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MODELLING THE SPATIAL AND TEMPORAL DISPERSAL OF *Cuscuta europea* (Cuscutaceae)

ABSTRACT: *Cuscuta* species are interestingly behaving plant parasites of very different plant communities all over the world. Under warmer climate conditions they can act as dangerous pests, while in the northern countries they are considered as threatened species. Moreover these plants have a special strategy to find their host, called foraging. Chemical clues emitted by the host plants attract the parasite shoots to the most proper host. Recent papers investigate the host preference of *Cuscuta* species. In our research, we examine the appearing spatial patterns with both experimental and modelling tools. Our objective is to reproduce this phenomenon in the virtual space and find the model, which best describes the emerging spatial patterns. For the modelling cellular automata are used, which are commonly used tools in spatial ecology. These are spatially explicit dynamic models, where both time and space are discrete. The graphical representation is a squared lattice. Every square - also called cell - in the lattice has a state (e.g. soil, plant, parasite) represented with an appropriate colour. In this paper we present the results of our field observations as well as the mathematical models considered.

KEY WORDS: *Cuscuta*, parasite, cellular automata, spatial pattern analysis

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1. INTRODUCTION

Cuscuta species are fast growing plant parasites of annual and perennial plant communities. Approximately 200 species are known worldwide from the tropics to the northern areas. Their ecological role changes with the latitudes due to the different climate conditions. Although they have a positive effect on the development of natural communities, they become dangerous pests on agricultural sites (Runyon 2009, Albert 2008). Air temperature and humidity are the main factors influencing the dispersal. Among some other species, they have an interesting behaviour, called foraging. This is a decision-based behaviour, meaning that these species are able to make decisions during their host finding, based on the chemical clues received from the potential host plants. This searching type behaviour and the fractal-like clonal structure of these shoot parasites make this issue a very complex modelling task. Investigating such processes through the appearing patterns could help to manage foraging organisms, both in nature conservation (Michelle 1997) and pest management (Lanini and Kogan 2005), (Aly 2007).

The modelling of the dispersal properties of *Cuscuta* species is not a new idea (Kelly 1990), (Kelly 1994), (Szymanski 1994), (Kelly 1999), however current works do not consider this issue from a two dimensional modelling point of view. Recent papers take spatial context into account (Li and Dong 2009)0, but there is still a lack of computer-aided simulations in this topic. Some cellular automaton models concerning other clonal plants already exists (Oborny 1994), (Kun and Oborny 2003), (Magyar and Kertész 2005), (Magyar and Oborny 2007), focusing on the spatial pattern formed by the individual decisions of the plants. Our aim is to study the attributes and spatial spreading of *Cuscuta* species by two dimensional cellular automaton models with graphical representation of their spatial structure.

2. MATERIAL AND METHODS

Our research includes three essential steps:

- Field observation documented on photographs
- Image processing to gain data
- Modelling and simulation to describe dispersion patterns of *Cuscuta*s

2.1. Field observations

An outdoor experiment was carried out to observe the patterns generated by the foraging behaviour within natural conditions. The object of our study was a big metapopulation of *Cuscuta europaea*, situated on a public square, called Honfoglalás Square in Békés, Hungary. GPS Coordinates: 46.769891, 21.125721. The area of the field is approximately 1000 square meters. The vegetation period of *Cuscuta*s starts around the end of May in Hungary. We observed the first shoots on 10 May, 2011. The two observation periods were between 17 May and 13 June and from 21 June to 1 July, 2011. In each observation period 10 randomly chosen permanent quadrats were marked out (one by one meter square). Digital photographs of the quadrats were taken every day, at the same time (15:30 pm). Due to the different light conditions, the colour balance of the pictures differs noticeably. There were 28 photos taken in the first time series, representing a 4 weeks long vegetation period. The second observation series contains 10 pictures of each marked quadrat, investigating a shorter time period. The flowering period started during our second observation period.

(Fig. 1)

2.2. Image processing

The raw pictures were taken in RAF format, with a Fuji Finepix 7000 digital camera, fixed on a stand at the edge of the quadrats. Due to this method the raw pictures are perspective distorted, hence perspective correction was necessary. For the image processing Gimp 2.6.12 (http://www.gimp.org/) and Wolfram *Mathematica* (www.wolfram.com) were used. Cropping was done to cut the photo edges and perspective correction to avoid inaccuracy in coverage measurement. In order to make *Cuscuta* shoots visible among the leaves and shoots of other plants colour transformation was necessary. Therefore the "Maximum RGB" function of Gimp software was used to mark *Cuscuta* cells with red colour, and all other plants and the soil with green or blue. On this way we could select the red pixels and ignore all the others. Frequency of the red pixels corresponds to the coverage of *Cuscuta* stems.

2.3. Modelling

Using Wolfram *Mathematica*, a simple cellular automaton model was constructed to study the dispersion pattern of *Cuscuta* patches and make some estimation about the colonization and extinction parameters of the general dispersion. Hence, essential simplifications were taken (see below), and the model can be considered as cellular automaton analogue of "SIR" models (**S**usceptible, **I**nfected, **R**ecovered) in epidemiology. The literature of SIR and other epidemiological models is very large (Farkas 2001), (Brauer 2008).

The cell-space is a 64x64 square lattice with Moorian neighbourhood (North; North-East, East,...) of the cells (Rácz and Karsai 2003). The boundary conditions are periodic, so the lattice is practically a surface of a torus. The environment is homogeneous; host cells provide equal quality for the parasites. The occupation is excluding, i.e., each cell can be occupied by either a host (marked with light grey), a parasite (grey) or becomes extinct (black ones).

Hence, the system enables 3 different states for the cells: host, *Cuscuta*, extinct. Due to the short time interval of both observations, some other simplifications are applied. As the development rhythm of the host species is usually much slower than that of *Cuscuta*, the host cells are assumed neither colonizing nor dying out.

To keep the model very simple we have only 2 parameters, *e* and *c*. The first parameter *e* refers to the extinction probability uniformly for any *Cuscuta* cells. Host cells don't become extinct. The second parameter, *c* refers to the colonization of the host. A host cell can be colonized by only the *Cuscuta* cells in its neighbourhood. The colonization depends on the neighbourhood according to the binomial distribution. Hence, let *c* mean the probability of colonization of a host cell, completely surrounded by only *Cuscuta* cells. Then for *k* (=0,1,2,...8) *Cuscuta* neighbours the probability is $1-(1-c)^{k/8}$. *Cuscuta* self-evidently cannot colonize empty cells, only host cells. Colonization of *Cuscuta* cells by host cells is also forbidden. Equations 1) and 2) contain the transition probabilities for the host and *Cuscuta* cells respectively; *k* is the current number of *Cuscuta* neighbours.

$$\mathrm{H} \to \begin{cases} 0 & \mathrm{P(H \to 0)} = 0 \\ \mathrm{C} & \mathrm{P(H \to C)} = 1-(1-c)^{k/8} \\ \mathrm{H} & \text{otherwise} \end{cases} \tag{1}$$

$$\mathrm{C} \to \begin{cases} 0 & \mathrm{P(C \to 0)} = e \\ \mathrm{H} & \mathrm{P(C \to H)} = 0 \\ \mathrm{C} & \text{otherwise} \end{cases} \tag{2}$$

Due to these simplifications this model has deficiencies. It cannot take the fibrous structure of the *Cuscuta* into account. The special role of shoot tips in colonization is also ignored. Despite of its deficiencies this model helps us to find the key parameters, mostly influencing the system.

3. RESULTS

Outdoor experiments are the only good tools to validate ecological models. In our case the result of the field work is a series of pictures about the development of *Cuscuta europaea* ramets. Due to the spatial structure of a metapopulation of clonal plants we do not know anything about the genetic variation of the units, however they are visibly distinguishable and seem to be independent. The modified pictures contain area information about the investigated *Cuscuta* patches. With pixel counting function of GIMP the area occupancy was registered, resulting 20 time series. The tendency is saturating, the particular shape depends on the initial size of the *Cuscuta* patches and the dispersal speed, which was influenced by the available host quality. Fig. 2 shows the results of pixel-counting; the proportion of the area occupied by *Cuscuta* is plotted with respect to the time.

(Fig. 2)

The simulation results of the cellular automaton model helped us to investigate and determine the most important properties influencing the spatial pattern. As it was given in the section "Methods", the probability of colonization of hosts by a single *Cuscuta* cell is $0 \leq c \leq 1$ and the uniform extinction probability of the parasite $0 \leq e \leq 1$. A detailed parameter scanning was done on the whole parameter space up to the total extinction (but maximum 250 time steps) of *Cuscuta* cells. The extinction time, the proportion of host and dead cells was recorded. The simulation was repeated 20 times for each parameter combination. The initial cell space was a 64×64 cells large square lattice with a 3x3 *Cuscuta* block in the centre, all the other cells are occupied by the host. Fig. 3 shows the dependence of the model on the parameters *c* and *e*. In particular, Fig. 3c shows the density plot of proportions of extinct cells with the contour lines at the values 0.05, 0.5 and 0.95 respectively. The following lines (colonization depends on extinction) are fitted to the experimental contours, where E denotes the basis of natural logarithm:

dead level 0.05: $c(e) = 0.9094 - 0.9584\, E^{-2.6511e}$
dead level 0.50: $c(e) = 0.9617 - 0.8453 E^{-2.6401e}$
dead level 0.95: $c(e) = 0.9928 - 0.7942 E^{-3.4646e}$

(Fig. 3)

It is well visible that there happens a dramatic "phase transition" at a sharp band in the parameter space. At low probabilities of colonization the host survives and *Cuscuta* becomes extinct, and for high probabilities the host cells become completely occupied by *Cuscuta* cells, which become extinct at the uniform extinction rate *e*. Along the band, separating these domains, the outcome is almost unpredictable. The extinction time and the deviation of it increase to huge values, see Fig. 4 which presents the average time of total extinction of *Cuscuta* cells and its standard deviation:

(Fig. 4)

To see what really happens in the cell space, Fig. 5 contains the space at the 100th time step at simulations with different parameter values crossing the phase transition band.

(Fig. 5)

The different dispersion parameters of *Cuscuta*s may correspond to various geographic latitudes. In northern Europe the weather is colder, providing lower rates of development and unfavourable conditions for dispersal of both hosts and *Cuscutas*. Hence, the spatial pattern at higher rates of extinction Fig. 5c-d was slowly emerging and more fractal like. The dispersal front is thinner due to the higher extinction rate. This caused, that ramets are less connected inside; the inner parts of the patches are quickly dying out. In contrast, another parameter combination for the other weather extreme, the tropics, can be found Fig. 5a. Plants grow much faster under warmer climate conditions and humidity is also a key parameter of the dispersal speed. Higher colonization and lower extinction rates cause different spatial patterns. The fractal-like forms disappear, because of the easiness of colonization. *Cuscuta* cells are able to overcolonize the host with greater probability and fewer neighbours are enough for the success than at the parameters for cold climate areas. This causes a simpler pattern and a more circle-like dispersal front. Inner parts of the patches are more connected due to the lower probability of extinction.

Finally, to compare our field work observations with our model, it can be easily found that the curves in Fig. 2 basically agree with the first increasing part of the proportion curves in Fig. 5. Note that the average extinction time of *Cuscuta* patches is much longer than our field observation period. The main differences are due to the different initial cell space configurations. Based on the first pictures of two particular observation series the initial spaces were defined and the appropriate colonization (c) and extinction (e) parameters were estimated by simulations (50 times repeated). Since *Cuscuta* patches in the investigated quadrats were separated, there was no immigration from other areas. Therefore, the simulation was done with plane topology instead of toroid cell space. By analyzing the pictures, some patches of worse quality hosts were found. They were taken into account as empty, uncolonizable patches in the simulations (in both cases their area is 20% of the total cell space). The results are shown on Fig. 6. Because the reasons detailed above the extinction rate was assumed to be very a small value, e=0.0001. Due to the similarity of patch development in the investigated quadrats, the colonization rates were assumed identical. The common value c=0.16 was confirmed by the simulations. Although the results have no power of statistical proof, they illustrate very well the applicability of our simple model in practice.

(Fig. 6)

4. DISCUSSION

Our cellular automaton model is a simple tool to study the spatial distribution pattern of *Cuscuta* patches. Simplifications helped to keep the model understandable, make the parameters investigable and to show the directions of next refinements of the model. This model doesn't take the fibrous structure of *Cuscuta*s into account. Also the special role of shoot tips is ignored. Even this simple model can show us which way to develop the model and which things worth more attention. Another experimental design is under development to investigate the smaller scale dispersal. The initial phase of the development seems to be very interesting. Special interests are to observe the host seeking strategies, especially if the host is heterogeneous or there are some artificial terrain features. Based on the field work and our first cellular automaton model, which approximately describes the spatial structure, a new model involving the fibrous structure of *Cuscuta*s is under development.

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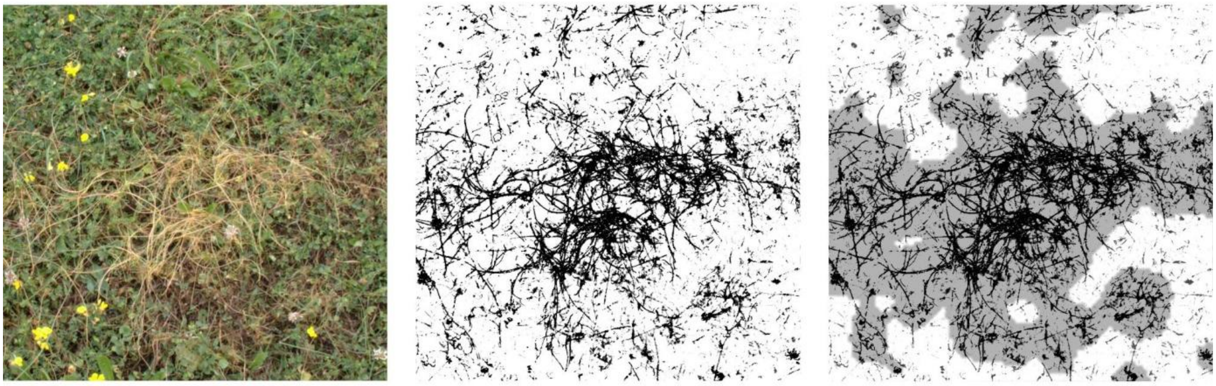
6. FIGURES



(a) (b) (c)

Fig. 1. Images: raw picture (a), detecting visible *Cuscuta* pixels (b), estimated *Cuscuta* patches (including hidden shoots) (c). The background consists of host and non-host plants.

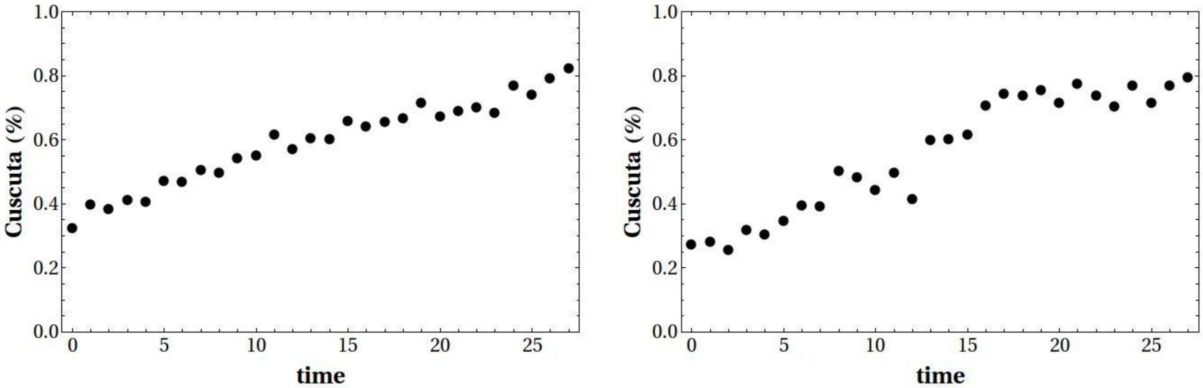
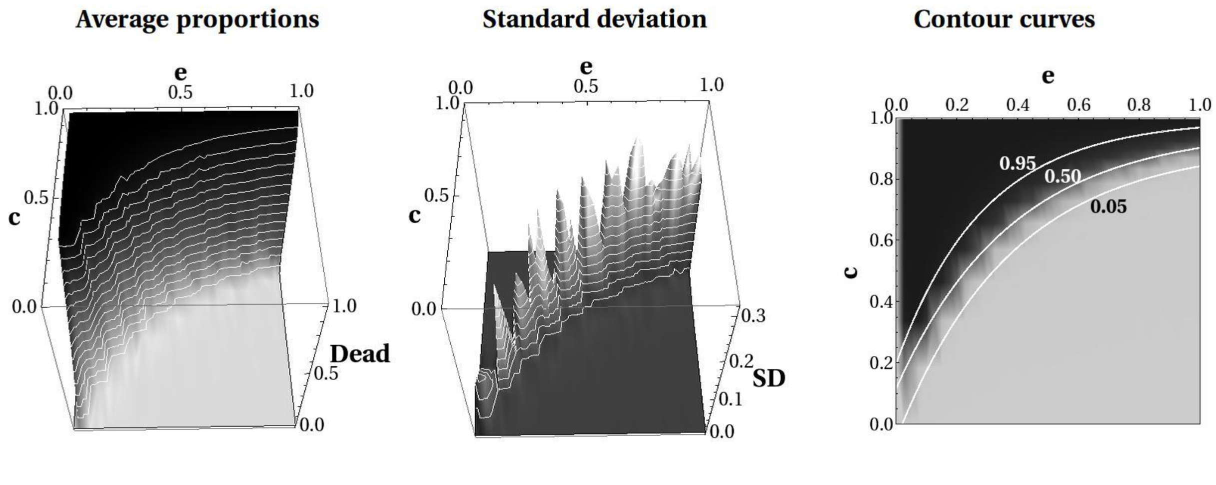
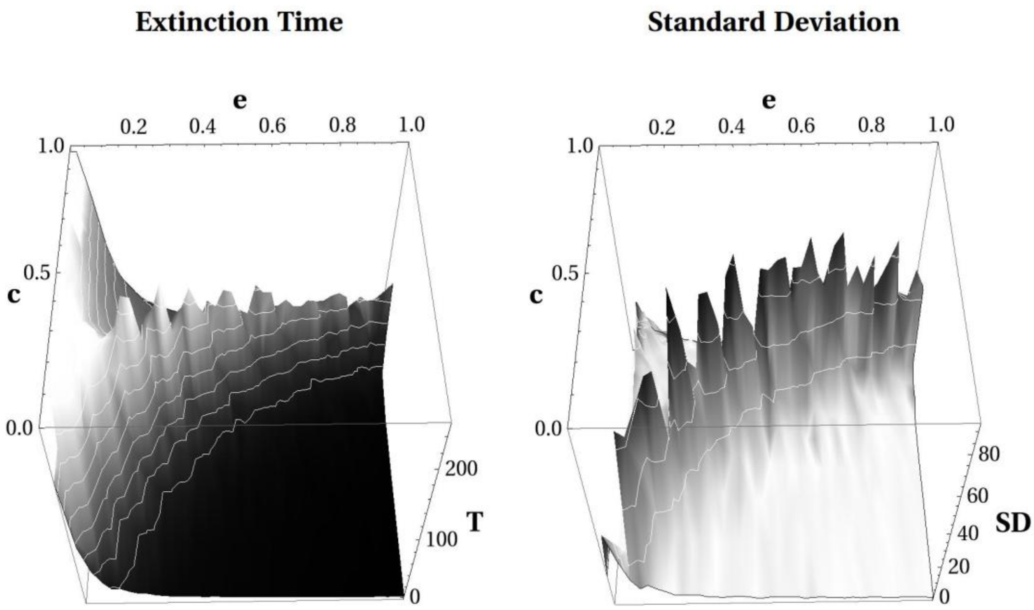


Fig. 2. Temporal change of the proportion of the area occupied by *Cuscuta* in two different measurements



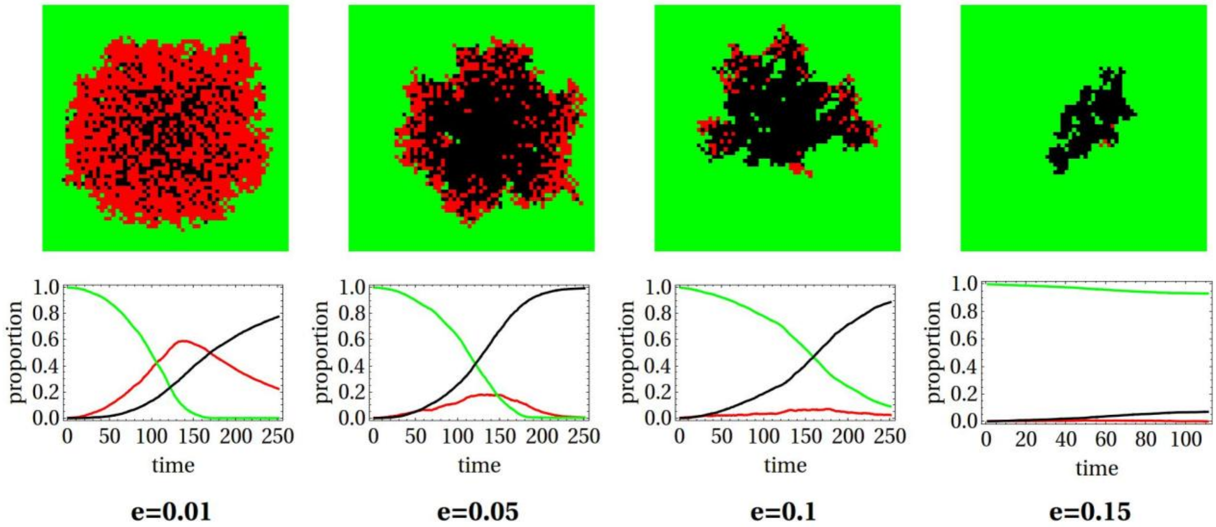
(a) (b) (c)

Fig 3. Parameter space scanning: Statistical details of number of extinct (black) cells at the time of complete extinction of *Cuscuta* cells with respect to the parameters *c* and *e*: average proportions (a), standard deviation (b) and contour curves of the average proportions of extinct cells (c). Grey level colouring according to the value of functions is used in order to express the dramatic changes. The precise values are well visible on the contour curves.



(a) (b)

Fig. 4. Extinction time of *Cuscuta* in time steps (a) and the standard deviation (b)



(a) (b) (c) (d)

Fig. 5. Pictures of the simulations at the 100th time step showing the area occupied by the host (light grey), *Cuscuta* (grey) and extinct (black) cells; and the average proportions in a 1square meter field area, at colonization *c*=0.35 and different *Cuscuta* extinction *e*=0.01 (a), 0.05 (b), 0.1 (c), 0.15 (d) (—— : Dead, – – : *Cuscuta*, – . – : Host)

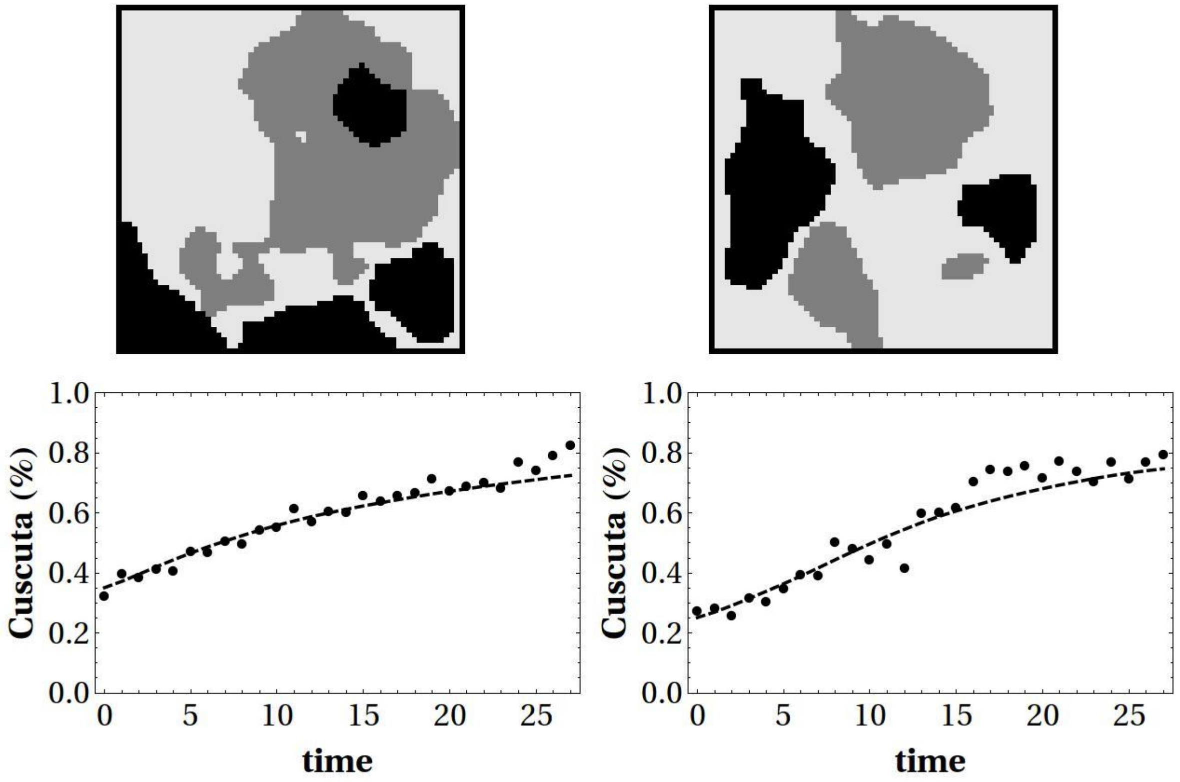


Fig. 6. Simulations using the original configuration detected on the field in two different quadrats, the development of *Cuscuta* patches from the detected initial space, the scatter plot is the same as Fig. 2. the dashed lines represent the model fit (‒ ‒ : average simulated density) at c=0.16 colonization rate and e=0.0001 *Cuscuta* extinction