

Spatial patterns of grasses and shrubs in an arid grassland environment

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Abstract. In the Chihuahuan Desert of Mexico and New Mexico, shrub invasion is a common problem, and once-abundant grassland ecosystems are being replaced by shrub-dominated habitat. The spatial arrangement of grasses and shrubs in these arid grasslands can provide better insight into community dynamics and can provide information on grass shrub interactions. To better understand the dynamics of the Chihuahuan Desert ecosystem and to provide information regarding the interactions between grasses and shrubs, we examined the spatial patterns of grasses and shrubs in remaining grass-dominated areas, interspersed with some shrubs. We developed 18, 10 × 20 m vegetation distribution plots by mapping the location of all grasses and shrubs on each and repeating the measurements three years later. Spatial patterns were then assessed for each plot using a second-order spatial statistic, Ripley's K-function, as well as any observed changes in the spatial patterns over a three-year period. We observed clumped grass distributions, indicating a lack of competition among grasses; random shrub distributions; and even grass distribution with respect to shrub locations, indicating competition between grasses and shrubs. We also observed a tendency for grass distributions to become more even over time, and grasses to become less even with respect to shrub locations over time. These changes occurred during a period of greater than average rainfall, indicating that greater water availability may lead to increased competition among grasses and decreased competition between grasses and shrubs.

Key words: arid grasslands; *Bouteloua eriopoda*; Chihuahuan Desert; grass and shrub interactions; Jornada Experimental Range; *Prosopis glandulosa*; Ripley's K-function; shrub expansion; spatial patterns; *Sporobolus* spp.

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INTRODUCTION

Arid grassland ecosystems, such as those found in North America throughout the Chihuahuan Desert, are able to support some mixed grass and shrub vegetation growth, but with low net primary production (McClaran 1995). Vegetation community composition varies depending

on specific climate conditions, but often includes grasses such as *Bouteloua* spp., *Sporobolus* spp., *Hilaria* spp., and *Eragrostis* spp. interspersed with shrubs such as *Prosopis* spp. and *Larrea divaricata* (McClaran 1995). Despite relatively low net primary production rates in these ecosystems, desert grasslands are important sources of food-production and have been heavily used as

rangeland for cattle since the 1800s. Research in these arid grasslands has largely focused on grassland degradation and invasion of woody species (Schlesinger et al. 1990, Larney et al. 1998, Schlesinger et al. 2000, Okin et al. 2001, Okin and Gillette 2001, Geist and Lambin 2004, Laliberte et al. 2004, Gibbens et al. 2005, Browning et al. 2008); however, many of the community dynamics of these ecosystems are still not well understood.

There has been considerable debate in the literature regarding the effects of competition in environments with low productivity, and to date, the role of competition in these ecosystems is still unclear. Grime (1973) and Huston (1979) initially proposed that competition would not be a factor in unproductive environments where environmental stress is high (e.g., arid environments with limited resources). Newman (1973), and later Tilman (1987), argued that competition would be equally as important in both productive and unproductive environments, but that competition in unproductive environments would be more related to belowground competition for resources such as water and nutrients instead of competition for light availability. Since then, much research has been conducted on the importance of competition in unproductive environments and results have been inconsistent (Kadmon 1995, Goldberg and Novoplansky 1997).

Whether competition is present in unproductive environments appears to depend on many factors, including resource quantity and distribution. For example, Goldberg and Novoplansky (1997) proposed a two-phase resource dynamics hypothesis, which suggests that the importance of competition for a community will depend on the nature of the available resources. Specifically, they proposed that competition is important in an unproductive environment when the length of time between resource pulses (e.g., rain events in arid environments) is sufficiently small and the availability of those resources is affected by the vegetation. Subsequent researchers have provided support for this hypothesis (Novoplansky and Goldberg 2001, James and Richards 2007).

In arid grasslands, where the invasion of woody shrub species is prevalent, whether grasses and shrubs directly compete for resources is a particularly relevant question. Walter

(1971) originally proposed the two-layer soil water model for savanna ecosystems, which suggested that grasses and trees/shrubs would not directly compete for water resources, because trees/shrubs have deeper roots and would utilize water from deeper soil layers, while grasses would be dependent on near-surface water. This was thought to provide an advantage for shrubs, because they would not be dependent on shallow water and seasonal rains for water resources. Many researchers have tested this hypothesis in arid and semi-arid ecosystems, and results suggest that shrubs actually do utilize shallow soil water as well as deeper water, and therefore, do compete to some extent with grasses (Belsky 1994, Le Roux et al. 1995, Golluscio et al. 1998, McCarron and Knapp 2001, Rodriguez et al. 2007). Whether grasses and shrubs directly compete for resources appears to be dependent on many different factors including location, species, annual rainfall amount, and seasonality of precipitation (Sala et al. 1989, Belsky 1994, Le Roux et al. 1995, Montaña et al. 1995, Weltzin and McPherson 1997, Golluscio et al. 1998, McCarron and Knapp 2001, Rodriguez et al. 2007).

Facilitation effects, where larger plants provide microhabitats with greater moisture and nutrient availability for smaller plants and seedlings, also appear to be important in environments with low productivity (Tielborger and Kadmon 2000, Bhark and Small 2003, Riginos et al. 2005, Maestre et al. 2005). It was initially proposed that competition would be more important in productive environments with greater resource availability, and that facilitation effects would dominate under greater environmental stress (Bertness and Callaway 1994). Recent research results do provide support for the importance of facilitation in unproductive environments (Riginos et al. 2005, Maestre et al. 2005, D'Odorico et al. 2007), and facilitation of forbs and grasses under shrub canopies does appear to be particularly common in arid environments (Tielborger and Kadmon 2000, Flores and Jurado 2003, Armas et al. 2008).

The spatial distribution of vegetation is commonly used by plant ecologists to determine relationships among plants and to better understand plant community dynamics (Ferreira et al. 2007, Scanlon et al. 2007, Wiegand and Moloney 2004, Caylor et al. 2003). Spatial patterns can be

used to assess whether plant communities show competitive interactions and/or facilitation effects. If competition is an important factor determining the spatial distribution of vegetation in unproductive environments, the distribution tends to be more uniform (i.e., regular distances between plants). If facilitation is important, the distribution tends to be clumped, and if neither competition nor facilitation effects are observed, the distribution is more likely random (Wiegand and Moloney 2004). Fowler (1986) reviewed the available literature on the spatial distribution of vegetation in arid and semi-arid regions and reported mixed results, but observed that more studies reported finding random distributions than uniform distributions. Further research indicates that facilitation is important in arid environments, and clumped patterns in vegetation are often observed (Maestre et al. 2005). The spatial distribution of vegetation in arid grassland environments, then, is determined by the combination of negative and positive effects (competition and facilitation) and will vary with location and depend on a variety of factors, including resource availability in space and time, as well as the species involved (Barbier et al. 2008). Additionally, it appears that these relationships can be quite complex and might change over time within single patches (e.g., move from facilitation-dominated to competition-dominated; Armas et al. 2008).

In the Chihuahuan Desert of Mexico and New Mexico, shrub expansion is a common problem, and once-abundant grasses such as *Bouteloua* spp. and *Sporobolus* spp. have been replaced by shrub-dominated habitat over the last 100+ years (Laliberte et al. 2004, Gibbens et al. 2005). Much research has been devoted to understanding the patterns and processes of this conversion (Yao et al. 2006, King et al. 2008); however, the basic dynamics of the remaining grass-dominated ecosystems and the interactions between grasses and shrubs in the Chihuahuan Desert are still poorly understood. In order to better understand the dynamics of this ecosystem, and to provide insight into the interactions among grasses and shrubs that may dictate eventual loss of grassland habitat, we developed detailed vegetation distribution maps in grass-dominated areas, interspersed with some shrubs, to observe spatial patterns. Previous research mapping vegetation

in this region has tended to rely on aerial photography (Lalibert et al. 2004, Gibbens et al. 2005, Bestelmeyer et al. 2006, King et al. 2008), small plots that do not broadly assess spatial patterns of vegetation (Yao et al. 2006), or more coarse, transect measures of vegetation that can only roughly estimate vegetation coverage (King et al. 2008).

We used 18, 10 × 20 m vegetation distribution plots in undisturbed grass-dominated habitat in the Chihuahuan Desert and mapped the locations and dimensions of every individual grass and shrub. We then used second-order spatial statistics to examine patterns of distribution for grasses and shrubs in these plots. Given that these ecosystems appear to be in transition, and temporal variation is also important in understanding ecosystem dynamics, we repeated these measurements three years later to examine any changes in the spatial patterns over time.

METHODS

Study area

We examined spatial patterns of vegetation on grass-dominated plots located at the Jornada Basin Long Term Ecological Research (LTER) station. The Jornada is an approximately 783-km² mixed desert grassland/shrubland habitat located in southeastern New Mexico in the Chihuahuan Desert. The region has a mean annual rainfall of less than 250 mm, with greater than 50% of this precipitation occurring during July through September. Mean maximum summer temperatures are 36°C, and mean maximum winter temperatures are 13°C (data available from Jornada Experimental Range, (<http://usda-ars.nmsu.edu/>)). Research indicates major increases in shrub coverage (particularly in mesquite dune habitat) and declines in once abundant grasses such as *Bouteloua* spp. and *Sporobolus* spp. over the last 150 years (Laliberte et al. 2004, Gibbens et al. 2005). Our experiment was established in Pasture 11 of the LTER site (32°56' N, 106°75' W) on what is commonly called the “sand sheet.” Soils at the site generally have a sandy clay loam texture.

Experimental design and data collection

We examined spatial patterns of vegetation in three adjacent areas located in Pasture 11. Each of

the three blocks were approximately 250×100 m, and were part of a larger, wind erosion experiment. Blocks were selected based primarily on high grass coverage and low shrub coverage, and were located near each other so that variables such as soil texture and moisture, topography, rainfall, and wind regimes were similar. All blocks were fenced throughout the four-year period of data collection to prevent any cattle grazing (although the mesh of the fencing was not small enough to completely exclude some grazing by smaller animals, such as rabbits). Dominant grasses in two of the blocks were *Sporobolus* spp., and the dominant grass on the third block was *Bouteloua eriopoda*. The dominant shrub on all blocks was *Prosopis glandulosa*.

In each block we established six, 10×20 m vegetation distribution plots oriented in the prevailing wind direction, 19° north of east, approximately 50 m apart (Fig. 1). On each plot, we used a Trimble 3600 total station (Trimble Navigation Limited, Sunnyvale, California, USA) to identify and record x, y coordinate data for every individual grass (all species) and *P. glandulosa* shrubs. We also measured plant widths parallel and perpendicular to the prevailing wind direction for all grasses (basal) and shrubs (canopy). Total station and dimension data for blocks 1 and 3 plots were collected during the summer of 2004. Block 2 data were collected in July, 2005. Measurements for all plots were recorded again during the summer of 2007. Vegetation plots were not disturbed throughout the data collection period. Rainfall data were also collected from a rain gauge located in pasture 11,

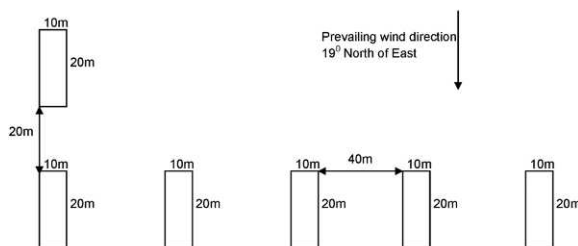


Fig. 1. Representation of one of three observation blocks. Rectangles represent approximate locations of the 10×20 m plots used to measure locations of all grasses and shrubs for spatial patterns analyses. Location data were collected on six vegetation distribution plots per block for a total of 18 plots.

near our blocks, for three years prior to and throughout data collection (2001–2007).

Spatial statistics

We used the second-order spatial statistics, Ripley's K-function, to examine spatial relationships among grass locations, shrub locations, and to compare grass and shrub distributions. Ripley's K-function gives a distribution of distances between pairs of points. Specifically, $K(r)$ shows the number of points of a given pattern within r distance of an arbitrary point within the study area. The bivariate K-function is equal to the number of points of a pattern located r distance from a point of a second pattern, or:

$$K(r) = \frac{A}{n_1 n_2} \sum_{i=1}^{n_1} \sum_{j=1}^{n_2} \frac{I_r(d_{ij})}{w_{ij}} \quad (1)$$

where n_1 is the number of points of one pattern, n_2 is the number of points of a second pattern, A is the study area, d_{ij} is the distance between the i th and j th points, I_r is a constant equal to 1 if $d_{ij} \leq r$ and 0 if $d_{ij} > r$, and w_{ij} is a weighted function used to correct for edge effects and is the proportion of the area of a circle found inside the study region located at the i th point with radius d_{ij} (Wiegand and Moloney 2004). For univariate analysis, pattern one is set as equal to pattern two. In order to remove scale dependence and stabilize variance, a square root transformation can be used, giving:

$$L(r) = \sqrt{\frac{K(r)}{\pi}} - r \quad (2)$$

where $L(r) > 0$ indicates a clumped pattern up to r and $L(r) < 0$ indicates over-dispersion or even distribution up to r . For bivariate analyses, $L(r)$ indicates attraction, repulsion, or independence of one pattern with respect to a second pattern (in this case the distribution of grasses with respect to shrub locations). For statistical analyses, the observed distribution of points is compared to a null model to determine significant deviation from a random distribution. Monte Carlo confidence envelopes for the appropriate null model are created, and values of $L(r)$ that are greater than or less than the enveloped values indicate clumped or even distributions, respectively (see Wiegand and Moloney 2004 for further details).

We used the software package *Programita* (Wiegand and Moloney 2004) to calculate the $L(r)$ functions for shrubs and grasses on each of our plots and to compare these to simulation envelopes for the null models of complete spatial randomness (CSR) for the univariate analyses (grass and shrub distributions) and CSR with antecedent conditions for the bivariate analysis (grass locations with respect to shrub locations). The software uses a grid based approach, with the study area divided into a grid, and cell size selected based on the size of the plants. We used cell size of 0.2×0.2 m to prevent multiple grasses occupying each cell in all but a few cases (Wiegand et al. 2006).

Wiegand et al. (2006) demonstrated that a point pattern approach to determining spatial relationships between plants of very different sizes, such as grasses and shrubs, is inaccurate. Based on their suggestions to correct for this error, we modified the point pattern analyses so that shrubs were represented as having finite sizes using our width measurements. The plant location data and dimension measurements were used to create vegetation distribution maps for each plot (Appendix: Figs. A1–A3). The *Programita* software was then used to construct grid-based, point patterns from each of the maps, where a given cell of the grid was assigned one type of point if it was covered by a shrub and another type of point if it was covered by a grass (Wiegand et al. 2006; Appendix: Figs. A1–A3). Shrub locations were held constant for the bivariate analysis and grasses allowed to overlap shrubs, as grasses are often observed growing within shrub canopies in this study area. All shrubs were given finite sizes and their shapes preserved for both the univariate and bivariate analyses. For analysis of shrubs of finite sizes, we selected the torus correction with guard cells as an edge correction method for cases where part of a shrub falls outside the study area (see Wiegand et al. 2006).

$L(r)$ statistics and confidence envelopes for each 10×20 m plot were calculated for all distances (r) up to 5 m from each point (grass or shrub location respectively). The results for the six replicate plots for each block were then combined to give $L(r)$ statistics and confidence envelopes for each block for both of the univariate analyses and the bivariate analysis.

These analyses were conducted for data collected in 2004 and 2005 and repeated for data collected in 2007 in order to examine any changes over time.

RESULTS

$L(r)$ functions for the univariate point pattern analysis for grasses were generally greater than zero and outside the confidence envelopes for all blocks for data collected during 2004–2005 at all spatial scales, indicating clumped distributions up to 5 m distances (Fig. 2). During 2007, the $L(r)$ functions for grasses on block 3 (the *B. eriopoda*-dominated site) were negative and outside the confidence envelopes up to a distance of 0.8 m, were within the confidence envelopes from 1 m to 1.4 m, and were positive and outside the confidence envelopes between 2 m and 3.4 m. Observed changes over time in spatial patterns from initial data collection for block 1 included a decrease in $L(r)$ up to 0.4 m distance and from 3.4 m to 5 m. $L(r)$ values for block 2 increased at all distances (r), while observed $L(r)$ functions for block 3 decreased for all distances (Fig. 2).

$L(r)$ functions from the univariate analysis for shrubs generally did not differ significantly from zero and were within confidence limits calculated for the null model of CSR for objects of finite size (Fig. 3). Two exceptions to the random distribution for shrubs were observed at small spatial scales. Specifically, the $L(r)$ function for block 1 was positive and outside confidence envelopes up to 0.2 m for initial data collection in 2004. $L(r)$ functions for shrubs on block 3 were also positive at small spatial scales for 2004 data. This tendency for clumping at small scales disappeared over time as shrub distribution became more even (decrease in $L(r)$ from 2004/2005 to 2007) for all blocks and all spatial scales, with the exception of block 2 between 1.8 m and 4.8 m (Fig. 3). Although the $L(r)$ functions decreased for all blocks, they remained within confidence envelopes.

$L(r)$ functions from the bivariate analysis evaluating grass locations with respect to shrubs were generally negative and outside confidence envelopes, showing grass distribution away from shrub locations (Fig. 4). Negative $L(r)$ functions were observed on blocks 1 and 2 for all distances up to 5 m for both years of observation (2004 and

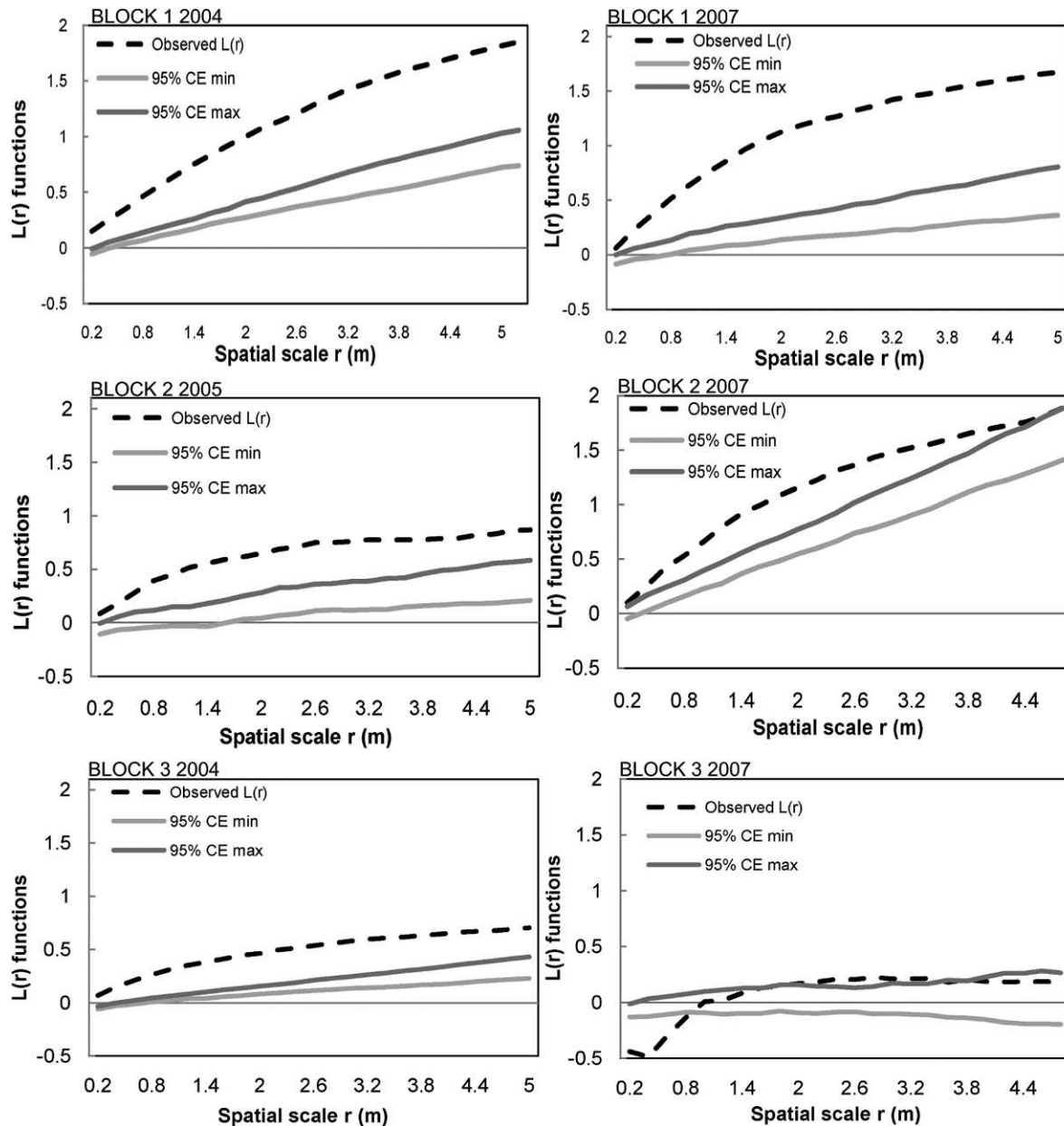


Fig. 2. Univariate pointpattern analysis of replicates for all blocks examining grass distribution for 2004/2005 and 2007 data using the Ripley method with 99 replicates for confidence limits. Observed $L(r)$ functions for grasses for each block (dashed line) are compared to constructed confidence envelopes for the null models of complete spatial randomness (CSR). Scale is in meters.

2007). For block 3, $L(r)$ functions were significantly negative for all distances up to 4 m for 2004 data and for all distances up to 2 m for 2007 data. Changes over time included a tendency for increasing $L(r)$ functions (becoming less negative) for all blocks at all spatial scales (Fig. 4).

Prior to the establishment of the plots and data collection, three years of below average rainfall were observed (2001–2003). Rainfall during 2004 was also below average, followed by three years of above average rainfall (2005–2007; Table 1).

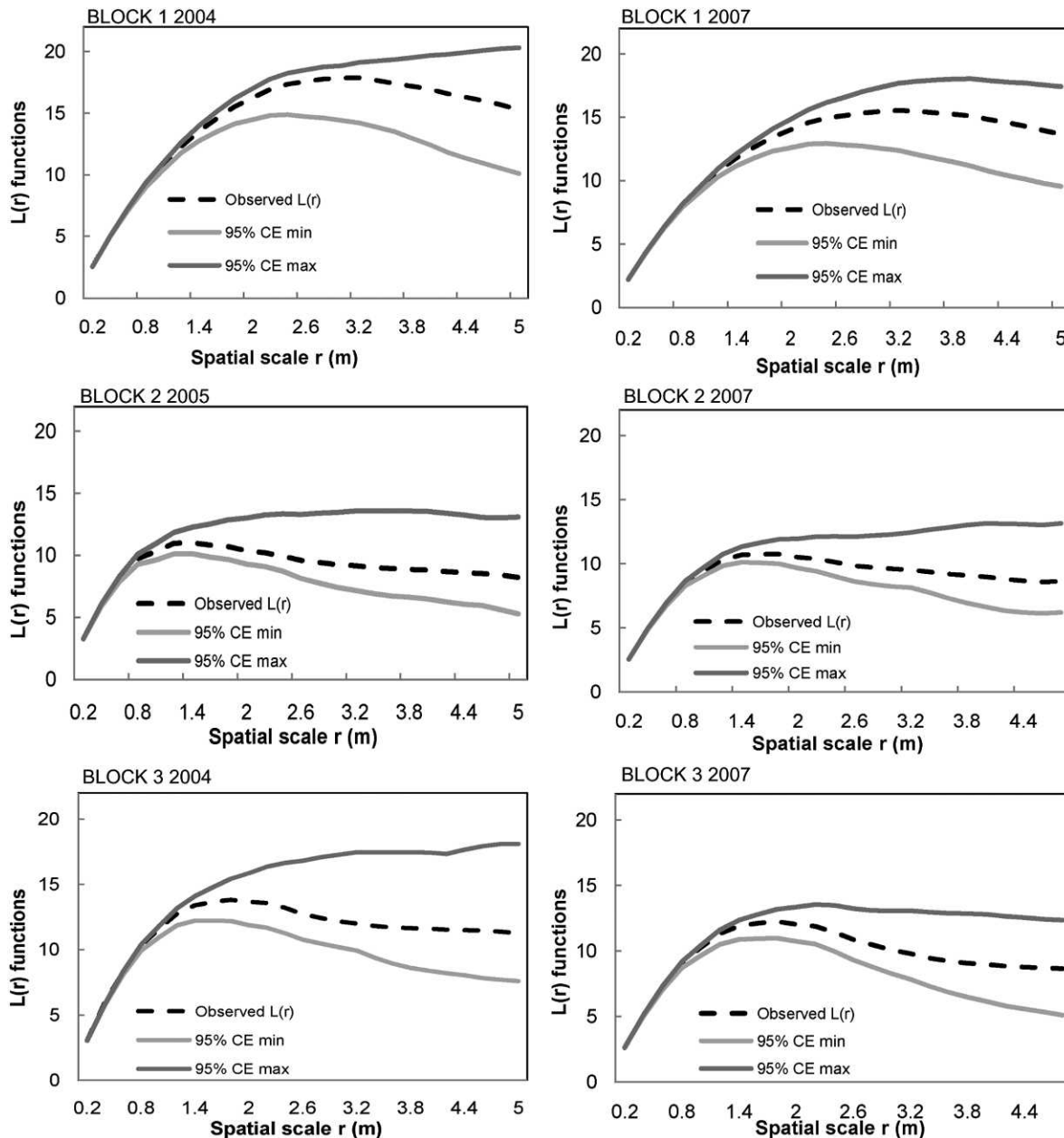


Fig. 3. Univariate analyses of shrubs with finite sizes for all blocks examining shrub distribution for 2004/2005 and 2007 data using the Ripley method with 99 replicates for confidence limits. The torus correction with guard cells was used as an edge correction method. Observed $L(r)$ functions for shrubs for each block (dashed line) are compared to constructed confidence envelopes for the null models of complete spatial randomness (CSR). The scale is in meters.

DISCUSSION

Our results indicate that grass distribution in this arid environment tends to be clumped, or

distributed closer together than would be expected if the distribution were random. These results illustrate a lack of competition among grasses, providing some support for the original hypoth-

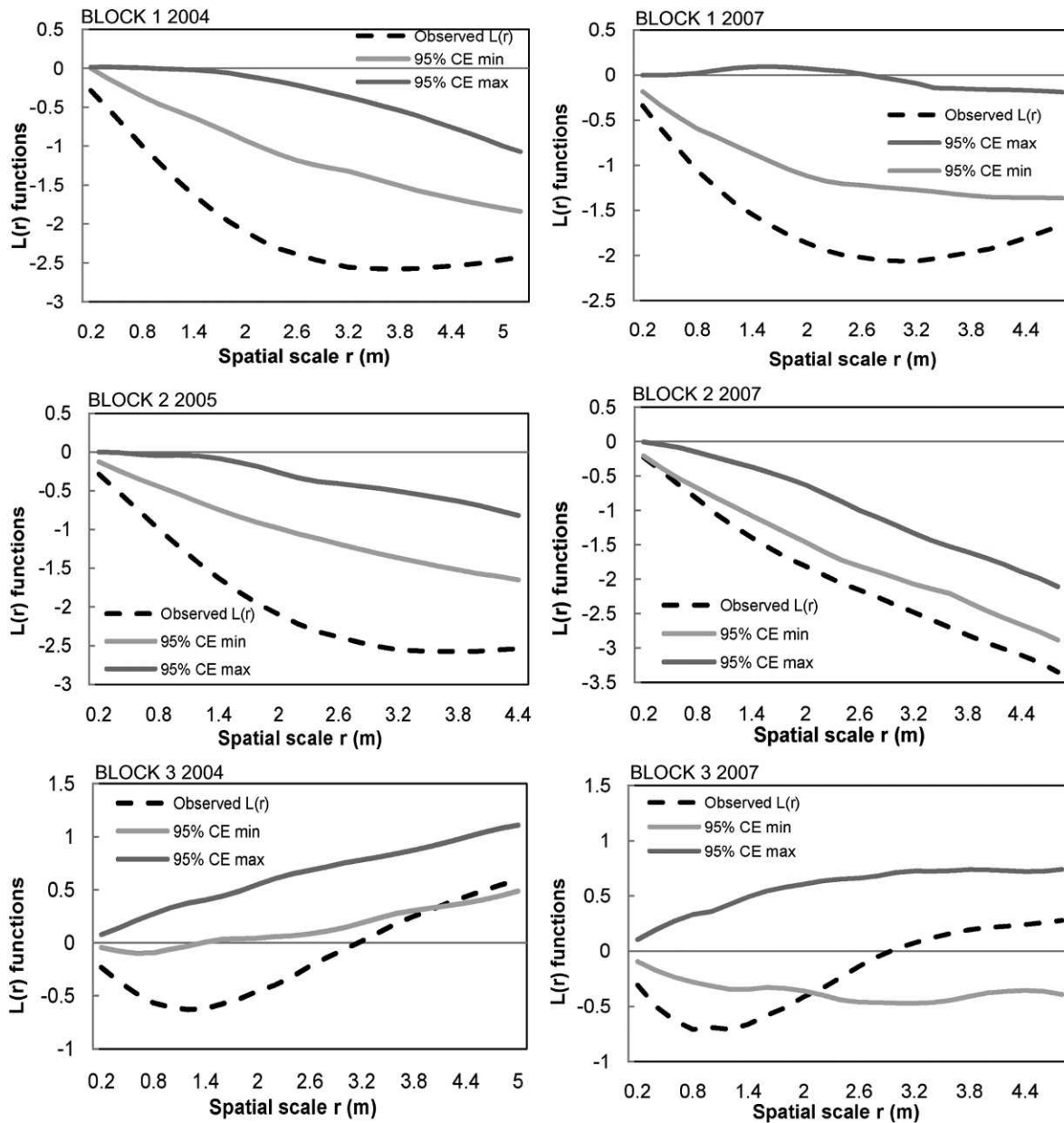


Fig. 4. Bivariate analysis of replicates for all three blocks comparing grass distribution to shrub locations for 2004/2005 and 2007 data, using the Ripley method with 99 replicates for confidence limits. The null model of CSR with antecedent conditions was used. The scale is in meters. Shrub locations were held constant and grasses were allowed to overlap shrubs.

esis proposed by Grime (1973) and further expanded by Huston (1979), suggesting that competition would be unimportant in unproductive environments. Facilitation effects among grasses appear to dictate spatial arrangement of grass clumps. This is likely caused, at least in

part, by seed dispersal close to parent plants, which is common for perennial grasses in arid environments (Bertiller 1998, Cheplick 1998, Marone 1998, Pazos and Bertiller 2008). Research in this study area has also demonstrated that soil nutrients tend to be clumped around grasses in

Table 1. Total annual rainfall data from a rain gauge in pasture 11 of the Jornada Experimental Range, 2001–2007, and percent deviation from long term average of 23.19 cm.

Metric	2001	2002	2003	2004	2005	2006	2007
Total rainfall (cm)	19.20	18.90	12.37	15.77	24.61	43.61	33.58
Deviation (%)	-17.21	-18.50	-46.66	-32.00	6.12	88.06	44.80

undisturbed areas (Li et al. 2008). The clumped distribution of soil nutrients would create relatively fertile microhabitats and facilitate the establishment of additional grasses near existing clumps. The clumped distribution could also be caused by the tendency for grasses to be distributed away from shrub canopies (discussed below) and may not necessarily be an inherent tendency for small-scale clumping, as larger-scale effects (e.g., larger holes) can influence the L-function at small distances.

Research on competition in arid environments indicates that resource timing and availability dictate whether competition will be important, and that competition will be important in these environments during times when resource availability is higher (Goldberg and Novoplansky 1997, Novoplansky and Goldberg 2001, James and Richards 2007). Although we did not specifically test this hypothesis, we did observe that the distribution of grasses on two of our three blocks became more uniform over time (2004 to 2007). Data collected during 2004 occurred after a three-year drought, while the 2007 data were collected after three years of above average rainfall (6%, 88%, and 45% above long term yearly averages for 2005, 2006, and 2007, respectively). The increased rainfall may have contributed to more uniform grass distribution over time. We did not observe this pattern for block 2, but initial observations for block 2 were made during 2005, after a year of slightly above average rainfall.

Although the distribution of grasses became more even for blocks 1 and 3 over time, grasses remained clumped at all spatial scales for block 1, while the distribution of grasses for block 3 changed from clumped during 2004 to even during 2007 up to 1m distances. It is interesting to note that most of the *B. eriopoda*, the dominant grass on block 3, which once covered much of the Jornada Experimental Range, has been substantially reduced over the last 150 years (Gibbens et al. 2005). We observed that changes in the spatial

patterns of *B. eriopoda* individuals were more extreme than the changes observed for *Sporobolus* spp., suggesting that these grasses may respond differently to resource distribution.

Mesquite shrubs in this arid grassland tend to be randomly distributed. This is not consistent with previous research at the Jornada Experimental Range (JER) showing regular patterns of shrub spacing (Okin and Gillette 2001, McGlynn and Okin 2006). We suggest that lack of competition effects among shrubs on our plots was likely the result of the very low shrub coverage (average areal coverage across all blocks: 2004 = 0.06; 2007 = 0.08). Previous examination of the distribution of shrubs at the JER has been conducted in large mesquite dune fields, and uniform shrub patches or shrub “islands” have been observed (McGlynn and Okin 2006). Our plots cover only a 10 × 20 m, so we may not have been able to effectively capture spatial patterns for Mesquite shrubs on a larger scale. However, our observations demonstrate that the pattern of shrub encroachment into grass-dominated habitat may be initially random at least on a small scale. We did observe some tendency for clumped distribution of shrubs for two of the three blocks for initial data collection at small spatial scales (<0.5 m), but not for 2007 data. Additionally, shrub distribution generally tended to become more even over time.

Given these observations, we suggest the following pattern of shrub expansion into grass dominated habitats: Small shrubs are initially randomly distributed through the grassland with some facilitation effects at small spatial scales, likely due to seed dispersal near parent plants (Bertiller 1998) and greater soil nutrient concentrations under shrub canopies (Li et al. 2008). As shrub coverage increases due to shrub growth and additional colonization, competition effects become increasingly important and the spatial distribution becomes more even. This is supported by our data as shrub coverage did increase slightly from 0.06 to 0.08 over the three-year

period, but the distribution became somewhat more even, and the facilitation effects initially observed at small spatial scales disappeared.

Grasses on our plots were distributed away from shrub canopies, indicating competition effects between grasses and shrubs. These observed competition effects were present for all blocks for both years of observation at almost all distances up to 5 m. This is consistent with previous research indicating that grasses and shrubs do compete for resources in arid environments (Belsky 1994, Le Roux et al. 1995, Golluscio et al. 1998, McCarron and Knapp 2001, Rodriguez et al. 2007), and does not provide support for the two-layer soil water model proposed by Walter (1971) for this particular environment.

Interestingly, we did not observe facilitation of grasses by shrubs, as grasses were over-distributed with respect to shrub canopies even at the smallest spatial scales. Although some grasses were found inside shrub canopies, the number observed was less than would be expected if shrubs actually facilitate grass growth. These results were not consistent with previous research examining spatial patterns in arid environments (Tielborger and Kadmon 2000, Flores and Jurado 2003, Riginos et al. 2005, Maestre et al. 2005, Armas et al. 2008), and may also be the result of the low shrub coverage on our plots.

Slight changes over time were observed, including an increase in $L(r)$ values for all blocks, indicating more clumping and a slight decrease in competition for grasses with respect to shrub locations. Although changes were not dramatic, it is interesting that we did observe minor changes given the small time-frame of the study (3 years). That increased precipitation correlated with a decrease in competition between grasses and shrubs from 2004 to 2007 could indicate that grasses are more severely affected by drought conditions than shrubs (greater competition effects during dry years). More controlled experiments that manipulate water availability for grasses and shrubs and determine the effects on spatial patterns are needed in this environment to support our preliminary observations.

The observed spatial patterns of vegetation on our plots provide some insight into the community structure of a desert grassland habitat with minimal shrub encroachment. Grass distribution

tends to be clumped, with shrubs randomly distributed throughout the grass dominated areas. Grasses are distributed further away from shrub canopies than would be expected if the distribution were random, providing support for the hypothesis that grasses and shrubs do compete for resources in this unproductive environment. Additionally, the changes we observed in the spatial patterns over time provide some insight into the mechanisms of shrub expansion in a desert grassland habitat. Specifically, the patterns observed showed increasing evenness among shrubs and among grasses, and decreased competition effects between grasses and shrubs. These changes coincided with an increase in water availability and indicate that, although competition within functional types (grasses or shrubs) increases with increasing water availability, competition between different functional groups (grasses and shrubs) may be greater when water availability is lower.

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APPENDIX

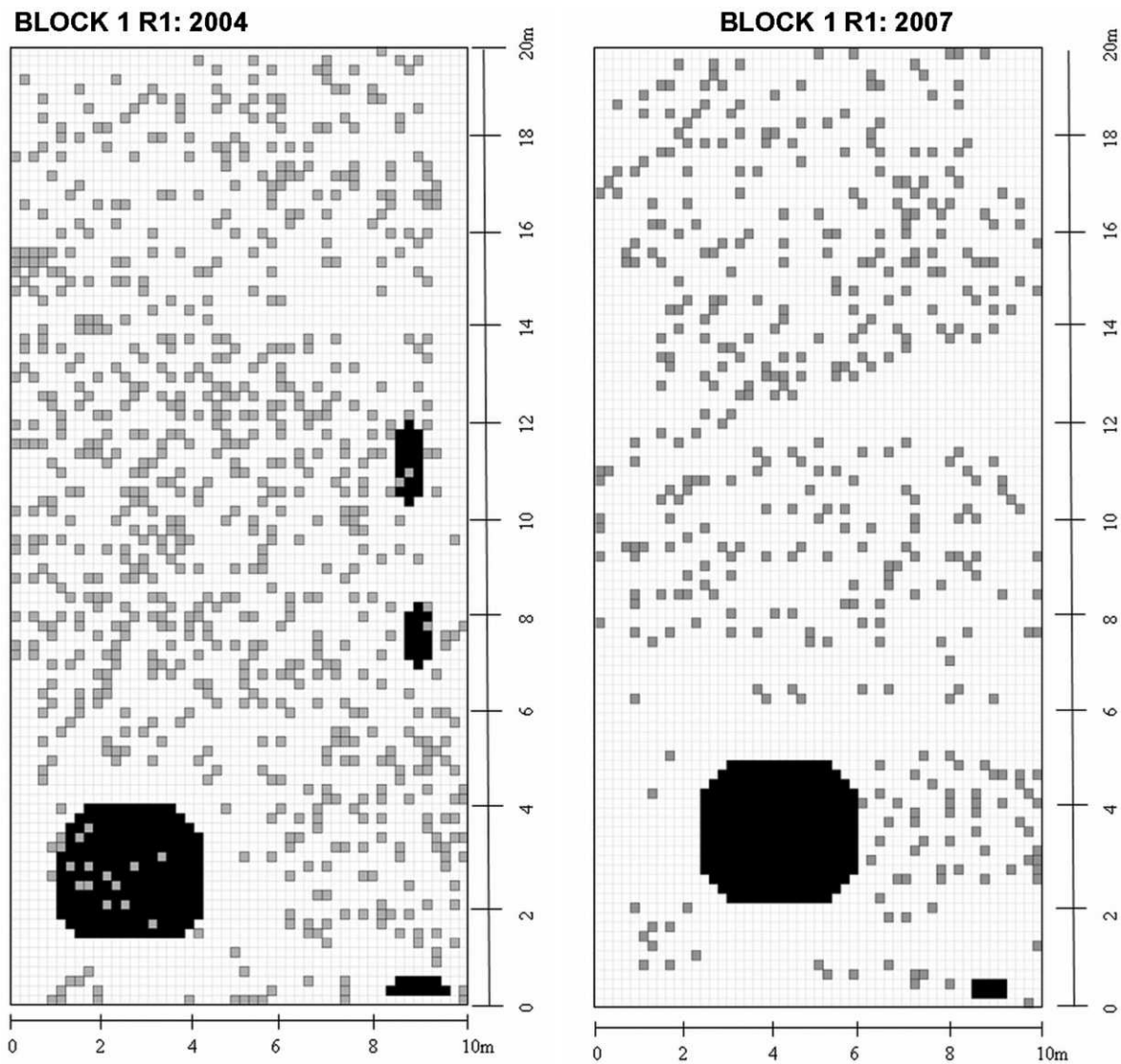


Fig. A1. Vegetation distribution maps (10×20 m) showing individual grasses as points (gray) and *Prosopis glandulosa* shrubs of finite size (black shapes) for block 1 for all replicate plots (R1–6) and for both years of data collection. These maps were used for the analysis of spatial patterns using the software package, *Programita*. Each cell is 0.2×0.2 m.

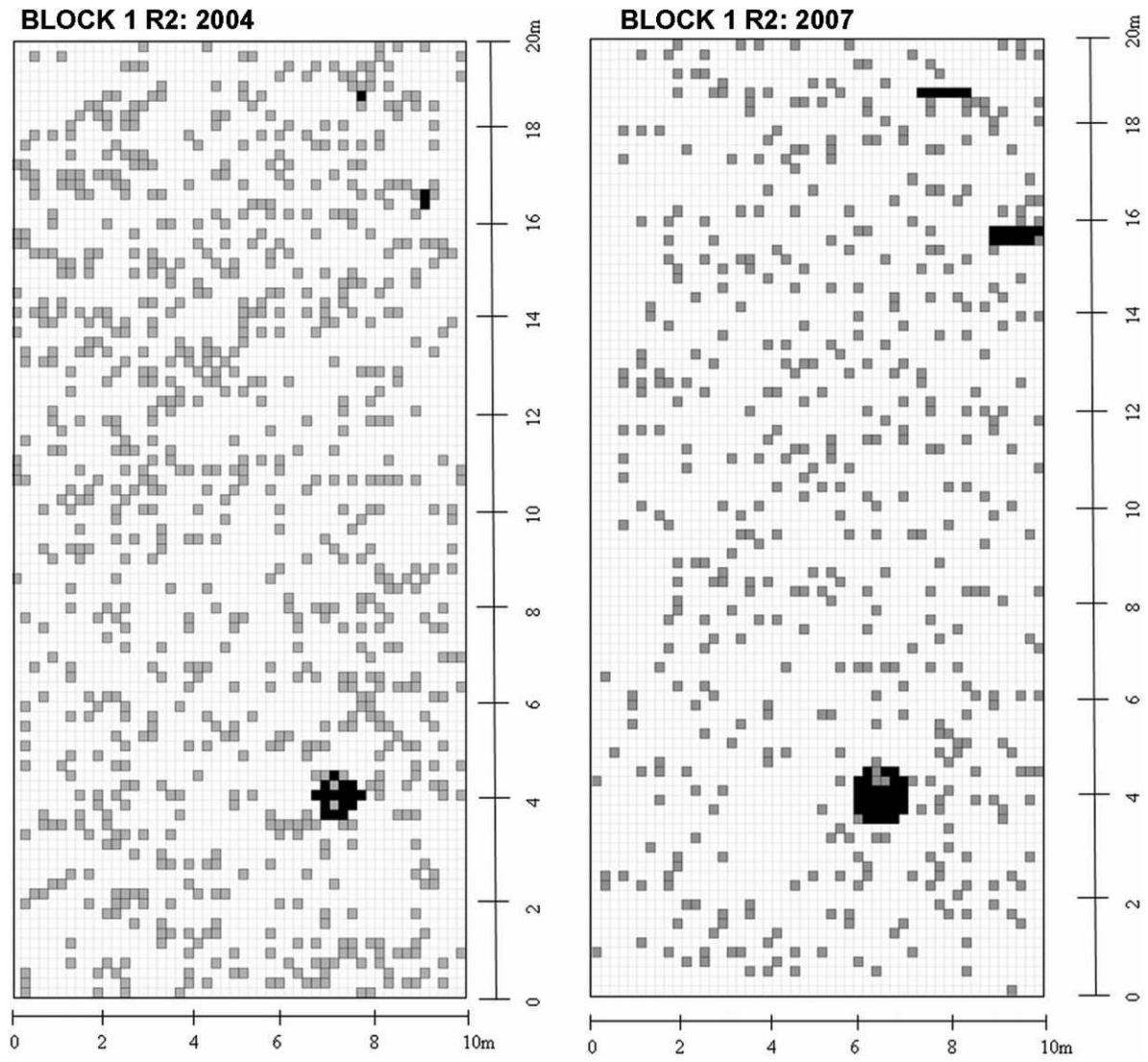


Fig. A1. Continued.

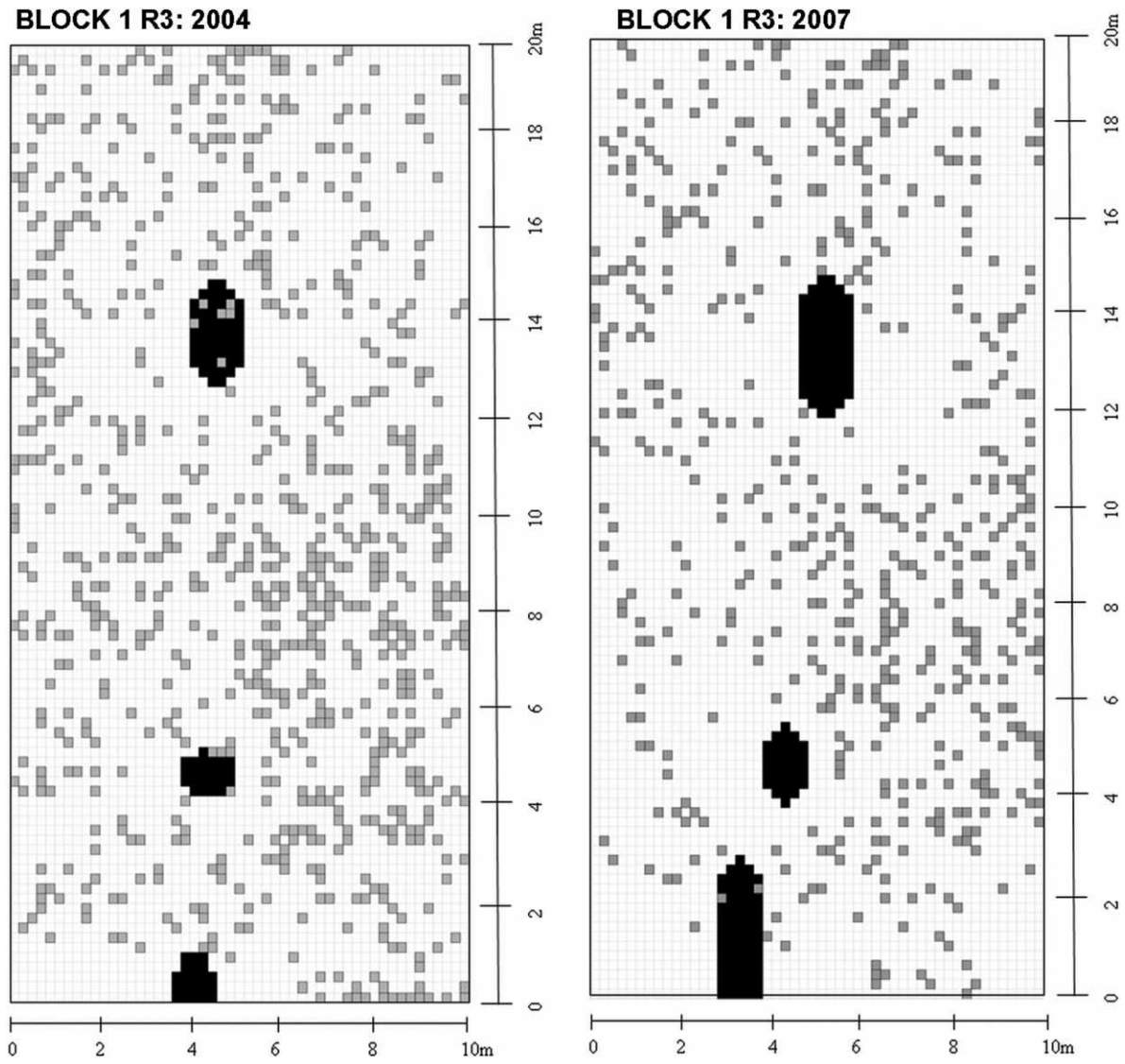


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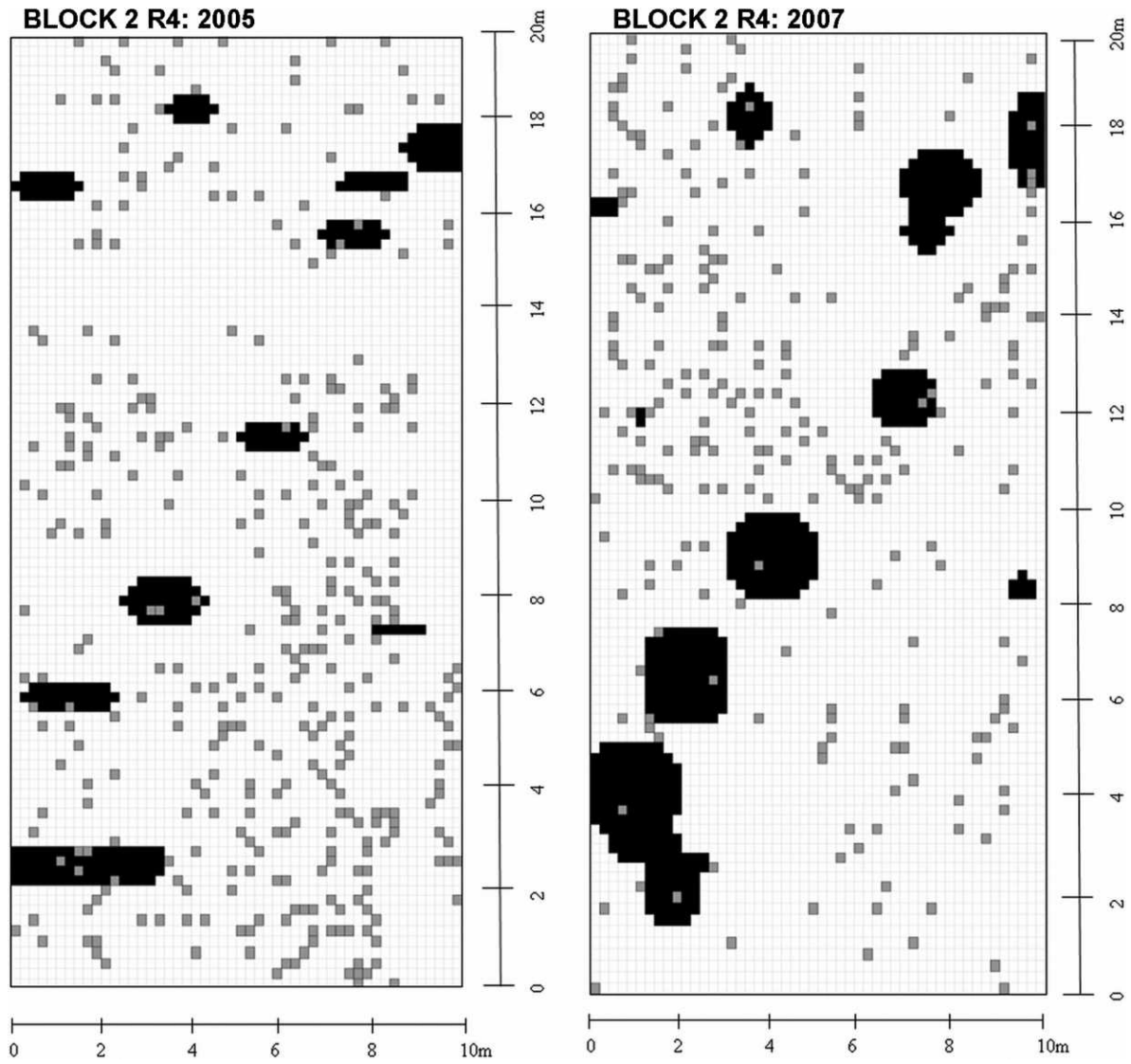


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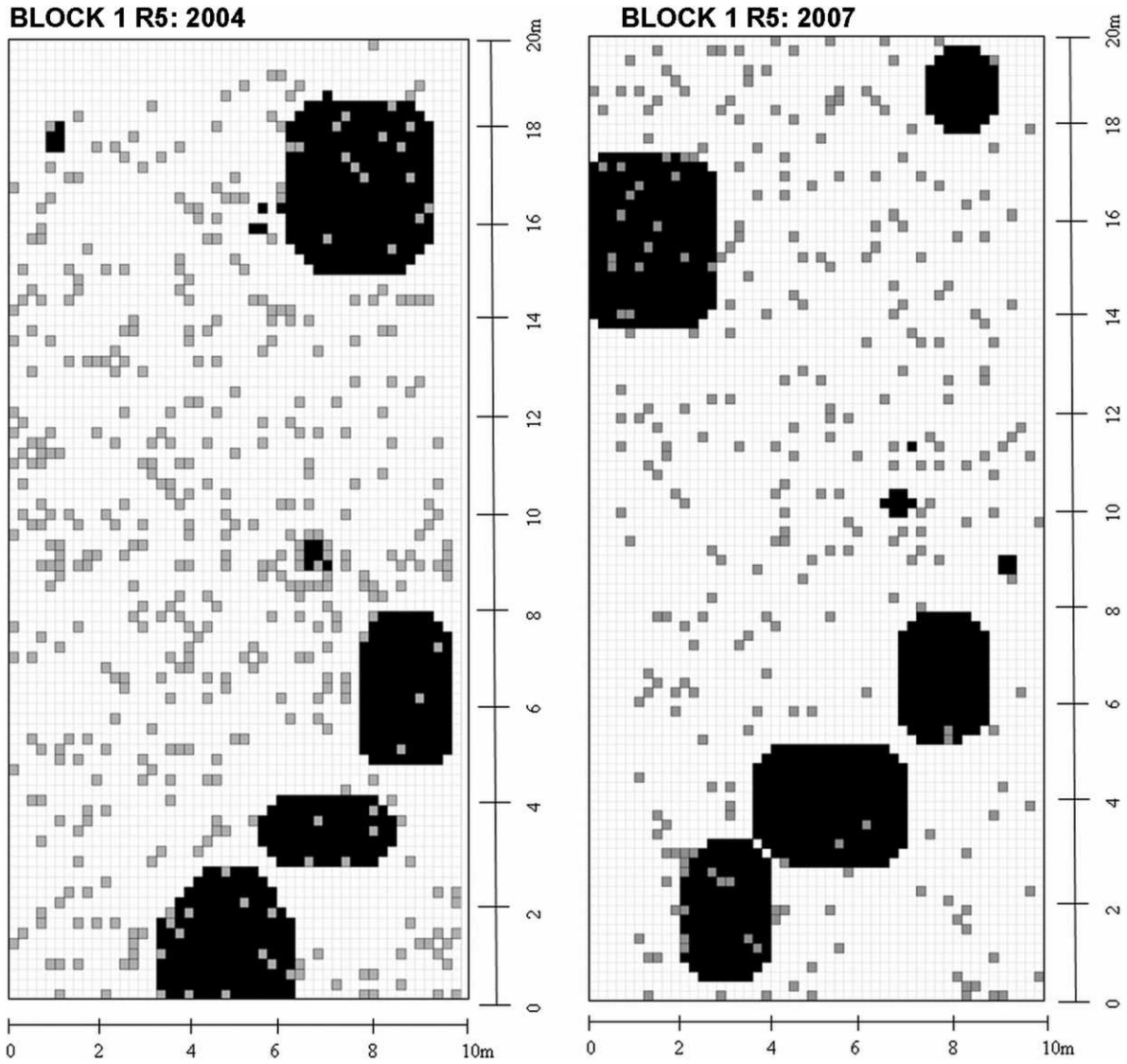


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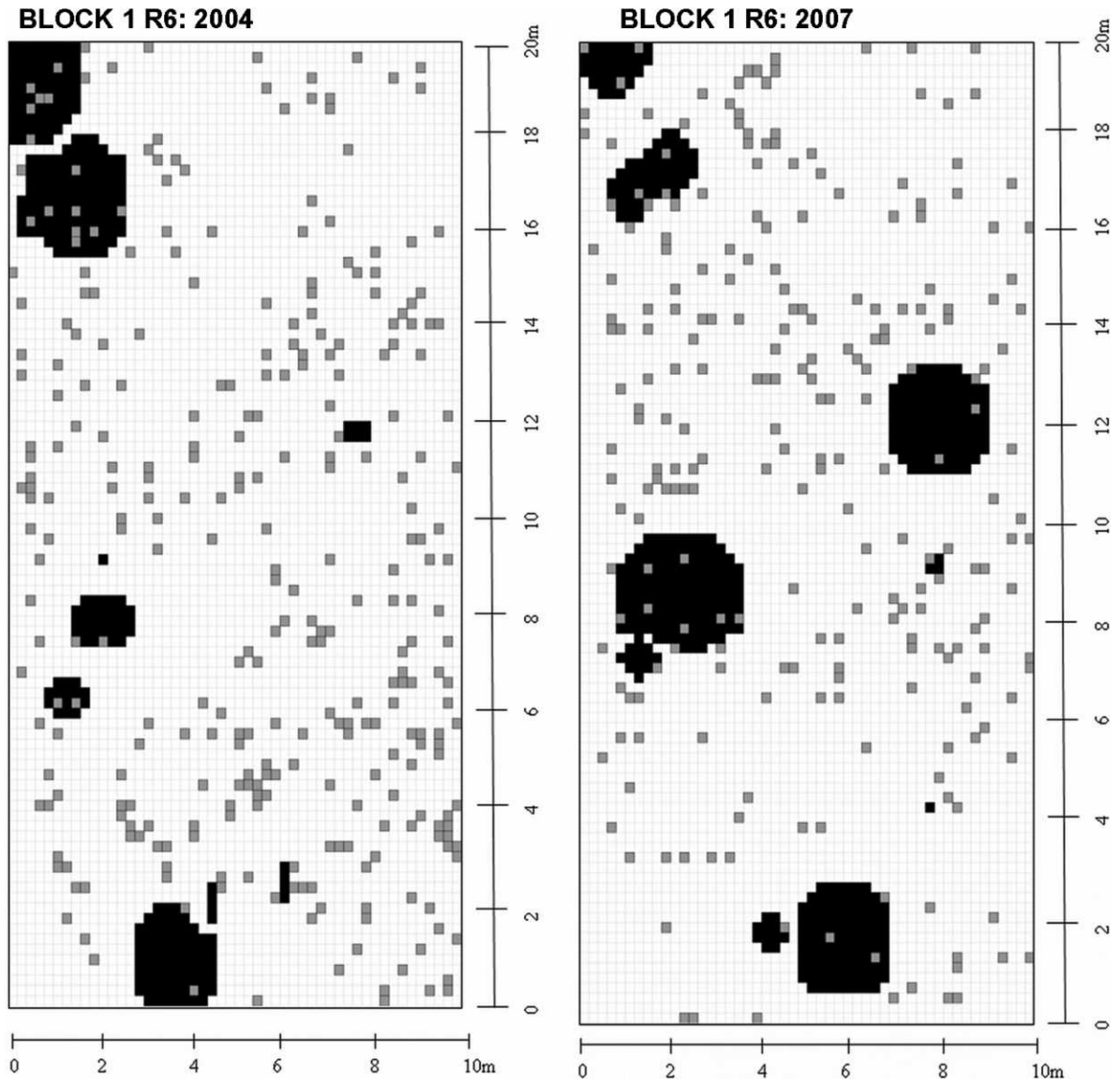


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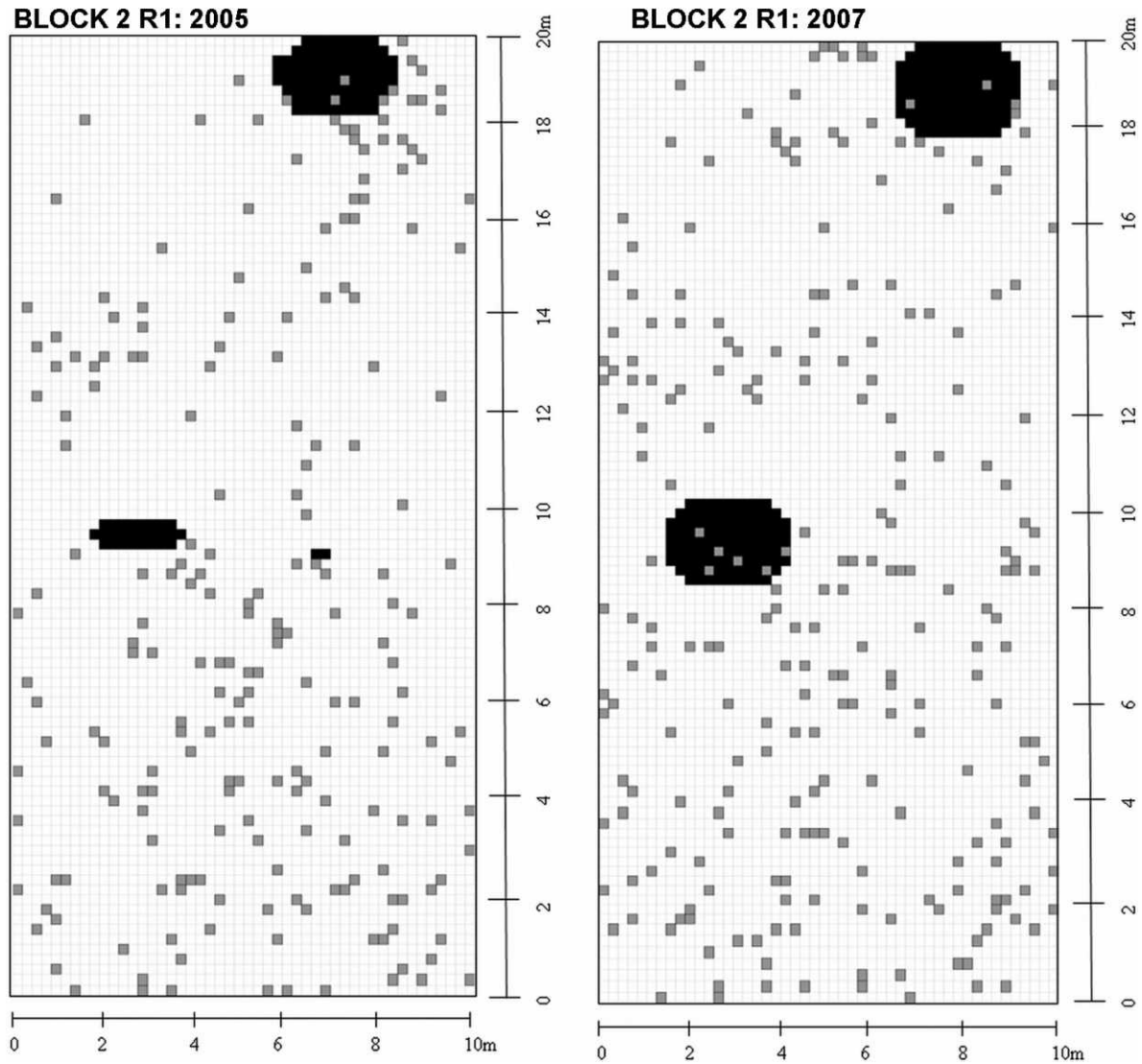


Fig. A2. Vegetation distribution maps (10×20 m) showing individual grasses as points (gray) and *Prosopis glandulosa* shrubs of finite size (black shapes) for block 2 for all replicate plots (R1–6) and for both years of data collection.

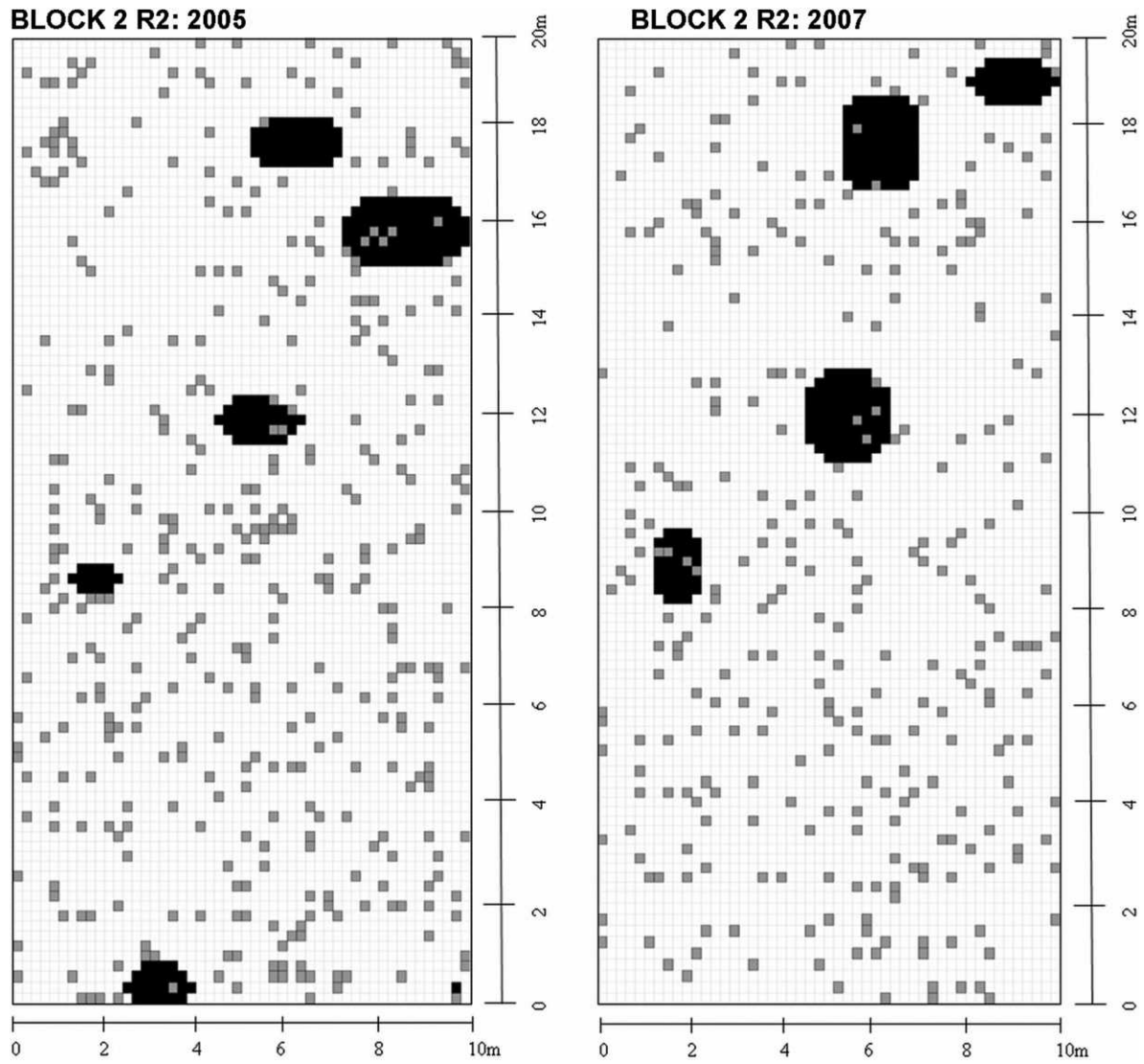


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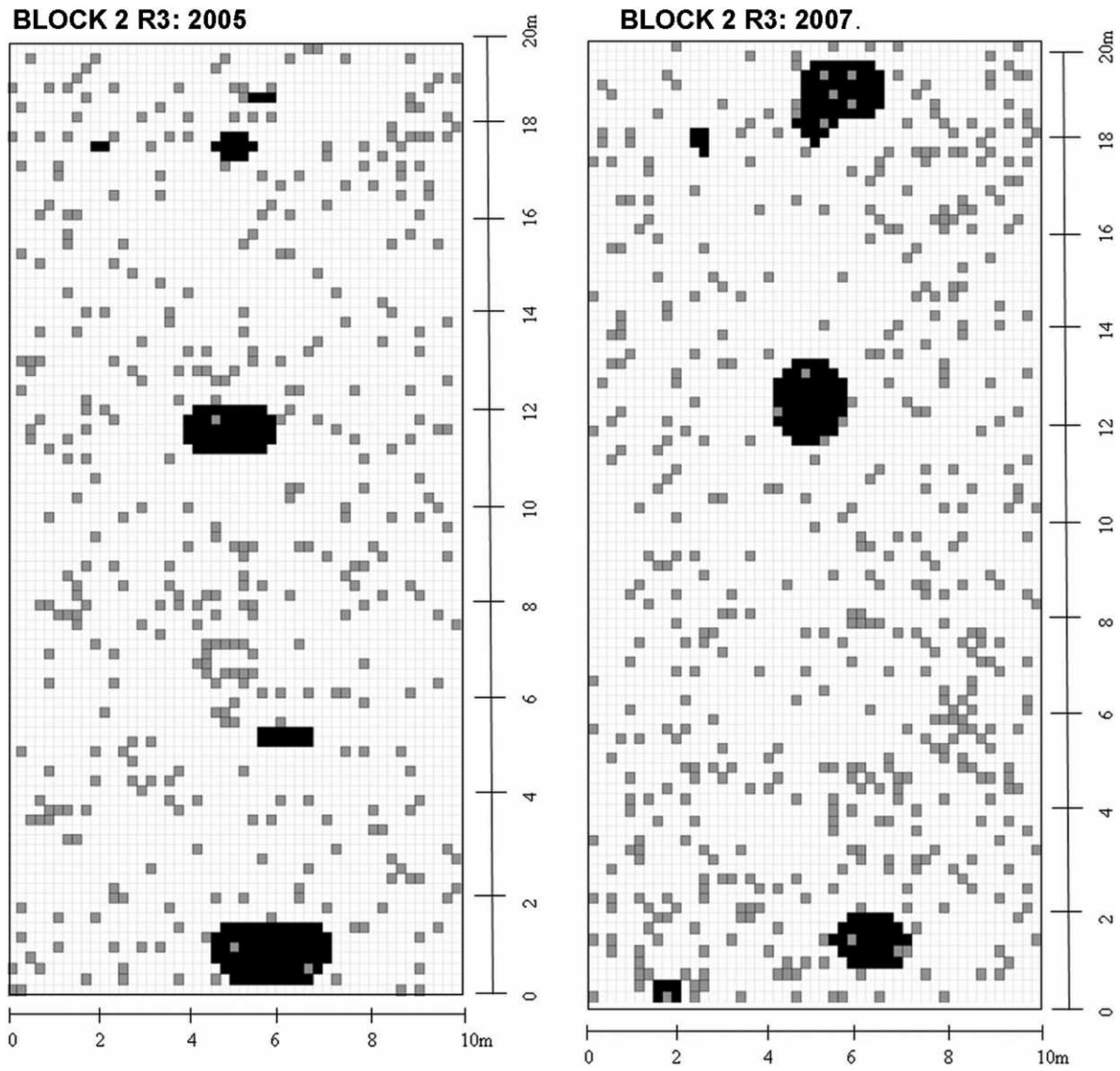


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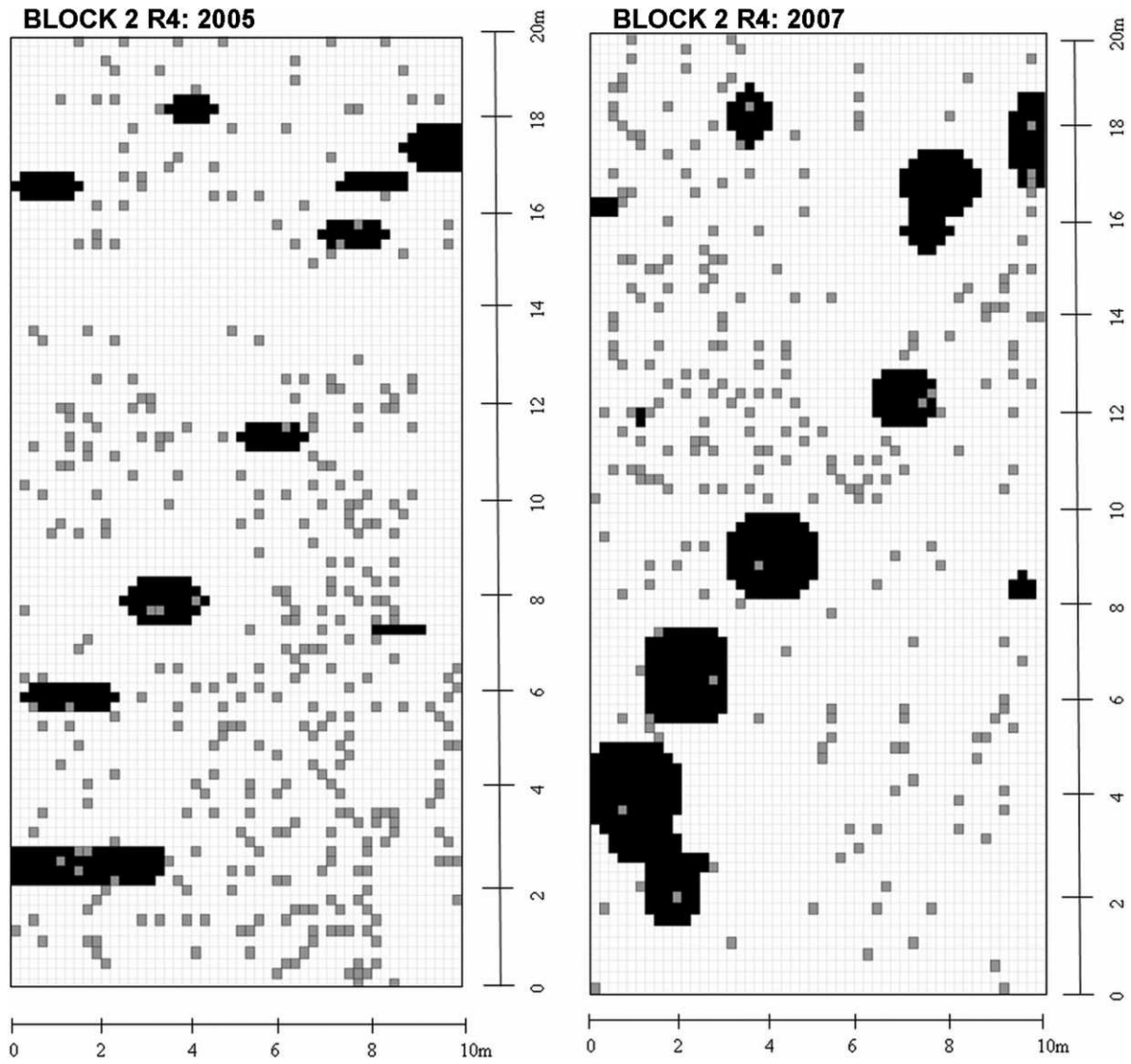


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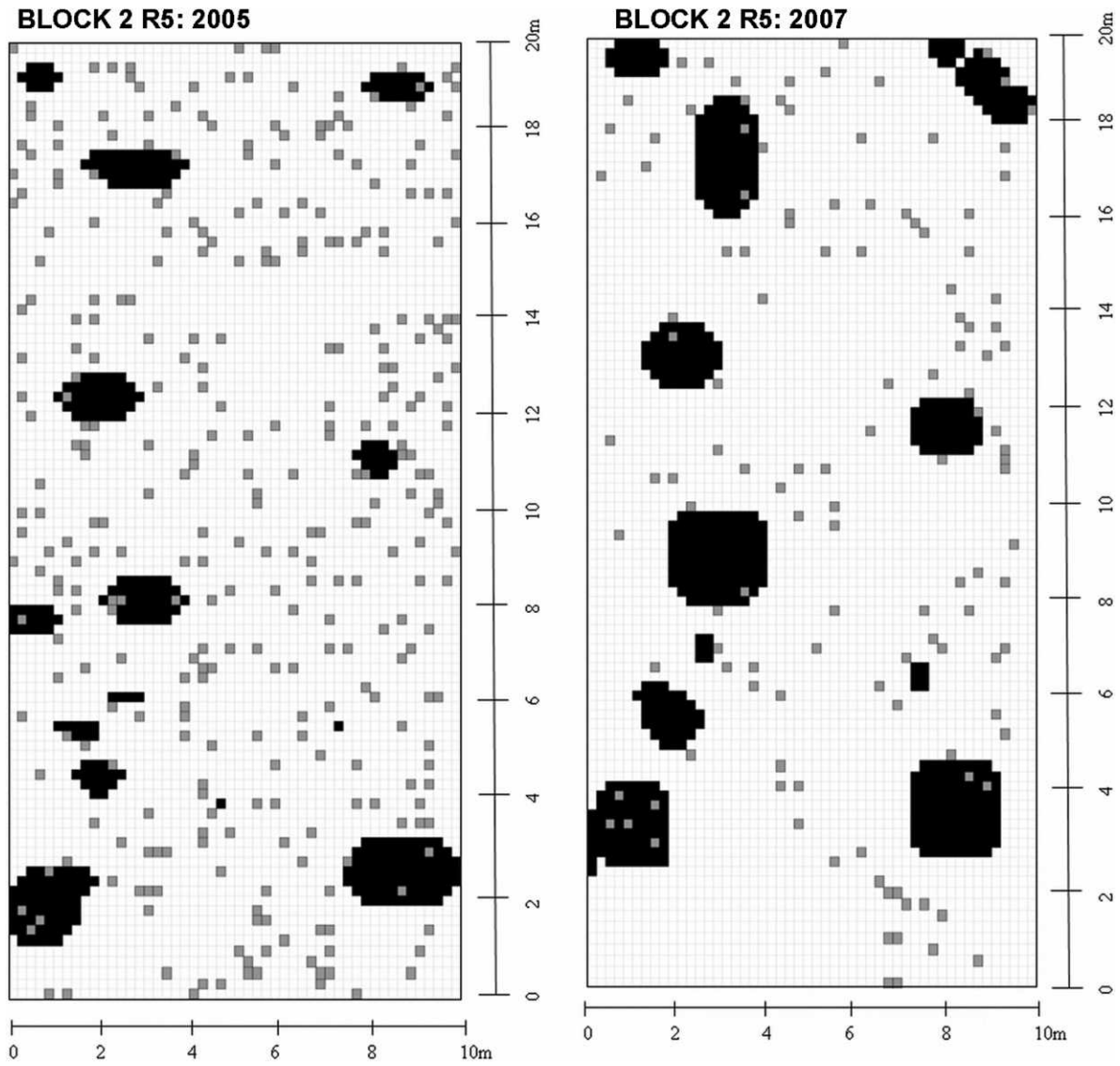


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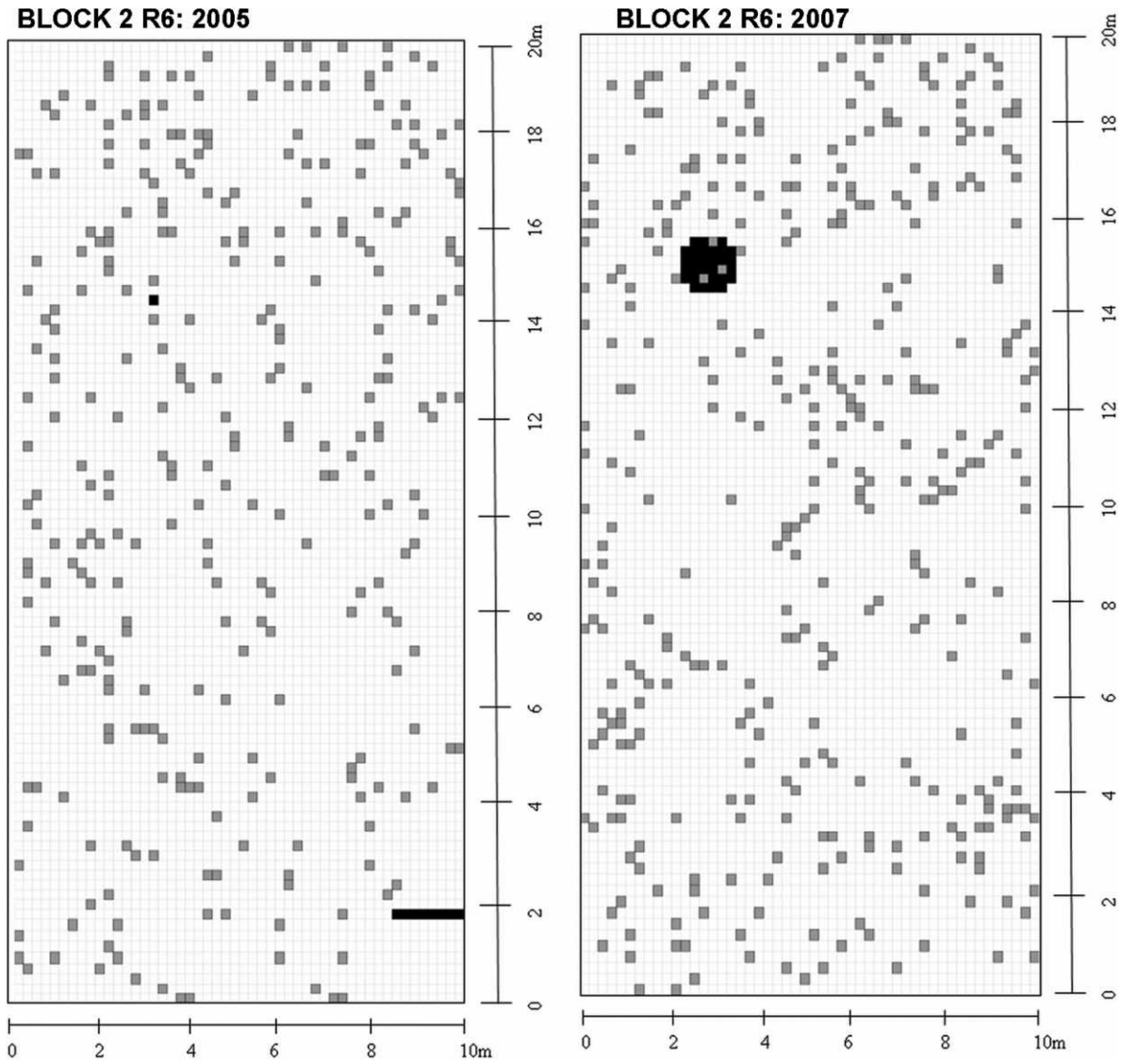


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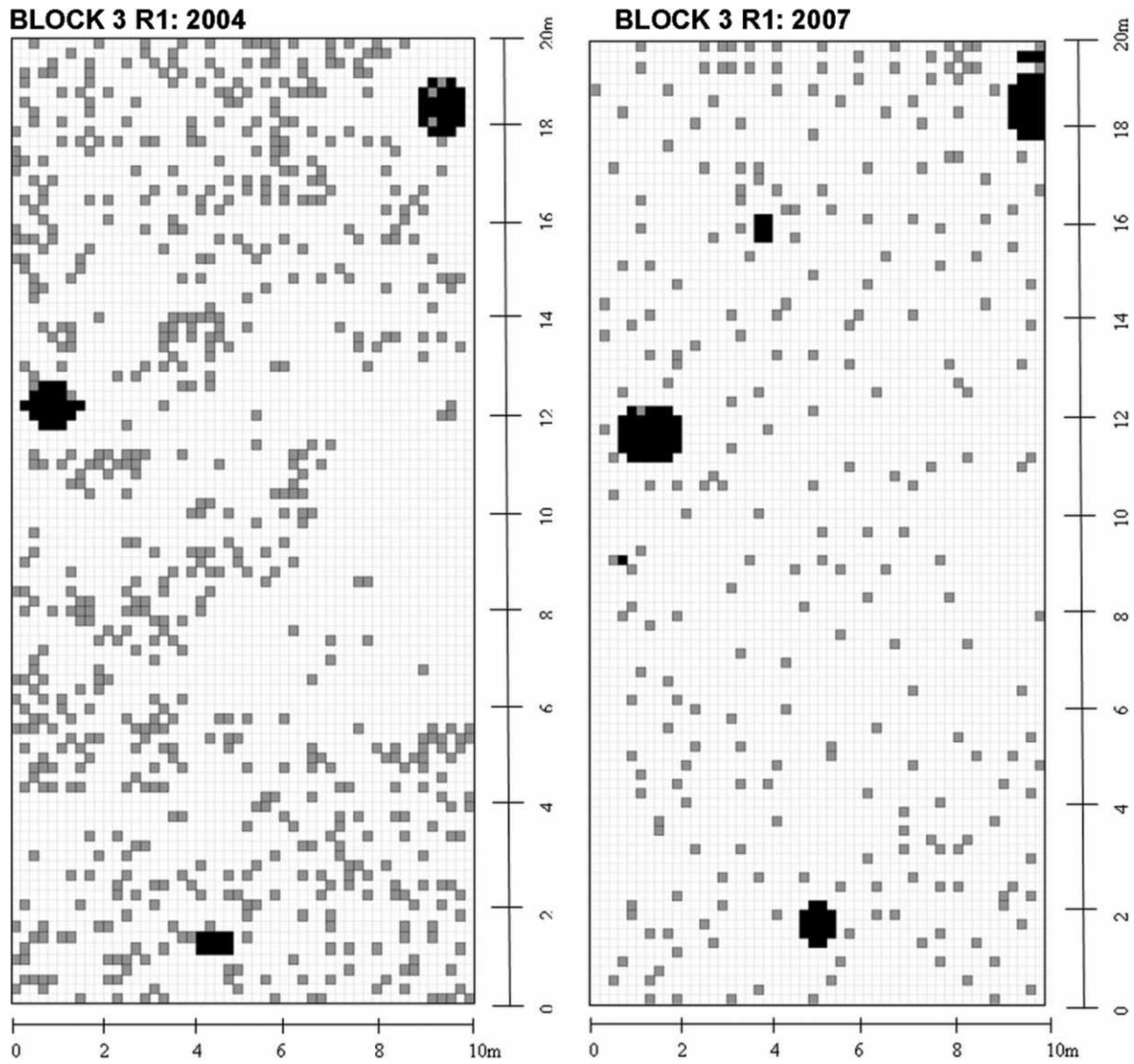


Fig. A3. Vegetation distribution maps (10×20 m) showing individual grasses as points (gray) and *Prosopis glandulosa* shrubs of finite size (black shapes) for block 3 for all replicate plots (R1–6) and for both years of data collection.

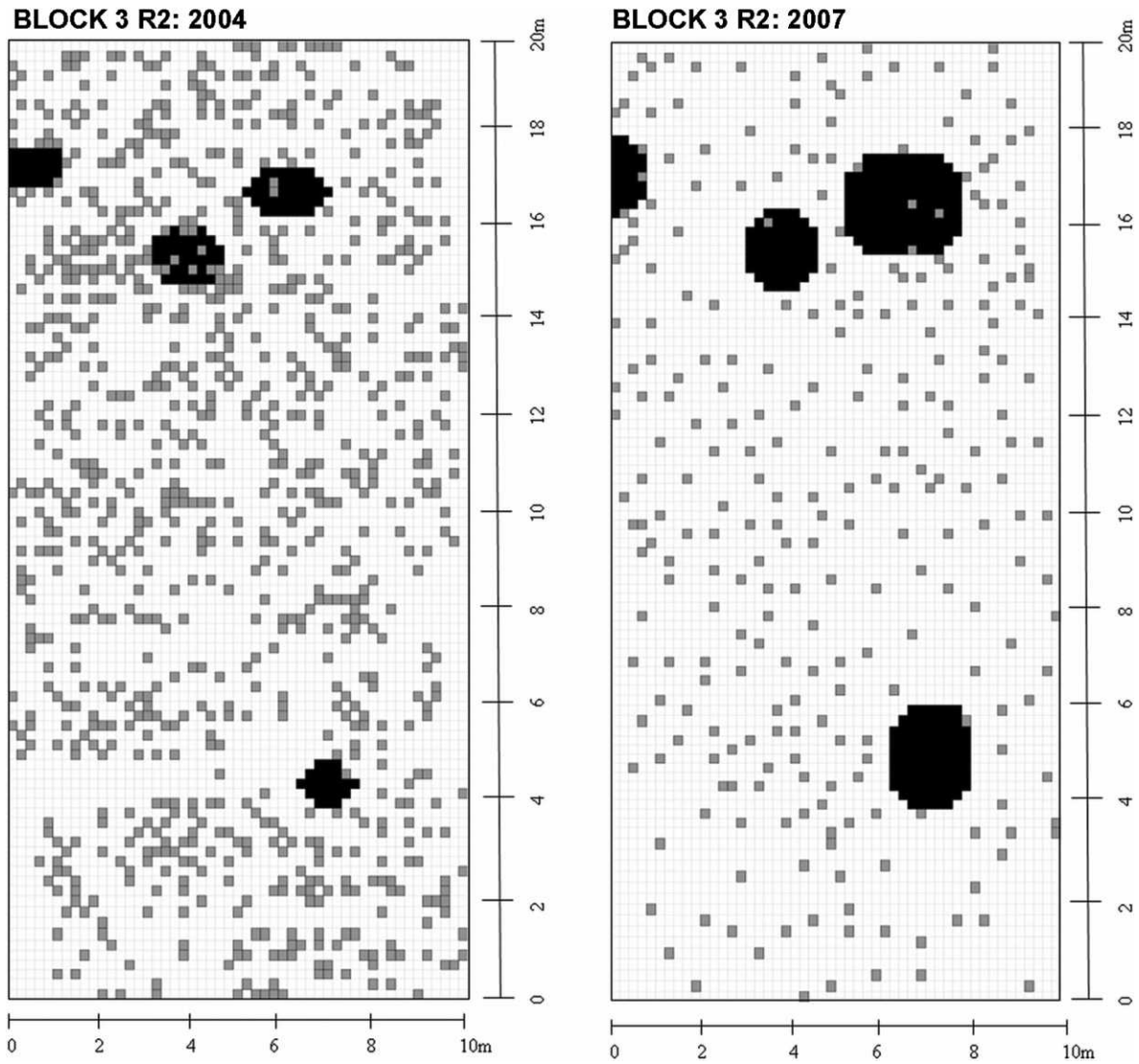


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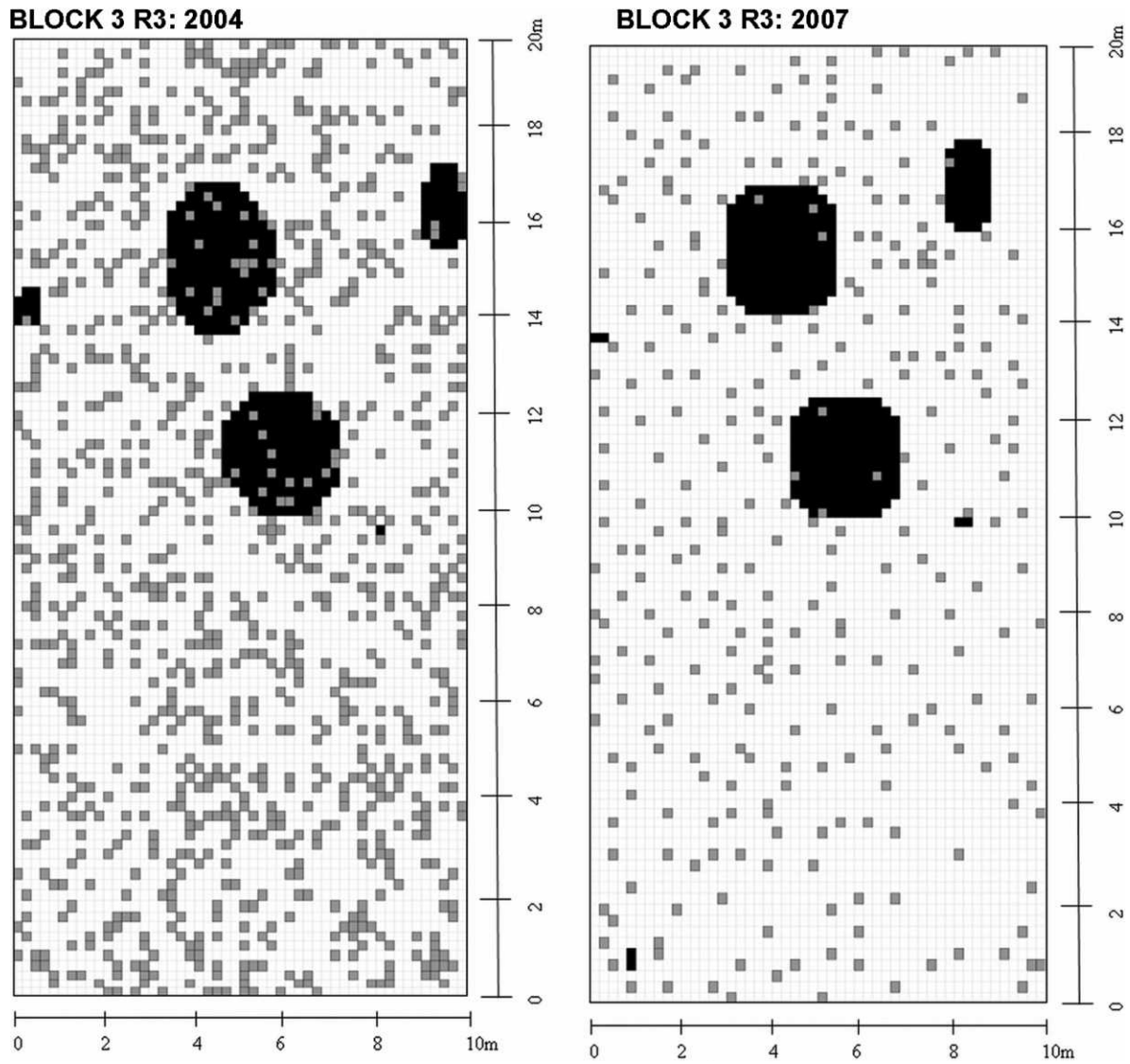
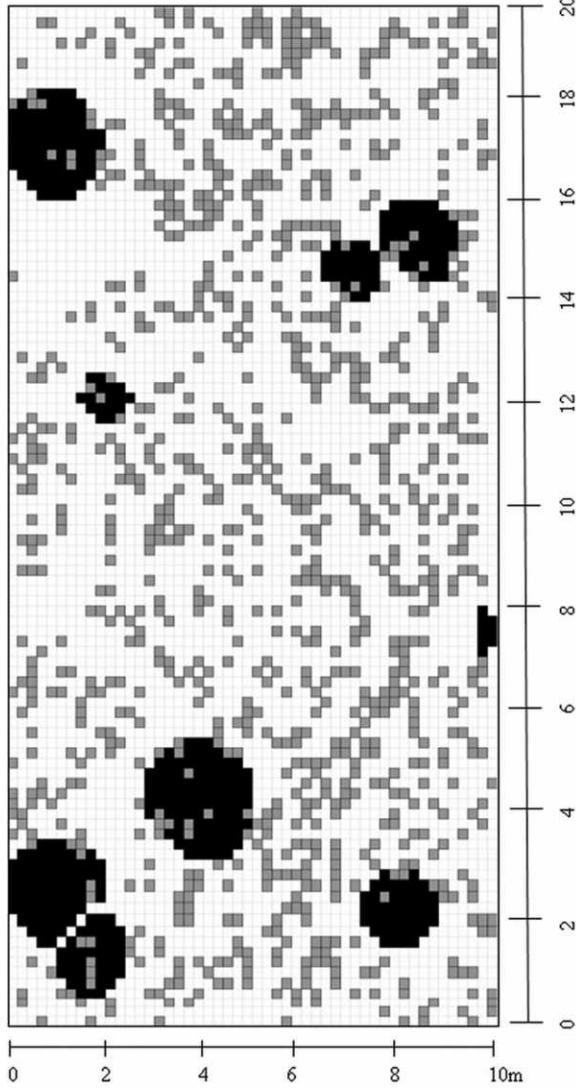


Fig. A3. Continued.

BLOCK 3 R4: 2004



BLOCK 3 R4: 2007

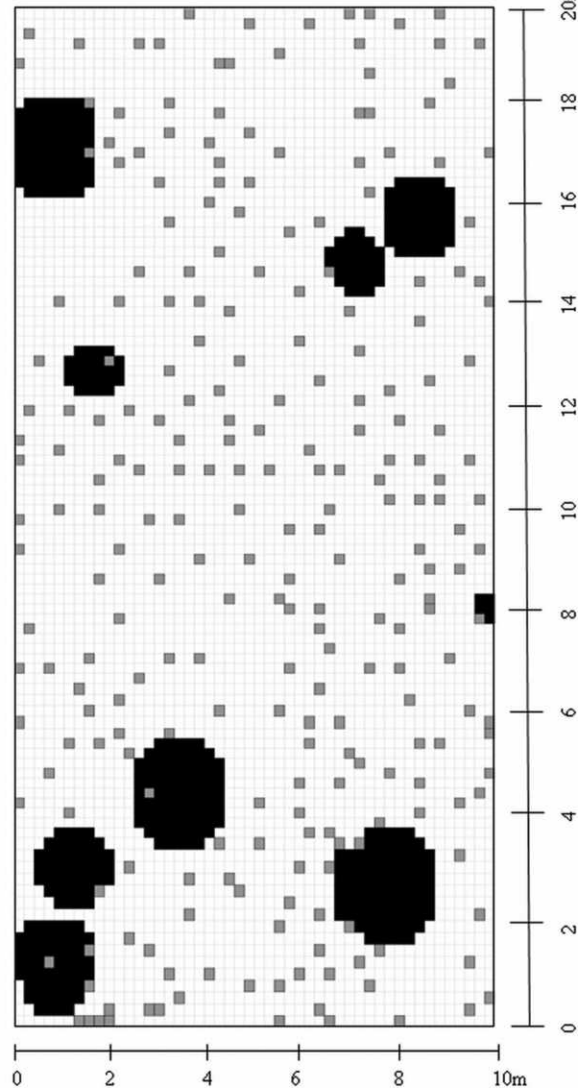


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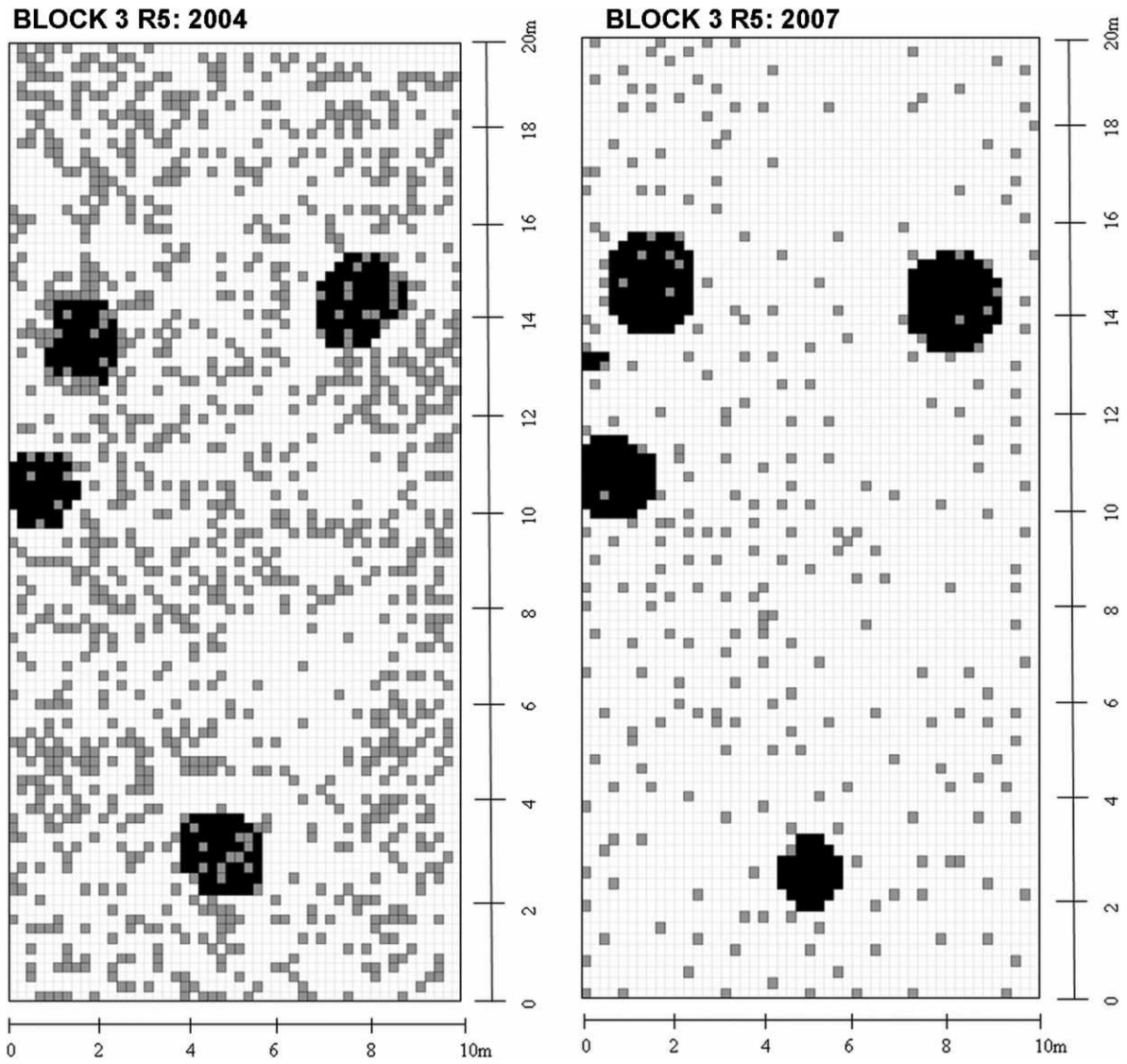


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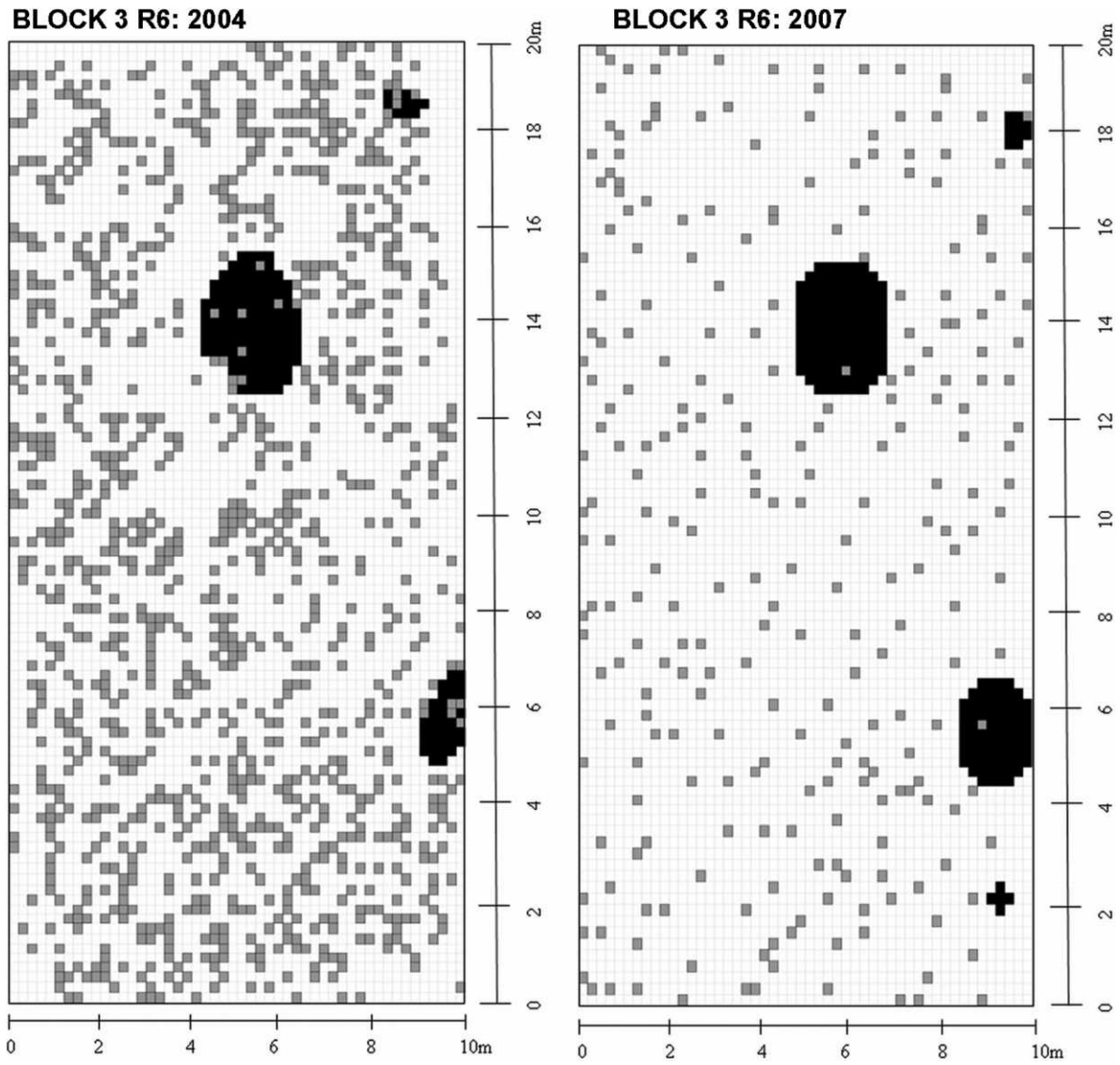


Fig. A3. Continued.