in 2001, 2002 and 2003. In 2001 and 2002 counts were also recorded after spraying. The spatial analysis focuses on the patterns before spraying, while pre- and post-spraying data were used to investigate a possible effect of soil heterogeneity on herbicide efficacy. Maize was grown at a row distance of 0.75 m. The four most abundant weed species in the observation plot throughout the three years of observation were *C. album*, *C. polyspermum*, *E. crus-galli* and *S. nigrum* (Heijting *et al.*, 2007). *C. album*, *E. crus-galli* and *S. nigrum* are some of the most important problem weeds in continuous maize cropping. Other weed species present were mostly dicot annuals. A full list of species and further details on weed counts and management of the field plots are given in Heijting *et al.* (2007).

Soil data: Sampling scheme
The field was divided into a 8 × 16 grid of quadrats measuring 1.5 m by 3 m each. A single soil sample was taken at a random position in each quadrat. Fourteen additional soil samples were taken at random positions in the plot, to increase the number of sample points at close range (30 pairs closer than 0.75 m) and improve estimation of the nugget in geostatistical analysis. Based on analysis of the 140 samples, a soil map of the plot was made using block kriging. Analyses of the relation between weed densities and soil variables were based on observed weed density (three years data) in the 140 quadrats in which the soil samples were taken and observed soil parameters in those same quadrats.

Soil data: Measurements
Soil samples were taken on 17 April 2003. They were taken with an Edelman soil drill

(Ø 7 cm) to 25 cm depth. The samples were air dried (40 °C), crushed and sieved to remove particles larger than 2 mm diameter. From each soil sample, a sub-sample of 200 g was further analysed. Soil pH and available nitrogen (as N-NO3, N-NH4 and N-total soluble), phosphorous and potassium content were determined by extraction with 0.01 M CaCl$_2$ solution. Magnesium content was determined with 0.01 M CaCl$_2$ solution (ICP-MS). Organic matter (OM) content was determined by loss-on-ignition (LOI) which was corrected for water bound to clay (Ball, 1964). Soil texture was characterized by particle size distribution as measured by sieve and pipet: clay/lutum (< 2 μm), silt (2–16 μm), loam (16–50 μm) and sand (> 50 μm).

Outline of data analysis
Analysis of weed counts and soil data proceeded in five steps: (1) Descriptive statistics were calculated for soil and weed data. (2) Soil data were subjected to geostatistical analysis to characterize and visualize heterogeneity of soil properties. (3) Relations between pre-spraying weed data (response variable) and underlying soil properties (explanatory variables) were then examined using regression analysis. Variables for use in regressions were selected stepwise in a Generalized Linear Model (GLM) with Poisson errors and a log link function. (4) The selected sets of variables from step 3 were used in GLMs in which the variance of the weed counts was modelled with Taylor's power law (TPL) and in which spatial correlations in errors were *not* taken into account. (5) Finally, GLMs were developed using the same explanatory variables and TPL as variance model, and taking into account spatial correlations in residuals from the regression. Parameters and *P*-values of these models were compared with those from the spatially uncorrelated models fitted in step 4.

Initial data analysis
Descriptive statistics were calculated: mean, SD, variance and maximum (minimum was zero for all weeds). In addition, mortality rates after spraying were calculated for 2001 and 2002.

Geostatistical analysis and visualization of soil data
Geostatistics was used to visualize soil patterns in the whole plot, based on the 140 samples. Spherical and Gaussian variogram models were fitted (Isaaks & Shrivastava, 1989, pp. 374-375). Predictions for unsampled locations were generated by block-kriging (Isaaks & Shrivastava, 1989, pp. 323-330) using a grid of 100 points per quadrat, i.e. 10 in every direction. The quadrat prediction for every quadrat was the average of the 100 corresponding point predictions. Calculated values of the soil variables were visualized with MatLab7.

Selection of soil parameters: GLM with Poisson distribution with log link

Relations between soil properties and weed counts were examined using the actual measured 140 data points for each combination of weed species and year separately. This was done for the fifteen weed species groups present (Heijting *et al*., 2007). The analysis was done in Genstat 9th edition (VSN International Ltd, UK) using a Generalized Linear Model with Poisson distributed errors and a log link (Schabenberger & Pierce, 2002).

The three textural fractions and OM are linearly dependent, adding up to 100%. To avoid possible effects of collinearity, four different sets of explanatory variables were examined separately as a starting point for the analysis of each weed species-year combination. Each set consisted of one textural fraction or OM and the soil parameters pH, Phosphorous, Potassium, Nitrogen Total soluble and Magnesium. Nitrogen-NH4 and Nitrogen-NO3 were discarded as they were strongly correlated with Nitrogen Total Soluble.

All possible model selection methods (stepwise backward, forward etc) were applied and dispersion parameter φ (used to calculate the variance) was estimated from the residual mean square to compensate for possible over-dispersion of the data. From the model outcomes, the best overall model per weed species was selected using R^2 as a primary criterion. In addition, significances of estimated regression coefficients were taken into account for the model selection. Possible relations between mortality of weeds (2001 and 2002) and soil variables were also investigated using the above described regression method.

Regression analysis: Non-spatial model

The combinations of selected soil parameters and weed species from the Poisson distributed GLMs with log link function, were used as a starting point for development of regression models with spatially uncorrelated and correlated error terms. Following Dalthorp (2004), the variance of the counts was modelled with Taylor's power law (TPL, Taylor, 1984). TPL has been found to give excellent descriptions of variability in weed counts (Berti *et al*., 1992; Clark *et al*., 1996; Heijting, unpublished results):

$$s^2 = a \times m^b \Leftrightarrow \log(s^2) = \log(a) + b\log(m)$$

where *m* is the mean counts and s^2 the variance. The *b* parameters of TPL were estimated from the data: 1.3351 for *C. album*, 1.3521 for *C. polyspermum*, 1.8313 for *E. crus-galli* and 1.8469 for *S. nigrum*. In the GLM, *a* is considered a scale factor which does not affect the estimates of the regression parameters and is, therefore, not incorporated into the variance function of the GLM. Therefore:

$$v(\mu_i) = \mu_i^{b} \qquad\qquad\qquad \text{(Dalthorp, 2004)}$$

where v is the variance function and μ_i is the expected mean density at location i.

The link function g, which transforms the linear combination of explanatory variables into an estimate for weed density, is:

$$\eta_i = g(\mu_i) = \frac{\mu_i^{1-b}}{1-b} \qquad\qquad \text{(McCullagh \& Nelder, 1989; Dalthorp, 2004)}$$

with the inverse link:

$$\mu_i = g^{-1}(\eta_i) = ((1-b)\eta_i)^{1/(1-b)} \quad \text{(Dalthorp, 2004)}$$

In the non-spatial model spatial dependencies in the response variable are not taken into account (Dalthorp, 2004). For every weed species we chose to include the same set of covariates for all three years, to enable comparison between the years.

Regression analysis: Spatial model

The same explanatory variables are used in the model with spatially correlated errors as in the model with spatially independent errors, to enable comparisons between the two models. The models with spatially correlated errors were constructed following the approach of Dalthorp (2004). For these models, assessment of regression parameters (β) and covariance matrix of the residuals of β (denoted as R) takes place in an iterative process, in which β and R are both alternately optimized until convergence is met for both. A spherical variogram model α (consisting of parameters a (range), c (sill) and γ_0 (nugget) is used to estimate the residuals of the predicted weed density. Parameter estimates $\hat{b}$ from the non-spatial model are used as initial values in the iteration. For technical details see Dalthorp (2004). Both β and α are estimated with Weighted Least Squares (WLS). Wald's statistic was used to test hypotheses $\beta_i = 0$. To enable comparisons, covariates are the same as in the non-spatial model for each weed species and in each year.

Software used

Soil sampling scheme was programmed using Compaq Visual Fortran v. 6.6. Block-kriging was performed in S-plus Spatial statistics module. Regression analysis using Poisson log link was done in Genstat. Soil data was visualized with Arc View GIS 3.3. A C^{++} program by Dalthorp (2004) was used to conduct regression analysis with TPL as link function.

RESULTS

Soil properties

Summary and spatial statistics of the soil properties are shown in Table 1. For pH, magnesium, OM and clay content the Gaussian model gave the best fit; for all other variables the best fit was obtained using a spherical model (using WLS). All soil properties except N-NH4 showed moderate (0.25 < nugget/sill < 0.75) to strong (nugget/sill < 0.25) spatial dependence. Range parameters varied from 1.2m for potassium to 10.9 m for OM content. Spatial patterns of the variables that were used in regressions are presented in Figure 1. Finer texture soil was found in the north-western part of the plot, and the coarser, sandier soil was found in the south-eastern part of the plot, coinciding roughly with the higher concentration of OM. Soil pH was highest in the north-west part of the observation area.

Weed species

Table 2 shows the summary statistics of the four patchy weed species during the three years of observation. Weed maps are given in Heijting *et al.* (2007), which also provides details on the summary statistics of other weed species.
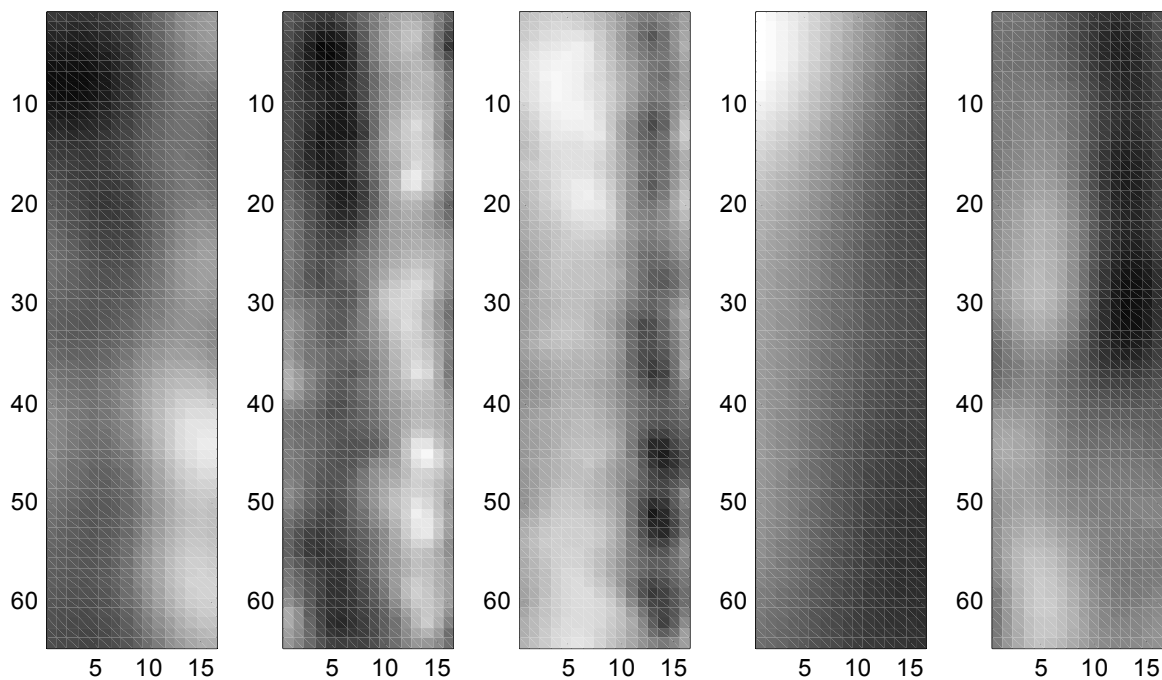
Figure 1. Soil variables. From left to right: clay (33–41%), silt (28–40%), sand (11–30%), organic matter (3–8%), and pH (6–7). White = low values; dark = high values.

Table 1. Summary and spatial statistics of soil variables (n=140).

	Clay	Silt	Sand	pH	N-NO3	N-NH4	Nts*	P	K	Mg	OM
	%	%	%		mg/kg	mg/kg	mg/kg	mg/kg	mg/kg	mg/kg	%
Mean	37.5	34.4	17.8	6.5	16.0	1.8	27.4	0.9	32.1	309.2	5.7
s.d.	1.9	3.0	4.0	0.2	3.9	0.3	4.1	0.3	6.9	37.5	1.2
Minimum	31.9	27.4	11.9	6.0	7.1	1.2	17.3	0.4	22.5	224.9	2.3
Maximum	41.5	40.0	29.0	7.0	26.6	3.4	41.0	2.0	83.1	365.9	7.7
Model	g	s	s	g	s	s	s	s	s	g	g
Range	5.8	8.2	8.5	5.2	9.4	7.3	9.2	5.1	1.2	5.4	10.9
Sill	2.4	9.0	17.0	0.0	6.5	0.0	9.2	0.1	47.9	1263.4	1.3
Nugget	1.0	0.4	0.0	0.0	8.3	0.1	7.5	0.0	1.4	433.3	0.5
N/(S+N)	0.3	0.0	0.0	0.1	0.6	0.8	0.4	0.2	0.0	0.3	0.3

s=spherical   g= gaussian

* N total soluble

Spatial dependence is expressed as N/(N+S). Values < 0.25 indicate strong spatial dependence, values between 0.25 and 0.75 indicate moderate spatial dependence and a value > 0.75 indicates weak spatial dependence of the data (Cambardella *et al.*, 1994).

Table 2. Summary statistics of weed counts (n = 1024). Mean of number of plants per 0.75 m × 0.75 m quadrat is given.

	year	mean	s.d.	maximum
C. album	2001	3.6	5.1	44
	2002	0.6	1.5	30
	2003	1.4	1.7	16
C. polyspermum	2001	2.6	3.7	26
	2002	1.0	2.2	41
	2003	3.7	5.4	65
E. crus-galli	2001	9.3	20.3	158
	2002	4.7	6.6	49
	2003	29.6	38.7	282
S. nigrum	2001	0.8	1.9	19
	2002	0.4	1.1	13
	2003	1.1	2.5	25

Stepwise regression: Selection of models using Poisson distribution with log link

The spatial patterns of four of the species present were related to soil variables (Table 3). These were the four most abundant weed species mentioned previously. For these weed species, models including two soil variables gave overall best results throughout the three years of study using R^2 as the primary criterion. The selected variables for two parameter models were highly consistent among years for a given weed species. Inclusion of additional explanatory variables in the regressions resulted in a less consistent selection of soil variables throughout the three years and a decrease in or loss of significance of regression coefficients. Thus, considering R^2 and parameter significance, the two-parameter models are optimal.

All weed species increased in density with soil pH (Table 3). The density of *C. album* decreased with higher organic matter (OM), *C. polyspermum* decreased with higher silt fraction, while *E. crus-galli* decreased with higher sand fraction. *S. nigrum* increased with clay fraction. The coefficient of determination, R^2, varied from 0.13 to 0.54, with a median R^2-value of 0.36, indicating modest strength of relationship. Regression coefficients showed consistent values for each species, throughout the three years of study, and all parameters and all models were significant.

The lowest value of R^2 was found for *C. album* in 2002 (0.13). This species had the lowest R^2, averaged over the three years, and it was the least spatially correlated of the four patchy weed species (Heijting *et al.*, 2007).

Table 3. Results of Generalized Linear Models with spatially uncorrelated errors (Poisson distribution and log link function) for weed response to soil variables.

Weed species and year	R-squared	RMSE	b_0 constant	b_1	b_2 soil pH
				value model parameters $\pm$ S.E.	
C. album				organic matter	
2001	0.19	1.70	$-12.43^{***} \pm 2.71$	$-0.23^{***} \pm 0.06$	$2.25^{***} \pm 0.42$
2002	0.13	1.55	$-23.49^{***} \pm 5.56$	$-0.33^{*} \pm 0.14$	$3.76^{***} \pm 0.87$
2003	0.25	1.25	$-17.69^{***} \pm 3.04$	$-0.31^{***} \pm 0.08$	$2.99^{***} \pm 0.48$
C. polyspermum				silt	
2001	0.37	1.62	$-7.48^{*} \pm 4.29$	$-0.16^{***} \pm 0.04$	$2.05^{***} \pm 0.52$
2002	0.42	1.22	-7.05 ± 4.92	$-0.24^{***} \pm 0.05$	$2.26^{***} \pm 0.60$
2003	0.51	1.67	$-9.50^{*} \pm 3.89$	$-0.18^{***} \pm 0.04$	$2.50^{***} \pm 0.47$
E. crus-galli				sand	
2001	0.54	3.33	$-21.36^{***} \pm 4.43$	$-0.45^{***} \pm 0.04$	$4.70^{***} \pm 0.71$
2002	0.35	2.37	$-23.59^{***} \pm 3.92$	$-0.24^{***} \pm 0.03$	$4.47^{***} \pm 0.64$
2003	0.33	4.68	$-20.22^{***} \pm 3.22$	$-0.15^{***} \pm 0.03$	$3.98^{***} \pm 0.53$
S. nigrum				clay	
2001	0.23	1.25	$-43.18^{***} \pm 7.43$	$0.38^{***} \pm 0.08$	$4.29^{***} \pm 0.79$
2002	0.42	0.93	$-77.82^{***} \pm 9.96$	$0.69^{***} \pm 0.10$	$7.60^{***} \pm 1.02$
2003	0.45	1.28	$-67.77^{***} \pm 8.17$	$0.51^{***} \pm 0.08$	$7.26^{***} \pm 0.84$

*** $P < 0.001$; ** $P < 0.01$; * $P < 0.1$

No significant relationships between soil variables and densities of the other weed species were found, with R^2 not exceeding 0.10 and regression coefficients being not significant.

Herbicide efficacy and relations with soil properties
Herbicides resulted mostly in 100% mortality, leaving no room for regresison analysis, However in a few cases, incomplete control was recorded: *E. crus-galli* in 2002 (84%), *Poa annua* 2001 (81%) and *P. aviculare* 2001 (81%). Relations between these mortalities and soil variables were not significant. For *E. crus-galli* (2001) mortality was incomplete as well. However, the mortality could not be precisely calculated due to the presence of many late germinating plants that could not be distinguished from plants surviving the herbicide treatment.

Taylor's power law as a link function: Non-spatial models
Table 4 shows the results of the generalized linear models in which Taylor's power law is used as a link function. Model convergence was attained using the estimated values of the parameter *b* of TPL. However, for *S. nigrum* 2003, a lower value of *b* (1.3500 as opposed to 1.8469) was necessary to make the model converge.
Values of regression coefficients were comparable to those given by the GLM using a Poisson distribution with log link function for *C. album*, *C. polyspermum* and *S. nigrum*. For *E. crus-galli*, values of regression coefficients showed approximately a 10-fold decrease compared to the Poisson log link. Significances of regression coefficients of the GLM using TPL were overall lower than for GLM using Poisson log link.

Taylor's power law as a link function: Spatial models
The results for the regression models with spatially correlated error terms are presented in Table 5. Values of regression coefficients of models with spatially correlated errors (Table 5) were overall similar to those of models with spatially uncorrelated errors (Table 4). Significances of the models with spatially correlated errors were in general similar or slightly lower than those of the models with uncorrelated errors and in a few cases much lower. The largest difference in significance between spatial and non-spatial models was found for *C. polyspermum*. For this species in particular, discarding spatial correlation of the response variable (weed counts) would result in substantial overestimation of model significance.
The expected plant density per quadrat of *C. polyspermum* according to the spatial model is plotted in Figure 2 for 2001, 2002 and 2003, separately. The expected values for three levels of soil pH (6, 6.5 and 7) are shown. With a decreasing silt fraction, plant density increased steeply.

Table 4. Characteristics of regression models with spatially uncorrelated error terms with Taylor's power law as a link function.

Weed species	Year	b (TPL)	$b_0 \pm$ SE (constant)		$b_1 \pm$ SE		$b_2 \pm$ SE (soil pH)		P-value
					organic matter				
C. album	2001	1.34	–11.14**	± 1.90	–0.16** ± 0.05		1.51**	± 0.30	0.0070
	2002	1.34	–28.85**	± 9.91	–0.38 ± 0.23		4.15**	± 1.40	0.0116
	2003	1.34	–18.39***	± 2.75	–0.27*** ± 0.07		2.60***	± 0.43	0.0004
					silt				
C. polyspermum	2001	1.35	–7.11*	± 3.45	–0.11*** ± 0.03		1.32**	± 0.41	0.0000
	2002	1.35	–8.02	± 5.30	–0.24** ± 0.05		1.93***	± 0.64	0.0000
	2003	1.35	–7.51**	± 2.73	–0.19* ± 0.03		1.42*	± 0.32	0.0000
					sand				
E. crus-galli	2001	1.83	–2.55**	± 0.79	–0.05**** ±0.01		0.48****	± 0.12	0.0000
	2002	1.83	–6.51**	± 1.71	–0.05**** ± 0.01		1.08***	± 0.19	0.0000
	2003	1.83	–1.62***	± 0.26	–0.01** ± 0.00		0.26****	± 0.04	0.0004
					clay				
S. nigrum	2001	1.85	–59.690*	± 12.72	0.52*** ± 0.14		5.73*	± 1.30	0.0144
	2002	1.85	–146.44**	± 31.95	1.31* ± 0.32		13.95*	± 3.19	0.0192
	2003	1.35	–69.83***	± 9.01	0.52** ± 0.10		7.05***	± 0.91	0.0000

*** $P < 0.001$; ** $P < 0.01$; * $P < 0.1$

Table 5. Characteristics of regression models with spatially correlated error terms with Taylor's power law as a link function.

Weed species	Year	b (TPL)	$b_0 \pm$ SE constant		$b_1 \pm$ SE		$b_2 \pm$ SE soil pH		P-value
					organic matter				
C. album	2001	-	-		-		-		-
	2002	1.34	-28.37**	± 9.78	-0.37	± 0.26	4.06**	± 1.53	0.0282
	2003	1.34	-18.42***	± 2.87	-0.26***	± 0.07	2.61**	± 0.45	0.0004
					silt				
C. polyspermum	2001	1.35	-8.80*	± 4.15	-0.08*	± 0.04	1.39**	± 0.50	0.0017
	2002	1.35	-6.89	± 5.51	-0.24*	± 0.05	1.76**	± 0.67	0.0000
	2003	1.35	-5.32*	± 2.83	-0.07**	± 0.02	0.88*	± 0.37	0.0130
					sand				
E. crus-galli	2001	1.82	2.62**	± 0.82	-0.05***	± 0.01	0.49***	± 0.13	0.0000
	2002	-	-		-				..
	2003	1.83	-1.05**	± 0.35	-0.01**	± 0.00	-0.17**	± 0.06	0.0048
					clay				
S. nigrum	2001	1.85	-50.90*	± 20.03	0.42*	± 0.21	4.85*	± 2.09	0.0458
	2002	1.85	-118.08**	± 41.10	1.23**	± 0.43	10.22*	± 4.09	0.0129
	2003	1.35	-66.14***	± 11.05	0.48**	± 0.11	6.77***	± 1.12	0.0004

*** $P < 0.001$; ** $P < 0.01$; * $P < 0.1$
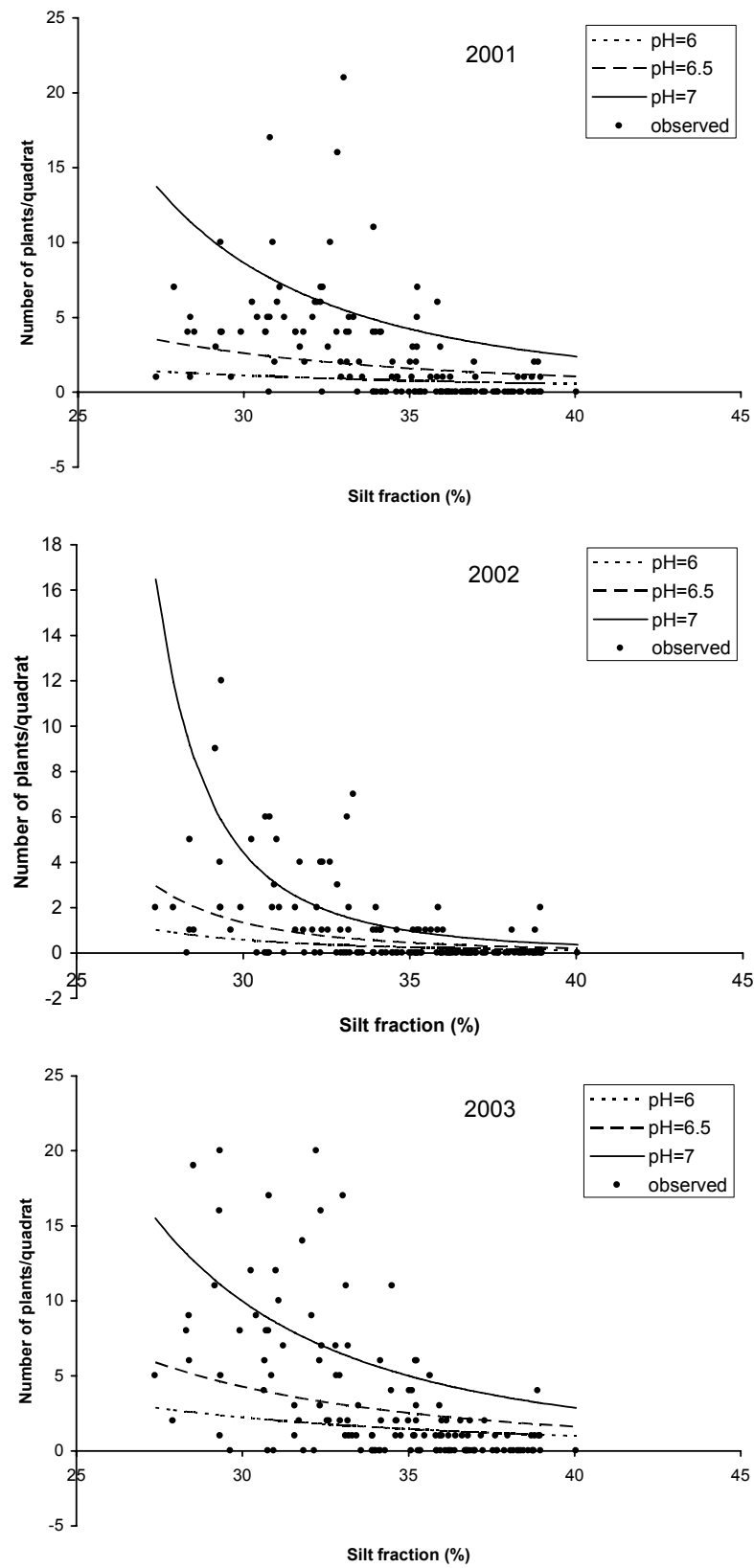
Figure 2. Observed and expected plant density of *C. polyspermum* based
on a GLM with spatially correlated error terms for 2001, 2002 and 2003.

    As examples, the actual weed patterns of *C. polyspermum* 2002 and *E. crus-galli* 2001 are shown in Figure 3 and Figure 4, respectively, along with the patterns predicted from the regressions and the resulting residuals. Location and density of weeds is predicted relatively well. But the sharp spikes in the actual weed density are not accounted for by the regressions. Generally, the response surfaces in the regressions are more smoothed and less spiky than the observational surfaces. As a result, spatial dependence was left in the residuals for most species~year combinations (Figures 3 and 4). Addition of quadratic components to the models did not result in sharper peaks of the model (not shown here).

    The spatial models of *C. album* (2001) and *E. crus-galli* (2002) did not converge as there was too little spatial correlation left in the residuals to fit a variogram to. In Figure 5, variograms are presented of count data, model (spatially uncorrelated errors) and residuals of *E.crus-galli* in 2002. The range of spatial dependence present in the weed data coincides largely with that of the selected explanatory soil variables that appear to govern large scale variation. After accounting for the large scale factors, spatial dependence in the residuals is evident only for a short distance spanning less than 1.5 m, suggesting that the small scale variation is governed by dispersal or other factors intrinsic to the population.
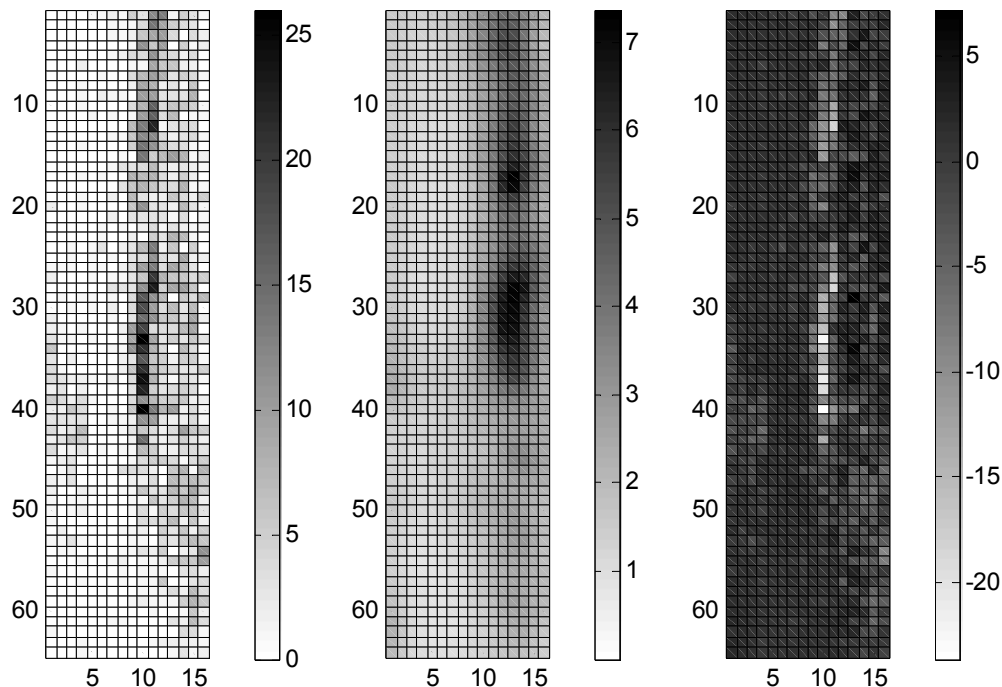
Figure 3. *C. polyspermum* 2001: Actual weed density pattern (left), predicted weed density pattern with model with spatially correlated errors (middle) and residuals (right).
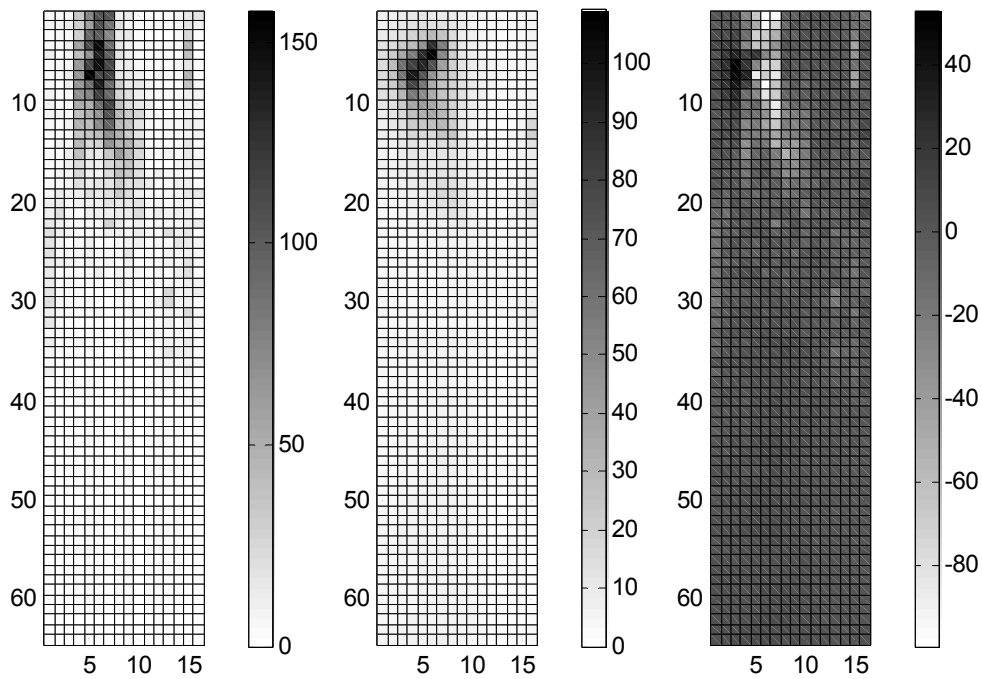
Figure 4. *E. crus-galli* 2001: Actual weed density pattern (left), predicted weed density pattern with model with spatially correlated errors (middle) and its residuals (right).
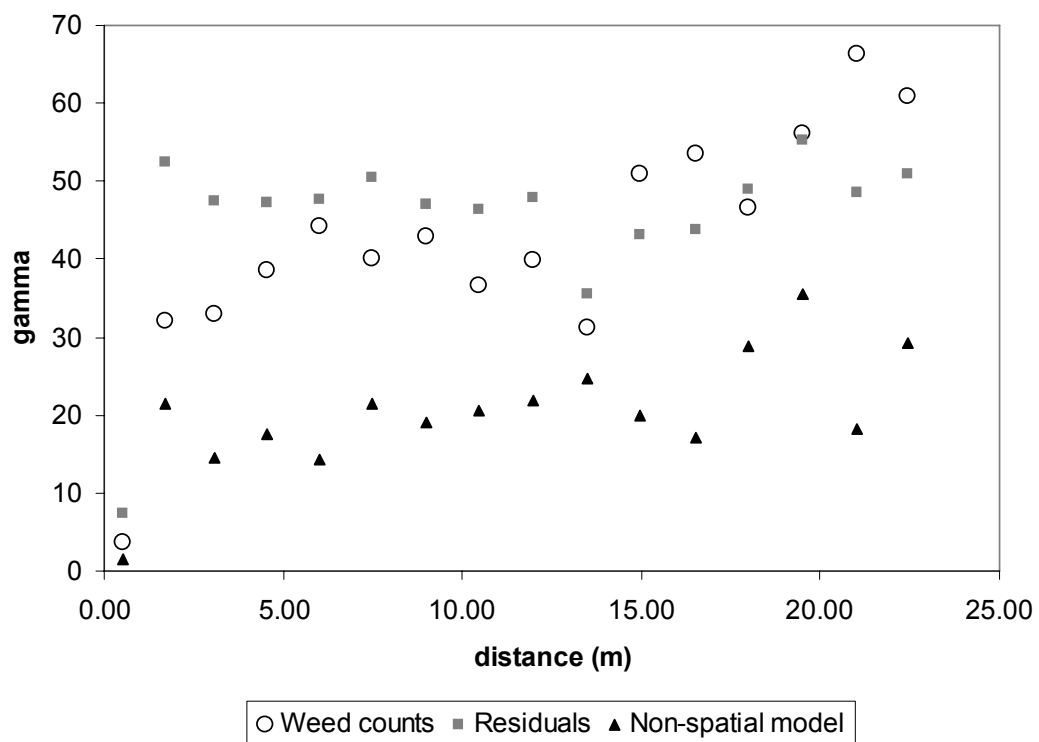
Figure 5. Empirical variograms for *E. crus-galli* 2002, weed counts, non-spatial model and its residuals.

DISCUSSION

In this study small scale variation in density of four patchy weed species, *C. album*, *C. polyspermum*, *E. crus-galli* and *S. nigrum,* was related to heterogeneity of underlying soil properties. Densities of these species were related to soil pH, soil texture or OM. They were the patchiest weed species throughout the three years of study in a plot 12 m × 48 m plot in continuous corn, reaching the highest densities of all weed species present (Heijting *et al*., 2007).

A statistical method was used to determine whether soil variables could provide a sufficient explanation for patchiness in these weeds. In most cases, patterns in soil variables did explain some part of the variation in weed density, but a substantial proportion of the variability in weed densities remained unexplained. Moreover, in most cases, spatial correlation was noticeable in the residuals of the regression, indicating that although the soil covariates were significantly correlated with weed densities, they could only partially explain for weed patchiness. For *C. album* (2001) and *E. crus-galli* (2002), the spatial model failed to converge as there was little spatial correlation left in the residuals. In these cases, it could be argued that the soil factors did account for the patchiness in the weeds. But the finding that in other years, the spatial model for these species did converge indicates that the soil factors are only a partial explanation for weed patchiness. For one weed species, *C. polyspermum*, large differences in *P*-values (> 10 fold) between spatial and non-spatial models indicate that there is a strong degree of spatial correlation that is not accounted for by the selected soil parameters. The results of *C. polyspermum* and effect of years illustrate that it may be important to account for spatial correlation if weed patterns are associated to soil factors. If these spatial correlations are not accounted for, inflated *P*-values may result.

Relationships between densities of weed species and soil factors can be interpreted in the light of the ecological requirements and ecological niche of these species. *E. crus-galli* showed decreasing plant densities with increasing sand fraction in the observation plot. This species is known to like wetter habitats (Mitich, 1990) which could explain its preference for the areas of finer texture in our study. *S. nigrum* prefers clay soils (Oberdorfer, 1970), which is in line with our findings as it was found to be positively related to clay fraction. *C. album* was negatively related to OM, which is in agreement with results of Andreasen *et al*. (1991). *C. polyspermum* is generally associated with river flood lands and moist, heavier soils (Oberdorfer, 1970) but in our study plot, with a rather high percentage silt and clay, the species occurred in higher densities in the part of the observation area where the soil was relatively coarser. Reproducing plants of *C. polyspermum* were not found in the plot during the years of observation and its seeds are relatively persistent. The pattern of *C. polyspermum* may,

therefore, be a relict from historic field levelling processes which will be described further on, during which weed seeds may have been introduced with soil.

Texture fractions and organic matter affect soil moisture content (Andreasen *et al.*, 1991; Walter *et al.*, 2002), thus are likely to influence weed germination, establishment and growth (Albrecht & Pilgram, 1997; Dieleman *et al.*, 2000b). The observation plot was situated near the headlands and stayed wetter than the rest of the field after rain, which may have favoured all four weed species. Variations in patch expansion/shrinkage between years were present (Heijting *et al.*, 2007) possibly as result of annual variation in precipitation and temperature. Annual variations in soil-weed relations were also reported in other studies (Andreasen *et al.*, 1991, Dieleman *et al.*, 2000a; Medlin *et al.*, 2001; Walter *et al.*, 2002).

All four weed species were positively related to soil pH. Soil pH varied over a rather narrow range (6–7) which makes it difficult to explain the patterns in terms of ecological requirements. Interference of soil pH, organic content and texture fraction with herbicide efficacy has been shown in other studies (Novak *et al.*, 1997; Dieleman *et al.*, 2000a; Williams II *et al.*, 2001). In this study, no relation between soil factors and herbicide effectiveness was found. Still, the weed seedbank could reflect past failures in herbicide effectiveness that could be linked to soil.

Results of correlative studies between weeds and soil factors are expected to be scale specific. The spatial relations between soil factors and weed distributions were examined here at a detailed level of scale in a sub-field area. A comparable but slightly coarser scale was used by Burton *et al.* (2005). They found significant spatial relations between the distribution of *Helianthus annuus* and the topography and soil organic matter content in a 64 ha field. Number of weeds were counted in transects with contiguous quadrats of 1 m × 1.52 m. In each of the three separate *H. annuus* patches, transect intersections were established in the high-density centre. Most studies examined soil-weed relations at field scale using sampling grids often coarser than our entire study plot (Dammer *et al.*, 1998; Dieleman *et al.*, 2000a, b; Dunker & Nordmeyer, 2000; Gaston *et al.*, 2001; Walter *et al.*, 2002; Nordmeyer & Häusler, 2004). At field scale (≈ 10 ha) using a 20 m × 20 m sampling grid, spatial relations between various weed species and soil parameters were present in two Danish fields (Walter *et al.*, 2002). They pointed out that if a finer sampling scale were used, possibly more relations would have been established between soil characteristics and weed species. Intensive sampling schemes as used in the current study are very costly, but too coarse schedules could result in missing relations. A combination of two levels of scale (Burton *et al.*, 2005) is costly but might be valuable for obtaining a better understanding of soil-weed relations.

Ranges of spatial dependence of soil parameters in our study were much smaller

than those reported in other studies (Cambardella *et al.*, 1994; Cambardella & Karlen, 1999; Gaston *et al.*, 2001; López-Granados *et al.*, 2002; Walter *et al.*, 2002) but similar to findings by Trangmar *et al.* (1987) and Campbell (1978). Historic land use (Albrecht & Pilgram, 1997), cropping practices (Andreasen *et al.*, 1991), sampling scheme, and geological past can all affect the scale of variability of soil properties and thus influence relations with vegetation. To illustrate this, the dynamic history of our small field was examined. During World War II much earth was moved on this particular field as it was bordered by a deep ditch (3 m) to trap tanks. After the war the field was used as a pasture during several decades. Narrow north-south oriented ditches (20 cm wide) were present at intervals of approximately 12 m for drainage. Plant debris was removed from the ditches periodically and dumped adjacent to the ditch, likely resulting in a local build up of organic matter over time. The field was equalized using soil from an unknown origin in the early 1980s and was from then on used for arable farming. Although the exact location of the channels and other events is unknown, they are likely still reflected in the present spatial patterns of soil parameters.

The fact that throughout the three years of study, consistent relations between soil properties and important weed species could be established, and that weed patchiness largely coincided with heterogeneity of the field is promising for site-specific management of weeds. Areas favourable to weeds can be identified and treated accordingly. Weed monitoring can be facilitated once weed sensitive areas have been detected. With advancing technological developments, it is likely that machinery will be able to adapt to this level of detail.

CHAPTER 5

Seed dispersal by forage harvester and rigid-tine cultivator in maize[*]

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Summary

Harvest and tillage operations are a major factor in seed dispersal in agricultural crops. We studied the effect of harvesting and cultivation on seed dispersal in continuous maize. A suite of cultivated plant species were used as model weed species to avoid potential sampling problems. Dispersal on the entire field was assessed by counting emerged seedlings in contiguous quadrats. Species that had the seeds on the plant at the time of harvest (*Sinapis alba* and *Phacelia tanacetifolia*) were spread further in the traffic direction by harvest + cultivation combined, as judged by the 50, 90 and 95 percentile of the cumulative dispersal distribution, than species whose seeds had been placed on the soil surface. Harvesting alone did not have this effect. The use of cultivator after harvesting significantly increased the distance travelled in the driving direction for three species with ripe seeds at harvest time (*Eschscholzia californica*, *Linaria maroccana*, *Linum usitatissimum*). Kernels resulting from cultivator operations were long tailed, extending over the whole of the sampled area, and they were quite variable. The headlands accumulated plant debris that had been collected and dragged over the field by the cultivator. Implications for the ecology, patterns and management of weeds are discussed.

Keywords: Harvest combiner, rigid-tine cultivator, weed dispersal, headlands.

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[*] Submitted to Weed Research.

INTRODUCTION

A better understanding of weed spatial behaviour can help to support integrated weed management strategies such as site-specific weed management (Humston *et al*., 2005). The results of experiments on dispersal of *Helianthus annuus* L. (common sunflower) by harvest in a soybean-maize rotation showed that a reduced weed dispersal can be achieved if densities of weed patches are kept under control (Humston *et al*., 2005). Apart from initial weed density, the interaction between harvest machinery and weed biology is important for dispersal of weeds (McCanny & Cavers, 1988; Woolcock & Cousens, 2000; Blanco-Moreno *et al*., 2004; Humston *et al*., 2005; Barroso *et al*., 2006). Seeds of species whose seeds are strongly attached to the mother plant, such as *Lolium rigidum* are thought to disperse further by machinery (Blanco-Moreno *et al*., 2004) than seeds that shatter easily such as those of *Avena fatua* and *A. sterilis* (Barroso *et al*., 2006) because plant material is more easily spread than seeds. A model study by Woolcock & Cousens (2000) predicted that in cereal cropping, weed plants that shed their seeds prior to harvest will be dispersed less far than plants that shed seeds during harvest. Although the results obtained in different cropping systems are generally in line with the idea that seeds that are on the plant are spread further than seeds that are on the soil, there are no comparative studies in a single system that provide empirical support.

Most studies on dispersal by harvest have been performed in cereals. An important crop in north-western Europe, however, is maize. For example, in The Netherlands 10% of the agricultural land is sown with maize. Maize is mainly harvested for silage production and it is often grown continuously without rotating crops. At present, continuous maize cropping is mainly depending on herbicides for weed control. Full dependence on mechanical weed control as commonly practiced in organic maize cropping results in huge increases of the weed seed bank (Barberi *et al*., 1998). One means to reduce herbicide input is by site-specific weed management, i.e. taking into account weed spatial distribution when spraying.

For silage maize the entire crop is harvested, with a cutting height of approximately 10 cm. No crop material is emitted back to the field. This contrasts with cereal harvesting, where the combiner emits Material Other than Grain (MOG) (Shirtliffe & Entz, 2005). This MOG includes both crop material and weed seeds. Chaff collection can significantly reduce the spread of weed seeds (Blanco-Moreno *et al*., 2004; Shirtliffe & Entz, 2005). A forage harvester as used for silage maize may contribute to spread of weed seeds by dragging weed plants over the field if weed plants have ripe seeds at time of harvest. This would mainly cause longitudinal spread in the direction of the field traffic. Lateral spread, perpendicular to the field traffic, could occur if emitted maize silage is spilt between the harvest combiner and lorry, e.g. due to human

failure or wind. No research has been done on this harvest system specifically.

Soil tillage provides another means for seed dispersal is tillage. In several studies (e.g. Rew & Cussans, 1997; Grundy *et al.*, 1999; Marshall & Brain, 1999), tillage moved the majority of seeds a few meters or less and only a few were transported over larger distances. Spread of seeds of *A. fatua* and *A. sterilis* was mainly caused by soil tillage practices (Barroso *et al.*, 2006). Steinmann & Klingebiel (2004) showed that cultivation contributes to seed dispersal of *Bromus sterilis* in an arable field. A common practice in The Netherlands in silage maize on sand is to cultivate the soil with a rigid-tine cultivator a few weeks after harvest. This loosens the soil and ensures water is drained well in the winter. It furthermore facilitates cultivation with the plough in spring. We expected that the cultivator could also be an important vector of weed material as the tines can potentially drag plant and seed material across the field.

The aim of our study was to determine the contribution of both forage harvester and rigid-tine cultivator to the dispersal of weed seeds in a field cropped with continuous maize. The effect of timing of seed shedding in relation to harvest was examined. To avoid bias by seeds already present in the seed bank of the field, we used non-weedy species which were not present in the field before the experiment started, to study dispersal.

MATERIALS and METHODS

Field experiments

Two field trials were conducted on a sandy soil field 'Meenthoeve 14' on the Meenthoeve farm near Achterberg, The Netherlands. The field (2 ha) was 200 m long and 100 m wide. During the two years of the study, silage maize was grown. The crops were grown with conventional methods (Table 1). In the field, seeds of experimental plant species ('model weeds') were released, either by laying out seeds before harvest of the crop, or by seeding plots with the species in the spring, after clearing 3 m × 3 m patches of crop from all maize plants. All field traffic in the course of the experiment was counter clockwise. Thus, dispersal was essentially in one direction from the established sources. During chemical weed control the plots with introduced plants were shielded with plastic foil. Weeds in these plots were removed by hand and hoe. The crop was harvested with a Claas forage harvester with a Champion cutting bar, harvesting 6 rows in one pass. Cutting height was 10 cm.

Experimental design 2002
This first experiment measured the dispersal of the seeds of two plant species that were sown in each of four source plots, and three species of seeds that were each laid out in

a single source plot. The combined effect of harvesting and cultivation was studied.

The source plots were laid out in mid May. Each plot of sown experimental plants measured 6 m × 6 m and was sub-divided in four sub-plots of 3 m × 3 m (Figure 1). On 30 May, *Sinapis alba* (cv. Carnival) and *Phacelia tanacetifolia* (cv. Amerigo) were sown, each in two of the sub-plots, using a row distance of 15 cm. *S. alba* was sown at a seed density of 1.5 g m^{-2}, and *P. tanacetifolia* at 0.8 g m^{-2} (Table 2), following seeding densities used in practice.

Table 1. Details on field management in 2002 and 2003 on Meenthoeve 14.

Operation	Machinery/details	2002	2003
Ploughing	Kverneland LD115 3 plough shears, 6.5 km/h Furrow width: 40 cm Ploughing depth: 24 cm Skim coulter depth: 3 cm	15 Apr	18 Mar
Fertilizer		22 Apr: 500 kg/ha 27% KAS	24 Apr: 600 kg/ha 27% KAS 9 May: 150 kg/ha 23/23 N/P
Seed bed preparation	Rotary harrow Kverneland 12300, working width: 3m Working depth: 4-5 cm		
Sowing maize	cv. Lima top Row spacing 75 cm 0.13m within row spacing	25 Apr	9 May
Tine harrow	Hatzenbichler, 6m wide	8 May	Mid May
Sowing of model plants	By hand	30 May Row spacing 0.15 m	4 Jun +additional on 3 Jul Row spacing 0.4 m
Spraying		31 May 300 g/ha sulcotrione 40 g/ha nicosulfuron 300 g/ha pyridaat 100 g/ha bromoxynil	12 Jun 300g/ha sulcotrione 96 g/ha dicamba 30 g/ha nicosulfuron 320 g/ha dimethenamid-P
Placing of seeds on soil		24 Sep	11 Sep
Harvest	Claas Jaguar 7 km/h Maize cutting height: 0.1m 6 rows in one go	25 Sep Claas Mega Jaguar + Champion 4500	12 Sep Claas Jaguar 890 Speedstar + Champion 345
Mapping		-	2 & 3 Oct
Rigid-tine cultivator	Rumpstadt, 2 rows, 5 tines each at 40 cm apart. 15-16 cm depth 12.8 km/h	10 Oct	16 Oct
Mapping		15, 19 & 20 Nov	20, 24 & 25 Nov
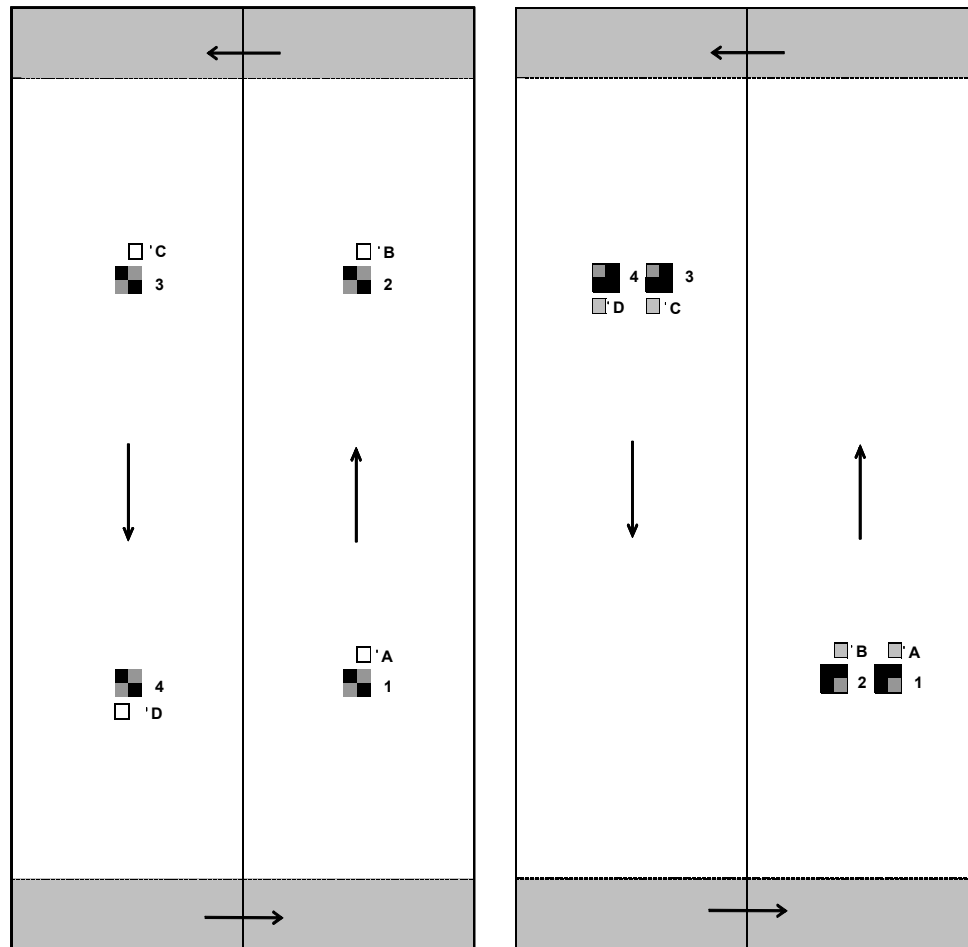
Figure 1. Experimental design in 2002 (left) and 2003 (right) on Meenthoeve 14. The entire field measures 100 m × 200 m. Driving direction is indicated with arrows. Headlands are grey. Foci are indicated with grey tones and numbers correspond with kernel numbers. Plants with ripe seeds in 2002: *S. alba* (grey), *P. tanacetifolia* (black). Letters indicate in 2002: initial location of seeds of *B. officinale* (A), *S. marianum* (B), *V. sativa* (C) and *D. stramonium* (D). Plants with ripe seeds in 2003: *C. officinale* (black), *E. californica* (crosshatch), *L. usitasitsimum* (grey) and *L. maroccana* (stripes). Initial location of seeds in 2003: *A. hybridum* (A), *L. coronaria* (B), *H. vulgare* (C) and *L. angustifolius* (D).

At harvest, both *P. tanacetifolia* and *S. alba* plants had ripe seeds on the plant. *P. tanacetifolia* also had flowers. Just before harvest, seeds of *Borago officinale*, *Datura stramonium*, *Silybum marianum* and *Vicia sativa* were placed on the soil surface, each in one 3 m × 3 m plot, downstream from the plots with the seeded source plants (Figure 1). Details on seeds of the species used in this experiment are provided in Table 2. The crop was harvested on 25 September 2002 (Table 1). First, the headlands were harvested. The driving direction on the headlands was pursuant to the counter clockwise movement schedule of the whole field (Figure 1). On 10 October 2002, the field was cultivated with a Rumpstadt rigid-tine cultivator (Table 1). On 3 November

Table 2. Information on plant species used.

Plant species	1000-seed weight (g)	Seeds (g) per 9 m^2
A. hybridum	4.07	720
D. stramonium	7.15	236
B. officinalis	19.79	1000
C. officinalis	7.00	50
E. californica	1.53	25
H. vulgare	46.58	1000
L. maroccana	0.07	18.75
L. usitatissimum	5.64	25
L. angustifolius	132.42	2670
P. tanacetifolia	2.37	7.2
S. marianum	30.45	1000
S. alba	5.50	13.5
V. sativa	73.56	1400

2002, the entire field was scouted and blue plastic rods were placed near seedlings and plants of the introduced species to make an initial mapping. On 15, 19 and 20 November, the dispersal pattern was mapped by counting the number of seedlings and plants on the entire 2 ha field using 1.5 m × 1.5 m quadrats. Four metal 1.5 m × 1.5m quadrats were placed on the soil adjacent to each other and counts were made per quadrat. The metal frame was shifted until the whole field had been mapped. Fixed poles were present on all four sides of the field to enable correct placement and alignment of the quadrats. To secure positions in the field, lines were attached and fixed between these poles, and tape measure was fixed along these lines.

Experimental design 2003
This experiment measured the dispersal of the seeds of four plant species that were sown in each of four source plots, and four species of seeds that were each laid out in a single source plot. The effects were studied of harvesting alone and harvesting plus cultivation.

The field was managed identically as in 2002 (Table 1), but the design of the experiment was slightly adjusted. Taking into account the large dispersal distances observed in 2002, source plots were not placed downstream of other source plots as in 2002, but in parallel (Figure 2). To avoid confusion with possible seedlings of experimental plant species used in 2002, four other species were used as model weeds: *Calendula officinalis*, *Eschscholzia californica*, *Linaria maroccana* and *Linum usitatissimum*. Each of these had ripe seeds on the plant during harvest.

Just before harvest, seeds of *Abutilon hybridum*, *Lignis coronaria*, *Lupinus angustifolius* and *Hordeum vulgare* were placed on the soil surface in plots of 3 m × 3 m downstream of the plots with the seeded source plants. These four species represent weeds that shed their seeds prior to harvest. On 2 and 3 October, the spatial pattern of seedlings of introduced species was mapped using the same method as described for the 2002 experiment. Dispersal patterns of all introduced plant species were monitored a month after cultivation of the field. Wind speed during harvest was low: 1–2 Beaufort.

Data analysis and visualization

Dispersal patterns of the plant species were visualized using ArcView GIS 3.3 (ESRI, Redlands, CA, USA). The analysis will focus on the dispersal of seeds in the driving direction of the machines. Due to the unexpectedly far dispersal of plants in the 2002 experiment (Figure 1), kernels 1 and 3 were truncated in the driving direction at the start of the source plot of kernels 2 and 4. Kernels 2 and 4 were continued up till the field edge and thus included part of the headlands. The width of kernel 2 and 4 full field (measured cross-row) determined also the width that was considered in the headlands. Boundaries of the other kernels of the 2002 and 2003 experiments were clearly apparent from the experiment. For each species in each source plot, the cumulative frequency distribution was constructed. The counts were summed cross-row to obtain the cross-row integrated longitudinal kernel. The 0-point was taken in the middle of each of the 3 m × 3 m source sub-plots, or as the combined middle of two sub-plots of the same species (*S. alba* and *P. tanacetifolia* in the 2002 experiment). Seedlings that must have came from another source than the nearest one, i.e. the odd ones located tens of meters upstream of a source, were discarded in the calculations. From each kernel, the mean distance travelled, the maximum distance and the 50, 90 and 95 percentiles were determined.

The Mann-Whitney *U* test was used to test the following three null hypotheses:

(*i*)   There is no difference in dispersal distance by harvester + cultivator between seeds that were on the soil or on the plant at the time of harvest (2002 experiment).

(*ii*) There is no difference in dispersal distance by harvester alone between seeds that were on the soil or on the plant at the time of harvest (2003 experiment).

(*iii*) The dispersal distributions caused by the harvester or by the harvester + cultivator are the same (2003 experiment).

The cumulative dispersal distributions of harvester alone and of harvester plus cultivator (2003 experiment) were compared for each kernel and plant species separately, using the Kolmogorov-Smirnov test.
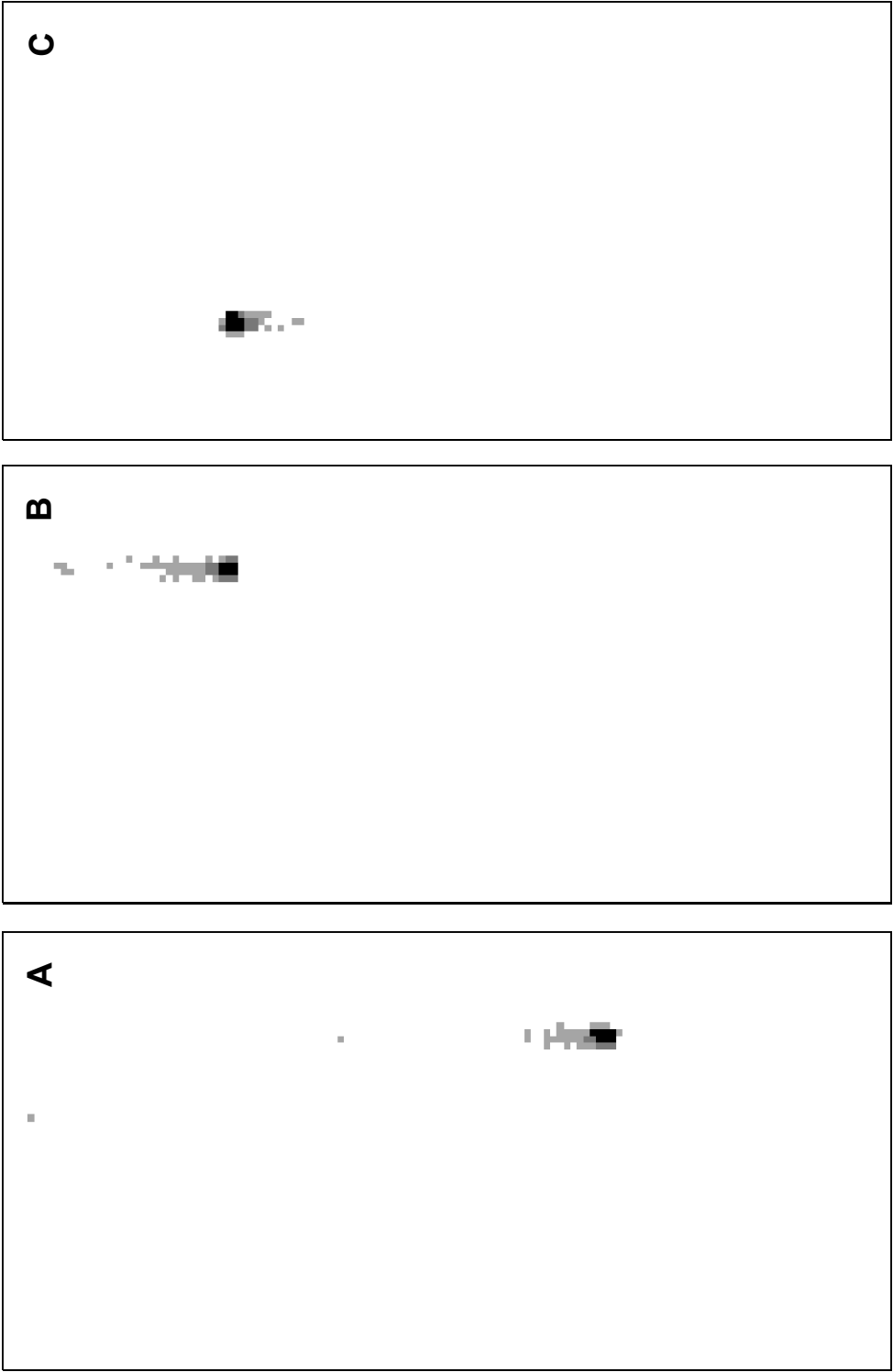
Figure 2. Results of the experiment in 2002. Location of *B. officinalis* (A), *S. marianum* (B), and *V. sativa* (C) seedlings after dispersal by harvest and cultivation. Number of plants per quadrat is indicated by grey tones:
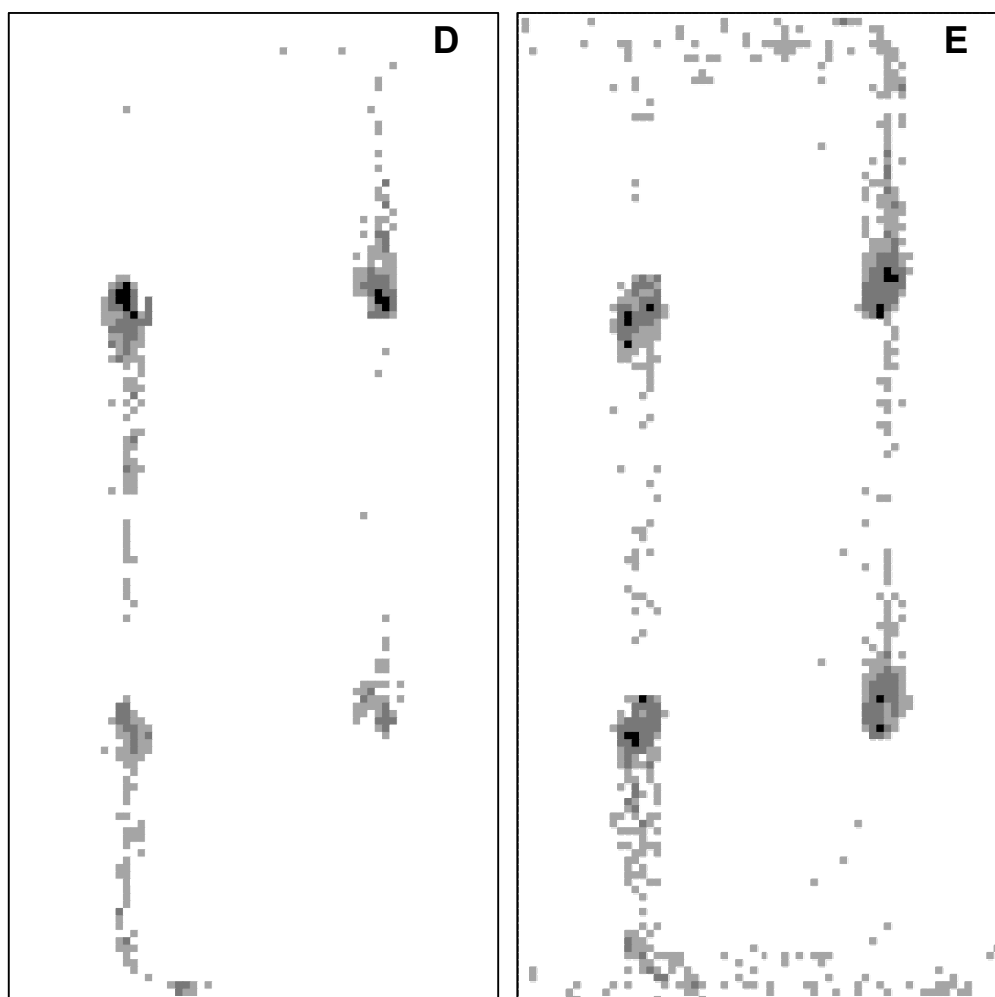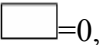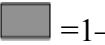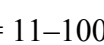
☐ =0, ▨ =1–10, ▨ =11–100, ◼ = 101–1500.

Figure 2. Continued. Results of the experiment in 2002. Location of *S. alba* (D) and *P. tanacetifolia* (E) seedlings after dispersal by harvest and cultivation. Number of plants per quadrat is indicated by grey tones: ☐=0, ▨ =1–10, ▨ = 11–100, ■ = 101–1500.

RESULTS

2002 Experiment

The seeds that had been placed on the soil in the 2002 experiment (*B. officinale, S. marianum, V. sativa*) dispersed less far than seeds that were attached to the plant at time of harvest (*S. alba, P. tanacetifolia*) (Table 3; Figures 2 and 3AB). The difference was significant for all dispersal parameters measured except the maximum distance travelled (Table 5). Thus at the scale of this study, all distance parameters were different between seeds on the soil and seeds on the plant, except the maximum distance measured. The true maximum distance could not be measured because it was constrained by the length of the plot. The 90 and 95 percentile showed a longer tail of

Table 3. Results of the 2002 dispersal experiment. Combined effect of cultivator and harvester on dispersal of plant propagules in the driving direction is shown. All distances are measured from the initial centre of the plot.

Machine	Location of ripe seeds	Weed species	Kernel	Length of plot (m)	Number of plants	Mean distance (m)	SD	Maximum distance (m)	Percentile (m) 50	90	95
Harvester+cultivator	soil	*B. officinalis*	1	137.5	6943	0.84	2.24	131.75	–0.03	1.85	2.17
	soil	*S. marianum*	1	51.5	6872	0.76	1.88	39.75	–0.15	1.77	2.16
	soil	*V. sativa*	1	149.5	7881	0.40	1.22	15.75	–0.47	1.38	1.93
	plant	*P. tanacetifolia*	1	80.75	262	4.11	11.02	74.75	0.79	10.22	14.87
			2	57.5	1584	2.56	7.18	47.25	–0.60	11.30	17.82
			3	80.75	2088	4.36	9.20	65.75	0.86	9.58	26.85
			4	57.5	644	9.82	15.50	53.25	2.49	39.35	45.22
	plant	*S. alba*	1	80.75	1544	5.64	12.13	80.75	2.52	9.29	22.38
			2	57.5	2692	5.76	12.10	56.25	2.34	18.46	41.35
			3	80.75	1568	4.96	7.11	70.25	3.21	8.99	9.63
			4	57.5	2324	9.22	15.80	57.50	3.00	44.96	48.63

Figure 3A. Combined effect of harvest and cultivation on seed dispersal for 'soil-borne' plant species of the 2002 field experiment Cumulative frequency distributions are presented for each kernel of the plant species separately. On the *x*-axis distance in meters is shown. The *y*-axis presents the fraction of seedlings that were dispersed till the indicated distance.

the dispersal kernel for seeds that were on the plant at time of harvest (Table 3; Table 5). The 90 percentile of the dispersal distance of seeds that had been placed on the soil varied from 1.38 m to 1.85 m while the 90 percentile of the dispersal distance of seeds that were still on the plant at the time of harvest varied from 9 m to 45 m. In Figure 2, the 11 dispersal kernels, measured in this experiment, are shown, illustrating the major differences between the species that were subjected to harvesting as soil-borne seeds and those that were plant-borne.

There was substantial variation among the measured kernels (Figure 3B) within each of the two species used in 2002 with plant-borne seeds. Part of this variability is caused by the experimental set up, which did not allow for measurement of the full potential length of the kernels 1 and 3, and whose length may, therefore, have been underestimated. Another part is due to the occurrence of the headland in the tail of the kernels 2 and 4. The patterns (Figure 2) show that plants of *S. alba* and *P. tanacetifolia* were dispersed throughout the entire headland and even beyond. The pattern of *S. alba* reveals the presence of the headlands the most clearly (Figure 2): the tail of the kernel tapers steadily but has a discontinuity at about 40 m from the source. This is where the headland begins, and where there is a sudden increase in the number of seedlings observed per meter downstream from the source.

The dispersal kernel of *D. stramonium* could not be determined as seedlings of this species were killed by frost before mapping

2003 experiment: Harvest

The mean distance travelled by seeds that were on the soil at time of harvest was less than 0.5 m (Table 4). For species with seeds that were ripe at time of harvest, mean
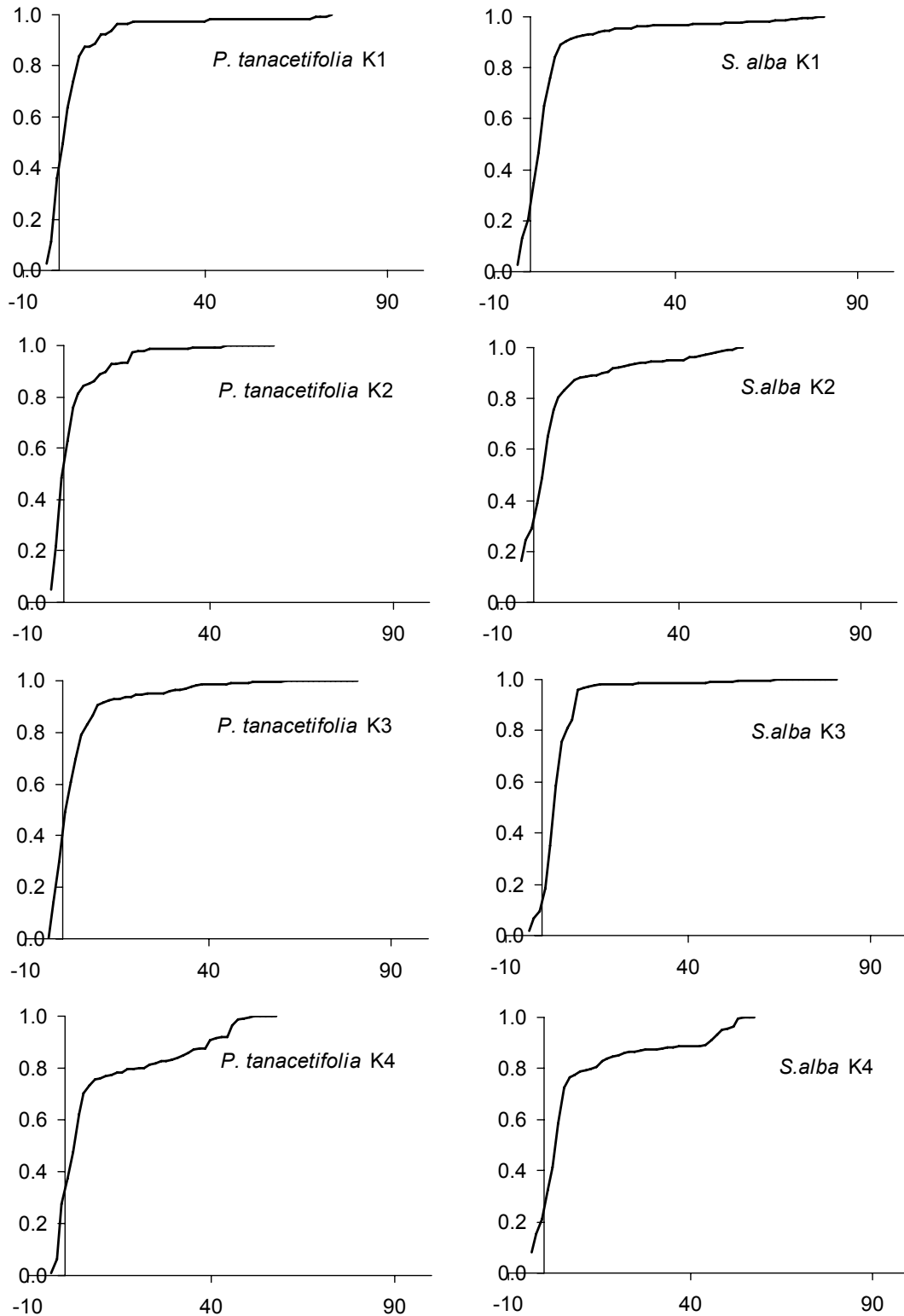
Figure 3B. Combined effect of harvest and cultivation on seed dispersal for plant species of the 2002 field experiment that carries ripe seeds at harvest time. Cumulative frequency distributions are presented for each kernel of the plant species separately. On the *x*-axis distance in meters is shown. The *y*-axis presents the fraction of seedlings that were dispersed till the indicated distance.
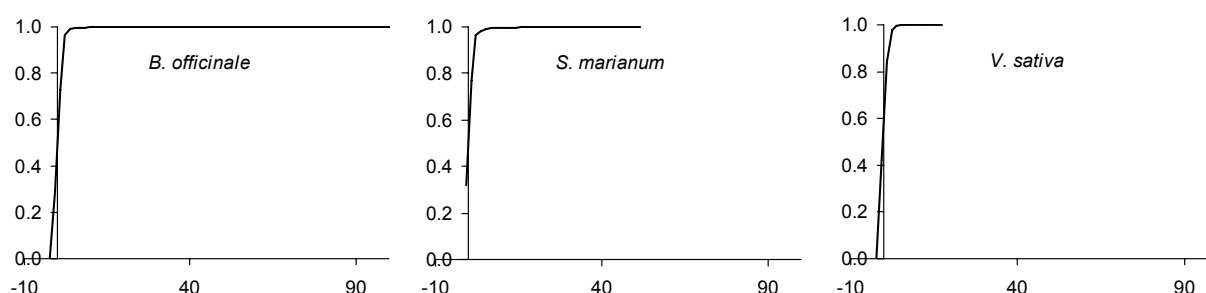
Table 4. Results of the 2003 dispersal experiment. Effect of harvest and the combined effect of cultivator and harvester on dispersal of plant propagules in the driving direction are shown. All distances are measured from the initial centre of the plot.

Machine	Location of ripe seeds	Weed species	Kernel	Length of plot (m)	Number of plants	Mean distance (m)	SD	Max. distance (m)	Percentile (m) 50	90	95
Harvester	soil	*A. hybridum*	1	137.5	94	0.49	1.88	11.25	–0.51	0.65	2.90
	soil	*H. vulgare*	1	137.5	248	0.38	2.91	27.75	–0.98	0.73	1.77
	soil	*L. angustifolius*	1	137.5	1705	0.07	0.85	11.25	–0.66	0.49	0.63
	plant	*C. officinalis*	1	142	63	2.04	2.15	14.25	1.20	2.10	2.21
			2	142	274	3.66	3.35	29.25	2.15	5.52	7.93
			3	142	131	5.54	14.04	94.25	1.60	6.30	34.43
			4	142	92	2.01	2.94	23.25	1.08	4.22	4.98
	plant	*E. californica*	1	142	260	0.08	1.02	5.25	–0.52	0.51	0.64
			2	142	458	0.61	3.00	14.25	–1.04	4.36	5.04
			3	142	83	1.51	6.15	39.75	–0.34	1.61	2.23
			4	142	222	0.98	2.74	30.75	–0.20	2.02	4.92
	plant	*L. maroccana*	1	145	1045	–0.49	1.01	5.25	–1.28	0.28	0.54
			2	145	4875	–0.79	1.39	42.75	–1.60	0.28	0.55
			3	145	1018	0.34	1.48	5.25	–0.33	1.58	2.13
			4	145	462	0.13	1.58	3.75	–0.86	1.72	2.13
	plant	*L. usitatissimum*	1	145	337	1.43	7.54	101.75	–0.26	2.21	5.27
			2	145	465	3.05	13.20	136.25	–0.10	4.91	9.67
			3	145	95	5.62	17.83	88.25	0.03	1.93	43.06
			4*	-	-	-	-	-	-	-	-
Harvester+ cultivator	soil	*H. vulgare*	1	137.5	19	7.49	27.85	124.25	–0.83	17.40	122.83
	soil	*L. angustifolius*	1	137.5	253	0.78	3.93	59.75	–0.26	1.33	2.09
	plant	*C. officinalis*	1	142	721	–0.12	1.25	6.75	–1.04	0.56	1.02
			2	142	798	2.48	15.46	134.75	–0.15	1.79	2.21
			3	142	108	1.82	2.61	15.75	1.02	2.20	4.20
			4	142	22	2.80	0.72	3.75	1.93	3.34	3.54
	plant	*E. californica*	1	142	4034	5.55	20.60	130.25	0.24	4.51	11.49
			2	142	4057	16.27	30.20	136.25	1.64	64.10	77.11
			3	142	3235	5.37	21.08	139.25	0.48	3.57	13.13
			4	142	4974	3.39	14.70	134.75	0.33	4.82	9.30
	plant	*L. maroccana*	1	145	489	2.37	18.66	136.25	–1.77	0.24	1.91
			2	145	66	28.70	44.43	143.75	2.55	131.30	132.76
			3	145	419	4.47	21.05	136.25	–0.15	1.65	2.22
			4	145	21	56.46	54.57	136.25	31.50	131.42	131.74
	plant	*L. usitatissimum*	1	145	64	41.71	62.54	134.75	–1.01	134.24	134.50
			2	145	339	4.48	21.86	137.75	–0.75	2.94	6.83
			3	145	95	4.82	23.04	133.25	–0.06	1.76	2.18
			4	145	83	15.77	40.52	134.75	–0.05	112.78	132.39

* Only three plants were retrieved of this kernel.

distance travelled was variable, with the lowest value for *L. maroccana* (–0.79 m) and the highest value for *L. usitatissimum* (5.62 m) (Table 4). Cumulative frequency distributions of all species are presented in Figures 4 and 5. No significant differences in dispersal by the forage harvester alone were found between species with
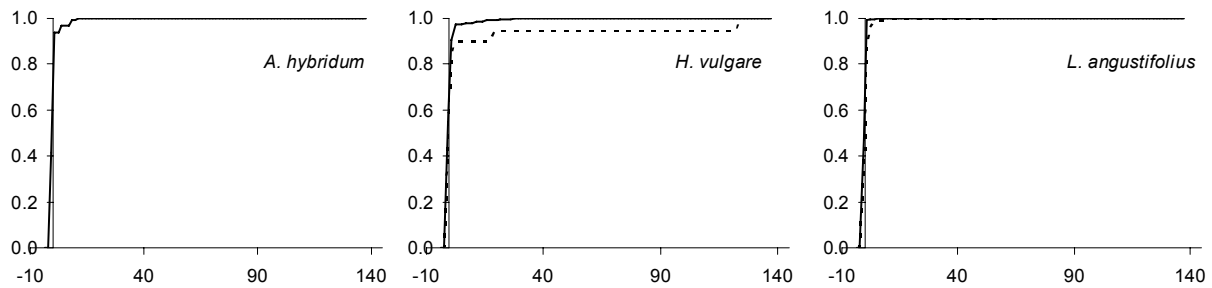
Figure 4. Effect of harvest and cultivation on seed dispersal in the 2003 field experiment for plant species with seeds on the soil before harvest. Cumulative frequency distributions of plant species are presented for harvest (solid line) and rigid-tine cultivator (dashed line) for each kernel of the plant species separately. On the *x*-axis distance in meters is shown. The *y*-axis presents the fraction of seedlings that were dispersed till the indicated distance.

ripe seeds at time of harvest and seeds on the soil were found (Table 5). *L. coronaria* did not germinate and could thus not be mapped.

2003 experiment: Harvest and cultivation

The effect of harvest machinery and cultivation on dispersal of *E. californica* is shown in Figure 6 and for *L. maroccana* in Figure 7. Both figures illustrate that the rigid-tine cultivator enlarged dispersal distances. Dispersal kernel 2 of *E. californica* shows fluctuating densities in the tail (Figure 6). This is reflected in its cumulative frequency distribution (Figure 5).

For species with ripe seeds at time of harvest, the distance parameters mean and maximum were larger for harvest + cultivator than for harvester alone (*P*<0.01) (Table 5). Overall the cultivator increased dispersal of seeds compared to the harvester (Figures 3 and 4; Tables 4 and 5), but for three of the four kernels of *C. officinalis* the cultivator dispersed seeds in the negative direction. The effect was small and most

Table 5. Comparison of dispersal distances for different treatments of 2002 and 2003 experiment. Comparisons were tested 1-sided with the Mann-Whitney *U* test.

				Percentile		
Year	H0	Mean	Maximum	50	90	95
2002	On soil< on plant	**	ns	*	**	**
2003	On plant harvest < on plant cultivator	**	**	ns	ns	ns
2003	On soil harvest < on plant harvest	ns	ns	ns	ns	ns

*$P < 0.05$; **$P < 0.01$; ns: not significant.
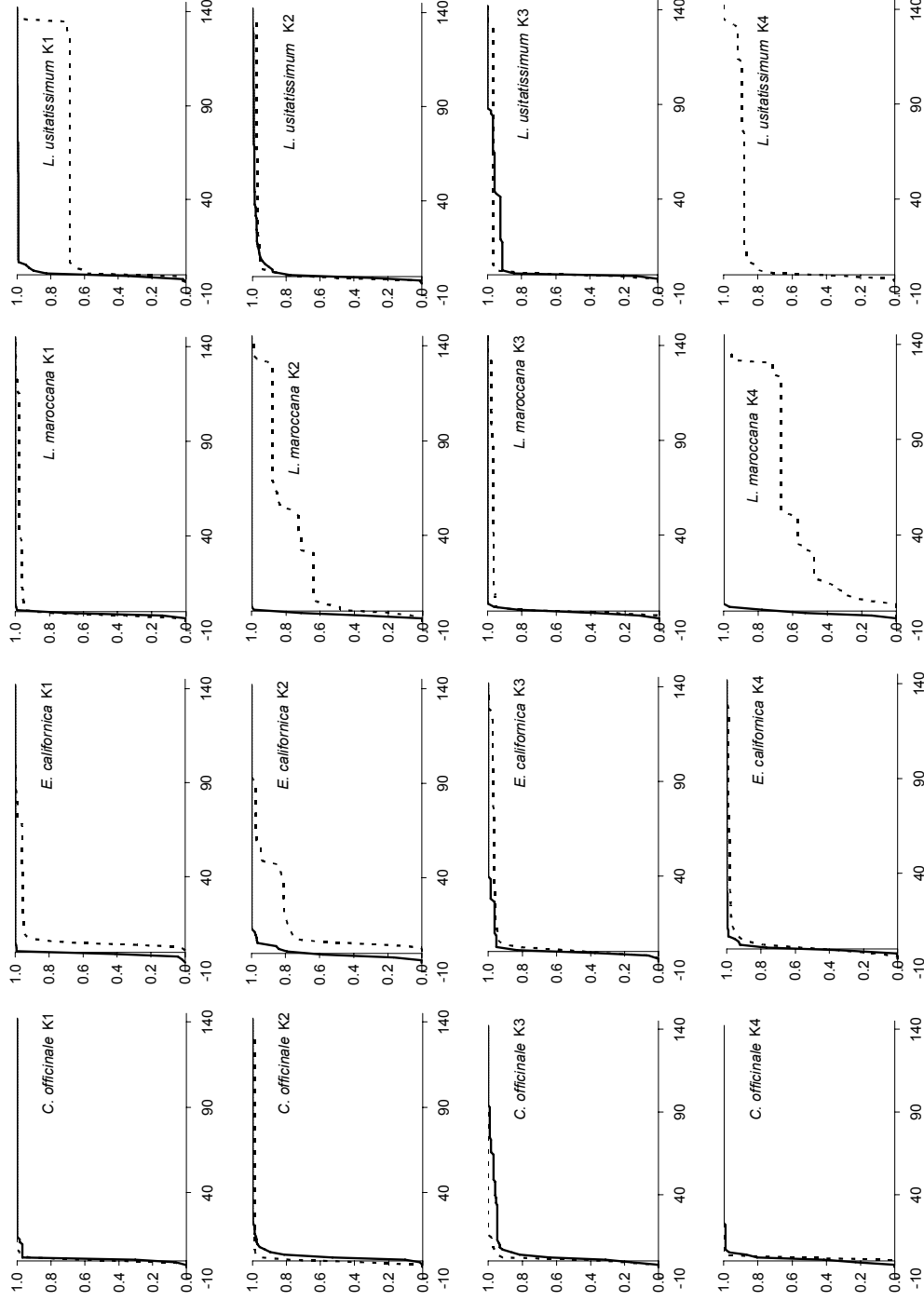
Figure 5. Effect of harvest and cultivation on seed dispersal in the 2003 field experiment for plant species with ripe seeds on the plant just before harvest. Cumulative frequency distributions of plant species are presented for harvest (solid line) and rigid-tine cultivator (dashed line) for each kernel of the plant species separately. On the *x*-axis distance in meters is shown. The *y*-axis presents the fraction of seedlings who were dispersed till the indicated distance.
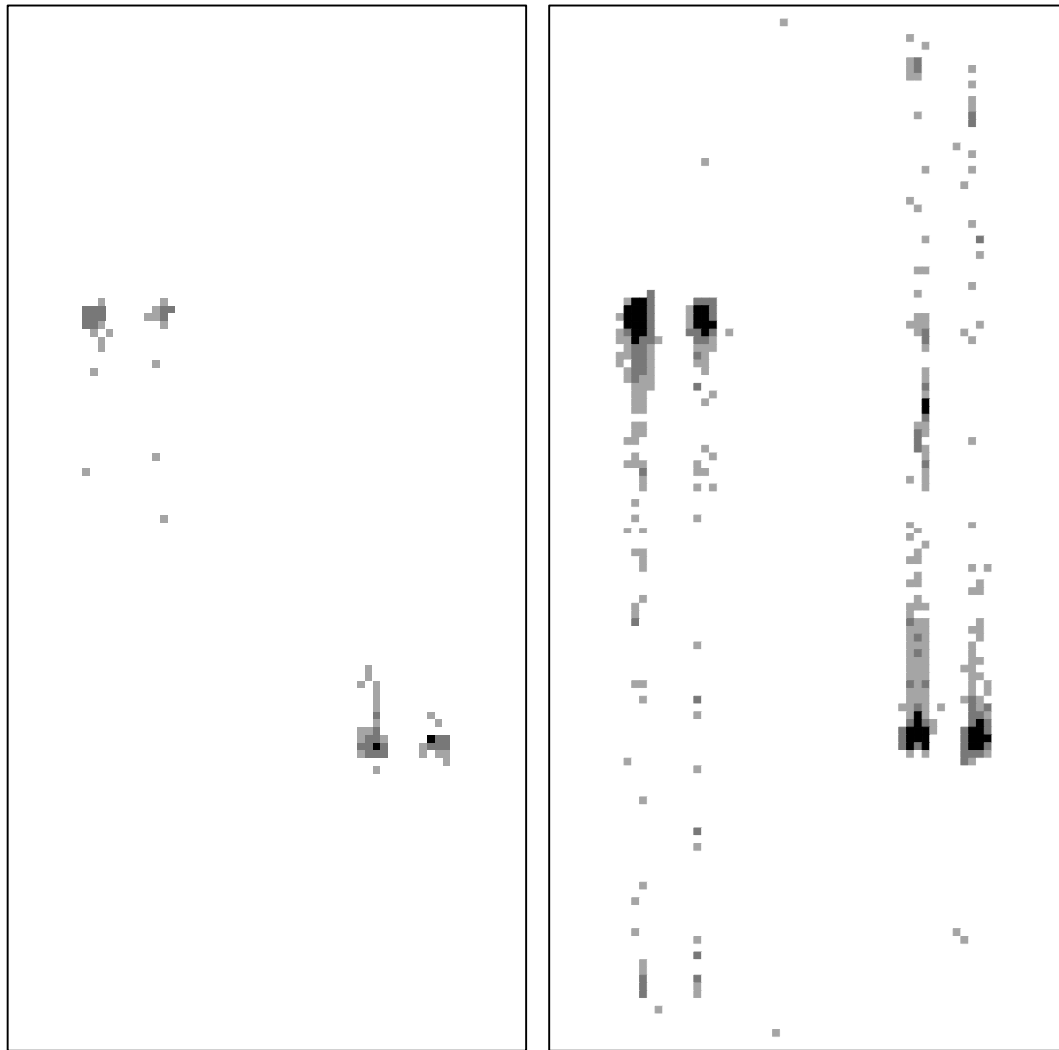
Figure 6. Results of the experiment in 2003. Location of *E. californica* seedlings after dispersal by harvest (left) and after harvest and cultivation (right). Number of plants per quadrat is indicated by grey tones: ☐=0, ▨ =1–10, ▧ = 11–100, ■ = 101–700.

likely partially caused by the choice of the origin in the centre of the 3 m large plot leading to an initial source between −1.5 m and +1.5 m. The Kolmogorov-Smirnov test for differences between the cumulative frequency distributions was significant at $P<0.01$ for all kernels except for *H. vulgare* (n.s.), kernel 3 of *L. usitatissimum* (n.s.) and *C. officinalis* (kernel 4 $P<0.05$) (details see Appendix 1).

For most seeds, the maximum distance travelled was beyond 130 m, covering the entire length of the field. The 90 and 95 percentile values of some kernels of *L. maroccana* and *L. usitatissimum* indicated that 5% to 10% of the seedlings were dispersed beyond 130 m.
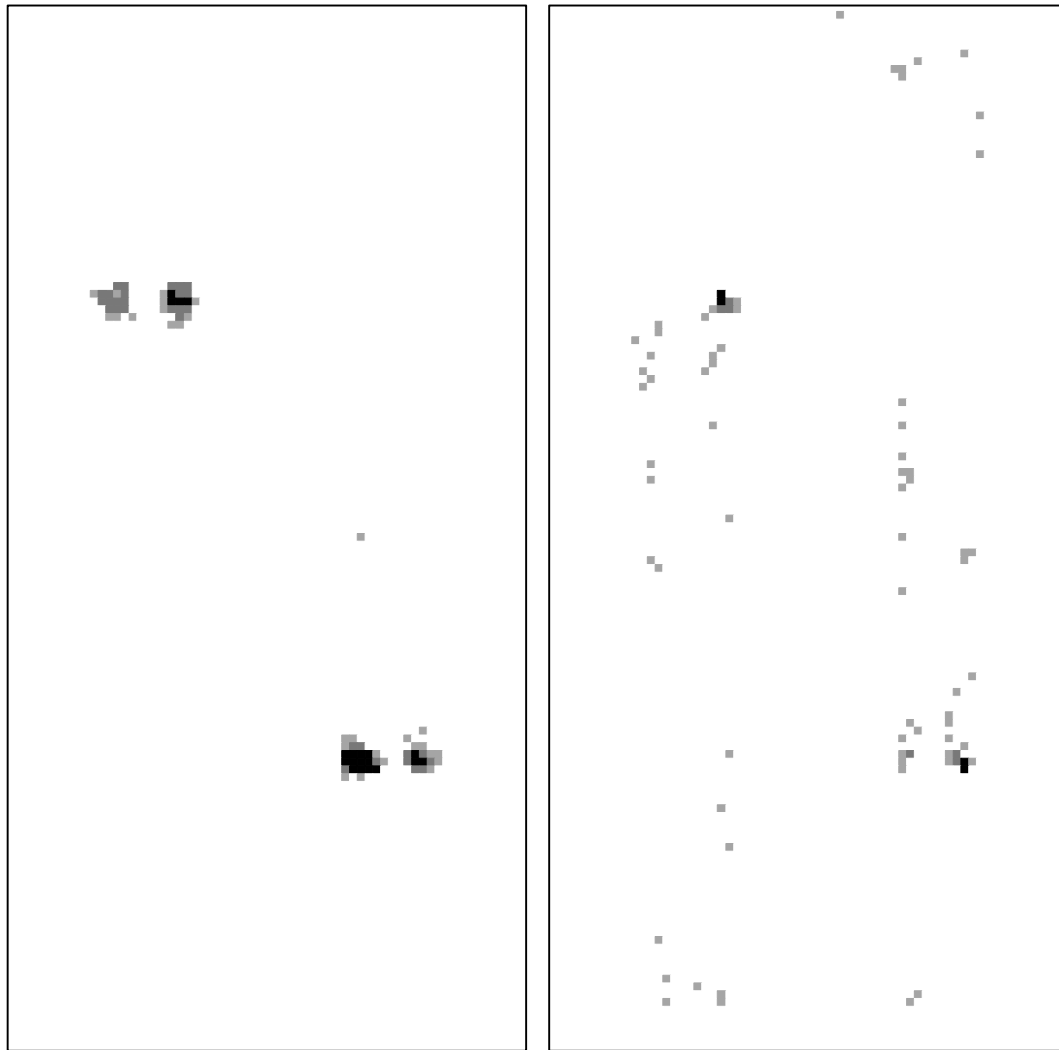
Figure 7. Results of the experiment in 2003. Location of *L. maroccana* seedlings after dispersal by harvest (left) and after harvest and cultivation (right). Number of plants per quadrat is indicated by grey tones:

□ =0, ▨ =1–10, ▨ = 11–100, ■ = 101–1100.

Figure 8 shows a comparison of the mean dispersal distances after harvesting and after harvesting plus cultivation in the 2003 experiment. This figure shows that the cultivation adds greatly to the average dispersal distance, but especially that it adds to the variability of the dispersal distance.

For seeds that were present on the soil surface the outcome was variable. The small sample number of seeds on soil (n=2) did not allow for statistical comparison with seed plants. The experiment with *A. hybridum* failed.
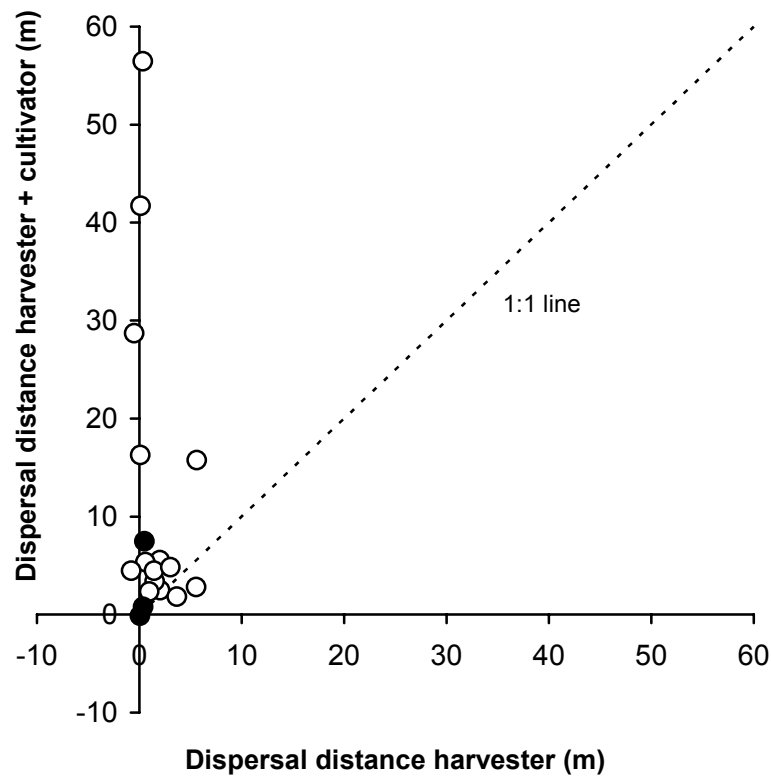
Figure 8. Comparison of mean dispersal distance due to harvester alone (*x*-axis) and harvester + cultivator (*y*-axis) in 2003 experiment, illustrating contribution to mean dispersal distance of the cultivation, but especially the contribution of cultivation to variability in the dispersal distance among different measured kernels. Open symbols: seeds on plant; closed symbols: seeds on soil.

DISCUSSION

The results of this study show that both harvesting and cultivating in maize can spread plant seeds over large distances of more than 100 m. The average dispersal distance in the working direction was often only a few meters, and sometimes the average displacement of the seeds was negative, i.e. upstream the driving direction, but with seeds on the plant and following cultivation, average dispersal distances of several tens of meters were observed in some kernels. Even though the sampled space in this study was fairly large when compared to other studies on plant dispersal in agricultural systems, the theoretical maximum dispersal distance was not attained, and several empirical dispersal kernels had not reached their end point at the end of the observed spatial support. Thus, it is concluded that harvesting and cultivating can make a substantial contribution to the long distance dispersal of weeds in maize. The observed dispersal kernels were quite variable, especially those following cultivation, indicating that chance effects play a big role in dispersal.

This chance element is consistent with direct observations that were made in the crop during the operations. Sometimes, during passage of the cultivator through the field, heaps of plant material were dragged from the source plots and subsequently deposited in the headlands when and where the tines of the cultivator were unearthed, to enable the driver to turn the tractor (Figure 9). The 'bumps' in the tails of the cultivator-induced dispersal kernels (Figures 3 and 5) are probably due to this phenomenon. The haphazard nature of this discrete event of dragging and dropping is a plausible explanation for the large variability of the dispersal kernels after cultivating.

Figure 9. (a) Rigid-tine cultivator in 2002 experiment at turning point in headlands where tines are unearthed. Plant material including seeds is attached to the tines. (b) Plant debris including seeds has fallen in headlands after disposal by tines of cultivator in 2002 experiment.

The timing of seed shed affected dispersal by machinery significantly. Seeds that were located on the plant at harvest time travelled further than seeds that were on the soil prior to harvest. This is the first study in which the effect of these two contrasting seed shed times on dispersal by machinery was tested simultaneously in a field experiment. Our study further showed that rigid-tine cultivator greatly contributes to the dispersal process if seeds are at the plant at time of harvest and that some kernels had long tails, covering the entire observation plot.

Nearly all the seeds that represent species that shed their seeds before harvest, and were placed on the soil in this study, stayed relatively close to their initial source plot. The short travel distance of the seeds of weed species that shed seeds prior to harvest will aid in patch persistence (Woolcock & Cousens, 2000; Humston *et al*., 2005) as primary dispersal of most seed shedding weed species results in seed shadows close their source. For example, the grass weeds *Bromus sterilis* and *Alopecurus myosuroides* shed their seeds within 1 m from the mother plant (Rew *et al*., 1996b; Colbach & Sache, 2001). Dispersal by machines will elongate weed patterns in the driving direction (see Humston *et al*., 2005), which was particularly reflected in the patterns shaped by the cultivator in the current study.

Although directionality was present in most dispersal patterns, the majority of the seeds in this study travelled less than a few meters from their initial position. Other studies on dispersal of weeds by agricultural equipment also reported that most seeds dispersed within a few meters from the source. For various types of cultivators, after a single pass, the bulk of seeds moved less than one meter from the initial source (Rew & Cussans, 1997) or only a few meters (Mayer *et al*., 1998; Marshall & Brain, 1999). Patch and or seed displacement by harvest combiner appeared to occur within approximately a few to 5 meter from the initial foci (Howard *et al*., 1991; Blanco-Moreno *et al*., 2004; Steinmann & Klingebiel, 2004; Humston *et al*., 2005; Barroso *et al*., 2006), depending on the machinery and weed species. For example, soil tillage caused larger dispersal of the seeds of *A. fatua* and *A. sterilis* than the combine harvester as the plant had shed over 90% of its seeds before harvest. The pattern that emerges is that the bulk of the weed seeds do not travel very far, but what may be more important is how far the tail of the distribution extends, because this has important ramifications for the rate of spatial population expansion (Kot *et al*., 1996). There are few data available concerning the spread of weeds at field scale, and the data provided here, which do demonstrate unequivocally the long travel distance of plant-borne seeds upon cultivating, are, therefore, valuable and important. This finding is especially striking as the harvesting method of maize (whole crop) would suggest that the chances of seed dispersal in this crop should be slim, compared to other crops, such as cereals, in which plant debris of weeds is – in principle – returned to the field

at harvest. The findings suggest that weeds that have plant-borne seeds that could get entangled in machinery during field operations have good prospects for rapid population expansion at field scale.

Our current study further illustrates that the interaction between design of the machine and weed biology should have major consequences for dispersing potential. Compared to harvesting alone, the rigid-tine cultivator caused the largest seed displacement for most species whose seeds were at the plant during harvest. There are several possible reasons for this. First of all, the maize silage forage harvester does not emit crop and weed material to the field on a structural basis as some cereal combiners do when emitting chaff and weed seeds with straw (see Blanco-Moreno *et al.*, 2004; Barroso *et al.*, 2006). Secondly, the cutting bar of the forage harvester cuts off maize plants at about 10–15 cm height. We noticed that introduced plants bent and gave way to the cutting bar of the harvester and were, therefore, cut off at a considerable greater height than 10 cm. As such, the harvester facilitates dispersal by rigid-tine cultivator. Until now, dispersal experiments to determine the spread of weeds by tillage equipment are performed with seeds placed on or buried in the top soil layer. Dragging plant material by cultivator seems to enhance dispersing potential compared to seeds travelling with soil on the machine. And indeed this was reflected in the contrast between the dispersal patterns of the two different starting positions in the 2002 experiment; on the soil or on the plant. The forage harvester was expected to also have plant dragging potential but this was not observed. In addition, we expected some spilling of seeds with silage maize by accident if wind blows the harvested material from the lorry accompanying the forage harvester. During the two years of this experiment, wind speed was close to zero in the critical periods and no such spilling was observed in the field.

For some species in this study, the combined effect of the two machines on dispersal of ripe seeds located at the plant at harvest, resulted in a small percentage of seeds travelling the entire length of the observation plot, exceeding 130 meters. Studies on the maximum dispersal distance (or tail length) are limited (Mayer *et al.*, 1998; Steinmann & Klingebiel, 2004; Guglielmini & Satorre, 2004). Experimental set up appears to determine the tail length with the maximum measured distance often coinciding with the length of the tail. Wild oats (*Avena fatua*) seeds were dispersed over 245 m by the cereal combine covering the full length of the observation plot (Shirtliffe & Entz, 2005).

For establishment of new patches, the length of the tail of the dispersal kernel is quite important, and tails which decrease less than exponentially with distance favour formation of new patches (Wallinga *et al.*, 2002). In our study, some kernels had 'bumps' in the tail (Figures 3 and 5). These bumps may be more important for the

formation of new patches than the taper of the tail. Rew & Cussans (1997) used the term 'guerrilla spread' to indicate the unpredictable dispersing behaviour of seeds travelling further than the bulk. In the study presented here, some predictability seemed present in the deposition of seeds by machines as for example shown by *S. alba*. This species carried ripe seeds during harvest time. A higher density of seedlings appeared in the headlands where the tines of the cultivator unearth and plant material is released (Figure 9). For the formation of new patches, higher density patches have more chance of successful establishing than lower densities (Humston *et al*., 2005). Patch size is also vital for establishment (Latore *et al*., 1998). Below a critical patch size, survival of a patch is unlikely if it depends too strongly on immigration, i.e. an Allee effect at patch level (Kot *et al*., 1996). If there is an Allee effect, population expansion is not so much driven by the 'pull from the tail' as by the 'push from the centre'. It is possible that the formation of new patches is strongly favoured if seed material is deposited in aggregations, overcoming this Allee effect, and allowing the tail of the distribution to pull the expansion.

The plant species used in the experiment as plants shedding seeds during harvest were cultivated plants and not weed species. This was done to ensure that the observed seedlings resulted from the introduced source, and did not occur already in the field. Differences in biology of cultivated plants and weeds species may be present, but given that a suite of species were used, we do not think that this choice has affected the applicability of the results. Some weedy plants drop their seeds easily (e.g. *A. fatua* and *A. sterilis*; Barroso *et al*., 2006), while others, e.g. *Lolium rigidum,* do not shed their seeds easily (Blanco-Moreno *et al*., 2004). The two exposure methods of seeds used in this study (on soil *versus* on plant) account for this variability in weeds. The large advantage of using cultivated plants is the ease of making observations, which allowed a greater number of kernels to be observed and a great spatial support than would otherwise have been possible. Some innovative findings in this study are a direct consequence of the choice of method.

In the current study, seeds of varying seed weight were used. Unfortunately, some lighter seeds such as *Lignis coronaria* failed to germinate. Both seed weight and the interaction with machines may influence dispersal distances and much depends on the system at study. Smaller seeds dispersed further than larger seeds by soil tillage machines (Rew & Cussans, 1997). Mayer *et al*. (1998) reported that lower seed weight affected carrying distance of some species positively but type of machine also influenced this. Relatively heavy weighted seeds of *Datura ferox* dispersed over nearly 100 m by combiner in soybean (Ballaré *et al*., 1987). Ideally, the hypothesis that seeds on the plant are dispersed further away from the source than seeds that are on the soil surface, should be tested in experiments that use the *same* seeds on the plant and on

the soil. With the setup used in this study, other attributes of the seeds, like seed weight and surface roughness, could also effect their dispersal. These are influences that our results do not rule out; however, the direct observation on the dragging and dropping of plant debris gives compelling support to the hypothesis that seeds that are attached to the plant have a better chance of travelling far when the field is tilled or when the crop is harvested. Observations on the kernels of the seeds of *Diplotaxis erucoides sylvetta*) and *Papaver rhoeas* (Heijting, unpubl. results), which both have low seeds weights, show that these seeds, when laid on the soil, do not travel very far under the influences of cultivation. This confirms the notion that the comparatively far dispersal of plant-borne seeds in this study is due to the fact that they were plant-borne, and not due to the fact that they were comparatively light when compared to the seeds that were placed on the soil surface.

Our study confirms the importance of timing of seed shedding for seed dispersal as was put forward and examined in other studies (McCanny & Cavers, 1988; Woolcock & Cousens, 2000; Blanco-Moreno *et al.*, 2004; Barroso *et al.*, 2006). It is shown that plant material with seeds can be dragged over large distances into the headlands. For species that bear viable seeds at the time of crop harvest, this could potentially lead to accumulation of plant material in the headlands. To prevent such sub-field weed transport, a clean crop at harvest appears advisable. This finding also sheds another light on the higher weed densities which are often encountered in headlands, which is often attributed to less efficient management, or introduction of species via the field entrance. This study shows that it may also be an effect of poorer management elsewhere in the field.

Appendix 1

Results of Kolmogorov-Smirnov test for the difference between the cumulative distribution functions of the dispersal distance attained by either harvest or harvest and cultivation of the 2003 experiment. Maximum difference between the two cumulative distribution functions and its significance is presented.

	Kernel	Maximum difference	Level of significance
H. vulgare	1	0.10	n.s.
L. angustifolius	1	0.15	$P < 0.001$
C. officinale	1	0.64	$P < 0.001$
	2	0.67	$P < 0.001$
	3	0.28	$P < 0.001$
	4	0.41	$P < 0.005$
E. californica	1	0.38	$P < 0.001$
	2	0.45	$P < 0.001$
	3	0.29	$P < 0.001$
	4	0.20	$P < 0.001$
L. maroccana	1	0.22	$P < 0.001$
	2	0.51	$P < 0.001$
	3	0.12	$P < 0.001$
	4	1.00	$P < 0.001$
L. usitatissimum	1	0.31	$P < 0.001$
	2	0.21	$P < 0.001$
	3	0.14	n.s.

CHAPTER 6

Predicting the weed-free proportion of the field area with Taylor's power law[*]

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Summary

Crop weeds are patchily distributed. In weed management it is important to be able to estimate the weed-free fraction of the total field area, because this fraction determines the potential saving on herbicides that may be achieved by site-specific application (and not spraying those patches with no weeds). In this chapter, we model the weed-free fraction by combining Taylor's power law (TPL) for the variance-mean relationship with a prediction of the zero class frequency according to the negative binomial distribution. The resulting predictions of occupancy were compared to observations on weed density and occupancy in 32 data sets on occurrence of agricultural weeds in The Netherlands. The results using weed species specific parameters for TPL provided strong validation for the approach, with $R^2_{prediction}$ varying between 0.735 and 0.998 for 13 of the 14 species groups. Estimates of the slope parameter b of TPL varied substantially between weeds (from 0.78 for volunteer potatoes to 1.95 for *Echinochloa crus-galli*), but only slightly between data sets. Predictions based on a common slope parameter still had high coefficients of prediction for most weed species. Based upon a spatially explicit data set collected using counts in contiguous quadrats, the effect of scale of the sample unit was analysed. At levels of scale relevant to decision making in weed management, the effect of scale on occupancy was minor. We conclude that the relationship between density and occupancy for arable weeds is strong, and that there is scope for prediction of the weed-free area and prediction-based weed management.

Keywords: Taylor's power law, negative binomial distribution, site-specific weed management.

INTRODUCTION

Weeds tend to occur spatially aggregated on arable land (Marshall, 1988; Wilson & Brain, 1991; Cardina *et al.*, 1995; Johnson *et al.*, 1995a, b), thus, offering scope for site-specific weed management (Christensen *et al.*, 1999). Costs and environmental impact can be reduced by adjusting herbicide application and dosage to weed occurrence and density. Aggregation of weeds can be assessed by examining the frequency distribution of numbers per spatial unit, e.g. a square meter. The negative binomial distribution (NBD) can often be used to describe the frequency distribution of weed counts (Marshall, 1988; Berti *et al.*, 1992; Mortensen *et al.*, 1992; Wiles *et al.*, 1992; Johnson *et al.*, 1996a). Its parameter *k* is an indicator of aggregation, with large values indicating randomness and small values indicating aggregation. The NBD can also be used to calculate the frequency of empty quadrat counts. For site-specific management the unoccupied fraction gives the minimum potential herbicide savings. Potential saving can be even greater if sprays are only applied when weed density exceeds a threshold. Parameter *k* depends on the mean weed count (abundance). In practice, the mean will generally be observation specific, so *k* will vary too. The weed-free fraction (which is 1 – occupancy) can be calculated without fitting the NBD if the relation between variance and sample mean has been established. For the mean-variance relationship Taylor's power law (Taylor, 1961) was chosen. Linking the model on mean and occupancy (NBD) with a model describing the relation between the mean and its variance was tested by He & Gaston (2003) on various species such as ticks, beetles and pine trees. Usefulness of the proposed model was further illustrated for distribution of arthropod species on the Azores (Gaston *et al.*, 2006).

Taylor's power law (TPL) (Taylor, 1961, 1984) characterizes the relationship between variance and mean for many organisms: $\sigma^2 = a\mu^b$. Parameters *a* and *b* are thought of as being characteristic to the species and the scale of sampling (Taylor, 1961; Binns *et al.*, 2000). Parameter *b* is considered an indicator for aggregation of the species at hand, with values > 1 representing aggregation. Parameter *a* is considered a scale factor. TPL has found wide application in animal ecology such as entomological research for IPM (Binns & Nyrop, 1992; Binns *et al.*, 2000). The use of TPL in plant ecology and in particular weed ecology has – so far – been limited (Clark *et al.*, 1996). TPL has proved useful in seed bank studies (Dessaint *et al.*, 1996; Ambrosio *et al.*, 1997) and weed plants (Berti *et al.*, 1992) to optimize sampling schemes. Clark *et al.* (1996) examined the effect of scale on parameters *a* and *b*, and found that although sample size and spatial scale affected values of parameter *a* and *b*, the effects were unpredictable.

We will investigate if the proportion of weed-free area can be predicted from weed density and spatial variance. Furthermore, we will examine the specificity of the

relations found and inquire how knowledge on weed-free fraction can be used in weed management. In a second part of the study the effect of scale of observation on level of occupancy will be studied for a detailed spatially explicit data set. Besides scale of the observation quadrats, the effect of the orientation of quadrats on the observed level of occupancy will be looked at.

MATERIALS AND METHODS

Data

Data were collected by Applied Plant Research, The Netherlands, as part of its herbicide efficacy trials (Table 1). A total of 32 data sets were collected between 1995 and 2002, at seven sites (Figure 1), with varying field histories, treatments, soil type, crop, quadrat size and time of observation. All weed counts used in this study were gathered in spring just prior to herbicide spraying. Number of plants per weed species was counted in quadrats, which were evenly distributed over the sampled area.

Additionally, weed count data prior to herbicide spraying were collected in contiguous quadrats over three years (2001, 2002, 2003) in a single field (Kortenoord II) on clay soil cropped with maize in Wageningen (location see Figure 1). These data were used to investigate the effect of size and shape of sample units on the weed-free fraction. The total area sampled with contiguous quadrats was 12 m wide and 50.25 m long. Each quadrat measured 0.75 m × 0.75 m. For full description see Heijting *et al*. (2007).

Analysis: Descriptive statistics and Taylor's power law

Descriptive statistics, including sample mean, variance, minimum, maximum, observed fraction of empty quadrats ($P(0)$) were calculated per weed species for all the data sets. TPL was fitted to the pairs of ^{10}log(sample mean) and ^{10}log(variance) of all data using linear regression (GENSTAT 8.1, Lawes Agricultural Trust, UK) and Weighted Least Squares (WLS) with number of quadrat count as weight. The results of this will be regarded as the general model or the null model (M_0). In a next step, species specificity of the intercept (log a) or slope (b) was examined by adding species as a factor to M_0, leading to M_a or M_b. Each species is regarded as a factor level (=14). Only weed species which occurred in at least 4 data sets were included in the analysis. The specificity of both parameter a and b was investigated simultaneously in a final step, leading to M_{a+b}. To determine a possible influence of data sets on the resulting model parameters, data sets were added as a factor to the general model. Each data set is a unique combination of year, crop, time of observation, field history, soil type, number of quadrat counts and size of quadrats used. The total number of data sets did

Table 1. Information on data sets: crop, soil type, geographic location, year, field and quadrat size, number of quadrats used and number of main weed species detected.

Observation code	Crop	Soil	Location	Year	Field size	Size quadrat (m^2)	Number of quadrats	Number of main weed species
AGV2347	leek	clay	Lelystad	2001	19.5m×198m	0.75	48	7
AGV3302	onion	clay	Lelystad	2001	19.5m×198m	1.08	40	8
AGV3352	sugar beet	clay	Lelystad	2001	18m×272m	0.3	112	7
AGV4050	sugar beet	clay	Lelystad	2002	18m×268m	0.5	128	11
AGV4051	onion	clay	Lelystad	2002	21m×123m	0.3	108	12
PAV3058	onion	clay	Lelystad	2000	19.5m×200m	0.25	68	5
met1	asparagus	sand	Meterik	2001	15m×48m	0.375	56	3
met2	asparagus	sand	Meterik	2002	15.3m×48m	0.35	56	5
KP480P1E1	fallow	sand	Valthermond	2000	36m×69m	0.8	36	2
KP480P1E2	fallow	sand	Valthermond	2000	36m×69m	0.8	36	2
KP480P2E1	fallow	sand	Valthermond	2000	36m×69m	0.8	36	2
KP480P2E2	fallow	sand	Valthermond	2000	36m×69m	0.8	13	2
KP481P1A	fallow	sand	Valthermond	2000	60m×147m	0.64	108	2
KP481P1B	fallow	sand	Valthermond	2000	60m×147m	0.64	108	2
KP481P2A	fallow	sand	Valthermond	2000	60m×147m	0.64	108	2
KP481P2B	fallow	sand	Valthermond	2000	60m×147m	0.64	32	3
KP500P1E1	fallow	sand	Valthermond	2000	39m×69m	0.64	36	3
KP500P1E2	fallow	sand	Valthermond	2000	39m×69m	0.64	35	4
KP500P2E1	fallow	sand	Valthermond	2000	39m×69m	0.64	36	4
KP500P2E2	fallow	sand	Valthermond	2000	39m×69m	0.64	36	6
KPG216	asparagus	sand	Valthermond	2001	39m×69m	0.25	64	6
PAGV4151AF	maize	sand	Heino	1995	60m×144m	0.75	16	6
PAGV4151BC	maize	send	Heino	1995	60m×144m	0.75	16	5
PAGV4151DE	maize	send	Heino	1995	60m×144m	0.75	16	6
REG3109	maize	sand	Heino	2000	36m×125m	0.5	48	7
PAGV4152AF	maize	sand	Cranendonck	1995	84m×100m	0.75	16	3
PAGV4152BC	maize	sand	Cranendonck	1995	84m×100m	0.75	16	2
PAGV4152DE	maize	sand	Cranendonck	1995	84m×100m	0.75	16	3
VP1008	maize	sand	Vredepeel	2001	97.5m×54m	0.75	120	10
VP1023A	black salsify	sand	Vredepeel	2002	27m×180m	0.15	80	3
VP1023B	black salsify	sand	Vredepeel	2002	27m×180m	0.15	80	3
ZW2369	onion	sandy clay	Colijnsplaat	2001	40.5m×90m	1.08	40	4

Figure 1. Geographic origins of data sets in The Netherlands: 1. Valthermond, 2. Heino, 3. Lelystad, 4. Colijnsplaat, 5. Vredepeel, 6. Meterik, 7. Cranendonck, 8. Wageningen.

not allow for further analysis on the latter characteristics separately. To ensure the model adequately described Taylor's power law, data sets with 4 or more different weed species were included. $R^2_{adjusted}$ was calculated for all models.

Calculation of weed-free fraction

TPL (Taylor, 1961, 1984) characterizes the relationship between variance and sample mean for organisms following

$$\sigma^2 = a\mu^b \tag{1}$$

The negative binomial distribution has parameter μ and k. The parameter k can be estimated from observed mean and variance as:

$$k = \frac{\mu^2}{\sigma^2 - \mu} \tag{2}$$

The zero class frequency of the negative binomial distribution is:

$$P(0) = \left(\frac{k}{k+\mu}\right)^k \tag{3}$$

Equations 1, 2 and 3 can be combined (He & Gaston, 2003; Gaston *et al.*, 2006) to obtain the following equation for calculating the zero class frequency, based on observed mean μ, and parameters a and b of TPL:

$$P(0) = \left(\frac{1}{a\mu^{b-1}}\right)^{\mu^2/(\sigma^2-\mu)} \tag{4}$$

Expected fraction of weed-free quadrats was calculated for each weed species-data set combination. $R^2_{predicted}$ (Turchin, 2003) was calculated between calculated and observed weed-free fraction of quadrats to determine the suitability of our approach to calculate the weed-free fraction.

Effect of scale and shape of observation quadrat
Kortenoord II data comprised three subsequent years. To determine the effect of scale and orientation on observed weed-free area fraction, quadrats were aggregated to gain higher level of scale according to the following scheme:

Scale	In-Row	Across-Row
1	1×1	1×1
2	2×1	1×2
3	3×1	1×3
4	4×1	1×4

The sign test ($P<0.05$) was performed to investigate on differences between the two directions (in-row and across-row). The effect of scale and orientation was investigated with Delphi (Delphi, Borland Inc., Scotts Valley, CA, USA).

RESULTS

Prediction of the weed-free fraction of the field
Throughout the data sets, *Chenopodium album*, *Polygonum persicaria*, *Poa annua*, *Stellaria media* and *Solanum nigrum* were the most frequent (Appendix 1) weed species. Fraction of empty quadrats ($P(0)$) varied largely depending on the observation. If counts of all weed species of a data set were summed, this fraction was smaller than 0.1 and often close to zero.

The general regression model M_0 adequately described ($R^2_{adjusted} = 0.96$) the relation between weed sample mean and its variance, with $^{10}\log a = 0.5160$ and $b = 1.3904$ (Table 2). If species were added as a factor, both slope (b) and intercept ($^{10}\log a$)

significantly differed ($P<0.05$) from the general model. The variance accounted for by the regression changed slightly but significantly when species specificity of both parameters was included in the model ($R^2_{adjusted} = 0.97$). Addition of data set as a factor to M_0 gave a similar effect as weed species (Table 3). Only 107 data points could be used as not all data sets comprised enough weed species for the regression analysis.

TPL could be fitted to 13 weed species and volunteer potato plants (*Solanum tuberosum*) (Figure 2; Table 4). $R^2_{adjusted}$ for the fitted species specific relationship were high, often above 0.91 with *Senecio vulgaris* attaining the maximum of 1.0. *Solanum tuberosum* was the exception with $R^2_{adjusted} = 0.79$. The latter weed gave the lowest b (0.78). For all other weed species the value of parameter b was between 1.18 (*Matricaria* spp.) and 1.95 (*Echinochloa crus-galli*). Values of parameter a varied between 1.54 (*S. tuberosum*) and 7.15 (*Polygonum convolvulus*).

Table 2. Details of the general model and species specific models for regression between ^{10}log(mean) and ^{10}log(variance) according to Taylor's power law, ^{10}log(variance) = $b \times$ ^{10}log(mean) + ^{10}log(a). Parameter b, ^{10}log(a), their s.e., significances, parameter a and $R^2_{adjusted}$ of the model is presented. The number of data points (N) was 146.

Model	b	s.e.	^{10}log(a)	s.e.	a	R^2_{adj}
M_0: not species specific	1.39	0.02	0.52	0.02	3.28	0.963
M_a: parameter a species specific	1.41	0.03	*see Table 4*			0.966
M_b: parameter b species specific	*see Table 4*		0.48	0.03	3.03	0.964
M_{a+b}: parameter $a+b$ species specific	*see Table 4*					0.97

Table 3. Details of the general model and data set specific models for regression between ^{10}log(mean) and ^{10}log(variance) according to Taylor's power law, ^{10}log(variance) = $b \times$ ^{10}log(mean) + ^{10}log(a). Parameter b, ^{10}log(a), their s.e., significances, parameter a and $R^2_{adjusted}$ of the model are presented. The number of data points (N) was 107.

Model	b	s.e.	^{10}log(a)	s.e.	a	R^2_{adj}
M_0: not data set specific	1.35	0.03	0.49	0.03	3.09	0.96
M_a: parameter a data set specific	1.30	0.03	-[*]			0.966
M_b: parameter b data set specific	-[*]		0.44	0.03	2.76	0.97
M_{a+b}: parameter $a+b$ data set specific	-[*]					0.97

[*] not shown here.
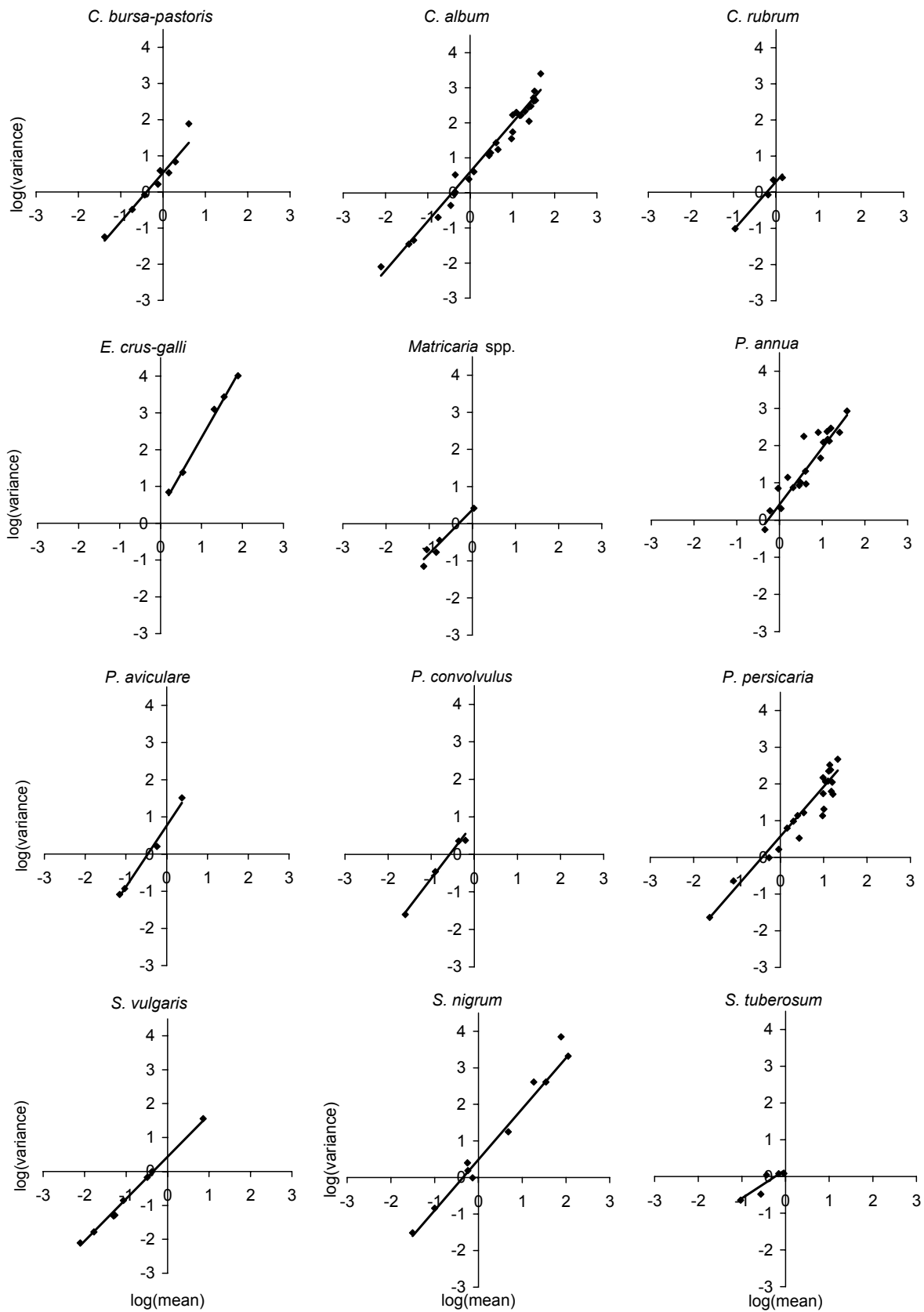
Figure 2. Species-specific results of fitting Taylor's power law.
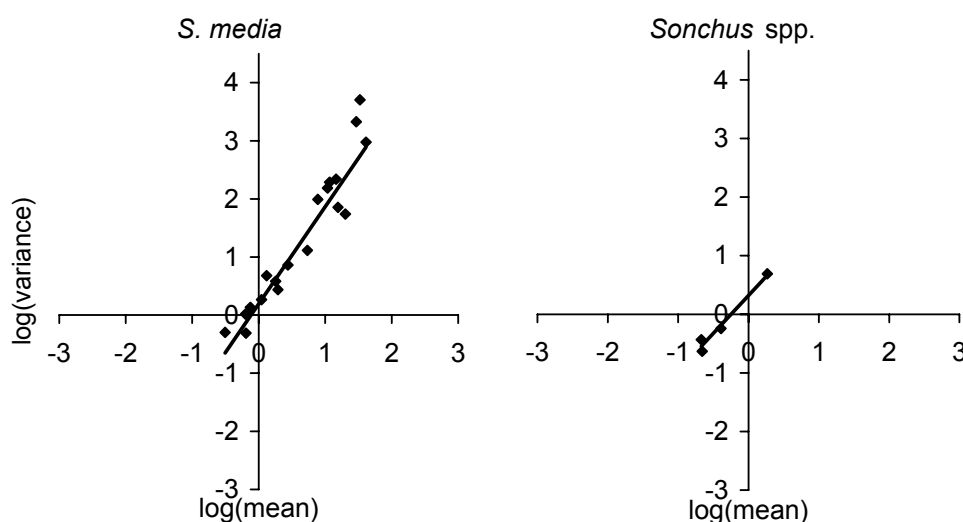
Figure 2. Continued. Species-specific results of fitting Taylor's power law.

Table 4. Results per weed species group for regression between $^{10}\log(\text{mean})$ and $^{10}\log(\text{variance})$ according to Taylor's power law. The parameters b, a, $^{10}\log(a)$ for the model $^{10}\log(\text{variance}) = b \times {}^{10}\log(\text{mean}) + {}^{10}\log(a)$, their s.e., significances and R^2_{adjusted} of the model and number of data sets included (N) are given.

Weed species	b	s.e.	P	$^{10}\log(a)$	s.e.	P	a	R^2	N
C. bursa-pastoris	1.36	0.13	<0.001	0.53	0.09	<0.001	3.42	0.94	8
C. album	1.40	0.03	<0.001	0.60	0.04	<0.001	3.95	0.98	30
C. rubrum	1.34	0.14	0.011	0.29	0.08	0.065	1.95	0.97	4
E. crus-galli	1.95	0.09	<0.001	0.37	0.07	0.015	2.36	0.99	5
Matricaria spp.	1.18	0.15	0.005	0.37	0.12	0.017	2.34	0.94	5
P. annua	1.59	0.12	<0.001	0.32	0.10	0.002	2.07	0.94	18
P. aviculare	1.67	0.15	0.006	0.78	0.12	0.016	5.98	0.98	4
P. convolvulus	1.50	0.11	0.004	0.85	0.11	0.051	7.15	0.98	4
P. persicaria	1.36	0.07	<0.001	0.57	0.07	<0.001	3.73	0.95	22
S. vulgaris	1.24	0.03	<0.001	0.43	0.05	<0.001	2.72	1.00	8
S. nigrum	1.39	0.07	<0.001	0.49	0.08	<0.001	3.08	0.98	10
S. tuberosum	0.78	0.20	0.028	0.19	0.12	0.23	1.54	0.79	5
Sonchus spp.	1.29	0.15	0.013	0.32	0.07	0.049	2.10	0.96	4
S. media	1.67	0.13	<0.001	0.19	0.12	0.113	1.57	0.91	19

Species specific values of parameter *a* and *b* (Appendix 2) were compared (*P*<0.05). Significant differences between weed species were present but weed species could not be grouped accordingly. This is probably caused by the limited number of these data sets. For some weed species only four data sets were available for regression of TPL (Table 4).

Proportion of weed-free quadrats was well predicted (Figure 3; Table 5) for all dicot weed species with values of $R^2_{predicted}$ between 0.87 (*P. convolvulus*) and nearly 1.0 (*S. vulgaris*). For grass weeds, $R^2_{predicted}$ had lower values; 0.74 for E. *crus-galli* and 0.37 for *P. annua*. The closer to 1 $R^2_{predicted}$ lies, the better the model performed in calculating the weed-free fraction. Values near 0 indicate the model did not contribute to a better calculation. And values of $R^2_{predicted}$ < 0 indicate that the calculation with our approach was poorer than using the mean. Using parameter values of the general model for prediction of the calculated weed-free fraction resulted in similar outcomes compared to the species specific model (M_{a+b}) for around half the weed species. For the remaining weed species, the general model gave a poorer performance in calculating the weed-free fraction. For *E. crus-galli* a negative value of $R^2_{predicted}$ was found, showing that for this weed species the general model was inadequate.

Table 5. Values of $R^2_{predicted}$ for the prediction of the weed-free fraction according to the species specific models and the general model of Taylor's power law for 14 weed species groups.

	$R^2_{predicted}$	
Weed species	Species specific model	General model
Capsella bursa-pastoris	0.891	0.895
Chenopodium album	0.976	0.976
Chenopodium rubrum	0.962	0.744
Echinochloa crus-galli	0.735	–0.335
Matricaria spp.	0.976	0.907
Poa annua	0.376	0.451
Polygonum aviculare	0.961	0.831
Polygonum convolvulus	0.868	0.393
Polygonum persicaria	0.954	0.957
Senecio vulgaris	0.998	0.997
Solanum nigrum	0.912	0.910
Solanum tuberosum	0.936	0.726
Sonchus spp.	0.981	0.845
Stellaria media	0.894	0.859
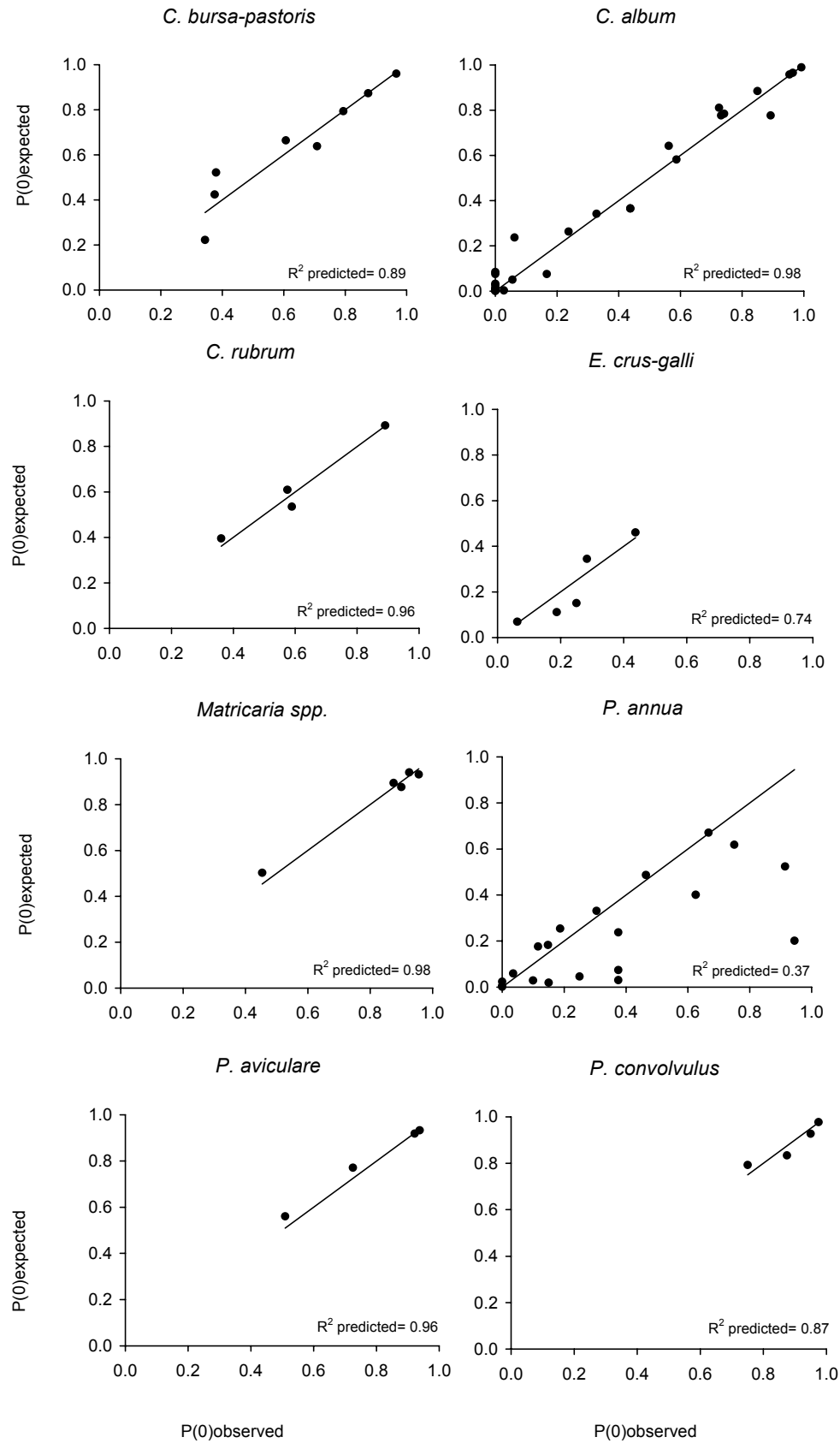
Figure 3. Observed and expected fraction of empty quadrats for 14 weed species groups, according to the species specific model. Each point in the graph represents a data set.
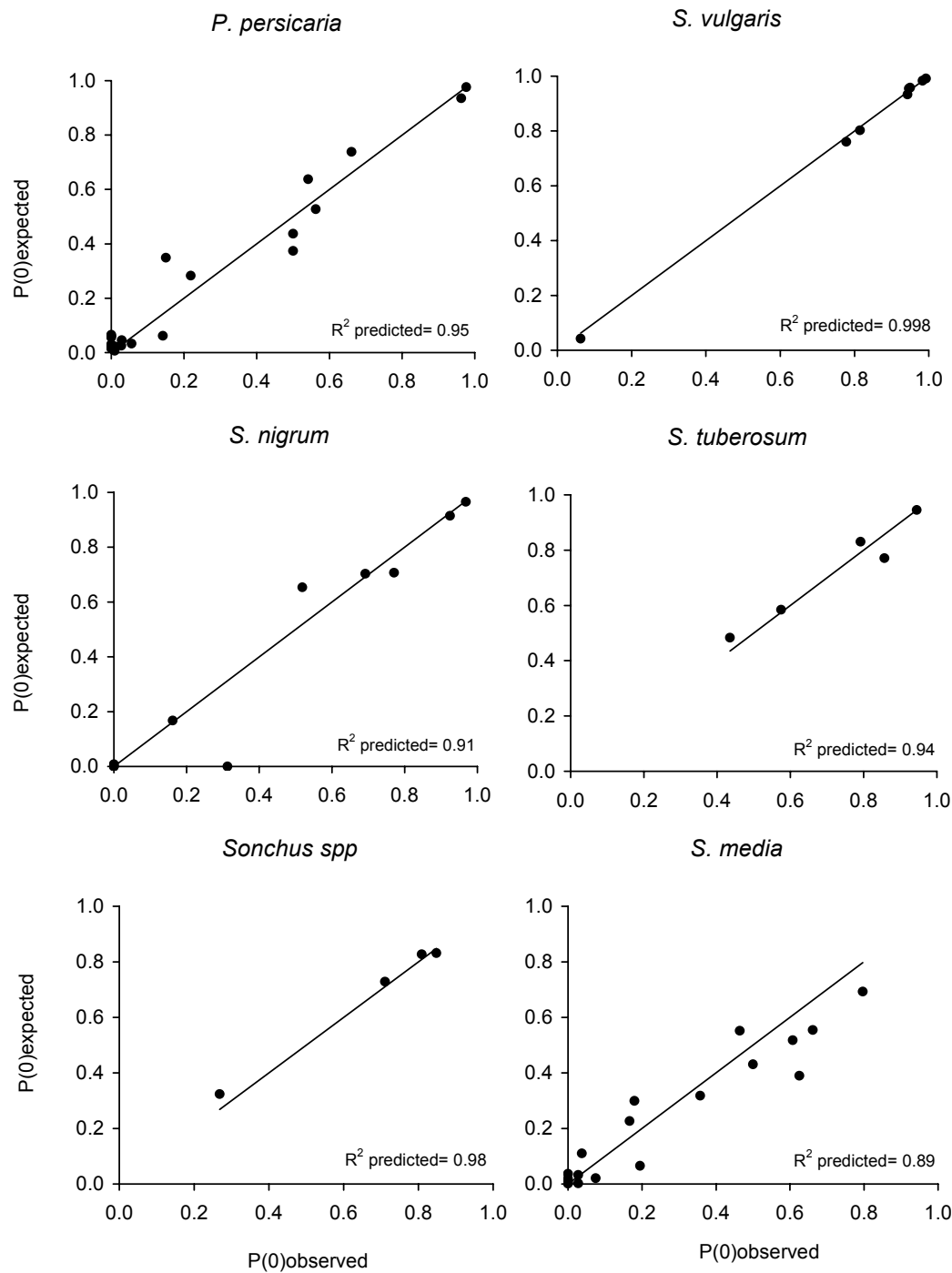
Figure 3. Continued. Observed and expected fraction of empty quadrats for 14 weed species groups, according to the species specific model. Each point in the graph represents a data set

Effect of scale and sample unit on observed fraction of empty quadrats

In Figure 4, the effect of orientation and scaling on observed occupancy fraction is presented for some important weed species. Although the difference between in-row and across-row aggregation was very small, it was significant for scale level 2, with
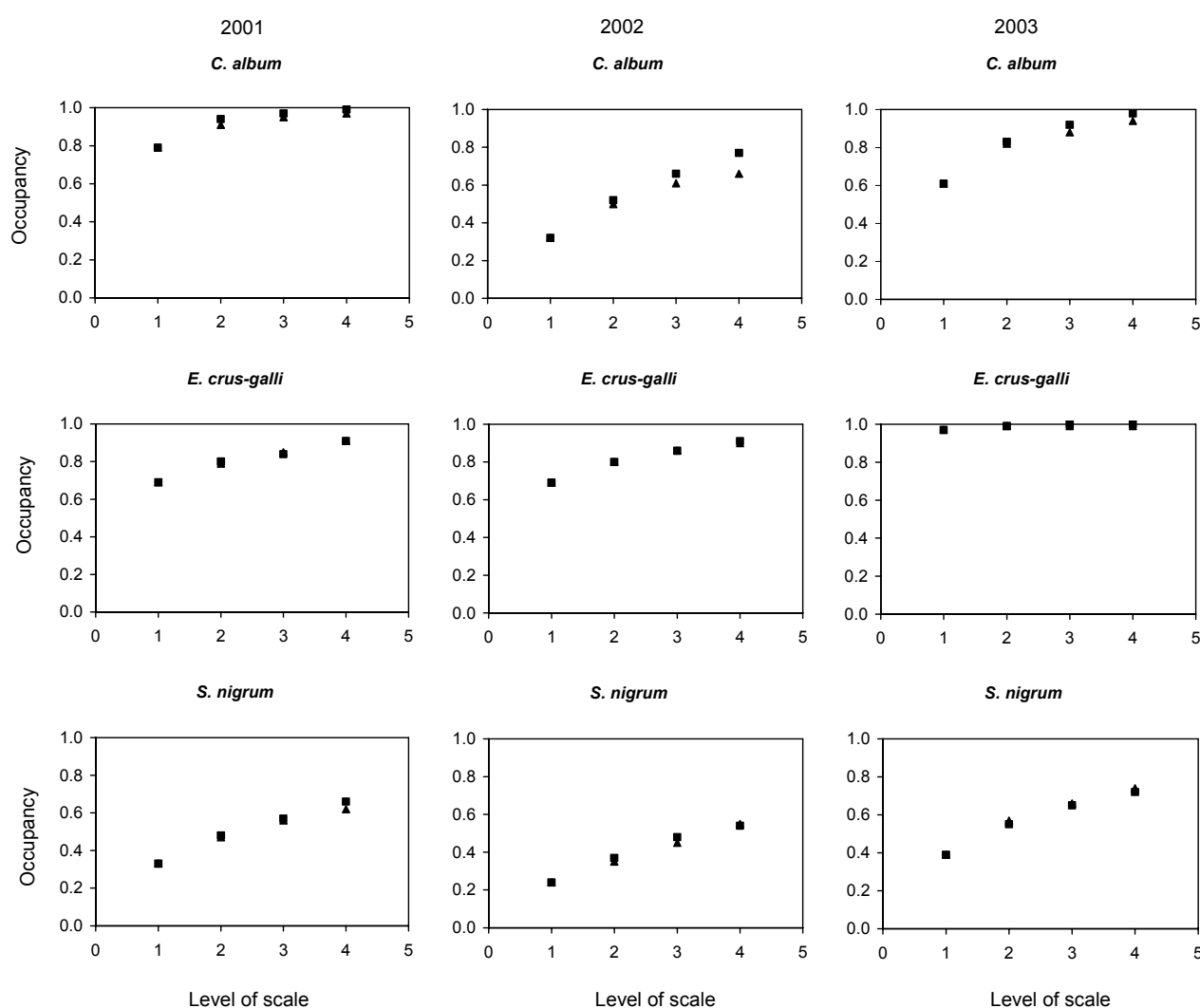
Figure 4. Effect of scale and direction of aggregation on observed occupancy. The two directions are cross-row (▲) and in-row (■).

$P(0)$ for in-row being smaller than across-row aggregation if all 6 examined weed species were regarded simultaneously. For the larger levels of scale, no significant differences occurred.

Aggregation of quadrats in larger observation units resulted in a quick decrease of weed-free fraction (Figure 5).

DISCUSSION

Overall, the weed-free fraction was predicted well using the observed mean density of a weed species combined with the general model of Taylor's power law. Some potentially large savings are possible as for most weed species a significant weed-free

fraction was present in the field. However, if the entire weed population is considered, the observed weed-free fraction is often close to zero. Therefore, in practice greatest reductions will be obtained if more than one herbicide is needed to kill most species of the weed population and a second herbicide is applied site-specifically to target the remaining weed species (Gerhards & Christensen, 2003).

The results on clustering quadrats into larger units showed that possible savings are quickly declining with increasing level of scale. This is in line with findings of Rew *et al.* (1997) and Wallinga *et al.* (1998). At one level of scale, aggregation of quadrats in a particular direction in the field did affect the observed weed-free area significantly, although the differences were very small. The presence of anisotropy in most of the observed weed patterns (Heijting *et al.*, 2007) could explain this detected significance.

Taylor's power law well described the relation between the sample mean and variance of the weed counts in this study, as it previously did for many other organisms (Taylor *et al.*, 1978) and weed plants (Berti *et al.*, 1992; Clark *et al.*, 1996). The parameter values for the slope and intercept of our general model ($s^2=0.52+1.39m$) were similar to those reported by Dessaint *et al.* (1996) for their general model for weed seeds in the seed bank ($s^2=0.45+1.41m$). Only for a few weed species the general model did not give an adequate prediction of the weed-free fraction and species specific parameters of Taylor's power law were required to obtain satisfactory output. Species specificity was significantly present in our study for both parameter *a* and *b*,
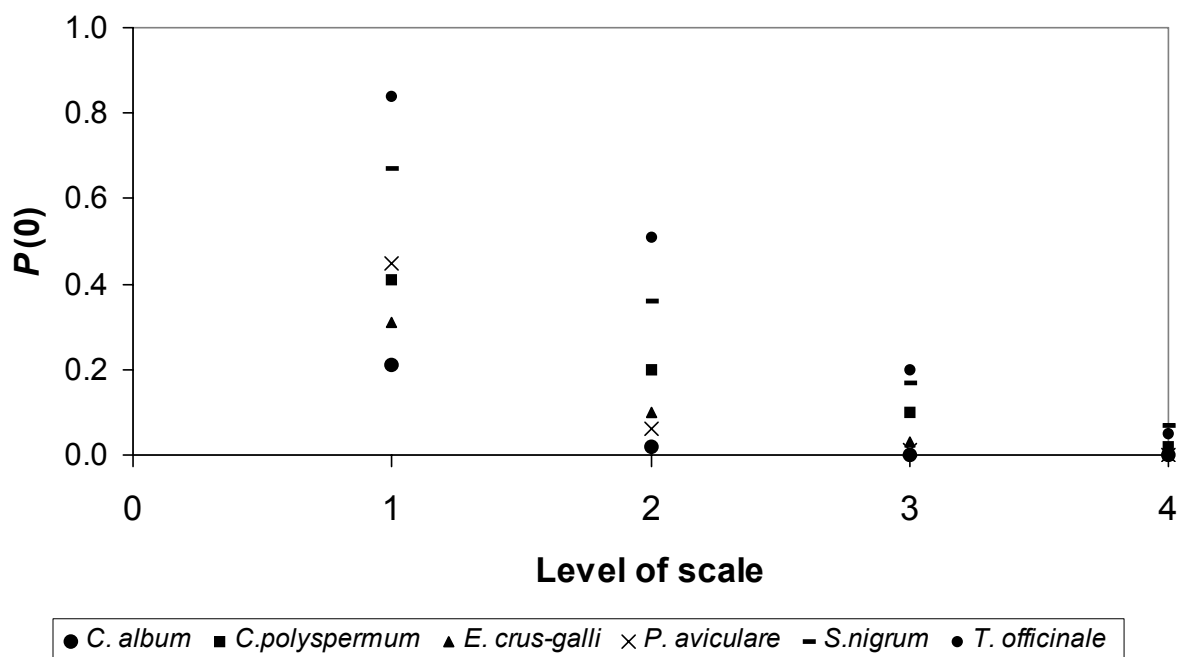
Figure 5. Fraction weed-free area ($P(0)$) as a function of scale for six weeds species on Kortenoord II 2001.

though no clear groups of weeds emerged from the significances found. This was probably caused by the limited number of variance/mean pairs in the regression analysis of some species. Species specific values for the two parameters of TPL were not found in other studies on weed plants (Berti *et al.*, 1992; Clark *et al.*, 1996) or weed seeds. Berti *et al.* (1992) reported that although in the overall regression no species specificity could be traced, some weed species emerged as locally significant weed species. It will be interesting to know if species specificity will filter out if weed counts have been gained under a very wide range of circumstances. The importance of extensive data for species specificity was been pointed out (Taylor *et al.*, 1988) as it will be difficult, if not impossible to keep conditions equal if various locations are examined.

The values we found for parameter *b* [0.78–1.95] coincided largely with the range indicated by Taylor *et al.* (1978) for plant species [0.82–1.48]. As Clark *et al.* (1996) pointed out, the range is expected to grow with an increasing number of plant species examined. *E. crus-galli* had the steepest slope of TPL (1.95). Volunteer potato (*S. tuberosum*) was the only species in our study with a slope < 1 (0.78) which most likely reflects the regular pattern in which the potatoes were planted in previous years. All other weed species in this study had slopes above 1.18, indicating some form of spatial aggregation. Wiles *et al.* (1992) mentioned that possible savings will depend on the spatial configuration of the weeds. Less advanced technological equipment is needed in the field if weeds are strongly positively correlated and have spatially aggregated patterns.

Besides species, data set as a factor had a slight but significant effect on the parameter outcome of Taylor's power law. Each data set comprised a combination of geographic location, field history, soil type, quadrat size and number, time of observation and crop, and any (combination of) these factors could have contributed to differences in TPL parameters. All these are known to affect the results found when fitting TPL. Berti *et al.* (1992) found that crop type, winter versus summer, significantly affected the outcomes of the parameter values. Mulugeta & Boerboom (1999) showed that differences in spatial aggregation existed between cohorts of the same weed population and these differences were reflected in parameter values of TPL.

The least good prediction of weed-free fraction, as indicated by $R^2_{predicted}$, was obtained for the two grass weed species that occurred in the data sets. A possible reason could be that with counting grass-weed plants it is more difficult to distinguish between individuals than for dicot weeds, which results in more inaccurate counts.

Besides its application to calculate weed-free area, knowledge on parameters of TPL for weeds can help for modelling on crop yield loss by weed densities (Clark *et al.*, 1996), and weed sampling programmes (Berti *et al.*, 1992; Dessaint *et al.*, 1996).

Furthermore, relations between environmental covariates and spatial patterns of organisms can be examined using TPL as was shown for insect larvae and organic matter by Dalthorp (2004). This approach was recently successfully applied to weed spatial patterns and soil characteristics (Heijting *et al*., 2005).

CONCLUSIONS

The weed-free fraction can be modelled by linking a model for the spatial variance with a model for the frequency distribution of weed counts, i.c. Taylor's power law (TPL), and the Negative Binomial Distribution. Predominant weed species throughout the spatial implicit data sets were *C. album*, *P. annua*, *P. persicaria*, *S. media* and *S. nigrum*. The weed-free fraction of the total weed population was approximately between zero and 0.1.

Using the general model of Taylor's power law to predict weed-free fraction gave similar results as the species specific models for the majority of the fourteen weed species examined here. The results show that the proposed model provides a valid tool for predicting occupancy in weeds.

Orientation of quadrats affected the total weed-free area at the lowest level of aggregation. This was caused by a stronger correlation in-row direction than cross-row. Clustering quadrats to higher scale levels resulted in a quick decrease in weed-free area.

Appendix 1

Summary statistics for 32 data sets. Mean, variance, minimum, maximum are expressed in number per quadrat. $P(0)$observed indicates fraction of empty quadrats of total number of quadrats. Rare weed species are omitted.

Data set	Weed species	mean	variance	min.	max.	$P(0)$observed
AGV2347	*C. bursa-pastoris*	0.19	0.33	0	3	0.88
	Matricaria spp.	0.15	0.17	0	2	0.88
	P. annua	0.46	0.55	0	3	0.67
	S. vulgaris	7.25	36.23	0	32	0.06
	S. nigrum	0.56	2.51	0	10	0.77
	S. tuberosum	0.27	0.33	0	2	0.79
	S. media	2.75	7.30	0	10	0.17
	Total weeds	11.63	42.96	0	34	0.04
AGV3302	*C. album*	0.18	0.20	0	2	0.85
	C. rubrum	0.65	0.85	0	3	0.58
	Matricaria spp.	0.08	0.07	0	1	0.93
	P. annua	0.60	1.78	0	6	0.75
	S. vulgaris	0.05	0.05	0	1	0.95
	S. nigrum	0.10	0.14	0	2	0.93
	S. tuberosum	0.70	1.19	0	4	0.58
	S. media	1.10	1.84	0	5	0.50
	Total weeds	3.45	5.28	0	11	0.08
AGV3352	*C. bursa-pastoris*	0.76	1.64	0	6	0.61
	C. album	0.04	0.03	0	1	0.96
	C. rubrum	0.87	2.19	0	9	0.59
	P. annua	4.21	9.32	0	14	0.12
	Sonchus spp.	0.21	0.37	0	4	0.85
	S. tuberosum	0.37	1.10	0	5	0.86
	S. media	1.79	3.82	0	9	0.36
	Total weeds	8.24	26.98	0	22	0.04
AGV4050	*C. album*	0.01	0.01	0	1	0.99
	C. rubrum	0.11	0.10	0	1	0.89
	C. bursa-pastoris	1.96	6.81	0	12	0.38
	P. annua	2.09	7.45	0	16	0.30
	P. aviculare	0.07	0.08	0	2	0.94
	P. persicaria	0.02	0.02	0	1	0.98
	S. vulgaris	0.01	0.01	0	1	0.99
	Sonchus spp.	0.41	0.57	0	4	0.71
	S. nigrum	0.03	0.03	0	1	0.97
	S. tuberosum	0.09	0.23	0	4	0.95
	S. media	1.95	2.74	0	8	0.18
	Total weeds	6.75	14.05	0	19	0.01

Data set	Weed species	mean	variance	min.	max.	$P(0)$observed
AGV4051	*C. album*	0.05	0.04	0	1	0.95
	C. rubrum	1.41	2.54	0	6	0.36
	C. bursa-pastoris	1.37	3.41	0	9	0.38
	P. annua	4.06	20.57	0	23	0.15
	P. aviculare	2.36	32.53	0	34	0.51
	P. persicaria	0.08	0.23	0	4	0.96
	Matricaria spp.	1.09	2.61	0	10	0.45
	S. vulgaris	0.32	0.67	0	5	0.81
	Sonchus spp.	1.85	4.89	0	16	0.27
	S. nigrum	0.73	0.98	0	4	0.52
	S. tuberosum	0.92	1.20	0	5	0.44
	S. media	20.18	54.97	5	43	0.00
	Total weeds	34.43	140.43	19	71	0.00
met1	*C. album*	0.45	3.27	0	10	0.89
	P. annua	1.09	2.05	0	6	0.46
	S. media	0.75	1.35	0	5	0.61
	Total weeds	2.29	4.86	0	11	0.16
met2	*C. album*	0.45	1.05	0	5	0.73
	P. persicaria	0.55	0.98	0	5	0.66
	P. annua	9.20	46.63	0	29	0.04
	S. vulgaris	0.05	0.05	0	1	0.95
	S. media	0.64	0.49	0	3	0.46
	Total weeds	10.89	47.92	1	29	0.00
KP480P1A	*C. album*	10.19	168.16	0	54	0.17
	P. persicaria	9.75	54.31	1	40	0.00
	Total weeds	19.94	209.77	2	65	0.00
KP480P1B	*C. album*	12.42	199.62	0	66	0.06
	P. persicaria	15.03	62.66	1	43	0.00
	Total weeds	27.44	227.51	5	77	0.00
KP480P2A	*C. album*	15.06	161.00	1	52	0.00
	P. persicaria	16.37	52.36	8	42	0.00
	Total weeds	31.43	184.25	12	67	0.00
KP480P2B	*C. album*	9.54	35.44	5	27	0.00
	P. persicaria	10.15	20.64	3	20	0.00
	Total weeds	19.69	78.23	13	47	0.00
KP481P1A	*C. album*	33.53	806.42	2	157	0.00
	P. persicaria	14.48	242.42	0	89	0.01
	Total weeds	48.01	1264.27	5	198	0.00
KP481P2A	*C. album*	24.31	277.60	1	85	0.00
	P. persicaria	15.79	111.29	0	49	0.01
	Total weeds	40.10	411.31	11	103	0.00
KP481P1B	*C. album*	46.62	2513.83	3	414	0.00
	P. persicaria	21.06	471.82	0	128	0.01
	Total weeds	67.69	3342.69	5	458	0.00
KP481P2B	*C. album*	16.09	166.54	1	60	0.00
	P. persicaria	9.44	13.61	3	18	0.00
	Total weeds	25.53	156.19	11	69	0.00

Data set	Weed species	mean	variance	min.	max.	$P(0)$observed
KP500P1A	*C. album*	32.00	416.23	6	85	0.00
	P. persicaria	13.08	225.11	1	53	0.00
	S. media	7.75	98.25	0	43	0.19
	Total weeds	52.83	743.80	13	118	0.00
KP500P1B	*C. album*	31.40	516.13	9	95	0.00
	P. persicaria	13.80	329.87	1	93	0.00
	S. media	11.66	193.41	0	59	0.17
	Total weeds	56.86	884.36	11	117	0.00
KP500P2A	*C. album*	35.31	438.16	9	96	0.00
	P. persicaria	12.61	119.62	0	33	0.06
	S.vulgaris	0.42	0.99	0	5	0.78
	S. media	33.36	5059.21	0	430	0.03
	Total weeds	81.69	5497.76	24	469	0.00
KP500P2B	*C. album*	27.31	297.63	4	84	0.00
	P. persicaria	11.06	116.11	0	51	0.03
	S. vulgaris	0.09	0.14	0	2	0.94
	S. media	29.29	2124.39	1	211	0.00
	Total weeds	67.74	2736.02	17	237	0.00
KPG216	*C. album*	3.06	13.90	0	16	0.33
	C. bursa-pastoris	4.05	77.06	0	54	0.34
	P. annua	2.91	8.56	0	15	0.19
	P. aviculare	0.09	0.12	0	2	0.92
	P. persicaria	3.45	16.51	0	25	0.22
	S. media	0.31	0.50	0	3	0.80
	Total weeds	13.88	132.68	2	58	0.00
PAV3058	*C. bursa-pastoris*	0.37	0.83	0	5	0.79
	Matricaria spp.	0.09	0.20	0	3	0.96
	S. nigrum	4.82	17.79	0	21	0.16
	Sonchus spp.	0.22	0.23	0	2	0.81
	S. media	0.63	1.04	0	4	0.66
	Total weeds	6.13	20.33	0	21	0.06
PAGV4151AF	*C. album*	2.81	11.63	0	11	0.44
	E. crus-galli	35.75	2713.67	0	170	0.19
	P. annua	8.06	226.20	0	60	0.38
	P. convolvulus	0.44	2.26	0	6	0.88
	P. persicaria	2.50	13.73	0	11	0.50
	S. nigrum	77.06	7020.46	0	210	0.31
	Total weeds	126.63	17308.78	0	361	0.06
PAGV4151BC	*C. album*	0.94	2.46	0	6	0.56
	E. crus-galli	20.50	1246.80	0	128	0.25
	P. annua	3.13	10.25	0	10	0.38
	P. persicaria	1.44	6.26	0	9.00	0.56
	S. nigrum	18.31	405.56	2	85	0.00
	Total weeds	44.31	1902.50	6	137	0.00
PAGV4151DE	*C. album*	2.81	13.36	0	12	0.44
	E. crus-galli	78.19	10194.03	0	320	0.06
	P. annua	10.63	123.85	0	40	0.25

Data set	Weed species	mean	variance	min.	max.	*P*(0)observed
PAGV4151DE	*P. convolvulus*	0.63	2.38	0	6	0.75
	P. persicaria	2.00	9.60	0	10	0.50
	S. nigrum	112.00	2089.47	37	185	0.00
	Total weeds	206.25	9891.13	85	399	0.00
PAGV4152AF	*C. album*	24.75	111.00	6	39	0.00
	P. annua	14.63	132.38	3	38	0.00
	S. media	10.88	153.45	1	47	0.00
	Total weeds	50.25	372.73	25	78	0.00
PAGV4152BC	*C. album*	4.56	17.33	0	12	0.06
	P. annua	1.56	14.00	0	15	0.63
	Total weeds	6.13	44.78	0	23	0.06
PAGV4152DE	*C. album*	19.88	212.38	4	56	0.00
	P.annua	13.06	239.80	0	40	0.38
	S. media	1.31	4.76	0	6	0.63
	Total weeds	34.25	816.20	4	86	0.00
REG3109	*C. bursa-pastoris*	0.85	3.91	0	11	0.71
	C. album	10.15	54.72	1	26	0.00
	E. crus-galli	1.58	7.01	0	15	0.44
	P. annua	38.08	849.01	11	154	0.00
	P. persicaria	0.92	1.65	0	5	0.54
	S. nigrum	34.77	408.90	5	89	0.00
	S. media	15.50	71.83	3	37	0.00
	Total weeds	101.85	957.66	40	200	0.00
VP1008	*C. bursa-pastoris*	0.04	0.06	0	2	0.97
	C. album	0.43	0.94	0	6	0.74
	E. crus-galli	3.52	24.17	0	26	0.28
	P. annua	13.43	148.00	0	65	0.10
	P. aviculare	0.58	1.61	0	8	0.73
	P. convolvulus	0.13	0.35	0	4	0.95
	P. persicaria	9.69	148.42	0	63	0.14
	S. vulgaris	0.02	0.02	0	1	0.98
	S. nigrum	0.58	1.54	0	8	0.69
	S. media	41.11	947.93	4	195	0.00
	Total weeds	69.51	1481.45	18	269	0.00
VP1023A	*C. album*	4.11	26.84	0	24	0.24
	P. annua	15.95	293.97	0	69	0.15
	S. media	14.54	217.44	0	75	0.08
	Total weeds	34.60	752.47	2	143	0.00
VP1023B	*C. album*	1.23	4.00	0	9	0.59
	P. annua	25.59	227.33	3	68	0.00
	S. media	5.38	12.97	0	17	0.04
	Total weeds	32.19	257.77	8	81	0.00
ZW2369	*C. album*	0.35	0.44	0	3	0.73
	P. persicaria	2.73	3.33	0	8	0.15
	P. convolvulus	0.03	0.03	0	1	0.98
	Matricaria spp.	0.18	0.35	0	3	0.90
	Total weeds	3.28	3.03	0	8	0.05

Appendix 2

Species specific values of parameters b *and* $^{10}\log(a)$ for the model $^{10}\log(\text{variance}) = b \times {}^{10}\log(\text{mean}) + {}^{10}\log(a)$, their s.e. and significances ($P < 0.05$).

Weed species	sign for b (0.05)	b	s.e.	sign for a (0.05)	$^{10}\log(a)$	s.e.
E. crus-galli	ab	1.95	0.09	abcdefghi	0.37	0.07
S. media	ab	1.67	0.13	e ghi	0.19	0.12
P. aviculare	abc e	1.67	0.15	abcd	0.78	0.12
P. annua	abc e	1.59	0.12	b efghi	0.32	0.10
P. convolvulus	abcdef	1.50	0.11	abcdefghi	0.85	0.11
C. album	bcde	1.40	0.03	abcd i	0.60	0.04
S. nigrum	bcde	1.39	0.07	bcdefgh	0.49	0.08
C. bursa-pastoris	bcde	1.36	0.13	abcd fgh	0.53	0.09
P. persicaria	bcde	1.36	0.07	abcd f h	0.57	0.07
C. rubrum	abcdef	1.34	0.14	b efghi	0.29	0.08
Sonchus spp.	abcdef	1.29	0.15	b defghi	0.32	0.07
S. vulgaris	cdef	1.24	0.03	abcdefghi	0.43	0.05
Matricaria spp.	bcdef	1.18	0.15	abcdefghi	0.37	0.12
S. tuberosum	def	0.78	0.20	efghi	0.19	0.12

CHAPTER 7

General discussion

INTRODUCTION

The main objective of the research, described in this thesis, was to obtain insight in spatial and temporal behaviour of weed patterns in arable fields. In Chapter 2, spatial aggregation and scale in weed patterns were investigated using Mead's test. In Chapter 3, 2-D correlograms were used to characterize spatial and spatio-temporal correlations in weed patterns. Relations between heterogeneity of soil properties and weed patterns were examined in Chapter 4. Chapter 5 addressed the effect of timing of seed shed on the dispersal of seeds by machinery used for harvest and tillage. Chapter 6 developed a method for predicting weed occupancy in a field, based on average weed density.

Here, the results presented in this thesis are reviewed and discussed. Strong points and possible short comings of the methodological approaches are discussed and avenues for further research are indicated. The issues are addressed in the following sections: *Methodology*, *characteristics of patterns* and *Causes of patterns*. In addition the consequences of our findings for site-specific weed control are discussed in a section *Implications for practice*. At the end of this chapter *Main conclusions* are drawn.

METHODOLOGY

Observation methods

Two approaches were used for collecting information on weed spatial distribution: spatially explicit maps obtained by monitoring weeds in contiguous quadrats (Chapters 2–5) and spatially implicit weed count data gathered by random quadrat counts (Chapter 6). Both types of data were gathered by direct observation.

The spatially explicit method allows a more elaborate analysis of characteristics than the spatially implicit method (Figure 1), but is also more labor intensive. We used contiguous quadrats to monitor weed patterns throughout subsequent years (Chapters 2 and 3) and this method was also applied to map dispersal of plants by machinery at the field scale (Chapter 5). Thus, it was ensured that all plants present in the defined area were counted. To avoid the presence of a time effect in the spatial pattern, all data was gathered within a few days.

The case study on weed spatio-temporal behaviour of weeds covered three years of observations on part of the Kortenoord II field near Wageningen. Similar case studies

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Observations on Spatial Patterns

Spatially explicit
Maps throughout years

Characterize:
• Mean density & variance
• Aggregation
• Occupancy
• Frequency distribution
• Spatial autocorrelation*
• Direction*
• Patch stability*
• Scale*

Spatially implicit
Random quadrat counts

Characterize:
• Mean density & variance
• Aggregation
• Occupancy
• Frequency distribution

Figure 1. Overview of aspects of observations and analysis of weed spatial patterns. Characteristics indicated with * are unique to spatially explicit data.

in which an area is mapped by counting in contiguous quadrats are scarce in weed science and this study therefore added substantial data on weed spatio-temporal patterns to the already existing datasets. The two other datasets are a multiple year observation on weed patterns of fourteen weed species in a crop rotation field in Australia by Cousens *et al*. (2002, 2004, 2006) and the spatial pattern of a single weed species (*Abutilon theophrasti*) in various year in continuous corn (Dieleman & Mortensen, 1999).

Ideally, individual locations of weed plants are determined to map weeds as this excludes possible effects of size of observation quadrats on weed patterns found (Bellehumeur *et al.*, 1997; Rew & Cousens, 2001). At present only two such data sets are known, both on the weed *Galium aparine* (Wallinga, 1995; Hamouz *et al*., 2007). Current developments on automated weed detection (Gerhards & Oebel, 2006) for precision weed management offer scope for an efficient gathering of data for the analysis of weed patterns.

Analysis

Depending on the research question and the quality of the data, different techniques were applied to determine the characteristics of weed patterns (Table 1). The weed patterns mapped on Kortenoord II were characterized using a number of techniques

Table 1. Relations between characteristics of spatial patterns and methodology.

Characteristics	Correlograms	Frequency distribution	Mead's test	Moran's *I*	Taylor's power law
Mean density and Variance	-/+	+	-	-	+
Aggregation	+	+	+	+	+
Occupancy	-	+	-	-	+
Spatial autocorrelation	+	-	-	+	-
Direction	+	-	+	+	-
Patch stability	+	-	-	-	-
Scale	+	-	+	-	-

(Chapters 2 and 3). In a first step (Chapter 2), Mead's test was used to categorize the patterns as random, aggregated or regular. Artificial patterns were studied to illustrate the result of Mead's test in certain standard situations. Mead's test proved to be a flexible tool for studying and characterizing weed patterns at various scales and various directions. In the same chapter Moran's *I* was used for comparison, describing autocorrelation of weed patterns in the two main directions. In Chapter 3, the 2-D correlograms were applied to study behaviour of 15 weed species groups both within and between years.

As some of the weed species patterns of Chapter 2 were also studied in Chapter 3, comparisons between the three techniques used (Mead's test, 2-D correlograms and Moran's *I*) can be made. Compared to Mead's test, 2-D correlograms greatly facilitated interpretation of weed pattern characteristics. The 2-D correlograms allowed inspecting spatial autocorrelation of patterns in all possible directions simultaneously. Mead's test, as implemented, is less flexible with respect to studying directions. However, it might be possible to further develop Mead's test to take account of patterns in which the axis of greatest correlation according to a null or alternative hypothesis is slanted with respect to the direction of field traffic. Studying the presence of directionality in patterns with Moran's *I* was limited to the two main directions, although in theory a further division of directions is possible until it resembles a 2-D correlogram. While Moran's *I* and Mead's test were calculated using actual weed count data, 2-D correlograms were applied by ranking the count data.

The three techniques were complementary as they represent different ways of looking at patterns but overall similar features of species patterns emerged. Species that showed strong aggregation in one test also did when analysed with another test.

Species which exhibited a random pattern, such as *T. officinale*, were categorized as such by all three techniques. But the nature of some lower density species emerged differently. The pattern of *P. aviculare*, for instance, showed significant aggregation and anisotropy when tested with Mead's test over several levels of scales, and weak spatial correlation when studied with the 2-D correlogram, but no spatial correlation when examined with Moran's *I*. It was discussed (Chapter 3) that low plant densities may affect detection of spatial correlation as a result of an increasing relative error in the data.

The effect of scale on weed patterns was examined both with Mead's test and with 2-D correlograms. Different levels of scale were obtained by merging smaller units into larger units, all within the observed area of 12 m × 50.25 m. Both in Chapters 2 and 3, scale of observation affected the outcome of the analysis. For example, the correlogram of the spatial pattern of *C. polyspermum* showed no spatial auto-correlation when units four time the unit of observation were used. On the other hand, for *P. annua*, a spatial correlated pattern emerged when resolution was decreased.

The effect of resolution on the occupancy of weeds on Kortenoord II in 2001 was analysed in Chapter 6. Occupancy quickly increased with the size of units.

CHARACTERISTICS OF PATTERNS

Patterns were monitored on Kortenoord II at a relatively small scale showing great differences between characteristics of weed patterns. Weed mapping in some other studies on weed patterns were done by sampling quadrats at interspersed distances that were greater than our entire study plot (Medlin *et al*., 2001; Wyse-Pester *et al*., 2002). Given the fact that within our plot, patchiness was present, the use of such a coarse schedule would have missed patterns in the field Kortenoord II, confirming a cautionary statement of Rew & Cousens (2001).

The presence of high peak densities appeared to be restricted to patterns of four weed species that showed the strongest spatial correlation. Most weed species exhibited only weak or no correlation at all.

It is important to keep in mind that these results only apply to Kortenoord II data. In another context, other weed species are likely to dominate. This was shown by the results of Chapter 6. The analysis of the spatially implicit weed counts in that Chapter showed that 14 out of 13 weed species examined showed aggregation at the quadrat level as parameter *b* of TPL was well above 1. A value of parameter *b* > 1 indicates patchiness at the level of the observation quadrat (Clark *et al*., 1996). Some of those weed species groups were classified as non-patchy in Chapter 3 (*C. bursa-pastoris*, *P. annua*, *S. vulgaris*, *Sonchus* spp. and *S. media*). A general model based on all weed species data predicted the percentage of empty quadrats well for most of these weed

species. This is surprising if one considers the differences in spatial autocorrelation between the weed species as observed on Kortenoord II. For a few weed species such as the grass weeds *E. crus-galli* and *P. annua* the general model for weed occupancy failed and the species specific relation between mean density and variance was needed to obtain a good prediction (Chapter 6).

Some weed species patterns showed anisotropy (Chapters 2, 3). Elongation of weed patterns in the driving direction of field traffic has often been found (e.g. Rew *et al.*, 1996a; Johnson *et al.*, 1996b; Dieleman & Mortensen, 1999; Colbach *et al.*, 2000) and seems common. Experiments on dispersal of weed seeds (Marshall & Brain, 1999; Chapter 5) indicate that this elongation is probably related to the much greater within-row than cross-row dispersal of weed propagules.

Only a few weed species displayed stable patch location. One weed species, *E. crus-galli*, seemed to shift from year to year.

CAUSES OF PATTERNS

Chapters 2, 3, 4 and 6 use observational data in unmanipulated field trials, resulting in a characterization of phenomena occurring in real fields, and generation of hypotheses. Chapter 5 uses a manipulative, experimental approach, using various non-weedy plants as 'model weeds' to investigate causes of patterns. Model plants shedding their seeds during harvest managed to disperse further in the driving direction than species shedding their seeds before harvest. This is the first field experiment in which the effect of the two contrasting release methods of ripe seeds (i.e. on soil vs. on plant) on dispersal by machinery was directly compared. Other field studies examining dispersal by machinery around harvest were restricted to a single species which had shed none of its seeds, such as *Lolium rigidum* (Blanco-Moreno *et al.*, 2004), or nearly all of its seeds, such as for example *Avena* spp. (Barroso *et al.*, 2006). The only study in which different weed species were compared was a model study by Woolcock & Cousens (2000). The model predicted a 16 fold increase in rate of spread of an annual weed if its seeds were taken up by the cereal harvest combiner.

Harvest equipment varies greatly between cropping systems. At the extremes are harvest machines that emit straw back to the field and machines which do not emit any plant material. Such differences will affect weed dispersal. The results of the studies described in this thesis showed that the tillage equipment used after harvest can also be of great importance as the use of cultivator after harvesting significantly increased distance travelled in the driving direction for species with ripe seeds at the time of harvest (Chapter 5).

Possible factors affecting the spatial distribution of seeds, seedlings and weed plants are presented in Figure 2. The complexity of the possible defining factors and their

interactions obstruct disentangling their contributions (Wiles & Brodahl, 2004). The added value of descriptive, empirical studies lies in the generation of hypotheses about possible processes governing the spatial dynamics of weed species (Cousens *et al.*, 2006). In an experimental set up or model this can then subsequently be tested. Model approaches such as performed by Woolcock & Cousens (2000) and Wallinga *et al.* (2002) elucidated the possible effect of some of the key processes on weed spatial and temporal behaviour. Thus, descriptive studies, experimental tests of hypotheses, and modelling studies, showing emerging properties of systems, all shed their own light on the complex world of weeds and may help to elucidate what causes patterns and help explain why patterns of weeds in farmers' field look how they look.

Wallinga *et al.* (2002) showed that localized seed shed of an annual weed controlled by herbicide application resulted in patch formation in a homogeneous environment. Density patterns of patchy weed species on Kortenoord II had relations with underlying soil properties. Several of the annual weed species on Kortenoord II did not show spatial aggregation and had no relation with underlying soil properties. Modelling studies that study the spread of weeds in spatially homogeneous and heterogeneous environments can help elucidate the role of soil heterogeneity in the causation of patterns in weeds.
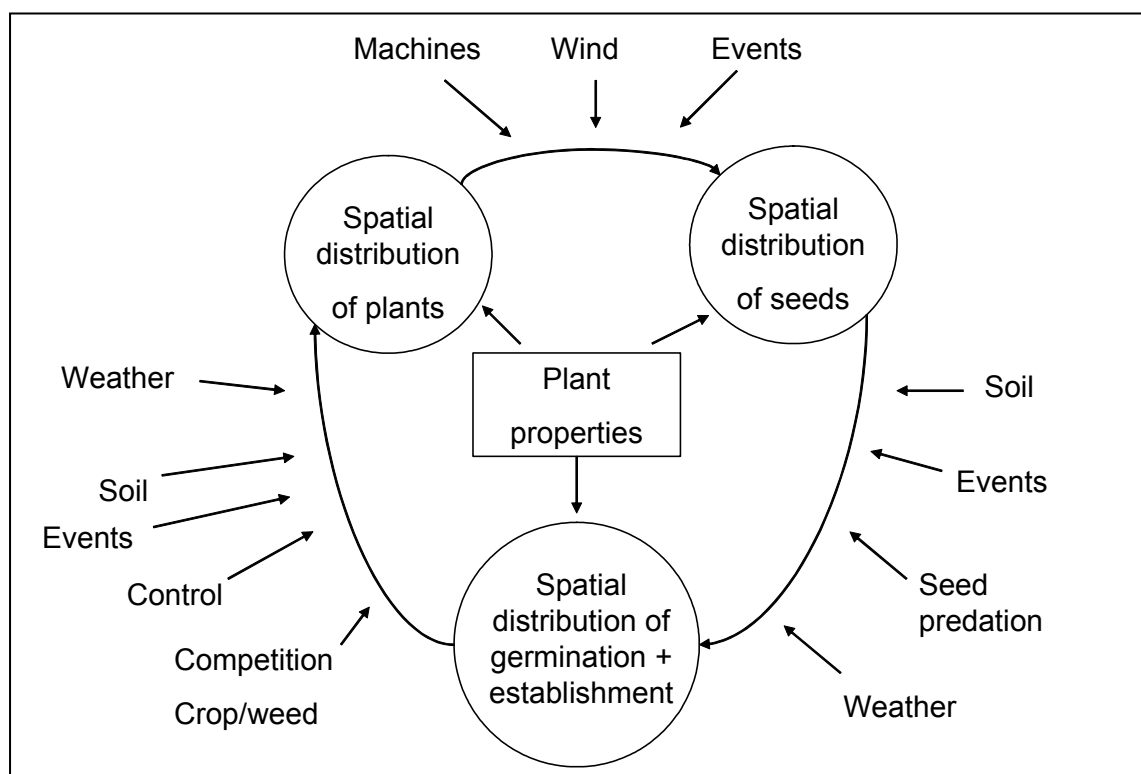

Figure 2. Causes of weed spatial distribution related to their influence on the various stages of the life cycle of weeds.

The visualized dispersal patterns and their cumulative frequency distributions (Chapter 5) displayed some irregularities in the tail. This may be important for establishment of new patches far from the source patch. This can be done in a model study or a field experiment. Questions such as: "Will clumps in the tail of the dispersal function result in new weed patches?" can be answered.

The role of events can be studied by querying farmers about the possible causes of weed patches on their land. For example, a patch forming event such as clogging of a spray nozzle may have taken place on a field and is still reflected in the weed pattern years after. Little has been done so far with knowledge of farmer's on patch forming events and historic land use. As was discussed in Chapter 3, knowledge on historic land use can facilitate the understanding of weed spatial dynamics.

The extent to which pattern forming processes and weed ecology affect weed spatial patterns could also be studied by combining information on the various components from different fields. Wiles & Brodahl (2004) used Classification and Regression tree analysis (CART) to compare and examine weed spatial distributions in eight irrigated corn fields. In this way, correlations between characteristics of the spatial distribution of seed banks, demographic aspects of species, features of the field and historic management were looked at simultaneously.

IMPLICATIONS FOR PRACTICE

Farmers become increasingly interested in using spatial information about their farm. More and more farmers use GPS when managing their fields. Examples of areas which receive much attention are the fine tuning of fertilizer application to the actual needs of the crop and local soil situation (see for example Godwin *et al.*, 2003).

On Kortenoord II, only a few weed species occurred at high densities which coincided with their patchy pattern. Most weed species in the observation area did not show strong spatial correlation. Each field appears to have its own patchy weed species and the cropping system will act as a filter. Spring sown crops will have a different weed community than crops sown in late spring or autumn. Continuous maize was grown on Kortenoord II during the course of the study and indeed weed species associated with continuous maize cropping such as *C. album*, *E. crus-galli* and *S. nigrum* were abundantly present on Kortenoord II. It is advisable for practice to ensure effective control of weed species that synchronize their life cycle with the crop to avoid dispersal of plant and seed material throughout the field (Chapter 5).

Judging from the results on stability of weed patterns (Chapter 3) and their relations with underlying soil properties (Chapter 4), prediction of weed patches appears promising but will possibly be restricted to a few patchy weed species in each field.

Reductions obtained in herbicide usage by targeting weed species site-specifically

will increase with increasing spatial resolution. At the level of observation (0.75 m × 0.75 m) a substantial reduction will be achieved, but savings at coarser resolutions will be too small to consider site-specific application of herbicides (Chapter 6).

The relation between TPL and the frequency distribution of weeds in quadrats, as examined in Chapter 6, lead to a simple model that allows evaluation of the weed free fraction of the field and the scope for site-specific control.

An element which has not been studied in this thesis but will be important for calculating the potential savings that can be achieved with site-specific management are associations between the patterns of different weed species. Site-specific management will be facilitated if weed species needing the same herbicide component co-occur in the same place. Control thresholds are another factor that influences the potential reductions.

With advancing technology, weeds may be recognized and controlled real-time. The major hurdle for implementing such techniques are the relatively high costs associated with it and the likely low resolution (down to plant level) that will likely be needed to reach substantial savings (S. Christensen; pers. communication). High costs, and – at least initially – a slow working speed of machinery that meets the required spatial resolution, will hamper uptake of technology by farmers. Therefore, weed ecologists may – at least initially – benefit more from technological advances in automated weed recognition than farmers.

MAIN CONCLUSIONS

Extensive data on weed count data were presented and analysed revealing various features of weed spatio-temporal behaviour. The main conclusions from this study, thus, are:

- Weed species with spatially aggregated patterns showed the highest densities.
- Two of the four weed species which attained high weed densities were persistent in location in time.
- Using 2-D correlograms facilitated interpretation of weed spatial dynamics.
- Variation in weed density was related to heterogeneity of soil properties and relations found were of moderate strength, but a substantial part of the spatial correlation in weeds was not explained by soil factors, and is probably due to autonomous processes in the weed population that operate in homogeneous environments as well as heterogeneous environments.
- The first study on the effect of weed biology on dispersal by harvest and rigid-tine cultivator showed that seeds can disperse very far as the dispersal kernels have

long tails. Dragging of plant material caused occurrence of clumps in some tails which may lead to establishment of new patches.

- Calculations showed that if too coarse a resolution is used, site-specific application of herbicides does not pay off.
- A model for predicting weed occupancy at quadrat level, based on average weed density, gave good predictions for most weed species.

Much remains to be done before weed ecologists can claim that weed patterns are fully understood. If weeds spread so well, as shown in Chapter 5, why are weeds patchy? Are these patches just a transient state, preceding occupancy of the whole field at high densities, or are they a stable state, representing equilibrium between recruitment and losses? Such equilibrium seems only possible if positive feedback mechanisms foster patch viability, while dispersal outside patches does not lead to establishment due to lack of sufficient survival or reproduction, i.e. a spatial Allee-effect. The presence of an Allee effect has recently been the objective of studies on spread of invasive plant species (for example, Cappuccino, 2004). Such effects have not been studied in a spatial context on a field or farm scale level for plant or weedy species. Evidence for positive density dependence has been reported for soil applied herbicides (for overview see Dieleman *et al.*, 1999) but such curvilinear relations could not be established for foliar applied herbicides (Dieleman *et al.*, 1999). Patterns observed in this thesis did not suggest density dependence of herbicide effects. Some evidence was obtained for patch *in*stability; the patches of *Echinochloa crus-galli*, the most successful weed in the experimental field Kortenoord II, was not stable in location. Also evidence was obtained for the presence of historical phenomena; the elongated patch of *Chenopodium polyspermum* may well have been a relict of leveling of the field in historic times, using soil (with plant propagules and associated soil factors) from elsewhere. It thus seems likely that any observed pattern in weeds could be due to a complex of causal factors, one more and another less important, but that can not be easily disentangled. This may, therefore, not be the last thesis on spatial ecology of weeds. Issues that are deserving of future work are (*i*) involving the farmers in a historically informed analysis of weed spatial patterns; (*ii*) a further search for positive density dependence as a factor shaping patchiness.

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Summary

Weeds in agriculture occur in patches. This thesis is a contribution to the characterization of this patchiness, to its analysis, and to prediction, and some of its results may be useful for weed management. Chapter 1, the introduction, presents the objectives of the work. The Chapters 2 through 4 try to answer ecological questions about weed patterns, and they use innovative statistics and a new and extensive spatially explicit data set on weed patterns in a maize plot over three years, to answer those questions. Chapter 2 develops a statistical test for pattern and applies it to artificial and real weed data. Chapter 3 develops the use of two-dimensional (2-D) correlograms to explore the spatial stability of patches through time. Chapter 4 looks at the relationship between patchiness in weeds and spatial heterogeneity in soil. In Chapter 5, measurements of the dispersal of weeds by machinery are presented. Chapter 6 analyses data on weed occurrence, collected in different fields over a range of years, to try and establish a predictive model for weed spatial occupancy in a field, based upon the mean density. A general discussion (Chapter 7) caps the work.

In Chapter 2, spatial patterns of six weed species are characterized, using Mead's test. The implementation of the test has a null hypothesis, the pattern is spatially random, and two alternatives: a regular pattern or an aggregated pattern. The test is conducted at various scales and with different shapes of basic units, in relation to the row direction of the field. To illustrate the functioning of Mead's test and facilitate interpretation, six artificial patterns were tested. Next, observed patterns of six weed species were subjected to Mead's test. These patterns had been collected in a 12 m by 50.25 m field plot in three years continuous maize cultivation. Weed counts were made using a 16×67 grid of contiguous quadrats, each measuring 0.75 m by 0.75 m. Five of the six analysed weed species showed aggregation at several levels of scale. The only wind dispersing species, *Taraxacum officinale* was random at all scales.

In Chapter 3, weed patterns were studied using 2-D space-time correlograms. Three years of count data on weed spatial patterns collected in contiguous quadrats for 15 weed species and weed species groups were analysed. The within years correlograms demonstrated large differences between weed species groups. Four summer annuals, *C. album*, *C. polyspermum*, *E. crus-galli* and *S. nigrum* were strongly aggregated. They also exhibited the largest incidence and highest maximum weed density of the species studied. Most other weed species showed weak spatial correlation or no correlation at all. Possible explanations for the apparent relationship between weed density and spatial pattern, including a density dependent signal to noise ratio, are discussed. Then, 2-D correlograms were applied to diagnose stability of patterns over

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time. *Chenopodium polyspermum* and *S. nigrum* were stable in location. Patches of one species, *E. crus-galli* appeared to shift from year to year. It is found that 2-D correlograms facilitate the visualization and interpretation of weed spatio-temporal behaviour.

Spatial patterns of the weeds that were analysed in Chapter 3 were further studied in Chapter 4, by analysing the relationship between weed pattern and spatial variability in the soil. Soil variables were selected using Generalized Linear Models with a Poisson log link to account for the non-normality of the weed count data. The four patchy weed species, *C. album*, *C. polyspermum*, *E. crus-galli* and *S. nigrum,* showed consistent relations with soil variables over the three years of study. Their density increased with pH and was related to soil texture or OM. Models with spatially uncorrelated and spatially correlated error terms were compared. Taylor's power law (TPL) was used as a link function. There were modest decreases in model significance (increases in *P*-value) when the spatial correlation in errors was accounted for by the regression model, and in a few cases, there were big differences in model significance, indicating that a model that would not account for spatial correlation in the response variable (which is common in weeds) would give inflated estimates of model significance. Spatial correlation remained in the residuals of the regression, showing that factors other than the selected soil variables contributed to the spatial correlation in the weeds.

Dispersal of weed seeds in fields by machinery was studied in continuous maize in Chapter 5. A range of plant species was used as model weeds. Plants with ripe seeds at harvest time dispersed their seeds further than species whose seeds were on the soil at harvest time. The cultivator significantly contributed to the dispersal in the driving direction, most likely by dragging plant material with seeds through the field. In some instances, seeds were found to have traveled the entire plot length. Irregularities were found in the tail of the dispersal kernels, probably as a result of different machine operation in the headlands and concomitant deposition of plant debris.

In Chapter 6, spatially implicit weed count data collected throughout The Netherlands were analysed using TPL which describes the relation between log(variance) and log(mean). TPL fitted the data well. Species specific models were fitted as well as an overarching "general" model. The general model accurately predicted the weed free fraction of the field for most weed species, but for some species, e.g. *E. crus-galli*, a species specific model was required to achieve adequate accuracy. Further data analysis illustrates that, if weeds are sprayed per species, herbicides can be saved by site-specific application. If all species are considered simultaneously, however, virtually no area on the field is weed free, and only minimal savings are possible. Calculations illustrate that if site-specific weed control is applied at a fine spatial resolution, much herbicide can be saved, but with increasing scale, savings drop drastically.

Samenvatting

Op akkerbouwpercelen komen onkruiden veelal onregelmatig, in plekken, voor. Dit proefschrift levert een bijdrage aan het karakteriseren van deze plekkerigheid, de analyse en voorspelling ervan en enkele resultaten kunnen bruikbaar zijn voor onkruidbeheersing. In Hoofdstuk 1, de algemene introductie, worden de doelstellingen van het werk gepresenteerd. In Hoofdstukken 2 tot en met 4 wordt getracht enkele ecologische vragen over onkruidpatronen te beantwoorden. Hiertoe wordt in deze hoofdstukken vernieuwende statistiek toegepast en uitgebreide ruimtelijk expliciete data sets van onkruidpatronen in maïs gedurende 3 jaar gebruikt. Hoofdstuk 2 ontwikkelt een statistische toets voor ruimtelijk patroon en deze wordt toegepast op kunstmatige en echte onkruiddata. Hoofdstuk 3 ontwikkelt het gebruik van twee-dimensionale correlogrammen om de stabiliteit van onkruidplekken door de tijd heen te bestuderen. Hoofdstuk 4 bekijkt de relatie tussen plekkerigheid van onkruiden en ruimtelijke heterogeniteit van de bodem. Hoofdstuk 5 presenteert metingen aan dispersie van onkruiden door machines. Hoofdstuk 6 analyseert gegevens over het voorkomen van onkruiden. De gegevens zijn verzameld in verschillende percelen en jaren en in dit hoofdstuk wordt getracht een voorspellend model voor het ruimtelijke voorkomen van onkruiden te maken dat gebaseerd is op de gemiddelde dichtheid. De algemene discussie (Hoofdstuk 7) sluit dit proefschrift af.

In Hoofdstuk 2 worden ruimtelijke patronen van zes onkruidsoorten gekarakteriseerd met behulp van de toets van Mead. De implementatie van de toets heeft als nul hypothese dat het patroon willekeurig is en heeft twee alternatieven: een regelmatig en een plekkerig patroon. De toets wordt uitgevoerd op verschillende schaalniveaus en met verschillende vormen van basiseenheid, in relatie tot de rijrichting in het veld. Om de werkwijze van de toets van Mead te illustreren en de interpretatie ervan te vergemakkelijken, worden zes kunstmatige patronen getest. Vervolgens worden zes echte patronen onderworpen aan de toets van Mead. Deze patronen waren verzameld in een stuk van 12 m bij 50.25 m gedurende 3 jaren in een veld met continue maïsteelt. De onkruidtellingen waren in een 16 × 67 grid van continue telvelden van ieder 0.75 m bij 0.75 m waargenomen. Vijf van de zes geanalyseerde onkruiden vertoonden aggregatie op verschillende schaalniveaus. De enige windverspreidende soort, *Taraxacum officinale* had een willekeurig patroon op alle geteste schaalniveaus.

Hoofdstuk 3 verkent onkruidpatronen met behulp van twee-dimensionale ruimte-tijd correlogrammen. Drie jaren van tellingen in continue telveldjes aan ruimtelijke onkruidpatronen van vijftien soorten werden geanalyseerd. Correlogrammen binnen jaren lieten grote verschillen zien tussen de onderzochte onkruidgroepen. De patronen

van de vier zomerannuellen *C. album*, *C. polyspermum*, *E. crus-galli* en *S. nigrum* waren sterk geaggregeerd. Deze soorten hadden tevens de hoogste bezettingsgraad en hoogste maximum onkruiddichtheden van alle soorten die waren bestudeerd. De patronen van de meeste andere soorten waren ruimtelijk zwak tot niet gecorreleerd. Het optreden van een dichtheidafhankelijke ruis als verklaring voor de relatie tussen onkruiddichtheid en ruimtelijk patroon wordt besproken. Vervolgens werden de twee-dimensionale correlogrammen toegepast om stabiliteit van patronen in de tijd te bepalen. De soorten *C. polyspermum* en *S. nigrum* waren stabiel in plaats. De plekken van één soort, *E. crus-galli* leek van jaar tot jaar te verschuiven. Het gebruik van twee-dimensionale correlogrammen vergemakkelijkt de visualisatie en interpretatie van het gedrag van onkruiden in ruimte en tijd.

De ruimtelijke patronen die in Hoofdstuk 3 waren geanalyseerd, werden verder bekeken in Hoofdstuk 4, door de relatie tussen onkruidpatronen en ruimtelijke variatie van bodemfactoren te bepalen. De bodemfactoren werden geanalyseerd door middel van een Generalized Linear Model met een Poisson functie als link om het niet normaal verdeeld zijn van de onkruiddata te verdisconteren. De vier plekkerige onkruiden, *C. album*, *C. polyspermum*, *E. crus-galli* en *S. nigrum* lieten consistente relaties zien met de bodem variabelen gedurende de drie jaren van de studie. De dichtheid van deze soorten nam toe met toenemende pH en was gerelateerd aan een textuur fractie of organisch stof. Modellen met ruimtelijke ongecorreleerde residuen werden vergeleken met modellen met ruimtelijke gecorreleerde residuen. Taylor's power law werd als verbindingsfunctie gebruikt. Er was een bescheiden afname in de significantie van de modellen (toename van de *P* waarde) als er rekening werd gehouden met de ruimtelijke correlatie van de residuen. Voor een paar gevallen waren de verschillen groot, wat aangeeft dat als geen rekening wordt gehouden met de ruimtelijke samenhang van de respons variabele, dit resulteert in een overschatting van de significantie van het model. Er bleef ruimtelijke autocorrelatie over in de residuen wat laat zien dat andere factoren dan de geselecteerde bodemvariabelen een bijdrage leveren aan de ruimtelijke samenhang van onkruidpatronen.

Dispersie van zaden door machines werd in Hoofdstuk 5 bestudeerd. Verschillende planten werden als modelonkruid gebruikt. Planten waarvan de zaden rijp waren tijdens de oogst werden over een grotere afstand verspreid dan soorten waarvan de zaden op de grond lagen tijdens de oogst. De cultivator leverde een significante bijdrage aan dispersie van zaden, waarschijnlijk door middel van versleping van plant materiaal met zaden door het veld. Zaden hadden in sommige gevallen de gehele lengte van de observatie plot afgelegd. Er waren onregelmatigheden in de staart van de dispersie verdeling, waarschijnlijk door andere handelingen van de machines in de kopakker en het laten vallen van plant materiaal.

In Hoofdstuk 6, worden ruimtelijk impliciete onkruidtellingen (verzameld door geheel Nederland), geanalyseerd met behulp van Taylor's power law (TPL) die de relatie tussen logaritme van het gemiddelde en variantie geeft. Zowel soortspecifieke als een algemeen model van TPL geeft een goede beschrijving van deze relatie voor onkruidtellingen. Het algemene model geeft een nauwkeurige voorspelling van de onkruidvrije fractie van een veld voor de meeste soorten, maar voor enkele soorten zoals *E. crus-galli* was een soortspecifiek model nodig om een goede voorspelling te krijgen. Een data-analyse illustreert verder dat als er per soort wordt gespoten, plaatsspecifieke toepassing van herbiciden een reductie in het gebruik geeft. Maar indien alle soorten gelijktijdig worden bespoten, blijft er bijna geen onkruidvrij stuk over in het veld. Berekeningen laten zien dat besparingen van herbiciden door pleksgewijze toepassing drastisch afnemen met een afnemende resolutie.

List of publications of the author

Refereed scientific papers

Heijting, S., Van der Werf, W., Stein, A. & Kropff, M.J. (2007) Are weed patches stable in location? Application of an explicitly two-dimensional methodology. Weed Research 47, 381-395.

Heijting, S., Kruijer, W., Stein, A. & Van der Werf, W. (2007) Testing the spatial significance of weed patterns in arable land using Mead's test. Weed Research 47, 396-405.

Kruijer, W., Stein, A., Schaafsma, W. & Heijting, S. (2007) Analyzing spatial count data, with an application to weed counts. Environmental and Ecological Statistics 14 (in press).

Submitted scientific papers

Heijting, S., Van der Werf, W. & Dalthorp, D. (2007) Does soil spatial heterogeneity explain patchiness in weeds? A regression approach accounting for spatial correlation.

Heijting, S., Van der Werf, W., Kempenaar, C., Withagen, J. & Van der Weide, R. (2007) Predicting the weed-free proportion of the field area with Taylor's power law.

Heijting, S., Van der Werf, W. & Kropff, M.J. (2007) Seed dispersal by forage harvester and rigid-tine cultivator in maize.

Conference papers

Heijting, S., Kropff, M.J., Stein, A. & Van der Werf, W. (2002) Spatial dynamics and site-specific management of weeds. In Proceedings 12th Symposium of the European Weed Research Society 2002, The Netherlands, pp. 400-401.

Heijting, S., Kruijer, W., Van der Werf, W. & Stein, A. (2005) Species specific spatial relations between weed species and soil characteristics. In Proceedings 13th Symposium of the European Weed Research Society 2005, Bari, Italy, CD-ROM.

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Other publications

Van der Weide, R. & Heijting, S. (2006) Eigen onkruid op kopakker. Machines verslepen onkruid over het veld. Loonbedrijf 10, 72-73.

Heijting, S., Van der Werf, W., Stein, A. & Kropff, M.J. (2005) Ruimtelijke dynamiek van onkruiden in continue maïsteelt. Gewasbescherming 36 (6), 272- 273.

Heijting, S., Van der Werf, W., Kempenaar, C., Withagen, J., Van der Weide, R.Y. & Van Evert, F. (2007) De bezettingsgraad van onkruiden op de akker en mogelijkheden voor pleksgewijze toepassing van herbiciden. Gewasbescherming, jaargang 38(3), 124.

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PE&RC PhD Education Certificate

With the educational activities listed below the PhD candidate has complied with the educational requirements set by the C.T. de Wit Graduate School for Production Ecology and Resource Conservation (PE&RC) which comprises of a minimum total of 32 ECTS (= 22 weeks of activities)

The C.T. De Wit Graduate School PE&RC

PRODUCTION ECOLOGY

& RESOURCE CONSERVATION
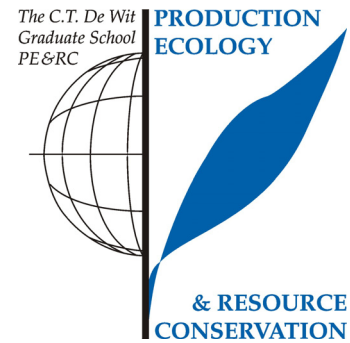
Review of Literature (4 credits)
- Spatial dynamics and site-specific management of weeds (2001/2002)

Writing of Project Proposal (4 credits)
- Spatial dynamics and site-specific management of weeds (2001/2002)

Laboratory Training and Working Visits (3.3 credits)
- Spatial aspects of weed ecology; University of Nebraska, USA (2001)
- Spatial aspects of weed ecology; Kansas State University, USA (2001)
- Automatic weed recognition/weed patterns; Universität Bonn, Deutschland (2001)

Post-Graduate Courses (9.8 credits)
- Spatio-temporal models in ecology; PE&RC (2001)
- Basic & advanced statistics; PE&RC (2001/2002)
- Spatial modelling in ecology; PE&RC (2002)
- Multivariate analysis; PE&RC (2004)

Deficiency, Refresh, Brush-up and General Courses (4.8 credits)
- Simulation of crop growth; Goudriaan, PPS (2001)
- Planmatig werken; NOW/FOM (2001)

Competence Strengthening / Skills Courses (5.2 credits)
- Scientific writing; PE&RC/CENTA (2002)
- Career perspectives; PE&RC/WGS (2005)
- Professional communication strategies; WGS (2005)

Discussion Groups / Local Seminars and Other Scientific Meetings (6.5 credits)
- Plant and crop ecology; PE&RC (2001-2005)
- Masterclass Julian Besag; PE&RC (2002)
- Masterclass agro-ecology Matt Liebman; PE&RC (2005)
- Masterclass integrated crop management; PE&RC, Ann Legere and Jon Marshall (2002)
- KNPV Najaarsvergadering (2005)
- KNPV Voorjaarsvergadering (2007)

PE&RC Annual Meetings, Seminars and the PE&RC Weekend (0.3 credits)
- PE&RC annual meeting (2002)

International Symposia, Workshops and Conferences (8.6 credits)
- 12th Symposium of European weed research society; the Netherlands (2002)
- Meeting of EWRS working group on site-specific weed management; Madrid, Spain (2003)
- EWRS/AAB Symposium on seed banks; Reading, UK (2003)
- 13th Symposium of European weed research society; Italy (2005)

Courses in Which the PhD Candidate Has Worked as a Teacher
- Populatie ecologie (2002,2003, 2004); 33 days
- Advanced crop and weed ecology (2002, 2003, 2004); 4 days
- Inleiding in de beta wetenschappen; 1 day

Supervision of MSc Student(s)
- Analysing spatial count data; 20 days; 1 student

Curriculum vitae

Suzanne Heijting was born on 4 May 1971 in Reeuwijk. She attended the secondary school in Emmen at the Gemeentelijke Scholengemeenschap Emmen where she graduated in 1989. Next she worked and lived in England for a year where she followed English language courses. In 1990, she started her study at (then called) Wageningen Agricultural University in Plant Pathology, specialization in Ecology and Epidemiology. Her theses subjects were in Entomology, Theoretical Production Ecology and Agricultural Law. Practical trainings were conducted in England (herbicide resistance) and Germany (entomology). In 1996, she graduated at Wageningen Agricultural University. From 1997–2000, she worked at Luxan BV, Elst, and next she worked for Koppert BV, Berkel en Rodenrijs. In 2001, she started at Wageningen University her PhD research under supervision of Dr. Ir. W. van der Werf and Prof. Dr. M.J. Kropff (Crop and Weed Ecology Group) and Prof. Dr. A. Stein (Biometris). The project concerned spatial analysis of weed patterns, and the research results are described in this thesis.

She is married to Jan Roelsma and they have three children.

Funding