Available online at www.sciencedirect.com

SCIENCE DIRECT®

Field Crops Research 96 (2006) 207–215

Field Crops Research

www.elsevier.com/locate/fcr

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

L. Kristensen [a], J. Olsen [a], J. Weiner [a,*], H.W. Griepentrog [b], M. Nørremark [b]

[a] Department of Ecology, Royal Veterinary and Agricultural University, DK-1958 Frederiksberg, Denmark
[b] Department of Agricultural Sciences, Royal Veterinary and Agricultural University, DK-2630 Taastrup, Denmark

Received 30 June 2005; accepted 2 July 2005

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,

---

* Corresponding author. Tel.: +45 3528 2822; fax: +45 3528 2821.
E-mail address: jw@kvl.dk (J. Weiner).

0378-4290/$ – see front matter © 2005 Elsevier B.V. All rights reserved.
doi:10.1016/j.fcr.2005.07.004

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