1998

When does the spatial pattern of weeds matter? Predictions from neighborhood models

Karen A. Garrett, *Oregon State University*
Philip Dixon, *University of Georgia*

WHEN DOES THE SPATIAL PATTERN OF WEEDS MATTER? PREDICTIONS FROM NEIGHBORHOOD MODELS

Karen A. Garrett[1,2] and Philip M. Dixon[2]

[1]*Department of Botany and Plant Pathology, Oregon State University, Corvallis, Oregon 97331-2902 USA*
[2]*Savannah River Ecology Laboratory, University of Georgia, Aiken, South Carolina 29802 USA*

Abstract. Good management models for postemergence weed control require good estimates of which weed density produces an economic threshold yield. Because intraweed competition increases if weeds are aggregated, weed spatial pattern may be an important factor for inclusion in management models. Mathematical models of weed–crop competition have demonstrated that this may be the case, but the small number of field studies examining the effect of weed spatial pattern have given variable results. These studies have used sampling units at arbitrary spatial scales for determining the level of aggregation in weed counts. We suggest that the neighborhood size for weed–crop competition is a natural scale for considering spatial pattern. We modeled crop yield resulting from weed competition as a function of the economic threshold, the level of competition within the neighborhood, neighborhood size, and the type and scale of weed pattern. From the model results, we predicted which weed traits would produce large shifts in threshold weed density as weed spatial pattern varies. For these weed species, consideration of spatial pattern in weed management models is predicted to be important. The systems most sensitive to weed spatial pattern are those with low economic thresholds, less competitive weeds, smaller neighborhoods, and aggregation at the scale of the neighborhood.

Key words: aggregation; area of influence; competition; economic thresholds; interference; neighborhood models; spatial pattern; spatial scale; weed–crop interaction.

Introduction

Weed management models can be effective tools for reducing both herbicide and tillage use in postemergence weed control (e.g., Lybecker at al. 1991; Wilkerson et al. 1991). Typically, decision making is based on estimation of the response of crop yield in experimental plots to a range of weed densities. An economic threshold is determined based on expected yield loss and the cost of an action to reduce the number of weeds (Mumford and Norton 1984, Zadoks 1985). Below the threshold weed density, money is likely to be saved by not taking action; above it, taking action is likely to result in profit. If several courses of action are available, with the more effective actions being more expensive, there may be a series of thresholds (e.g., Wiles et al. 1992*b*).

Traits other than weed density may also be useful in characterizing the weed population for yield prediction. There has been some debate about whether the spatial pattern of weeds is a useful consideration. Auld and Tisdell (1988) demonstrated mathematically that, for a yield response curve that is concave upward, variability in weed density from one sampling unit (SU) to another leads to less yield loss than for a homogeneous distribution of weeds. In other words, if weeds are more aggregated, less overall yield loss is predicted than if

they are systematically distributed. If estimates of yield response to weed density were constructed for systematically distributed weeds and applied to aggregated weeds, yield loss would be overestimated. Exaggerated estimates of yield loss could lead to unnecessary weed control measures if the shift takes the estimate of loss from below to above an economic threshold.

Studies of the importance of spatial pattern can be categorized by the scale at which pattern was considered. Studies of large-scale processes have focused on how some areas of a field may need no action while action may be economically justified in other areas. This scale of spatial structure may be important in the context of site-specific tillage or herbicide application (Thornton et al. 1990, Wilson and Brain 1991). On a smaller spatial scale, Brain and Cousens (1990) examined mathematically how a range of levels of aggregation affected yield loss, using different parameterizations of the negative binomial distribution to produce the range of levels. They began with the assumption that aggregation within a 1-m^2 quadrat was negligible and concluded that the effect of spatial pattern may be minimal for high economic thresholds. Hughes (1989) replaced mean population density in yield response models with Lloyd's (1967) ''mean demand,'' measured by the mean number per individual of other individuals in the same quadrat. Hughes considered arbitrarily sized spatial units, concluding that spatial pattern may be particularly important at low plant densities.
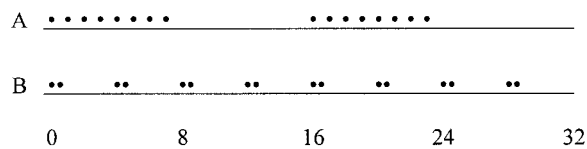
FIG. 1. Illustration of how the level of aggregation may vary depending on the spatial scale being considered. Points indicate weed positions for two types of patterns. (A) Greater aggregation at large scale, less at small scale. (B) Less aggregation at large scale, more at small scale.

Spatial pattern has rarely been considered in empirical studies of weed impact on crop yield. Hughes, in his 1996 review of the incorporation of spatial pattern of harmful organisms into crop loss models, states, "Wiles et al. (1992b) made what seems to be the only formal attempt to evaluate spatial information about harmful organisms (in this particular case, weeds) in the context of crop protection decision-making." Wiles et al. (1992b) looked at the effects of aggregation using 9.1 m length SUs in soybean weed control models and concluded, for their case, that the cost of ignoring spatial pattern in decision models may be low on average, but occasionally great.

One source of variable results in evaluations of the importance of weed spatial pattern is the scale at which pattern is assessed. The level of aggregation at one scale may or may not translate into a similar level of aggregation at a different scale. For example, the first pattern of weed positions in Fig. 1 has a systematic distribution for a SU of length 16, an aggregated distribution for a SU of length 8, and a lower level of aggregation for a SU of length 1. The second pattern has a systematic distribution for a SU of either length 16 or length 8 and an aggregated distribution for a SU of length 1.

We suggest that the size of the neighborhood for competition of a crop plant (e.g., Pacala and Silander 1985) is the natural scale for considering level of aggregation. At that scale, all weeds counted in a SU will influence the crop plant at the center of the SU. Weed scientists have considered the comparable concept of the weed area of influence (AOI), the range over which a weed impacts crop plant yield (e.g., Mercer et al. 1990, Pike et al. 1990), but not, to our knowledge, in the context of spatial pattern. If an arbitrary scale *larger* than the neighborhood is selected, undetected spatial pattern within the SU may be important. If an arbitrary scale *smaller* than the neighborhood is selected, weeds outside the SU may be having a great influence on yield within the SU. Under the yield response model that will be described below, the two weed patterns in Fig. 1 would each have the same predicted yield if the neighborhood is of length 16. If the neighborhood is of length 8, the predicted yield for weed pattern A would be the higher of the two. If the neighborhood is of length 1, predicted yield would be higher for weed pattern B.

TABLE 1. Notation.

Variable	Definition
λ	mean weed density (parameter for the Poisson distribution of weed density)
c	competition coefficient for effects of weeds on crop plants
d	length of neighborhood or area of influence (unit distance = spacing between crop plants)
h	length of sampling unit (unit distance = spacing between crop plants)
k	negative binomial parameter determining level of aggregation
m	density of weedss (no. weeds/crop plant)
N	total number of weeds in a neighborhood
t	economic threshold yield (expressed as proportion)

In addition to providing an appropriate scale for considering spatial pattern, the use of neighborhood models allows the characteristics of different types of weeds to be compared based on the shift they produce in threshold weed densities. "Types" of weeds can be defined in terms of an individual weed's AOIs (equal to the corresponding neighborhood diameters) and how competitive they are within their AOIs. We developed predictions as to when spatial pattern would be important and potentially a valuable factor for inclusion in management models. The influence of weed spatial pattern may be important in two different settings. First, competition coefficients have usually been determined for weeds planted or thinned to be systematically distributed (Hughes 1996). When these estimates are used in constructing economic thresholds for the management of fields where weeds are likely to be more aggregated, there is the question of whether an adjustment for that aggregation is needed. In this case, shifts in the threshold density from that for systematic distributions are of interest. Second, if weeds are generally somewhat aggregated in natural populations, shifts in the threshold density over the naturally occurring range of aggregation may be important to adjust models for particular fields.

The Model

Three main aspects of the agroecosystem were considered in this analytical model: (a) the level of competition, defined in terms of the size of the neighborhood or AOI and the intensity of competition exerted by the weeds, (b) the spatial pattern of weeds, defined in terms of weed density, whether weeds are systematically or randomly distributed or aggregated, and the spatial scale of aggregation relative to crop plants, and (c) the economic threshold for the use of an input to reduce the density of weeds. For a range of parameter values, we determined how large the shift in the economic threshold was in response to changing the level of aggregation. Notation is summarized in Table 1.

Analytical model of competition

Crop plants typically are planted closely enough to each other that competition between crop plants might be viewed as approximately constant in the absence of weeds. Competition of crop plants against weeds was also assumed approximately constant. Unit yield in the absence of weeds incorporates the constant effect of competition between crop plants. The distance between crop plants in the row was taken as unit distance, and neighborhood sizes were expressed in terms of the spacing between crop plants. The length of the AOI of the weeds, equivalent to the length of the neighborhood, was denoted by d. The inverse hyperbolic equation was used to model the individual crop plant yield response (Cousens 1985),

$$Y = 1/(1 + cN)$$

where N is the number of weeds within a crop plant's neighborhood, c is the competition coefficient of weeds against crop plants, and crop plant individuals have unit yield in the absence of weeds. The competitive effect of weeds against crop plants was approximated as constant regardless of the position of weeds relative to crop plants within the neighborhood (Pacala 1989). Use of the inverse hyperbolic incorporates the diminishing yield response to increasing weed densities that is likely to result from increased weed–weed competition. For each parameter combination, all weeds were assumed to be the same species or at least the same competitive type.

Distribution of weed counts within neighborhoods

It was assumed for simplicity that weeds fell in a line with the crop plants, as might be expected if there was postplanting tillage, and that they only influenced crop plants within their row. The mean weed density was denoted by m weeds per unit length of row, with unit length defined as the distance between crop plants. The scale at which plants interact was determined by the size of the neighborhood, d, also measured by unit length of row. So, for example, if the neighborhood is of length $d = 1$, each weed competes against only one crop plant.

The distribution of weed count per neighborhood was modeled as either systematic, random, or having one of three levels of aggregation. For systematic distributions, the number of weeds per neighborhood was nearly constant. This is the distribution under the assumption that an initial weed is equally likely to be positioned anywhere between two crop plants and that weeds are $1/m$ units apart from each other down the row. For random weed distributions, the number of weeds in a neighborhood was modeled as following a Poisson distribution. For aggregated weed distributions, a distinction was made between SU size and neighborhood size. The number of weeds per SU was modeled by the negative binomial (NB) distribution (Appendix A) so the variance in number of weeds per SU was higher than for randomly distributed weeds. We modeled the distribution of the number of weeds in a SU for the aggregated case as NB(k, hm), where k is the aggregation parameter as in Brain and Cousens (1990) and hm is the length of the SU multiplied by the mean number of weeds per unit length. The negative binomial distribution used in this way models aggregation at only one spatial scale. We have suggested that the level of aggregation at the spatial scale of the neighborhood size is likely to be the most useful measure. To model aggregation first at that scale, we used a SU size equal to the neighborhood size ($h = d$). Level of aggregation for SUs at a larger scale than the neighborhood may or may not reflect the level of aggregation at the scale of the neighborhood (Fig. 1), though the smaller the difference in scale, the greater the correspondence between the two measures. The effect of aggregation at a smaller scale than the neighborhood can be directly evaluated. For this case, we considered SUs of unit length ($h = 1$) so that neighborhoods encompass as many SUs as they are units long. The distribution of the total number of weeds in the neighborhood was then NB($dk/h, dm$) (Appendix A). Including this smaller SU example allows us to consider the effect as neighborhood size becomes large relative to aggregation at a fixed scale.

As an illustration of these distributions, suppose neighborhoods are of length $d = 10$ and mean weed density is $m = 1$ (Table 2). For systematically distributed weeds, $md = 10$ weeds appear in each neighborhood. For N following a Poisson distribution with mean m, variation in the number of weeds per neighborhood is introduced and weeds are randomly distributed. When the number of weeds per neighborhood follows the negative binomial, the level of aggregation for NB parameter $k = 1$ is somewhat higher than for the Poisson. Weeds are highly aggregated for $k = 0.01$, the majority of crop plants being exposed to no weeds. For unit-length SUs ($h = 1$), the level of aggregation within neighborhoods does not increase as rapidly as k becomes small because there are 10 chances for a SU with many weeds to occur within each neighborhood; the number of weeds per neighborhood is essentially averaged over ten draws so its variability is lower.

Estimating yield loss over parameter combinations

The distributions of the number of weeds in a neighborhood described above were used to determine the average yield over a range of parameters. Fields were assumed large enough that the number of crop plants was effectively infinite for purposes of this evaluation. The average yield was calculated as

$$E[Y] = \sum_{n=0}^{\infty} [1/(1 + cn)P(N = n)].$$

For this calculation, we used Maple version 5 (Char et al. 1991) to determine expected yields, using the forms

TABLE 2. Ten examples of neighborhood weed counts for each of eight spatial patterns, with weed density $n = 1$, neighborhood length $d = 1$, sampling unit length h varying, and negative binomial parameter k varying.

Systematic	10	10	10	10	10	10	10	10	10	10
Poisson	14	13	12	11	10	10	9	8	7	6
Negative binomial										
$h = 10$										
$k = 1.00$ (case 1)	29	18	16	13	9	6	5	3	1	0
$k = 0.10$ (case 2)	57	10	2	1	0	0	0	0	0	0
$k = 0.01$ (case 3)	72	0	0	0	0	0	0	0	0	0
$h = 1$										
$k = 1.00$ (case 1)	18	15	14	11	11	10	9	9	9	4
$k = 0.10$ (case 2)	21	18	16	14	9	9	8	5	0	0
$k = 0.01$ (case 3)	43	27	20	19	0	0	0	0	0	0

given in Appendix B. For each of three economic threshold levels (t), we found the threshold weed density that produced the threshold yield loss. This allowed us to determine how changes in the spatial distribution affect the threshold weed density. We found the threshold weed density over all combinations of representative parameter values of economic threshold $t = \{0.60, 0.90, 0.98\}$, competition coefficient $c = \{0.1, 0.2, 1.0\}$, length of SU $h = \{1.0, d\}$, neighborhood length $d = \{1.0, 2.0, 10.0, 20.0\}$, and spatial distributions systematic, random, or aggregated with NB parameter $k = \{0.01, 0.1, 1.0\}$.

Examples of parameter estimates from published empirical studies were assembled to guide the selection of parameter ranges for k (Table 3) and c and d (Table 4). In aggregation studies, the NB aggregation parameter k was either directly reported by the authors or calculated by us from reported estimates of the mean and variance of weed density using

$$\hat{\sigma}^2 = \hat{\mu}(1 + \hat{\mu}/\hat{k}).$$

Estimates of NB parameters at different densities may not be directly comparable (Taylor et al. 1979), and the size of SUs may not be that of neighborhoods, but these estimates give an idea of the likely range. For competition parameters, AOI studies were used. In this case, the competition coefficient (c) was estimated from reported yields by $1/(1 + cN) =$ mean yield within

neighborhood/mean yield in absence of weeds, assuming an asymptote of 0. The greatest distance reported as still yielding statistically different yield from crop plants in the absence of competition was taken as the radius of the neighborhood (AOI). This is only a rough estimate because it is influenced by the power of the experiment, and the resulting step function is only an approximation of the probably more complicated yield vs. distance function (Law and Watkinson 1987).

MODEL PREDICTIONS

Both aspects of the competitiveness of weeds have a straightforward influence on the yield response to weed density (Fig. 2). Increases in the competition coefficient (c) and the length of the neighborhood (d) function similarly to deepen the response curve. Spatial aggregation influences yield through its influence on the distribution of individual yields (Fig. 3). For the most aggregated case (Fig. 3D), almost all individuals have unit yield because they have no weeds in their neighborhood. A small number of plants have low yields because they are surrounded by many neighboring weeds. As the level of aggregation decreases (k increases), moderate yields become much more likely and fewer individuals have unit yield. These differences in probability distributions translate into differences in expected crop yield for a given weed density (Fig. 4).

TABLE 3. Estimates of spatial aggregation ($\hat{k}$) of weeds in agroecosystems. SU = sample unit.

Source	Crop	SU size	Weed	$\hat{k}$
Marshall 1988	*Triticum aestivum* L.	0.25 m^2	*Bromus sterilis* L.	0.15
			Bromus commutatus Schrader	0.025
			Elymus repens (L.) Gould	0.059
Wiles et al. 1992*a*	*Glycine max* (L.) Merr.	9.1 m	*Amaranthus retroflexus* L.	0.04–0.61
			Cassia obtusifolia L.	0.04–0.27
			Ipomoea spp.	0.14–2.79
			Sida spinosa L.	0.05–0.39
Dessaint and Caussanel 1994	*Zea mays* L.	625 cm^2	*Chenopodium album* L.	0.74
			Lolium perenne L.	0.12
			Polygonum persicaria L.	0.32
			Solanum nigrum L.	1.16
Cardina et al. 1995	*Glycine max* (L.) Merr.	2500 cm^2	*Chenopodium album* L.	0.76
		1000 cm^2		0.43

TABLE 4. Estimates of competition parameters of weeds in agroecosystems.

Source	Crop	Weed	$\hat{c}$	Radius†	$\hat{d}$‡
Mercer et al. 1990	*Gossypium hirsutum* L.	*Proboscidea louisianica* (Miller) Thellung	0.9	50 cm	10
Pike et al. 1990	*Glycine max* (L.) Merr.	*Xanthium strumarium* L.	0.2	100 cm	40
Byrd and Coble 1991	*Gossypium hirsutum* L.	*Xanthium strumarium* L.	0.6	60 cm	15
Stauber et al. 1991	*Oryza sativum* L.	*Echinochloa crus-galli* L.	0.07	25 cm	10

† Estimated radius in units from experiment.
‡ Neighborhood size parameter d scaled in terms of the spacing between crop plants in the row.

The shift in threshold weed density over the range of spatial patterns can be seen by following the horizontal dotted lines in Fig. 4. For this example weed system, there is little shift in threshold density at the 0.98 threshold. The point where the yield curve for the most aggregated case (case 3, $k = 0.01$) crosses the 0.98 threshold is somewhat shifted toward higher threshold densities, but the difference is relatively slight. At the 0.90 threshold, the moderately aggregated case (case 2, $k = 0.1$) is slightly offset from the less aggregated cases and the yield curve of the most aggregated case (3) does not even cross the threshold for the range of weed densities portrayed in the figure. At the low 0.60 threshold, even the systematic (S) and Poisson (P) cases are somewhat distinct from each other. Both the moderately aggregated (2) and highly aggregated (3) cases do not cross the threshold over the illustrated range of weed densities.

The above example incorporates differences in only threshold and spatial pattern; the shift in threshold yield over spatial patterns for all the parameter combinations is illustrated in Fig. 5. Each row of the figure shows the point where the yield curves cross the economic threshold for the indicated parameter combination, marking the threshold weed density as do the characters along the three horizontal dotted lines in Fig. 4. As in the example (Fig. 4), lower thresholds result in greater

shifts in threshold weed density over different spatial patterns, and the difference is greatest going from moderately aggregated (2) to highly aggregated (3). Larger neighborhood sizes (d) result in smaller shifts in threshold density as do larger competition coefficients (c). A given level of aggregation at a scale smaller than the neighborhood ($h = 1$) results in smaller shifts in threshold density than does the same level of aggregation at the scale of the neighborhood. (When $h = d = 1$, the SU length is the same as the neighborhood length, so there is no distinction.) The difference in threshold density shift in response to scale of aggregation is greatest moving toward the highest level of aggregation (3).

For which parameter combinations is there a large shift in threshold density when comparing systematic distributions to other distributions?

At the highest threshold (0.98), there is never an important difference in threshold density between the systematic distribution case (S) and any but the highest aggregation case (3). Even for this comparison, there is only a difference for weeds with small AOIs (d) and small competition coefficients (c). At the 0.90 threshold, there are added differences in threshold density between the systematic distribution case and the medium aggregation case (2) for less competitive weeds
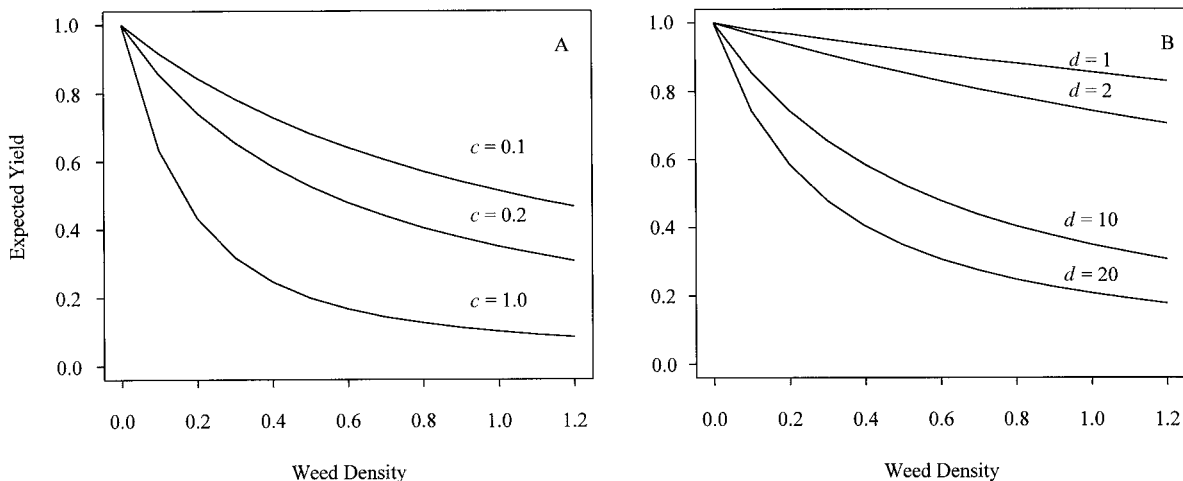

FIG. 2. Expected yield response to weed density (m) for randomly (Poisson) distributed weeds. (A) The competition coefficient (c) varies (neighborhood length $d = 10$). (B) The neighborhood length (d) varies (competition coefficient $c = 0.2$).
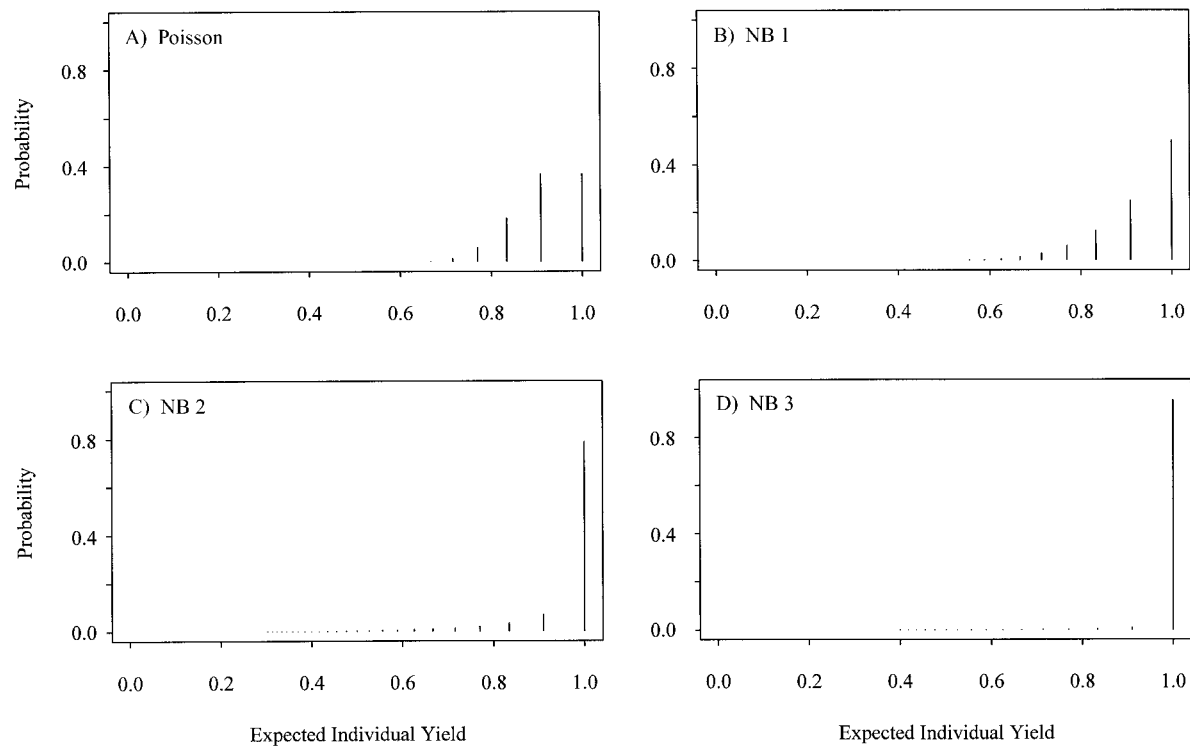
FIG. 3. Probability distributions of individual crop plant yields (competition coefficient $c = 0.5$, mean weed density $m = 1$, neighborhood length $d = 1$, and sampling unit length $h = 1$). Probabilities lower than 0.0001 are not depicted. (A) Randomly distributed weeds. (B) Aggregated weeds with NB (negative binomial) parameter $k = 1$. (C) Aggregated weeds with NB parameter $k = 0.1$. (D) Aggregated weeds with NB parameter $k = 0.01$.

(smaller d and c). The difference between the systematic case and the highest aggregation case is always great at this threshold when aggregation is at the scale of the neighborhood ($h = d$). For aggregation at the scale of smaller SUs ($h = 1$), this difference is great for less competitive weeds. At the lowest threshold considered (0.60), differences between the systematic case and the low aggregation case (1) are becoming important for less competitive weeds. Even differences

between the systematic case and the random case (P), though relatively small, are apparent.

For which parameter combinations is there a large shift in threshold density when comparing different levels of aggregation?

The pattern of response to differences between the aggregated cases is similar to that seen comparing the systematic cases to cases with other distributions. At
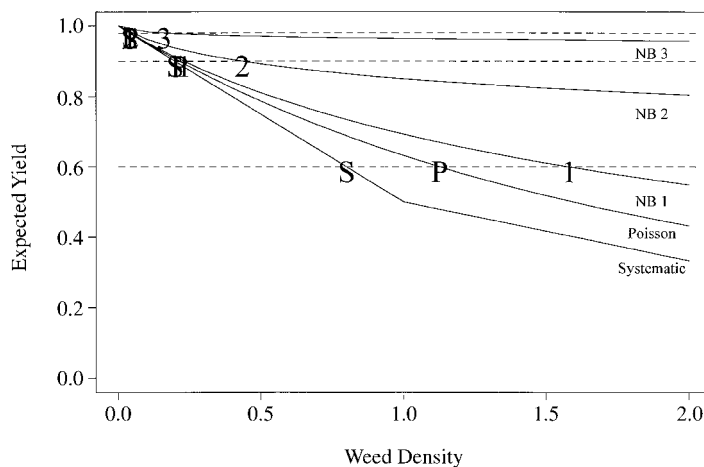

FIG. 4. Expected yield response to weed density as the level of spatial aggregation varies (competition coefficient $c = 1$, neighborhood length $d = 1$, and sampling unit length $h = 1$). Economic thresholds of yield loss $t = 0.98$, 0.90, and 0.60 are indicated by dotted lines. S = Systematic, P = Poisson, 1 = NB (negative binomial) with $k = 1.0$, 2 = NB with $k = 0.1$, and 3 = NB with $k = 0.01$.
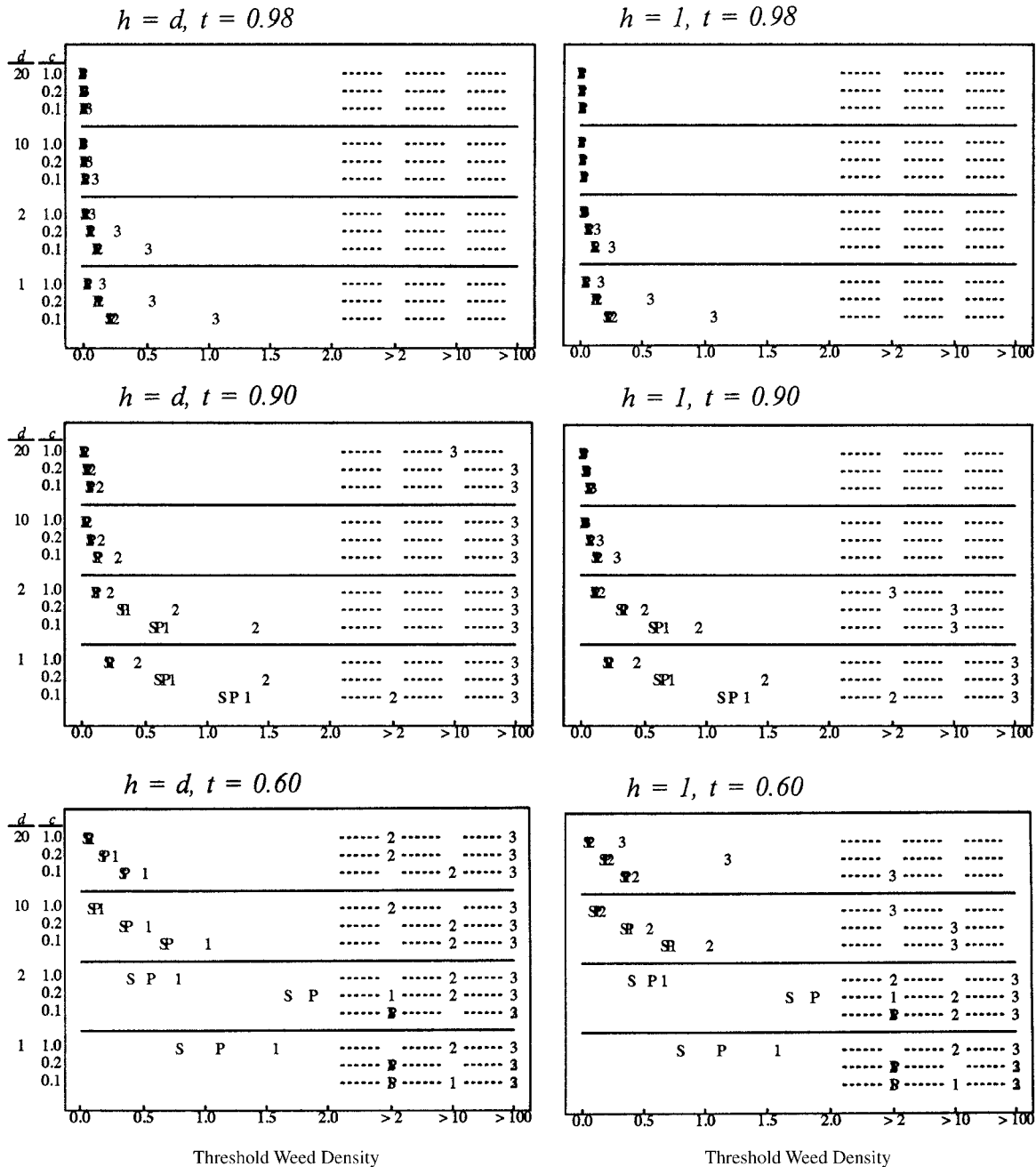
FIG. 5. The weed density at which the threshold yield is obtained. Within a box, four neighborhood lengths (*d*) are depicted, and within each level of *d*, there are three levels of the competition coefficient (*c*). S = Systematic, P = Poisson, 1 = NB (negative binomial) with $k = 1.0$, 2 = NB with $k = 0.1$, and 3 = NB with $k = 0.01$.

the highest threshold (0.98), the highest level of aggregation results in a threshold density different from the other aggregated cases for less competitive weeds. At the 0.90 threshold, each level of aggregation produces distinct threshold densities for the less competitive weeds and the highest level of aggregation is very distinct for the case of aggregation measured at the scale of the neighborhood ($h = d$). At the 0.60 threshold, the three levels of aggregation produce distinct results for every case except the most competitive weeds when aggregation is measured at a small scale ($h = 1$).

DISCUSSION

Our model predicts that shifts in threshold weed density between different spatial patterns can be large. For

less competitive weeds or low economic thresholds, yield loss in response to weed density, if estimated from studies using weeds planted in a systematic pattern, is predicted to be significantly overestimated if applied to aggregated weeds. Likewise, if less competitive weed species are present in different fields at different levels of aggregation, the threshold weed density may be very different for the different fields. Studies of the spatial pattern of weeds have found a wide range of levels of aggregation (Table 3). Researchers have reported quite different levels of aggregation between species, at least for limited sampling (e.g., Dessaint and Caussanel 1994). Within a weed species, Wiles et al. (1992*a*) found a range of levels of aggregation of weeds in different fields of soybeans. Though estimates of NB parameters may not be suitable for comparisons over a wide range of densities (Taylor et al. 1979), estimates of Taylor power law parameters for several agroecosystems also demonstrated a range of spatial patterns (Clark et al. 1996). These studies suggest that there exists a range of aggregation that could produce large differences in threshold weed density.

Our model predicts that a range of weed spatial patterns at the scale of the neighborhood results in larger shifts in threshold weed density than the same range of patterns at a smaller spatial scale than the neighborhood. It should be noted that this result is based on the assumption that all the weeds in the crop plant neighborhood compete with each other; pattern within the neighborhood would be more important if intraweed competition takes place only over a smaller distance than weed-crop competition. Differences in spatial pattern at both the neighborhood scale and smaller scales would then produce even larger shifts in threshold density. Studies of the AOI of weeds have generally found large neighborhoods (Table 4), though it is likely that the selection of weed species for AOI estimation has been based at least in part on their being competitive enough for a single individual to produce a measurable effect against a background of environmental variability. Other aspects of weed competitiveness are known to vary widely (e.g., Zimdahl 1980). The spatial pattern at a larger scale may influence spatial pattern at the scale of the neighborhood, though this is not necessarily the case (Fig. 1). Pattern at larger scales may be important if differential management at that scale is possible.

Weed scientists developing management decision models can use our model predictions as recommendations for when it would be worth investigating the impact of weed spatial pattern. When weeds are highly competitive in large neighborhoods and economic thresholds are high, it is probably not important to try to include information about weed spatial pattern. When weeds are less competitive in smaller neighborhoods and economic thresholds are lower, it is likely that weed spatial pattern is important and will shift where the threshold weed population lies. If parameters

describing competition between a particular weed species and crop are known confidently enough, and the inverse hyperbolic is known to describe the response to competition well, the estimates of shifts in threshold given here could be taken as approximations of how much the actual threshold would shift. It is more likely that parameters describing a crop–weed interaction are not well known enough and/or the inverse hyperbolic is not a good enough approximation to the functional response. In that case, our results give suggestions as to which crop–weed interactions require empirical studies of response to weed spatial pattern.

For those agroecosystems for which weed spatial pattern is predicted to be important, estimates could be made of yield loss in experimental plots with imposed spatial patterns. If there is typically only one level of aggregation at the neighborhood scale for a species of interest, that level should be reproduced in experimental plots rather than transplanting weeds into a systematic pattern. Perhaps a range of levels of aggregation are observed for a species. Different plots would then need to have different spatial patterns imposed, representing the set of patterns likely to be found in fields. Hughes (1996) discusses two approaches for incorporating spatial pattern into crop loss models. Yield may be estimated as the sum of yields at different weed densities weighted by the frequency of each density. Or the approach may be based on a description of yield loss per unit weed density and the relationship between an index of aggregation and the mean density.

The presence of several species of weeds in a field complicates estimation of the shape of yield response curves to weed populations, with or without consideration of spatial pattern. It may be possible to group weeds into competitive types based on individual biomass (Goldberg 1987). But it would be important to consider whether some species that are similar competitors tend to occur in different spatial patterns because they have different dispersal mechanisms.

Our model predictions could be tested empirically by measuring the importance of experimentally imposed spatial pattern for determining threshold density in experimental plots. The most straightforward tests would involve only one weed species per experimental plot. To test the prediction that weeds with smaller neighborhoods and lower competitiveness within neighborhoods result in greater response to spatial pattern, weed species for comparison should be of varying AOI and level of competition within neighborhood. To test the prediction that spatial pattern at scales smaller than the neighborhood is less important than spatial pattern at the scale of the neighborhood, the experimental plot could be split into subplots. Spatial pattern would then be imposed at the plot level in some plots and at the subplot level in other plots for comparison. VanGessel et al. (1995) performed an experiment in which naturally-occurring weeds were removed in strips (Garrett 1995) to introduce aggregation at a range

of scales. Even under this imposed scaling of aggregation, differences in yield between subplots with different spatial patterns were not detected. However, in this experiment the resulting density of weeds varied greatly (VanGessel et al. 1995) and there were a number of weed species present, with the proportions varying from plot to plot. Differences in species and genotype of weeds and differences in germination times will add a great deal of variability in competitive effect. One point that has been little addressed in the context of aggregated weed distributions is that such distributions may occur in part because of environmental heterogeneity in the field. Because of this, competition between weeds and crop plants may be occurring only in certain types of microenvironments within the field, rather than in average conditions for the field (Pacala and Tilman 1994). Likewise, observational studies using neighborhood or AOI analyses may be subject to environmental pseudointeraction effects when competition coefficients for weeds are estimated (Garrett and Dixon 1997). In other words, correlations between weed number or species and environmental variables may bias estimates of weed competitiveness. It may be important that weeds be either transplanted into experimental plots or sown and thinned to a desired density.

To summarize, our results corroborate Brain and Cousen's (1990) demonstration that threshold weed densities are likely to be more sensitive to spatial pattern for lower economic thresholds. We also predict that weeds with smaller AOIs and that are less competitive within their AOIs will result in greater sensitivity to spatial pattern. For these weed types, we predict that sensitivity will be greater to spatial pattern at the scale of the crop plant neighborhood than at smaller scales.

LITERATURE CITED

Auld, B. A., and C. A. Tisdell. 1988. Influence of spatial distribution on weeds on crop yield loss. Plant Protection Quarterly 3:81.
Brain, P., and R. Cousens. 1990. The effect of weed distribution on predictions of yield loss. Journal of Applied Ecology 27:735–742.
Byrd, J. D., Jr., and H. D. Coble. 1991. Interference of common cocklebur (Xanthium strumarium) and cotton (Gossypium hirsutum). Weed Technology 5:270–278.
Cardina, J., D. H. Sparrow, and E. L. McCoy. 1995. Analysis of spatial distribution of common lambsquarters (Chenopodium album) in no-till soybean (Glycine max). Weed Science 43:258–268.
Char, C. W., K. O. Geddes, G. H. Gonnet, B. L. Leong, M. B. Monagan, and S. M. Watt. 1991. Maple V language reference manual. Springer-Verlag, New York, New York, USA.

Clark, S. J., J. N. Perry, and E. J. P. Marshall. 1996. Estimating Taylor's power law parameters for weeds and the effect of spatial scale. Weed Research 36:405–417.
Cousens, R. 1985. A simple model relating yield loss to weed density. Annals of Applied Biology 107:239–252.
Dessaint, F., and J.-P. Caussanel. 1994. Trend surface analysis: a simple tool for modelling spatial patterns of weeds. Crop Protection 13:433–438.
Garrett, K. A. 1995. Selecting a sampling method for weed densities: the case of weed removal in strips. Weed Science 43:394–401.
Garrett, K. A., and P. M. Dixon. 1997. Environmental pseudointeractions: the effects of ignoring the scale of environmental variability in competition studies. Theoretical Population Biology 51:37–48.
Goldberg, D. E. 1987. Neighborhood competition in an old-field plant community. Ecology 68:1211–1223.
Hughes, G. 1989. Spatial heterogeneity in yield-weed relationships for crop-loss assessment. Crop Research 29:87–94.
———. 1996. Incorporating spatial pattern of harmful organisms into crop loss models. Crop Protection 15:407–421.
Kotz, S., and N. L. Johnson. 1969. Distributions in statistics: discrete distributions. Wiley, New York, New York, USA.
Law, R., and A. R. Watkinson. 1987. Response-surface analysis of two-species competition: an experiment on Phleum areanarium and Vulpia fasciculata. Journal of Ecology 75:871–886.
Lloyd, M. 1967. 'Mean crowding'. Journal of Animal Ecology 36:1–30.
Lybecker, D. W., E. E. Schweizer, and R. P. King. 1991. Weed management decisions in corn based on bioeconomic modeling. Weed Science 39:124–129.
Marshall, E. J. P. 1988. Field-scale estimates of grass weed populations in arable land. Weed Research 28:191–198.
Mercer, K. L., J. A. Pawlak, D. S. Murray, L. M. Verhalen, M. S. Riffle, and R. W. McNew. 1990. Distance-of-influence of devil's-claw (Proboscidea louisianica) on cotton (Gossypium hirsutum). Weed Technology 4:87–91.
Mumford, J. D., and G. A. Norton. 1984. Economics of decision making in pest management. Annual Review of Entomology 29:157–174.
Pacala, S. W. 1989. Plant population dynamic theory. Pages 54–67 in J. Roughgarden, R. M. May, and S. A. Levin, editors. Perspectives in ecological theory. Princeton University Press, Princeton, New Jersey, USA.
Pacala, S. W., and J. A. Silander, Jr. 1985. Neighborhood models of plant population dynamics. I. Single-species models of annuals. American Naturalist 125:385–411.
Pacala, S. W., and D. Tilman. 1994. Limiting similarity in mechanistic and spatial models of plant competition in heterogeneous environments. American Naturalist 143:222–257.
Pike, D. R., E. W. Stoller, and L. M. Wax. 1990. Modeling soybean growth and canopy apportionment in weed-soybean (Glycine max) competition. Weed Science 38:522–527.
Stauber, L. G., R. J. Smith, Jr., and R. E. Talbert. 1991. Density and spatial interference of barnyardgrass (Echinochloa crus-galli) with rice (Oryza sativa). Weed Science 39:163–168.
Taylor, L. R., I. P. Woiwod, and J. N. Perry. 1979. The negative binomial as a dynamic ecological model for aggregation, and the density dependence of k. Journal of Animal Ecology 48:289–304.
Thornton, P. K., R. H. Fawcett, J. B. Dent, and T. J. Perkins. 1990. Spatial weed distribution and economic thresholds for weed control. Crop Protection 9:337–342.
VanGessel, M. J., E. E. Schweizer, K. A. Garrett, and P. Wes-

tra. 1995. Influence of weed density and distribution on corn (*Zea mays*) yield. Weed Science **43**:215–218.

Wiles, L. J., G. W. Oliver, A. C. York, H. J. Gold, and G. G. Wilkerson. 1992*a.* Spatial distribution of broadleaf weeds in North Carolina soybean (*Glycine max*) fields. Weed Science **40**:554–557.

Wiles, L. J., G. G. Wilkerson, H. J. Gold, and H. D. Coble. 1992*b.* Modelling weed distributions for improved post-emergence control decisions. Weed Science **440**:546–553.

Wilkerson, G. G., S. A. Modena, and H. D. Coble. 1991.

HERB: decision model for postemergence weed control in soybean. Agronomy Journal **83**:413–417.

Wilson, B. J., and P. Brain. 1991. Long-term stability of distribution of *Alopecurus myosuroides* Huds. within cereal fields. Weed Research **31**:367–373.

Zadoks, J. C. 1985. On the conceptual basis of crop loss assessment: the threshold theory. Annual Review of Phytopathology **23**:455–473.

Zimdahl, R. L. 1980. Weed–crop competition: a review. International Plant Protection Center, Corvallis, Oregon, USA.

APPENDIX A

THE DISTRIBUTION OF N UNDER AGGREGATION

If the weed count in a sampling unit (SU) of unit length has a Poisson distribution conditional on the rate for that SU and the rate is distributed following a gamma distribution, then the unconditional distribution of the count is negative binomial (Kotz and Johnson 1969). If the size of the SU is scaled by a factor $h,$ the conditional distribution of the count is then

$$P(N = n \mid \lambda) = [\exp(-\lambda h)(\lambda h)^n]/n!.$$

If the rate parameter λ follows the gamma distribution with mean density m weeds per unit length of row,

$$f_\lambda(\lambda) = (1/m)^\alpha/\Gamma(\alpha)\lambda^{\alpha-1} \exp(-\lambda/m)$$

where $\Gamma(x) = (x - 1)!$ is the gamma function, then the unconditional distribution of the number of weeds in a SU of length h is

$$P(N = n)$$

$$= \int_0^\infty \Big([(\lambda h)^n \exp(-\lambda h)/n!][(1/m)^\alpha/\Gamma(\alpha)]$$

$$\times \lambda^{\alpha-1}\exp(-\lambda/m) \; d\lambda\Big)$$

$$= \Gamma(n + \alpha)/[n!\Gamma(\alpha)]\{[1/(hm)]/[1 + 1/(hm)]\}^\alpha$$

$$\times \{1/[1 + 1/(hm)]\}^n$$

which is the probability density function of the negative binomial distribution. Brain and Cousens (1990) used a different notation for the negative binomial:

$$P(N = n) = \frac{\Gamma(n + k)}{n!\Gamma(k)}[m/(m + k)]^n[k/(m + k)]^k.$$

In this form, decreasing the parameter k increases the level of aggregation. The distribution derived above, allowing for SU size to vary proportionately with $h,$ can be reparameterized for SU counts in the functional form used by Brain and Cousens (1990) as

$$P(N = n)$$

$$= \frac{\Gamma(n + k)}{n!\Gamma(k)}[(hm)/(hm + k)]^n[k/(hm + k)]^k.$$

If SU size is the same as neighborhood size ($h = d$), the distribution of the number of weeds in a neighborhood is NB(k, dm). If SUs are of size $h < d,$ so that d/h SUs fall inside a neighborhood, the distribution of the count within one of these smaller SUs is NB(k, hm). Because the sum of identically distributed negative binomial random variables is also distributed following a negative binomial (Kotz and Johnson 1969), the distribution of the total count within a neighborhood over h small SUs is

$$NB[(dk)/h, dm].$$

APPENDIX B

FORM OF YIELD EXPECTATION FOR EVALUATION

We used the probability generating function, $G(z),$ to change the evaluation from over an infinite sum to over a finite integral as in Brain and Cousens (1990),

$$E[Y] = 1 - \int_0^1 z^{1/c} G'(z) \; dz$$

where $G'(z) = dG(z)/dz.$ In our case, the probability distribution function for the negative binomial is

$$G_{NB}(z) = [[(dk)/h]/[(dk)/h + dm(1 - z)]]^{(dk)/h}$$

with derivative

$$G'_{NB}(z) = dm[[(dk)/h]/[(dk)/h + dm(1 - z)]]^{(dk)/h+1}.$$

For the Poisson distribution, the generating function is

$$G'P(z) = \exp[-dm(1 - z)]$$

$$G'_p(z) = dm \exp[-dm(1 - z)].$$

For the systematic distribution, at most two levels of N are possible so a finite sum is appropriate:

$$E[Y] = \sum [1/(1 + cn)P(N = n)]$$

$$P(N = \text{int}(dm)) = 1 - \text{re}(dm)$$

and $P[N = \text{int}(dm) + 1] = \text{re}(dm),$ where $\text{int}(dm)$ gives the integer part of dm and $\text{re}(dm)$ gives the remainder.