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Describing the spatial pattern of crop plants with special reference to crop–weed competition studies

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Abstract

The spatial distribution of individual crop plants in the field is important for crop growth, yield production, and crop–weed interactions, but the role of spatial pattern has not been appreciated in agricultural research. A quantitative measure of degree of spatial uniformity/aggregation of individual plants would be very useful in this context. We digitized photographs of field plots of weed-infested spring wheat sown in uniform, random and normal row patterns at three densities (204, 449 and 721 seeds m^{-2}), and described the locations of individual wheat seedling as *x*- and *y*-coordinates. We analyzed the spatial pattern of these plant locations in two ways. One approach is based on Voronoi or Thiessen polygons (also called tessellations or tiles), which delimit the area closer to each individual than to any other individual. The relative variation (coefficient of variation) in polygon area and the mean shape ratio (ratio between the circumference of the polygon and that of a circle of the same area) of the polygons are measures of spatial aggregation. The other approach was Morisita's index of dispersion, which is based on the mean and variance in number of individuals in sampling units (quadrats). The CV of polygon area, the mean shape ratio of these polygons and Morisita's index of dispersion, all performed well as descriptions of the degree of spatial aggregation of crop plants. Models using one of these measures of uniformity and sowing density as explanatory variables accounted for 74–80% of the variation in crop biomass production. Despite its simplicity, models with Morisita's index performed slightly better than models using polygon parameters, accounting for 80–86% of the variation in weed biomass. Simple spatial analyses of individuals have much to offer agricultural research.

Keywords: Individual plants; Morisita's index; Spatial analysis; Voronoi polygons

1. Introduction

Agricultural production is the result of the growth, development and yield of individual plants in the field. The spatial distribution of crop plants is important for these processes, but the role of crop spatial pattern remains poorly investigated. In a series of recent studies, we have shown that a highly uniform pattern of crop plants suppresses weeds 30% better on average than plants distributed in standard 12 cm rows, and that further improvements in weed suppression can be achieved by also increasing crop density (Weiner et al., 2001; Olsen et al., 2005, in press). But it is not clear what degree of uniformity is necessary to achieve major improvements in weed suppression (Olsen et al., 2005). Addressing this question requires a meaningful and useful measurement of the degree of spatial uniformity of individual plants.

Spatial analysis of individuals is an important tool in plant ecology (Tilman and Kareiva, 1998; Dieckmann et al., 2000) but not yet in agricultural research, where the underlying spatial patterns of individual crop (or weed) plants are usually described in very general categories. More detailed information on the pattern of individual plants in the field and appropriate analytical methods are needed if we are to understand and evaluate the effects of spatial pattern on crop performance. Here we ask the following question: is it possible to describe the degree of spatial aggregation/uniformity with a simple quantitative measure, which can then be used to compare different spatial crop patterns?

A wide range of methods is available for quantifying spatial patterns (e.g. Ripley, 1981; Krebs, 1989; Cressie,

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1993; Leibold and Mikkelson, 2002; Perry et al., 2002). In most ecological studies, the objective is to reveal underlying spatial patterns to make inferences about mechanisms and interactions (see Perry et al., 2002). Often it is important to describe a pattern at several scales, and therefore, a method depending on a single scale is not considered optimal.

In this study, we have a different goal. Agricultural engineers have studied the performance of sowing machinery and the resultant crop patterns of seedlings, but most of these investigations have been primarily concerned with the evenness of within-row seed spacing, and therefore, the analyses have been one-dimensional (Panning et al., 2000; Pasternak et al., 1987). The implicit assumption is that more even within-row spacing will result in a more uniform two-dimensional spatial pattern. There has been little two-dimensional spatial analysis of seeding patterns (Heege, 1970; Griepentrog, 1999).

There are three general categories of two-dimensional point patterns: (1) uniform (hyperdispersed), (2) random, and (3) clumped (aggregated). It would be useful to describe the degree of two-dimensional spatial uniformity/aggregation of crop plants with a single measure on a continuous scale, which is independent of the sowing method used (Olsen et al., 2005). Here, we apply two well-known and accessible methods to evaluate the spatial distribution of individual crop plants in agricultural experiments. These are Morisita's index of dispersion (Morisita, 1959, 1962; Cressie, 1993; Tsuji and Tsuji, 1998) and Voronoi or Thiessen polygons (Guibas et al., 1990; Green and Sibson, 1978). Both these methods can be applied to x, y point-referenced data.

1.1. Voronoi polygons

For given collection of points in a plane, Voronoi polygons (also called Thiessen polygons or tiles) delimit all points in the plane that are closer to each of the given points than to any other point. If coordinates of individual points (here representing individual plant locations) are known, Voronoi polygons can be calculated from a Delaunay-triangulation (Lee and Schachter, 1980) which is based on the perpendicular bisectors of lines connecting neighbouring plants (Mithen et al., 1984).

Properties of potential interest for the analysis of plant populations include (i) the area of the polygon, (ii) the general shape of the polygon (from relatively round to highly elongated), and (iii) the eccentricity (the location of the point within the polygon relative to the center; Griepentrog, 1999). Here we investigate the first two of these. To quantify how much a polygon shape deviates from a perfect circle, a ''shape ratio'', S, is calculated. The shape ratio is the ratio between the circumferences of the observed polygon and the circumference of a circle of the same area (modified from Griepentrog, 1999):

$$S = \frac{C_{\text{polygon}}}{C_{\text{circle}}}, \tag{1}$$

where C_{polygon} is the circumference of the polygon, and C_{circle} is the circumference of a circle of the same area $= 2\sqrt{\pi A}$, where A is the polygon area.

The above-mentioned polygon parameters have been used to evaluate the competition among plants (Mead, 1966; Mithen et al., 1984). Fischer and Miles (1973) modelled a plant's exploitation of resources in two dimensions as an expanding circle, centered at the point of seedling emergence. They predicted that sowing of crops in a triangular pattern would result in the most efficient exploitation of space by crop plants and in the least amount of space available for weed growth. Consequently, every plant would ideally be positioned on an equilateral triangle, which results in a ''beehive'' pattern of hexagonal individual areas.

There are two disadvantages of the polygon approach. First, border effects have to be handled prior to data analysis. Polygons near the edge of the sample area cannot be calculated, so these points cannot be used in the analysis. Second, while polygons are an intuitive and simple way to describe point patterns, their analysis is not straightforward. Polygon analysis does not give us a convenient single measure of uniformity/aggregation. Non-uniformity can be manifested in several ways, such as variation in polygon area, mean and variation in polygon shape, or mean and variation in eccentricity. We do not know which of these is most useful, nor do we know of any measure that combines several of these aspects of non-uniformity. Here, we consider variation in polygon area and the mean polygon shape ratio as simple measures of non-uniformity, and ask the following questions:

(a) What is the degree of spatial uniformity of individual crop plants sown in highly uniform, random and standard row patterns at different densities?
(b) Are there major differences between the two approaches to spatial pattern when applied to these different crop-sowing patterns?
(c) Do the derived indices and parameters provide information relevant to crop and weed performance?

1.2. Morisita's index of dispersion

Morisita's index of dispersion (I) has been extensively used to evaluate the degree of dispersion/aggregation of spatial point patterns (Morisita, 1959, 1962; Cressie, 1993; Tsuji and Tsuji, 1998; Tsuji and Kasuya, 2001). Morisita's index is based on random or regular quadrat counts, and is closely related to the simplest and oldest measures of spatial pattern, the variance:mean ratio (Krebs, 1989; Dale et al., 2002) and to other dispersion indices, such as David and Moore's index of crowding, and lacunarity analysis (see Dale et al., 2002). Because Morisita's index can be calculated for different quadrat sizes, the scale of the analysis is not inherent, and it can be used to investigate pattern over a range of densities and scales. Many spatial patterns are uniform at one scale, but clumped or random at other scales (Dale et al., 2002).

Morisita's index of dispersion (sometimes called I_δ, here we call it I),

$$I = Q\frac{\sum_{i=1}^{Q} n_i(n_i - 1)}{N(N-1)}, \quad (2)$$

where Q is the number of quadrats in the sampling area, n_i is the number of plants in quadrat I, and N is the total number of plants in the sampling area.

Morisita's index requires that quadrats be small relative to the scale of pattern to be described (Cressie, 1993). It ranges from 0 (completely uniform) over 1 (random) to Q (the most clumped arrangement when all plants occur in one quadrat, and the index equals the number of quadrats). Morisita's index has several limitations. Considerable information is lost when point-referenced data (x-, y-coordinates) is converted to counts within quadrats (Cressie, 1993). Morisita's index is a population measure based on sampling units that are independent of individual points, so it is not possible to evaluate pattern on the individual plant level, as in polygon analysis. Border/edge effects are not a problem when using Morisita's index, and it has the advantage of simplicity as a single measure of uniformity/aggregation.

2. Materials and methods

We analyzed crop spatial data from a field experiment on the effects of crop density and sowing pattern on crop–weed competition. The experiment was performed at the Royal Veterinary and Agricultural University's research farm in Taastrup, Denmark (55°40′N, 12°18′E). The soil is a sandy clay loam typical of eastern Zealand. The climate is temperate/maritime with a mean temperature of 0 °C in January and 16.5 °C in July, and a mean annual precipitation of 613 mm.

Three crop sowing methods were used to establish (1) a highly uniform pattern, (2) a random pattern, and (3) normal row pattern (clumped pattern), at three seeding rates (204, 449 and 721 seeds m^{-2}) of spring wheat (*Triticum aestivum* L. cv. Leguan). We modified a precision seed drill (Kverneland Accord Corporation, Soest, Germany) to sow wheat in a highly uniform pattern (Weiner et al., 2001). This was achieved through a combination of narrow row spacing and even individual placement of seeds within rows. The ratio of inter- to intra-row distance was about 1:1 for the low and medium density and 5:4 for the high density.

To create a random sowing pattern, we used a modified conventional grain seeder (Kongskilde Nordsten, Sorø, Denmark) in which the coulters were removed and a bar mounted below the outlets. The wheat seeds were dropped from a height of 72 cm and bounced off the bar before falling to the ground. The soil was then covered with 4 cm of topsoil.

We used a standard plot research grain drill (Hege, Waldenburg, Germany) with 12.8 cm row spacing to sow in the normal rows.

The experiment was sown on 9 April 2002. Plots were 1.31 m × 8.0 m and there were four replicated blocks. After sowing the wheat, the soil was rolled and levelled before weeds were sown in a random pattern on the soil surface. The weed seeds were sown the same way as the random wheat pattern. After sowing the weed seeds on the soil surface, the soil was rolled again. To achieve high weed pressure, *Sinapis arvensis* L. was sown at a density of 350 seeds m^{-2}. The plots were fertilized at a rate of 80 kg N ha^{-1}, 14 days after sowing.

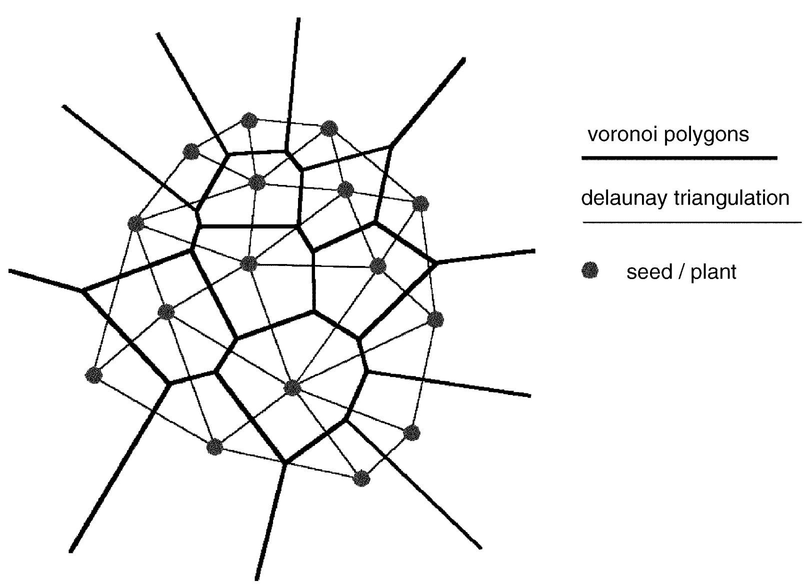

Fig. 1. Delaunay triangulation. Every point in the plane within the Voronoi polygons (thick line) is closer to the plant (dot) within the polygon than to any other plant in the plane. Thin lines represent Delaunay triangulation helping lines to construct the polygons (Lee and Schachter, 1980, modified).

Table 1
Mean and CV of polygon area and mean polygon shape ratio resulting from different sowing patterns and densities

Sowing pattern	Sowing density (seeds m^{-2})	Mean emergence (plants m^{-2})	N	Mean area (cm^2)	CV (area) (%)	Mean shape-ratio
Uniform	204	217	83	47.0	31.1	1.1507
	449	445	281	22.9	36.0	1.1535
	721	636	425	16.9	37.1	1.1580
Random	204	150	54	66.7	44.7	1.1860
	449	370	241	26.4	47.1	1.2020
	721	502	335	19.8	61.2	1.2181
Row	204	204	101	50.4	69.0	1.2982
	449	396	232	26.4	63.4	1.2930
	721	516	397	16.8	69.9	1.3291

Sowing density is determined by the sowing method used; N is the number of polygons contributing to the calculations.

On 2 May, after seedlings had emerged, we took photographs with a digital camera mounted on a camera stand in a fixed position 90 cm above ground, pointing directly downwards and centered over a 50 cm × 50 cm frame. The pictures were digitized and referenced using the program Surfer© Version 7.0 (Golden Software, Golden, Colorado, USA) giving the (x, y) point-referenced data for each crop plant. Polygons were generated using the software MatLab (MathWorks, Natick, Massachusetts, USA) and modified standard routines (Griepentrog and Nielsen, unpublished results; Fig. 1) were used to calculate area and circumference of each polygon. The number of whole polygons analyzed per treatment ranged from 54 to 425 (Table 1). Spatial analyses were performed only on crop plants, not weeds.

A later measurement of field emergence was made on 6 May (four days after photographing) by counting the number of seedlings per meter row to ask whether differences in emergence at the time of photographing were due to variation in emergence speed or actual differences in post-emergence plant density.

The point-referenced (x, y) data from the digitized photos were also used to calculate the Morisita's index of dispersion (I), after dividing the total plot area into quadrats. Since Morisita's index can be sensitive to scale, i.e. sample unit size (Krebs, 1989; Dale et al., 2002), we used three different quadrat sizes: 10 cm × 10 cm (25 quadrats), 5 cm × 5 cm (100 quadrats), and 2.5 cm × 2.5 cm (400 quadrats) within the 0.25 m^2 sampling area. This range of resolutions is based on the average area per individual over the range of densities from approximately 100 to 1000 seeds m^{-2}, which includes our actual range of sowing densities used in the study, as recommended in studies of Morisita's index (Cressie, 1993).

2.1. Statistical analyses

We analyzed mean polygon area (=1/[seedling density]) and the following measures of spatial aggregation: CV of polygon area, mean polygon shape ratio, and Morisita's index (at three different resolutions), for the three sowing patterns at the three densities with four replicate blocks. Data were analyzed using analysis of variance.

We also analyzed the spatial parameters influence on crop and weed performance. In a general linear model, sowing density was included as a class variable (factor with three levels) and the measures of spatial aggregation (derived from polygons or Morisita's index) as continuous variables. To achieve homogeneity of variance the weed biomass was square root transformed.

Two plots (one random pattern, low density, and one uniform pattern, low density) were excluded from the analysis due to errors in sowing, which resulted in totally inappropriate seedling densities.

Table 2
Morisita's index of dispersion (I) calculated for three different quadrat sizes for each sowing pattern and sowing density

Pattern	Density (plants m^{-2})	N	Size of sampling unit (quadrat)		
			10 cm × 10 cm	5 cm × 5 cm	2.5 cm × 2.5 cm
Uniform	204	3	0.8141	0.3872	0.7741
	449	4	0.8897	0.7252	0.4615
	721	4	0.9326	0.7216	0.5115
Random	204	3	0.8869	1.1238	1.0152
	449	4	0.9349	1.0590	1.1585
	721	4	1.0063	1.1211	1.2498
Row	204	4	1.3403	2.1096	3.7566
	449	4	1.0903	1.9005	3.1709
	721	4	1.0577	1.8896	2.8451

Table 3
Effects of quadrat size on Morisita's index

	Num-DF	Den-DF	10 cm × 10 cm		5 cm × 5 cm		2.5 cm × 2.5 cm	
			F-value	*P*-value	*F*-value	*P*-value	*F*-value	*P*-value
(a) Source								
Pattern	2	29	7.95	0.0023	57.62	<0.0001	24.31	<0.0001
Density	2	29	0.29	0.7488	0.01	0.9859	0.38	0.6858
(b) Least squares means								
Uniform vs. random				0.4142		0.0011		0.1658
Uniform vs. row				0.0009		<0.0001		<0.0001
Random vs. row				0.0081		<0.0001		<0.0001

(a) Analysis of variance, type 3 fixed effects of sowing density and sowing pattern on Morisita's index (I) for different sampling unit (quadrat) sizes: 10 cm × 10 cm, 5 cm × 5 cm and 2.5 cm × 2.5 cm. (b) Least squares means comparisons of sowing patterns for the different quadrat sizes. The intermediate quadrat size distinguishes the best among the sowing patterns.

3. Results

3.1. Polygon-derived pattern parameters

The polygon parameters clearly distinguish among the three patterns (Table 1). There were unexpected and significant differences among patterns in both measures of crop density: mean polygon area (Table 1) and field emergence. The random pattern was significantly lower in density, as measured by number of polygons, than the row pattern ($p = 0.002$), especially at lowest sowing density. Four days later, the emergence percentage, based on the intended sowing densities, was 98.8% in uniform, 92.8% in random and 89.8% in row patterns, but these differences were not significant ($p = 0.1987$; data not shown).

Both CV of polygon area and mean shape ratio distinguished clearly among the sowing patterns ($p < 0.0001$, all pair-wise comparisons $p < 0.002$).

3.2. Morisita's index

Quantifying spatial aggregation with Morisita's index also makes a clear distinction among the different sowing patterns (Tables 2 and 3a). However, pair-wise tests (Table 3b) indicate that random and uniform patterns are only different at one of three resolutions (5 cm × 5 cm).

3.3. Crop and weed biomass

In all cases, both sowing density and spatial parameters had highly significant effects on both crop (Table 4) and weed biomass (Table 5). All densities were significantly different from each other. Models based on each of the spatial parameters and density accounted for much of the variation in both crop (Fig. 2; Table 4) and weed biomass (Fig. 2; Table 5). In general, the models accounted for over 74% of the variation in crop biomass production (Table 4) and over 80% of the variation in weed biomass (Table 5).

Table 4
Analysis of variance (type 1 fixed effects) of crop biomass on density and a measure of spatial aggregation (a polygon parameter or Morisita's index)

Measure of spatial aggregation	Source	DF	SS	*P*-value	r^2
CV of polygon area					0.7703
	Block	3	72505	0.0644	
	Density	2	731075	<0.0001	
	Aggregation	1	90599	0.0036	
Mean shape-ratio (S)					0.7458
	Block	3	74085	0.0818	
	Density	2	695074	<0.0001	
	Aggregation	1	62956	0.0180	
Morisita's index (I), 10 cm × 10 cm quadrats					0.7729
	Block	3	55694	0.1223	
	Density	2	613876	<0.0001	
	Aggregation	1	93372	0.0030	
Morisita's index (I), 5 cm × 5 cm quadrats					0.7812
	Block	3	68821	0.0651	
	Density	2	653337	<0.0001	
	Aggregation	1	101973	0.0018	
Morisita's index (I), 2.5 cm × 2.5 cm quadrats					0.8090
	Block	3	77373	0.0294	
	Density	2	584703	<0.0001	
	Aggregation	1	131087	0.0003	

Table 5
Analysis of variance (type 1 fixed effects) of square root of weed biomass (g m^{-2}) on density and a measure of spatial aggregation (a polygon parameter or Morisita's index)

Measure of spatial aggregation	Source	DF	SS	*P*-value	r^2
CV of polygon area					0.8537
	Block	3	44.20	0.0021	
	Density	2	329.04	<0.0001	
	Aggregation	1	34.34	0.0006	
Mean shape-ratio (*S*)					0.8136
	Block	3	39.83	0.0111	
	Density	2	313.43	<0.0001	
	Aggregation	1	17.75	0.0021	
Morisita's index (*I*), 10 cm × 10 cm quadrats					0.8535
	Block	3	36.90	0.0054	
	Density	2	279.26	<0.0001	
	Aggregation	1	34.84	0.0006	
Morisita's index (*I*), 5 cm × 5 cm quadrats					0.8517
	Block	3	40.15	0.0038	
	Density	2	298.71	<0.0001	
	Aggregation	1	34.07	0.0007	
Morisita's index (*I*), 2.5 cm × 2.5 cm quadrats					0.8609
	Block	3	46.55	0.0012	
	Density	2	272.53	<0.0001	
	Aggregation	1	38.01	0.0003	

Models including both CV of polygon area and mean polygon shape-ratio (data not shown) did not account for more variation in crop or weed biomass than did models with either of these alone.

4. Discussion

4.1. Describing the degree of spatial aggregation

Morisita's index has been used extensively in ecology, but it has recently come under criticism. The major criticism has been that indices like Morisita's do not show characteristics of patterns at multiple scales very well (Cressie, 1993). In many experimental studies in agriculture, such as those on crop–weed competition, scale is not a major issue, because most comparisons are made at the same scale—the experimental plot as a sample of an agricultural field. While there may be differences in crop and weed densities and local conditions at higher scales in the field, it is reasonable to assume that these effects do not alter the nature of crop–weed competition at the local scale.

In many ecological studies, the objective of spatial analysis is to measure deviations from complete spatial randomness, and to describe the type of aggregation observed. In our studies, we already have much control over and information about the spatial pattern. Morisita's index is well suited for our purpose, and it distinguished clearly among the different patterns (Table 3). Morisita's index provides a simple quantitative description of pattern, which may be useful in future studies of crop and weed performance.

In general, sowing pattern is highly significant determinant of all polygon-derived parameters (Table 1). The CV of polygon area, mean of shape-ratio and standard deviation of shape-ratio, also provide a quantitative description of pattern, which may be useful in studies on crop and weed performance. The significant difference in mean polygon area among patterns (Table 1) were most likely due to differences in germination rate and speed resulting from the different sowing technique used rather than differences in sowing rates. The use of precision seeders is known to give higher field emergence values (Heege and Billot, 1999).

The spatial analyses used here are two-dimensional, and do not consider the relative height of crop and weed (Mohler, 2001). In models based on polygons, it is assumed that all plants utilize resources in the same way and have the same initial sizes and growth rates. Size differences that exist before the onset of competition have a major influence on subsequent competitive interactions (Weiner, 1990), but it is difficult to include such differences in analyses in which all points are equal except for their locations.

4.2. Timing of spatial analyses of crop plants

Photographs to be used in analyses of crop spatial pattern have to be taken before plants develop so much that it becomes difficult to distinguish individual plants when digitizing the photos, but late enough to ensure that all seedlings have emerged. In our study, the plants were sown on 9 April and plots photographed on 2 May, but there was additional emergence in the random pattern over the

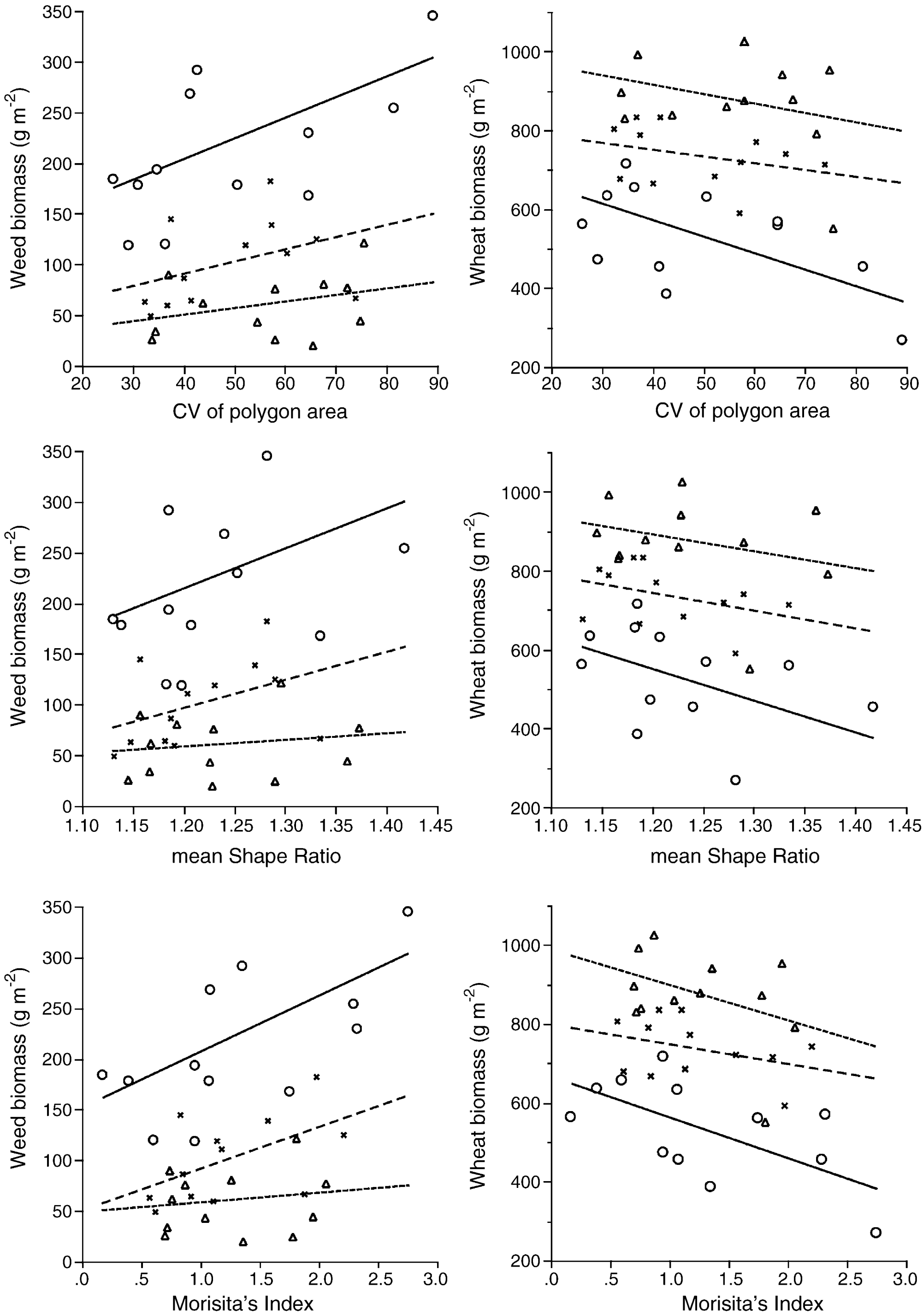

Fig. 2. Weed biomass (left column) and crop biomass (right column) plotted against CV of polygon area; mean shape ratio (middle) and Morisita's index at 5 cm × 5 cm quadrat size (bottom) at high density, 721 plants m^{-2} (triangles); medium density, 449 plants m^{-2} (crosses); low density, 204 plants m^{-2} (circles). Lines are least-square regressions for each quadrat size.

following 4 days. The difference in germination/actual density at the time of photographing the plots were primarily caused by a delay in germination in the random treatment, where the seeds were dropped on the soil surface and subsequently covered with soil. Seeding depth was apparently greater in this case, resulting in slower germination.

4.3. Crop and weed biomass

Crop density was a major determinant of both crop and weed performance, as reported in numerous previous studies (e.g. Radford et al., 1980; Samuel and Guest, 1990; Blackshaw, 1993; Murphy et al., 1996; Doll, 1997; Weiner et al., 2001; Olsen et al., 2005, in press).

Together with sowing density, models including either Morisita's index, CV of polygon area, mean polygon shape-ratio or standard deviation of polygon shape ratio accounted for 75–81%, the observed variation in crop biomass (Table 4), and 81–86% of the variation in weed biomass (Table 5). While the effect of density was much stronger, measures of spatial aggregation made a significant contribution to accounting for variation in crop and weed biomass in every case. Thus, we consider the use of both Morisita's index and the polygon-derived pattern parameters presented here as appropriate analytic tools in research on impacts of spatial pattern on crop–weed competition. Morisita's index appears to perform slightly better than polygon-based parameters.

Improving the spatial distribution of crop plants in the field can have significant agronomic advantages, such as improved germination and yield uniformity and quality, as well as increased weed suppression. Such improvement may be relatively easy to achieve, but neither uniform nor random sowing patterns are currently used in grain production. There is a need for new sowing methods to realize the potential advantages of a more uniform spatial distribution of crop plants. Such new methods would most likely be based on a decrease in row width accompanied by an improved distribution of seed spacing within the row. The quantification of spatial pattern should prove useful in comparing different sowing techniques (Griepentrog, 1999).

In conclusion, research on plant production needs to go beyond the description of crop spatial pattern as a qualitative variable or in only one dimension. The quantitative measures of pattern used in the present study provide a useful basis for further and more generalized comparison of the spatial patterns of individual plants in agricultural studies. Morisita's index has the advantage of being a single value, whereas Thiessen polygons provide much more detailed information at the individual scale, but we do not yet know how to best summarize this information in the most biologically and agronomically meaningful way.

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