A Spatially Explicit Individual-Based Model of the Population Dynamics of the greenhouse whitefly (*Trialeurodes vaporariorum*), *Encarsia formosa* and tomato powdery mildew (*Oidium neolycopersici*) in Tomato Crops.

Dissertation

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Summary

The greenhouse whitefly *Trialeurodes vaporariorum* – Westwood is one of the most important insect pests in crops. The spatial dynamics and population grow of the insects are affected by different biotic and abiotic factors like the host plant quality, the control by natural enemies or the presence of another kind of pest such as mildew fungus. Patterns of the population behavior in tomato crops were used to develop an age-structured, spatially explicit, individual-based model with a description of the developmental biology of the whitefly individuals. The model comprises three types of entities: 1) plant leaves, 2) pest insects, 3) parasitoid insects and the presence of the fungus *Oidium neolycopersici* (powdery mildew). The plants are modeled only as space units with a dynamic size to store insects. The insects' populations are modeled in an age-structured design to mimic their growth and development as in real systems. For the pest insects, the key process is the dispersal, in which the individuals decide where to move, for this purpose four different basic rules under density dependent and density independent context were tested with respect to their ability to create patterns similar to the patterns observed in nature. The parasitoid insect *Encarsia formosa* is also modeled in an age-structured population and its effect on the pest insect is implemented to affect the second stage of nymphs, mimicking host-feeding, and the third and fourth stage of nymphs, representing the parasitization. The mildew fungus, that affects the behavior of *E. formosa* is modeled as present or absent in the leaves and its effect on the behavior of the insects was tested. The results show that whitefly dispersal follows rules probably related with chemical or visual cues to orient their flights and these rules can be used to represent population growth patterns and spatial distribution. The effect of biocontrol by *E.formosa* is important and varies with the three dispersal rules tested, where the exponential function gives the more realistic representation of the parasitoid foraging behavior. Furthermore, the presences of mildew in the leaves affecting the parasitoid foraging activity result in an increase of dispersion of the whitefly population. As the interaction between the fungi and whiteflies is not

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explicitly modeled in this study the results suggest that the presence of mildew have a negative direct effect on the parasitoids foraging behavior and a positive indirect effect on the whiteflies increasing its dispersion probably because the presence of mildew makes the infected leaf a protected refuge for the whitefly. This interaction deserves more research in the field and in real experiments in order to get more details to be included later in the simulations to study a more realistic scenario. The severity or incidence of mildew in the crop related with the dynamics of whiteflies and parasitoids in real-like experiments could help to improve the knowledge about these multitrophic interactions. The main conclusion is that this research tool can be used to orient the future research on this system. Some gaps in knowledge were found that can be important to better understand the function of the systems.

1   General Introduction

The crop production losses to pests can vary from 7% (Oliveira et al., 2014) up to 80% (Oerke, 2006). Tomato crops are often affected by pests like the greenhouse whitefly *Trialeurodes vaporariorum* – Westwood and tomato powdery mildew *Oidium neolycopersici*. *T. vaporariorum* is one of the most important phytophagous insects in vegetables and ornamentals (Greenberg et al., 2009). One of the successful methods to reduce the impact of *T. vaporariorum* on crops is the biological control strategy using the parasitoid *Encarsia formosa* - Gahan (van Lenteren et al., 1996). *O. neolycopersici* is known to cause problems in tomato since the 1980´s in Europe, especially in greenhouses (Mieslerová et al., 2004). Additionally, the presence of *O. neolycopersici* affects the interaction between *T.vaporariorum* and *E. formosa* by reducing the parasitization rate (Focke, 2000).

Different approaches have been used to study the dispersal process of insects in agriculture, showing the importance of factors like wind, humans, or the interactions with other organisms (Mazzi and Dorn, 2012; Schellhorn et al., 2014). Until now the dispersal patterns of *T. vaporariorum* and *E. formosa*, as well as O. neolycopersici in tomato crops, have been studied separately (Chelal and Hau, 2015; Jiang et al., 1999), but the interactions between the pathogens and insects and the effects on their spatial distribution in crops have not been studied yet. To my knowledge, this is the first study to approach this complex system in a way that includes the pest, parasitoids, and phytopathogens, building up from the simple pest – crop model to the most complex pest – parasitoid – fungus – crop model.

Insect pest *Trialeurodes vaporariorum*

The dispersal process of whiteflies *Trialeurodes vaporariorum* (Hemiptera: Aleyrodidae) has been studied in laboratory and greenhouses (Gabarra et al., 2004; Rincon et al., 2015). *T. vaporariorum* foraging times spent on the leaves show a preference for young leaves and

shorter times on old leaves for experienced adults. The within-plant movement takes place mainly one day after the emergence of the adult and can be on average 2.5 leaves up. The between-plants movement also starts on the day of emergence and can reach the distance of up to 125 cm from the plant of emergence. This pattern can explain the aggregated distribution observed in crops (Noldus et al., 1986a, 1986b, 1985; Pérez et al., 2011a). Factors such as temperature and insects density can affect the pest movement length (Bonsignore, 2014) but also chemical and visual cues from plants can be used by the pest to orient the flight (Bleeker et al., 2009).

The whitefly flight and dispersal are very complex processes and therefore, it is important to understand their functioning in crops more than in well-studied laboratory conditions. However, the experiments already conducted in crops prove it difficult to collect the data, due to the small size of the insects and the difficulty to intercept all the flights (Bonsignore, 2014). Therefore, in this study, I used the simulation approach in order to elucidate the components that could be playing an important role in the dispersal process. Furthermore, I tested the effects of different dispersal behavior rules of whitefly adults on the dynamics of its population.

Insect parasitoid *Encarsia Formosa*

Encarsia formosa (Hymenoptera: Aphelinidae) is a successful biological control agent for *T. vaporariorum* in crops. As primary parasitoid, *E. formosa* reproduces parthenogenetically by the parasitization of nymph stages of whiteflies like *T. vaporariorum* (van Lenteren et al., 1996). The foraging behavior of *Encarsia formosa* in the crop is a crucial aspect to understand and explain the success of biocontrol in the system. The behavior of the parasitoid in the leaves is well studied (Fransen and Lenteren, 1993; van Lenteren et al., 1995; van Roermund et al., 1997) but its ability to distinguish between infested and uninfested leaves from a distance seems unclear. Studies in wind tunnel reported contradictory results, for example, according to (Noldus and Van Lenteren, 1990) the presence of the host pest on leaves has no influence on plant choice. However, another

study shows differences in the plant selection when the host pest is present (Guerrieri, 1997).

As insects´ dispersal is difficult to follow in field studies, some insights can be inferred from simulations based on parameters and observations of the behavior and distribution of the insects. In an individual-based simulation model of *E. formosa* and *T. vaporariorum* Roermund et al. (1997) assumed a random search dispersal for *E. formosa* in the leaf and the same exponential empirical function to move between plants for both pest and parasitoid differing only in one parameter that described the decrease in the probability to find a new plant as the distance between plants increases. Though this simulation study shows good control of the pest by the parasitoid, the parasitoid's dispersal behavior remains unclear. Therefore, I extended the whitefly - tomato model to include the effects of the parasitoid on the dispersion and biocontrol of *T. vaporariorum*.

Tomato powdery mildew *Oidium neolycopersici*

The tomato powdery mildew, *Oidium neolycopersici*, is reported as a pest in greenhouses since the 1980´s (Fletcher et al., 1988). *O. neolycopersici* is an obligate biotrophic pathogen in more than 60 plants species, making white lesions in leaves and stems in the glasshouse and open field crops (Jones et al., 2001). The optimal conditions for development range from 15 to 25°C and 60% to 90% relative humidity in experimental conditions for the spore germination, appressoria formation, and sporulation. The increase in temperature and/ or relative humidity reduces the activity and success of the pathogen in the leaves (Jacob et al., 2008; Whipps and Budge, 2000). However, the inhibition of development of *O.neolycipersici* was not observed in six different plant genera including 10 species of the genus Lycopersicon, but a delay in development was present in some cases. Furthermore, low light intensity and dark periods can delay or inhibit the development of the pathogen (Mieslerová and Lebeda, 2010; Mieslerová et al., 2004).

The effect of *O. neolycopersici* on its host plant tomato and the synchrony of the disease with the host plant growth seems to be important to understand the dynamics of this plant

disease and its damage to the crop. The importance to take into account not only the pathogen but also the host-plant dynamics was highlighted as a more realistic approach as opposed to the epidemiological studies about the disease alone (Chelal and Hau, 2015). The presence of *O. neolycopersici* can also negatively affect the parasitization rate of *E. formosa* on whiteflies in experimental conditions (Focke, 2000). Thus, to understand the dynamics of pest and parasitoid in crops it was necessary to extend the model by adding *O. neolycopersici*. The aim was to study the effects of *O. neolycopersici* on the dispersion of pest and parasitoid populations.

Simulation model approaches

Simulation models are versatile tools used to develop theory and to perform virtual experiments that can be difficult in nature (Zurell et al., 2010). They can help to identify gaps in knowledge or guide the design of real experiments (Peck, 2004). Individual-based and differential equation population-based models are used to study different aspects of ecosystems, for example, the individual-based model of aphid population dynamics used to study the interactions between aphids with different landscapes configurations (Parry et al., 2006) or the population-based model used to study mass rearing mites population growth under different management aspects (Bustos et al., 2016). The individual-based approach is suitable to use when the individual behavior or the variability between individuals is essential to answer the research question (DeAngelis and Grimm, 2014).

Individual-based models have been used to study the spatial distribution of immature stages of whiteflies in tomato plants (Rincon et al., 2015). They generate a more realistic distribution than the simple assumption of uniform distribution based on laboratory experiments, showing a good match between simulation and real data of insects distribution on plants. A similar individual-based approach was used to study the biocontrol effect of *E. formosa* on *T. vaporariorum* (Roermund et al., 1997). The results show the complexity of the system, and the importance of parameters like the number and the size of leaves, or the time of the parasitoid to leave the leaflet, as well as the number of release strategies of the parasitoid that are necessary for the successful biocontrol.

Epidemiological models to study the conditions for population development of *O. neolycopersici* (Jacob et al., 2008) show that temperatures between 15 and 25°C for one to four weeks are positively correlated with the development of the epidemics in crops. Furthermore, differential equation-based models (Chelal and Hau, 2015) shows the importance of the synchrony between the disease progress curve and the host plant growth curve. However, there are no studies at crop scale about the influence of the *O. neolycopersici* on other organisms like insects.

Most of the studies about *Trialeurodes vaporariorum*, *Encarsia formosa* and *Oidium neolycopersici* in tomato deal with population dynamics in a laboratory or experimental conditions and only a few in crops (Eggenkamp-Rotteveel et al., 1982a; Gabarra et al., 2004; Pérez et al., 2011a). At the same time, different explanations are given for the individual movement of *T. vaporariorum*, i.e random search within a range of nearest neighbor plants or following cues from plants (Bleeker et al., 2009; Roermund et al., 1997). The individual behavior of the parasitoid is even less studied and is usually assumed to be similar to the whitefly for the between plants movement (Roermund et al., 1997). Although, more recent studies show that chemical volatiles from infested plants could be used by the parasitoid to guide the search behavior from a distance (Birkett et al., 2003). Furthermore, the presence of *O. neolycopersici* on the plants can affect the volatiles emitted by infested plants and in consequence affects the ability of the parasitoid to find the infested plant (Focke, 2000).

Aims

The aim of this study was to understand : 1) the flight and dispersal processes of whitefly in an applied setting i.e. in crops; 2) the foraging behavior of the parasitoid; 3) the dynamics of mildew and its effect on parasitization rate of the whitefly and finally to overcome the difficulties in empirical research by using a simulation approach.

2 Methods

2.1 Patterns and model structure

2.1.1 Characteristic patterns

Pattern 1: The spatial distribution of whiteflies in crops is clumped at the beginning of the infestation and follows a negative binomial distribution afterward. This pattern is based on the actual spatial distribution of the pest observed in controlled experiments in small greenhouses and sample studies in commercial greenhouses (Basso et al., 2001; Noldus et al., 1986a)**.**

Pattern 2: The whitefly population increases exponentially in the absence of control strategies but the growth can be reduced by the introduction of the parasitoids (Roermund et al., 1997)**.**

2.1.2 Model structure from patterns

The dynamic and spatially explicit model represents the population size changes over time by taking into account the whitefly densities in different plants. The foraging process of individual whitefly adults drives the observed patterns, and therefore, should be included with an individual-based modeling approach. One day time step mirrors the usual frequency of surveys in greenhouse experiments.

2.2   Model validation

2.2.1 Spatial distribution

In order to compare the model outputs for adults spatial distribution with field data, a field experiment and a virtual experiment following a setup from literature (Noldus et al., 1986a) were conducted (See table 1).

The field experiment used "artificial plants", which are tomato leaves placed individually in a test tube and three of these leaves placed on a wood stick to emulate real plants. In consequence, the plants and leaves are not growing. The setup consisted of an arrangement of 10 x 10 plants with 3 leaves each. At time zero 762 adults of whitefly were introduced in the central plant. The position of the insects was followed daily for eight days.

2.2.2 Population growth.

The simulation outputs for population growth were compared with six different experimental data sets reported in the literature (Roermund et al., 1997) with three different setups as follows (See Table 1):

a. Two datasets of experiments with five plants infested with 50 females (Approx. 10 females/plant). The population surveys were done at 35, 48 and 63 days (Joosten and Elings, 1985).

b. Three datasets of experiments with 10 plants infested with 100 females (Approx. 10 females/plant). The surveys were done at 40, 47, 60, 93 and 95 days (Elzinga, 1982; Joosten and Elings, 1985).

c. One dataset of one experiment with 15 plants, infested with 300 females (Approx. 20 females/plant). The surveys were done at 53 and 93 days (De Ponti and Steenhuis, Unpub.).

2.2.3 Final population size

To calculate the final size of the whitefly population, a simulation experiment with an arrangement of 10 x 10 plants and an initial population of 10 females in the central plant was run for 340 days. The adults used the eight nearest neighbor dispersal rule under density-independent option.

Since the maximum carrying capacity of one plant is 371654 individuals (21862 individuals X 17 leaves) the modeled system was above the computing capacity of the computer. To overcome this limitation the carrying capacity of each plant was limited to 8925 individuals (525 individuals per leaf).

2.3   Model description

The model description follows the ODD (Overview, Design concepts, Details) protocol for describing individual- and agent-based models (Grimm et al., 2010, 2006).

2.3.1 Purpose

The model´s purpose is to test the effects of different dispersal rules of the insect pest *Trialeurodes vaporariorum* – Westwood on its spatial and temporal distribution in tomato crops. Additionally, the model tests the effects of the initial density and location of insects on population's development over time.

2.3.2 Entities, state variables, and scales

2.3.2.1 Entities

There are three types of entities: leaves, plants, and pests. Each leaf is characterized by its spatial coordinates (x, y, and z) and a carrying capacity. A plant is composed of a group of leaves with the same x and y coordinates but different z coordinate. A pest is a mobile individual with state variables for location, degree-days, stage of development, eggs per degree day, sex and age. The number of leaves, their carrying capacity and the number of insects change over time.

The temperature, time step, distance between plants, and the order of the execution of the processes for the three entities are managed by the greenhouse class (Figure 1; Section: 2.2.6.7). The temperature is defined as constant from the beginning of the simulation (Table 1) and maintained for all simulations.

Table 1. Initial conditions of pest simulation experiments.

| Parameter	Experiment (Section)				
	Spatial distribution 100 plants *(section 2.2.1)*	*Population growth*			*Population analysis* 100 plants *(section 2.2.3)*
		5 plants (section 2.2.2a)	*10 plants (section2.2.2b)*	*15 plants (section 2.2.2c)*	
Simulation time (days)	8	70	100	100	340
Number of plants	100	5	10	15	100
Initial number of pest (♀)	762	50	100	300	10
Time of infestation	0	0	0	0	0
Pest initial spatial distribution	Aggregated (central plant)	Random	Random	Random	Aggregated (central plant)
Leaf carrying capacity	21862	21862	21862	21862	525
Pest dispersal rule	(See section 2.3.6.4)	(See section 2.3.6.4))	(See section 2.3.6.4))	(See section 2.3.6.4))	Eight nearest neighbor - density-independent
Reference	(Noldus et al., 1986a)	(Joosten and Elings, 1985)	(Elzinga, 1982; Joosten and Elings, 1985)	(De Ponti and Steenhuis, Unpublished.)	-
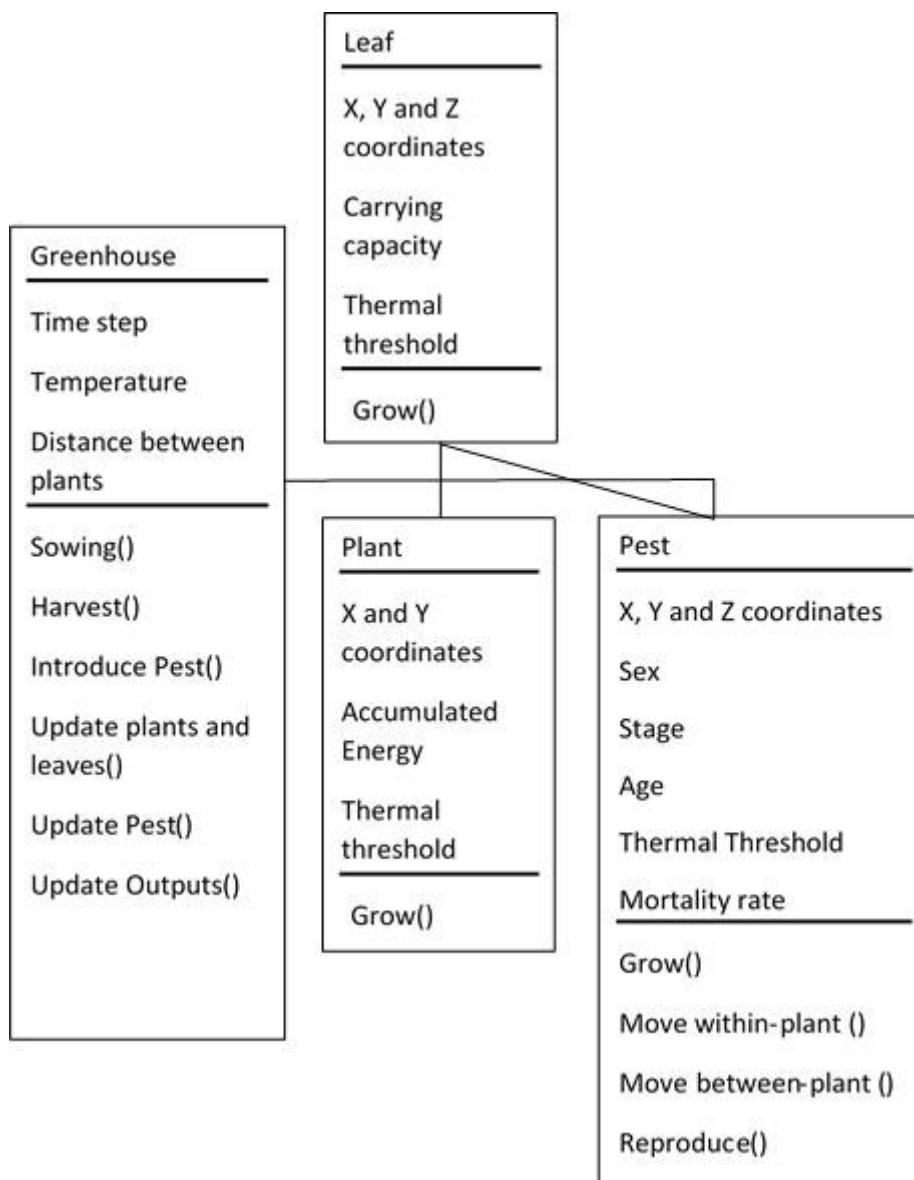
Figure 1. Static structure of the spatially explicit model of whitefly dispersion in Unified Modeling Language (UML). Each class is represented by one box, the first part of the box corresponds to the class name, the second to the key attributes and the third to processes. Every individual (instance of a class) in the model has its own values for each one of the attributes. Links signify association.

2.3.2.2 State variables

Degree-days variable is used for all entities and is defined as the accumulation of thermal units over the lower thermal threshold of development. Age in days, stage of development and sex are also used to represent characteristics of the individuals.

2.3.2.3 Scales

The spatial extent is *n* by *n* plants in a grid (Figure 2), with the same distances between plants (i.e. one meter). Space is represented as toroidal: insects going beyond the edge jump to plants at the opposite edge. The smallest space unit is one leaf.

All events in the model happen in discrete 1-day time steps with no explicit difference between day and night. The simulation duration varies depending on the experiment (See Table 1).

n				
…				
3		X		
2				
1	2	3	…	n

Figure 2. A grid representation of the plants´ arrangement in the greenhouse. Each cell represents one plant placed in the center of the cell and the "X" an infested plant.

2.3.3 Process overview and scheduling

For each time step, the following actions happen in the same order. All state variables are updated as soon as the new value is calculated in each process.

Plants' growth. Plants produce new leaves based on the accumulation of degree-days (thermal units over the lower thermal threshold, Section 2.1.7.8)**.**

Leaves' growth. The growth of the leaves is not explicitly modeled but each leaf has a certain carrying capacity to store individuals, that changes over time until it reaches its maximum (Section 2.1.7.5.1).

At the beginning of the crop cycle, each leaf has an initial carrying capacity (Table1). Thereafter, in each time step, the leaf grows 1/21 of the maximum carrying capacity until it reaches the maximum carrying capacity. New leaves produced by a plant start with a carrying capacity of zero following the same grow process until they reach the maximum carrying capacity (Table 1).

Pests' mortality. Insects die with a constant probability, dependent on the life stage (Table 2).

Pests' growth. The ageing process is modeled by changing the "stage variable" when a number of necessary degree-days for the stage is reached (Table 2).

Pests' dispersal. Dispersal is executed only by adult females and comprises two types of movement: a) within the plant and b) between plants.

Pests' reproduction. Adult females reproduce each time step during the whole adult stage under the condition that the number of insects in the current leaf is smaller than the carrying capacity of that leaf.

Harvest. If the plant has more than 21 leaves, the three lowest leaves are removed to simulate the pruning of leaves that follows the fruits harvest in real crops.

2.3.4 Design concepts

Basic principles: In the dispersal submodel, to reproduce the observed population dispersion pattern, adult females choose to move according to four alternative rules.

Emergence: The whiteflies' spatial distribution and population size emerge from the number of plants and leaves in the crop and the dispersal behavior of whitefly adults.

Adaptation: The dispersal and reproduction processes are the adaptive behavior for this model. The insects decide which is the next leaf to visit and if they oviposit or not each day.

Sensing: Adult insects sense the space availability for oviposition on their leaf.

Stochasticity: Stochasticity is included to simulate variability in the duration of stages, the daily probability of insect mortality and in the direction of female dispersal behavior.

Observation: Summary statics of the number of leaves per plant, the insect population size per leaf, stages, and location of insects are saved after each time step.

2.3.5 Initialization

At time zero, one plant is a group of 3 leaves sharing x and y coordinates but with different z coordinate. The carrying capacity of each leaf is set to the initial value (Table 2). The number of plants, time step for insect infestation, stage of insects infesting the plants and their location are assigned according to the experimental design (see Table 1).

2.3.6 Submodels

The following subsections describe in detail how the processes are simulated in the model.

2.3.6.1 Plants' growth

Plants grow by accumulating degree-days over the lower thermal threshold (see section 2.1.7.8). The variable accumulated energy is obtained by the multiplication of accumulated degree-days by the node initiation rate. When the accumulated energy is more than 1.00 a new leaf is produced and one unit is discounted from accumulated energy, the remained fraction is kept in the variable for the next time step.

All new leaves have the carrying capacity equal to zero and the value increases each day by 1/21 of the maximum carrying capacity value (Table 2). Each leaf grows for 21 days.

2.3.6.2 Pests' mortality

To calculate the value of mortality per degree-day for each stage, the mortality values for each developmental stage (Roermund and Lenteren, 1992) were divided by the duration of the stage in degree days. Each time step, insect mortality is the mortality per degree-day multiplied by the number of degree-days of that day.

2.3.6.3 Pests' growth

The insects have five immature stages (Egg and four nymph stages) and the adult stage. For each new insect, the values in degree days for the duration of each stage of development are assigned randomly within the range of values for each stage (Table 2). The insects grow by accumulating degree days over the lower thermal threshold (see section 2.1.7.8). When an individual accumulates the necessary amount of degree days to complete a development stage, the state variable stage changes to the next stage value mimicking the aging process. When the individual reaches the adult stage, the sex is assigned randomly (with a probability of 0.48 for a female) (Table 2).

2.3.6.4 Pests' dispersal

Dispersal is the key process in this model and is executed exclusively by females. The males of whitefly stay in the plant where they emerged and only the females search for different plants (Roermund and Lenteren, 1997). In this model, males are included only to occupy space on leaves but not in reproduction or dispersal processes.

The location of individuals is followed over successive time steps and the dispersal process is executed 73% of times, the remained 27% the individuals stay in the plant where they emerge (Noldus et al., 1985).

The dispersal process happens: 1) independent of density when individuals execute the move action every day (Figure 3a), or 2) dependent on density when the move action is executed only if there is no space for oviposition on the current leaf where the insect is (Figure 3b). The individual can move: a) within-plant or b) between-plants (Figure 3). Once any of these actions is executed, it is counted and can be repeated until the insect finds a suitable host plant or the maximum number of attempts is reached (Table 1).

a) Within-plant movement: If there are leaves above the location of the leaf where the insect is, then the individual moves up one or two leaves maximum (Bonsignore, 2014), otherwise the between-plants movement is executed.

b) Between-plants movement is executed using one of the four different rules as follows:

2.3.6.4.1   Random uniform

A random uniform probability is used to let the individuals choose the next plant to visit. In consequence, all plants in the crop can be chosen with an equal probability. This behavior is used as a baseline assumption to compare with other behaviors in which different rules are followed by insects to find a new plant.

2.3.6.4.2   Eight nearest neighbors

Eight nearest neighbors dispersal behavior allows the individuals to choose a random plant from the eight nearest plants.

2.3.6.4.3   Negative exponential

A negative exponential function (Roermund et al., 1997) Is used,

$$P\ (r) = \propto\ exp^{(-\alpha r)/2\pi r}$$

where r is the distance between two plants, $\alpha = \dfrac{0.3}{Plant\ distance}$.

This function assumes that the highest probability lies on the source plant (where the individual is) and decreases with the distance from the source plant, making it less probable to move to a more distant plant.

2.3.6.4.4   Following cues

Following cues, behavior represents the interaction between plants and insects, where insects follow chemical and visual cues from plants as a guide to finding new plant resources (Bleeker et al., 2009). In this behavior, when the insect searches for a new plant, 25% of the time the individual stays on the same plant, otherwise it uses the eight nearest neighbors dispersal rule (2.1.7.4.2).

2.3.6.5 Pests´ reproduction

Reproduction is executed before dispersal behavior in density-dependent cases and always executed after dispersal behavior in the density-independent cases (see Figure 1). Females reproduce only if the number of individuals on the leaf is lower than the current carrying capacity. The value of oviposition per day at a given constant temperature is expressed here as eggs per degree-day (Table 2). The number
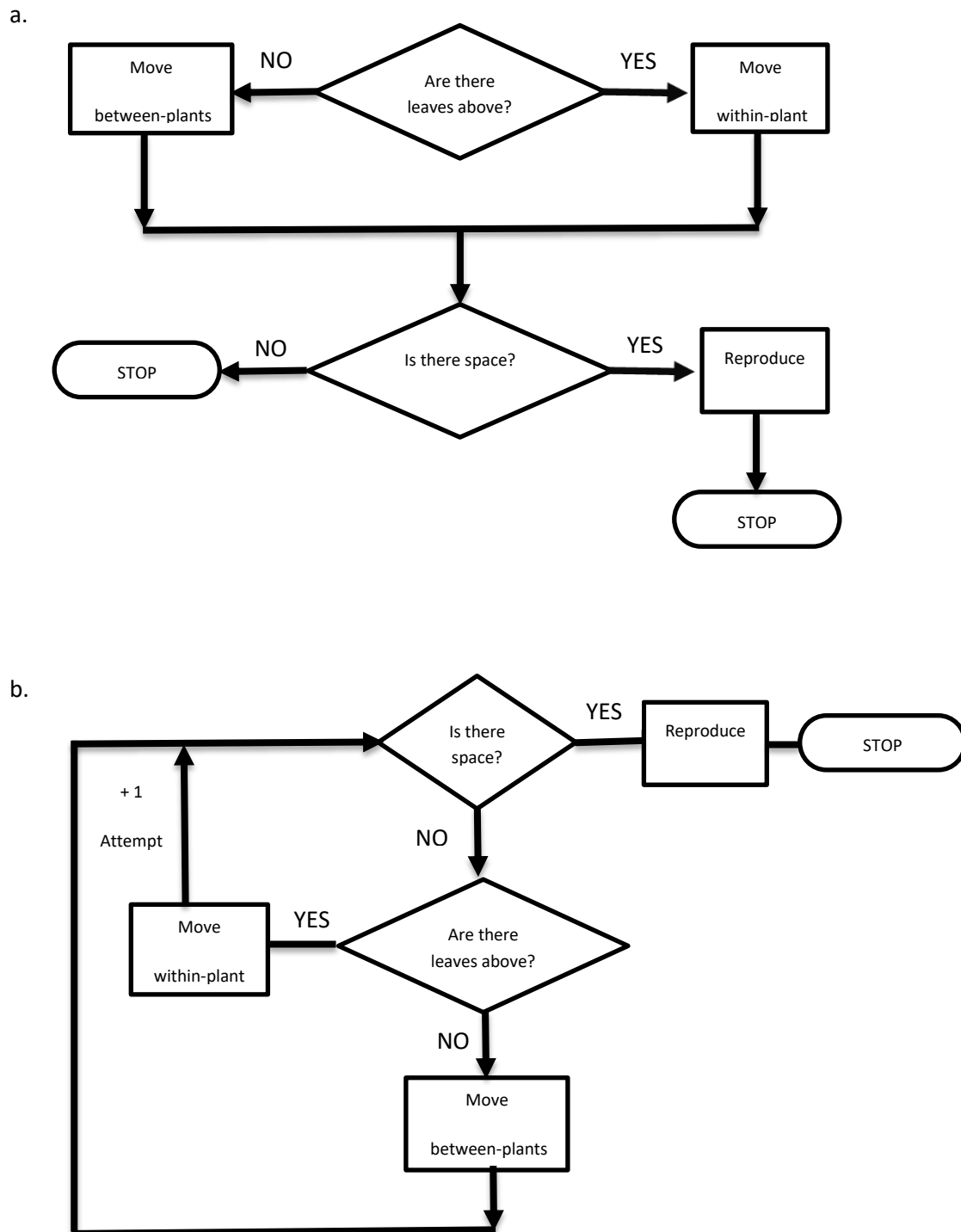
a.

b.

Figure 3. Daily basic dispersal and reproduction rules for female adults: a) density-independent where the decision to move is priority over the reproduction, b) density-dependent where the space for reproduction is priority over dispersal and the maximum number of attempts per time step is eight (Bonsignore, 2014)

of eggs per degree-day is multiplied by the number of degree-days of the current time step to give an integer number of eggs to be placed in the current leaf. The decimal part of this calculation is saved and added to oviposition in the next time step.

2.3.6.5.1   Calibration of carrying capacity

The number of individuals that can be on a tomato leaf was estimated with mean leaf area (Decoteau, 2007) and the size of nymph 4 (Cardona et al., 2005), resulting in a potential range between 10046 and 80974 individuals per leaf. All leaves of the same age have the same carrying capacity.

The carrying capacity for leaves was calibrated by testing percentages of the above-mentioned values until the simulation outputs represented the trends of empirical data used for validations. The final value after the calibration was 27% of the initial values, which means between 2712 and 21862 individuals per leaf. Hereafter, these values are used in all simulation experiments.

2.3.6.6 Degree-days calculation

This model uses the averaging method (Arnold, 1960) when the lower thermal threshold of the individual is less than the minimum temperature of the day. Otherwise, the single sine method is used (Allen, 1976).:

$L_T = Lower\ threshold$

$minT = minimal\ temperature\ of\ the\ day$

$maxT = maximal\ temperature\ of\ the\ day$

The formula for average method is $degree\ days = \frac{minT+maxT}{2} - L_T$

And the single sine method formula is:

$$\alpha = \frac{maxT - minT}{2}$$

$$\theta_1 = \frac{Sin^{-1}\left[\left(L_T - \frac{maxT + minT}{2}\right)\right]}{\alpha}$$

$$degree\ days = \frac{1}{\pi}\left[\left(\frac{maxT + minT}{2} - L_T\right)\left(\frac{\pi}{2} - \theta_1\right) + \alpha\cos\theta_1\right]$$

Table 2. Parameters of the plants and pest used in the model.

Parameter	Value		
	Initial	Minimum	Maximum
Greenhouse			
Temperature	20°C		
Plant			
Lower Thermal Threshold (Zotarelli et al., 2009)		10.00 °C	
Node initiation rate (Roermund and Lenteren, 1992)		$0.031 dd^{-1}$	
Number of leaves per plant	3		17
Distance between plants	1.0 m		
Number of plants	(see Table 1)		
Leaf			
Carrying capacity	2712 insects	0	21862 insects
Lower Thermal Threshold (Zotarelli et al., 2009)		10	
Pest			
Lower Thermal Threshold		5.2 °C	
Stages (number of degree-days)			
Egg		113.43	184.76
Nymph 1		53.89	100.19
Nymph 2	assigned randomly within the range	37.55	74.59
Nymph 3		53.10	128.93
Nymph 4		125.72	218.10
Female		141.79	789.69
Male		Female * 0.5	Female *

		0.5
Intrinsic mortality (% of individuals entering the stage) (Roermund and Lenteren, 1992)		
Egg		3.70
Nymph 1		4.20
Nymph 2		2.60
Nymph 3		3.70
Nymph 4		7.30
Sex ratio (♀ proportion in offspring) (Roermund and Lenteren, 1992)		0.48
Oviposition (Burnett, 1949)		1.2+/-0.42
Attempts (Bonsignore, 2014)	8	

2.3.6.7 Software

The model was implemented in C++ language with Qt-Creator development environment (Qt-Creator 5.5) using the object-oriented programming approach. There are four classes: greenhouse, plant, leaf, and pest. The greenhouse class is used as a manager of the processes taking place in the crop, and the individuals are created by creating objects in each one of these classes (Figure 1).

2.4   Simulation procedures

Under two decision options, (1. Density-independent and, 2. Density-dependent) for adults to execute the between-plants movement, four dispersal behaviors were tested (Section 2.3.6.4, Figure 3, and Table 3). Every virtual experiment was repeated five times.

Table 3. Dispersal behaviors of whitefly adults tested in each one of the virtual experiments.

Decision option for adults	Experiment number	Between-plants behavior (Section 2.3.6.4)
Density-independent	1	Random uniform
	2	Eight nearest neighbors
	3	Negative exponential
	4	Following Cues
Density-dependent	5	Random uniform
	6	Eight nearest neighbor
	7	Negative exponential
	8	Following cues

3   Results and discussion

3.1   Model validation

3.1.1 Spatial distribution

The experimental data show that the most intensive dispersal of adult whiteflies happens during the first three days after infestation (ref.). Afterward all plants are colonized in similar quantities. This means that the first few days of insect-spread are very important for determining the dispersion pattern.

The simulations data with four different dispersal rules for whitefly adults tested under density-independent (Figures 4 – 7) and density-dependent (Figures 8 - 11) options give insights about this pest's behavior. Neither of the results representing dispersal behaviors in the density-dependent option (Figures 8-11) nor the random uniform behavior in the density-independent option (Figure 4) show agreement with the experimental data. However, the other three dispersal behaviors in the density-independent option (eight nearest neighbors, cues following and exponential function) were able to recreate the experimental distribution.

Adults' decision to select the next plant to visit randomly resulted in a uniform distribution in both density-dependent and independent option (Figures 4 and 8). The random uniform distribution was far from the experimental data trend. This shows that the insects do not move randomly in the crops and instead follow certain rules.

In the density-independent option, if the insects moved according to the eight nearest neighbors rule, dispersing individuals initially stayed on the plants around the starting plant but the area of colonized plants increased every time step (Figure 5). However, in the density-dependent option, the individuals stayed in the same central plants during the whole simulation time (Figure 9). Even though in the density-independent option, on the day 1, the number of individuals on plants around the starting plant was overestimated compared to the

experimental data, the distribution of the individuals matched the experimental trends already from day 2.

The negative exponential function used by insects as a rule to choose the new plant, in the density-independent behavior, was able to closely reproduce the experimental data trend except day 2 where the simulation showed a smoothed curve while the experimental data showed more aggregated distribution around the starting plant (Figure 6). Conversely, for the density-dependent option, this behavior overestimated the population size in the first three days but matched the experimental data for the rest of the simulation time (Figure 10).

In density-independent option, the simulations of the following cues dispersal behavior resulted in the general trend similar to the experimental data (Figure 7). Only on day 1 the number of individuals on the starting plant and the closest neighbors was overestimated. However, this dispersal behavior under density-dependent option overestimated the size of the population during the whole evaluation period (Figure 11).

The density-dependent option did not match the experimental data with any of the four behaviors tested. This suggests that at this short time scale density-dependence is not playing a role in the distribution of insects. On the other hand, density-independent option matched the experimental data well, especially for following cues behavior. Therefore, the dispersal behavior of the insects can be explained here as an initial phase of colonization where the rules for movement within and between plants are not playing a role or at least are not easy to identify.

The dispersal rules that reproduced the experimental data (following cues, exponential function, and eight nearest neighbors) fit the well-known aggregated distribution of whiteflies reported in different studies (Eggenkamp-Rotteveel et al., 1982a; Noldus et al., 1986a; Pérez et al., 2011a; Rincon et al., 2015). This distribution is explained by the foraging behavior of the insects, where the new emerging adults fly short distances to neighbor leaves or plants, where they settle for several days to oviposit (Noldus et al., 1986a), similar to the eight nearest neighbors and following cues dispersal behavior used here. Also, the preference of whiteflies for

new leaves in the upper part of the plants (the higher content of nutrients and water) causes the individuals to aggregate there frequently (Noldus et al., 1986b) resulting in a dispersal pattern similar to following cues behavior.

The whiteflies´ search behavior and movement between leaves and plants suggest that short flights of the insects are more common (Bonsignore, 2014). This can explain the uniform distribution obtained in the simulations after 3 or 4 days. Nevertheless, short time and small spatial scale allow clarifying only one part of the complex dispersal behavior.

The following cues dispersal behavior uses a complex mix of factors including the density-independent decision to move, the probability to stay in the current plant, the probability to find a new plant using chemical and visual cues from the plant and finally the choice of the new plant within the nearest neighbors. The fact that this behavior closely replicated the experimental data shows that even at the small scale some dispersal rules are important.

3.1.2 Population growth

In the simulation with five plants, for all four dispersal behaviors in the density-independent option, the model was able to reproduce the trend of experimental data (Figures 12a, c, and 13a, c). In density-dependent option, only the eight nearest neighbors' dispersal behavior fitted the experimental data while the other three behaviors overestimated the population size (Figures 12b, d, and 13b, d).

In the second experiment with 10 plants, the population growth was also well reproduced by all dispersal behaviors in the density-independent option (Annex 1, Figures 1a, 1c, 2a and 2c) and also the random uniform dispersal behavior in the density-dependent option (Annex 1, Figure 2b). Meanwhile, for eight nearest neighbors and negative exponential function, the model replicated the population trend but an exponential growth at the end of the experiment overestimated the population size (Annex 1, Figure 1b and 1d). The following cues behavior

under the density-dependent option resulted in the faster increase and an early overestimation of the population size (since the day 60).

The results of the third experiment using 300 females growing on 15 plants fitted the first data point at 53 days with almost all dispersal behaviors in density-dependent and independent options. Only following cues behavior in density-dependent option did not fit the data because of the faster growth of the population size (similar to the experiment with ten plants) (Annex 1: Figures 3 and 4). Though, the second data point, at 93 days, was reproduced only by eight nearest neighbors and negative exponential dispersal behaviors in the density-dependent option. However, the experimental data reported two different values (400.000 and 800.000 individuals) at 93 days and the simulations reached only the lower value. Unlike the two previous experiments with 5 and 10 plants, in this case, all behaviors in density-independent option underestimated the population size (Annex 1: Figures 3a, 3c, 4a, and 4c).

In the experiments with 5 or 10 plants, all dispersal behaviors under density-independent option reproduced the experimental data. In the experiments with 15 plants, the density-dependent behaviors: eight nearest neighbors and exponential function represented the data better than density-independent rules, while the following cues behavior showed earlier growth and the larger population size than the experimental data.

 Density-independent options consider one movement per time step, while density-dependent options represent a more intensive search for places to oviposit (up to eight times per day). Because these conditions allow more attempts they lead to a higher population size especially when the density of insects on the leaf is close to the carrying capacity.

There are approximately 10 individuals per plant to infest in the five and 10 plants experiments and approximately 20 individuals per plant in the 15 plants experiment. Initially, in low densities, a low search effort represented by density-independent rules can reproduce the experimental data while in a more populated experiment the more intense search for space is important to reproduce the experimental data. As the population size increases the role of the dispersal behavior of insects becomes more relevant to the population growth in all experiments.

The development of integrated pest management programs has recently considered the pests´ dispersal, which shapes the pests´ spatial distribution (Mazzi and Dorn, 2012). Making the decision to disperse, pest insects consider several characteristics of the environment, for example, the host quality (Noldus et al., 1986b). As implemented in this study, the host quality causes the insects to move upward. In the case of within-plants movement, the insects follow the chemical and visual cues from plants (Bleeker et al., 2009). Therefore, following cues behavior implemented in the model, works better for the spatial experiments than for population growth analysis. All these factors can be important in low densities of the insects in early stages of colonization of the crop. On the other hand, the results for population growth show that density-dependent dispersal process can play a role at high densities of pest insects because the population growth speeds up the decrease in plant quality (Stewart, 1996).

In conclusion, the dispersal behavior of the insects is a complex process that can be dependent on its density but also on the environmental factors and availability and quality of resources. The dispersal behavior deserves further studies to determine the exact interplay of all known factors. However, according to the results of this study, early stages of pest colonization in crops with low densities of the pest can be controlled using the traditional approach On the other hand, in the advanced stages of population development new strategies oriented towards insect dispersal behavior would highly improve the pest control.

3.1.3 Population analysis at theoretical equilibrium

The empirical data from literature as well as laboratory experiments usually deal with short time frames while the field experiments are difficult to conduct without intervention or control measures for the pest. Therefore, a virtual experiment can provide some insights about the population size at equilibrium and measure the effect of different dispersal rules.

Three increases in population size are evident in this experiment (Figure 15a), at 40, 80 and 120 days when adults and eggs were the most abundant stages in the population (Figure 14a) corresponding to the first, second and third generation of the population. The population size increased for approximately 150 days, afterward it oscillated around 200000 individuals. As the plants are growing all the time and the lower 3 leaves are pruned from the plants weekly the amount of available resources changes causing the oscillating pattern in population size trajectory (Figure 15a).

After 150 days, instantaneous growth rate started oscillating around 1.0 and intrinsic growth rate close to zero (Figure 14b). The growth rates, variation in population size (Figure 15a) and stages distribution (Figure 14a) changes were affected only by pruning procedure. These results show that the population reached the equilibrium point in this system and did not increase above 200000 individuals. Interestingly, the initial adult population colonized up to 40 plants and the first generation increased the number of colonized plants up to 60 (Figure 15c). However, the following generations were not able to colonize more than 60 plants. The population of adults at equilibrium was about 300adults/plant, but approximately 500 adults/infested plant (Figure 15b and 15d).

The equilibrium point in the development of a pest population cannot be reached due to the management of the crop but also due to other factors like changes in environmental conditions, the presence of other competitor or natural enemies. However, this analysis shows the synchrony of the pest population growth with the crop growth, the discrete generations were present even though only one infestation happened. The knowledge of generations' cycle is very important to properly apply the control measures and break the life cycle of the pest.
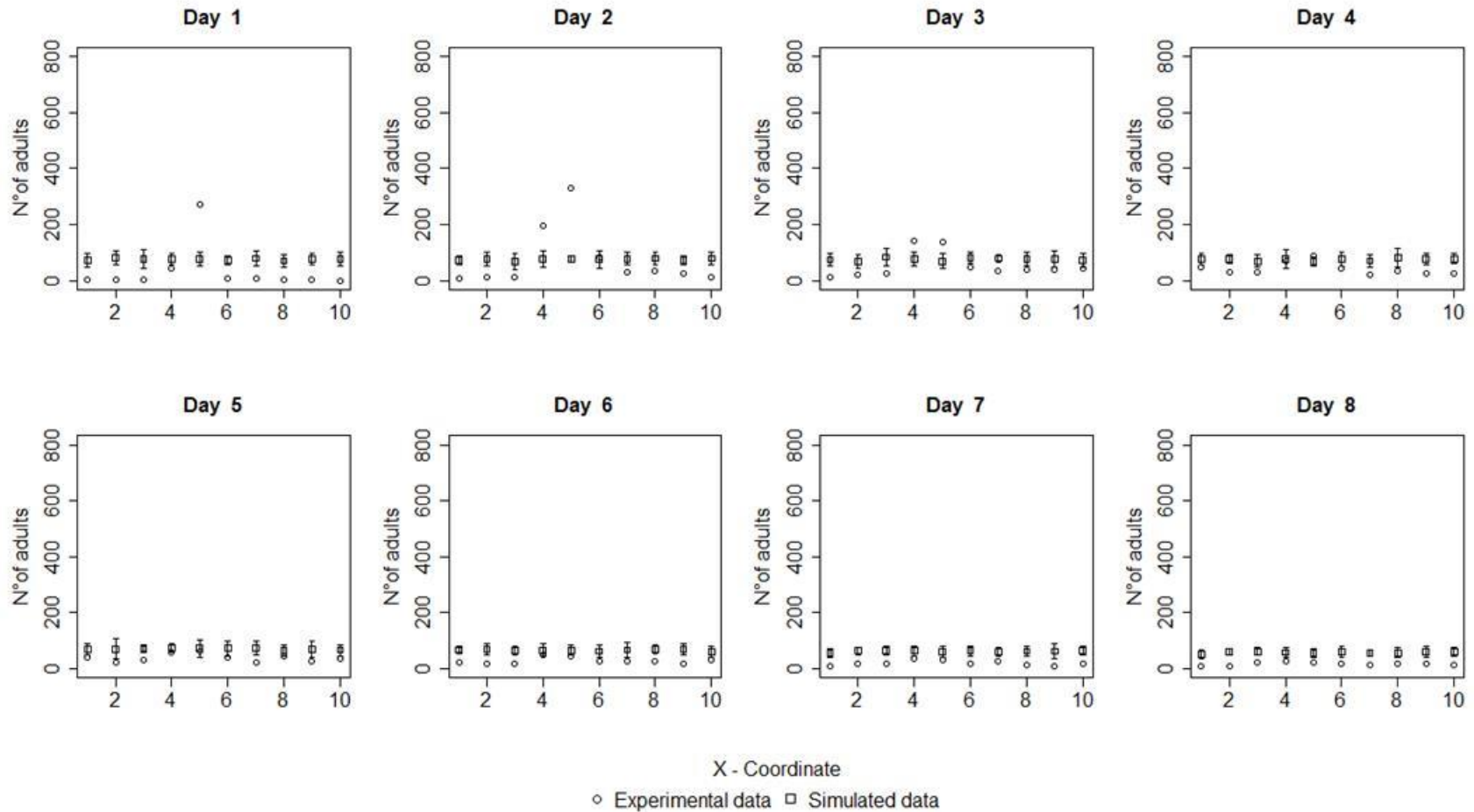
Figure 4. Distribution of whitefly adults for the random uniform dispersal behavior under density-independent option (Experiment number 1, Table 3) in an arrangement of 10 x 10 plants and 762 adults in the central plant at time zero, followed during eight days.
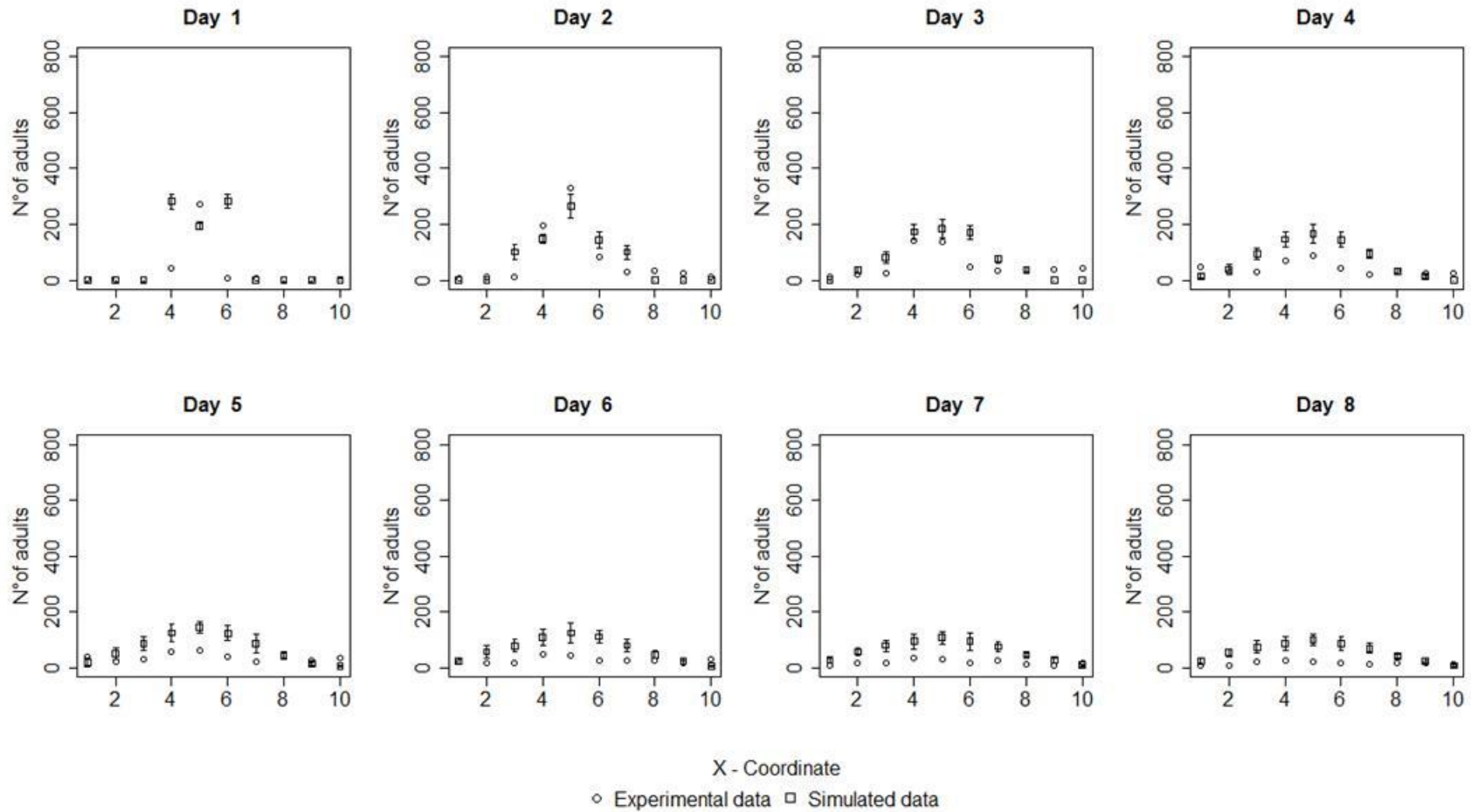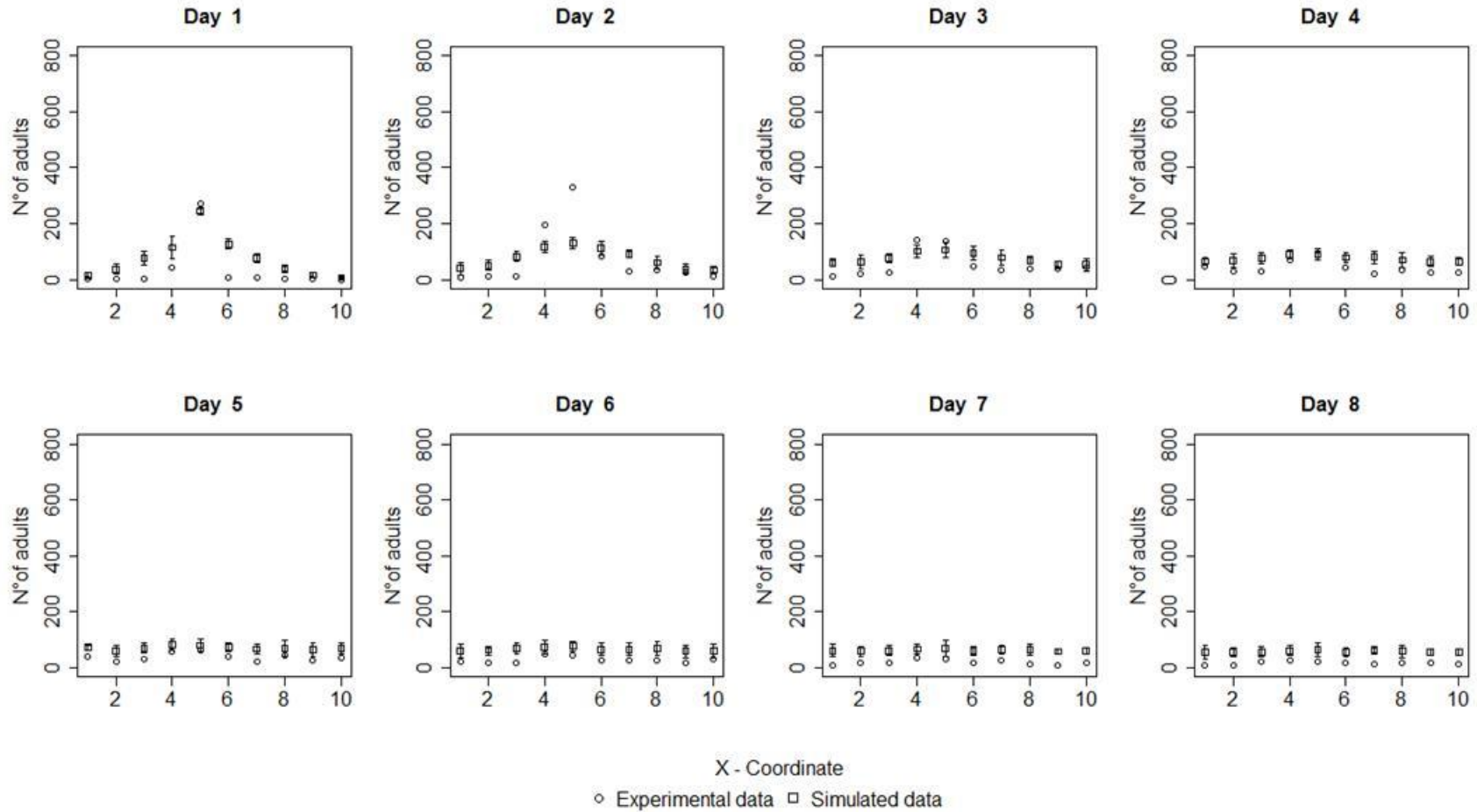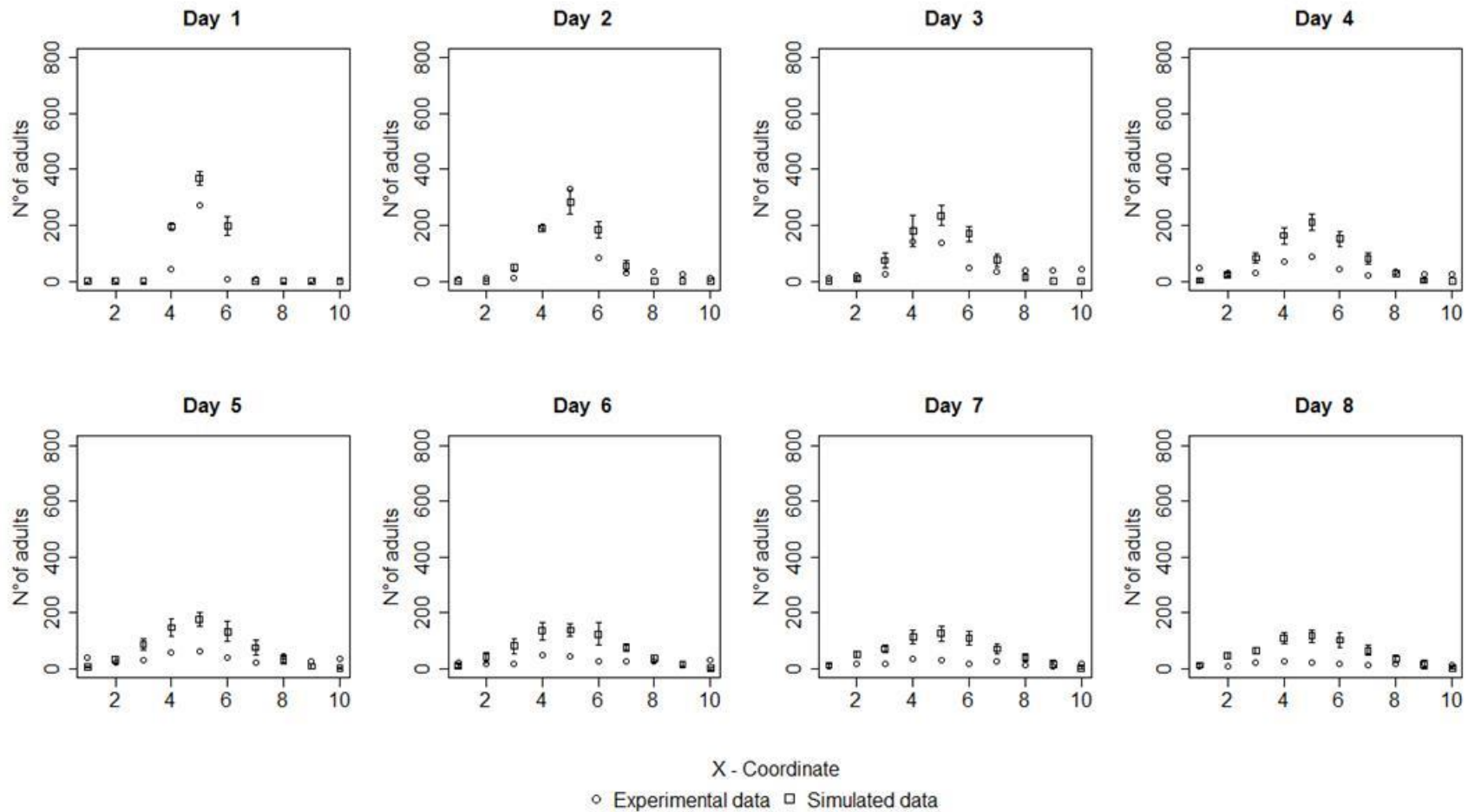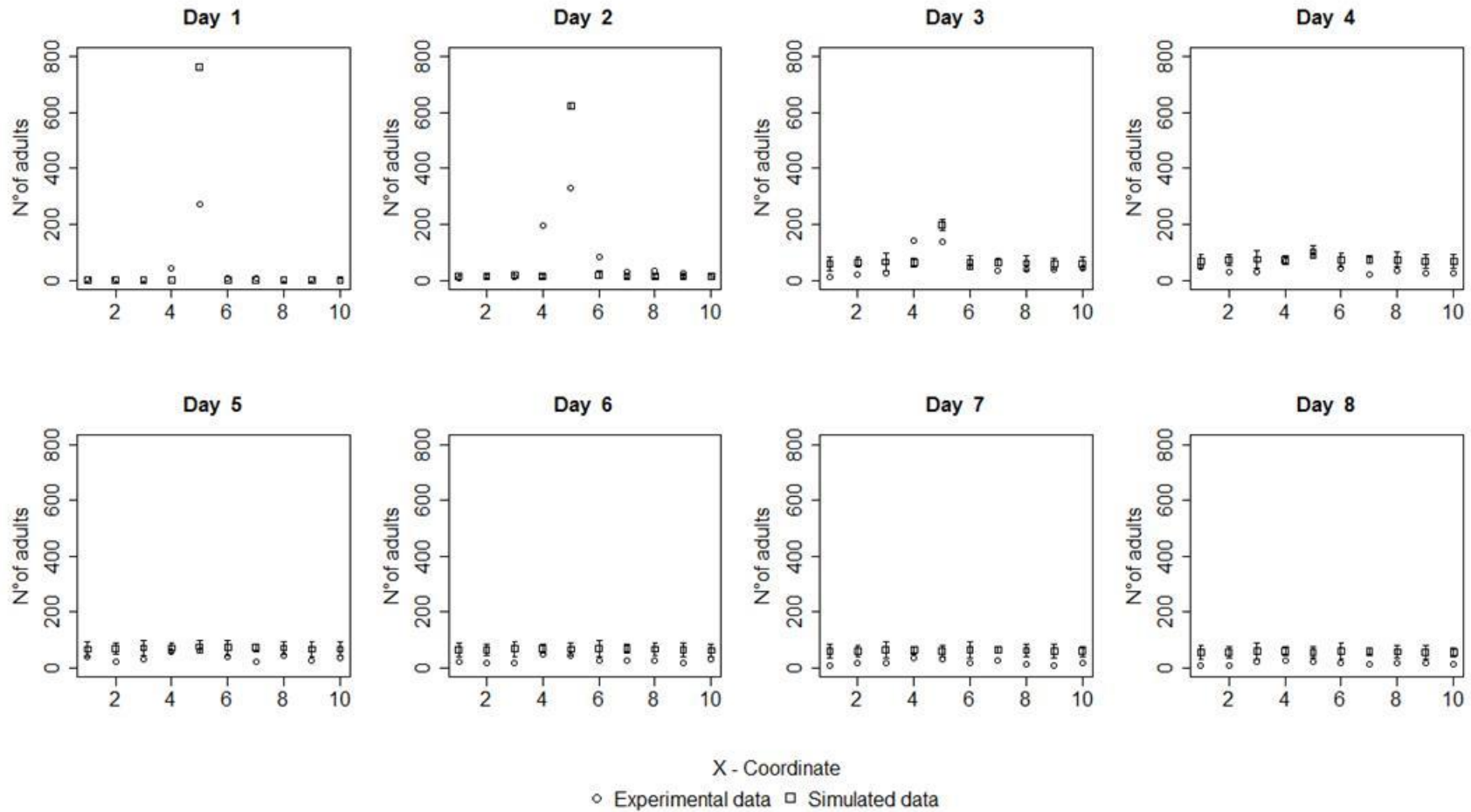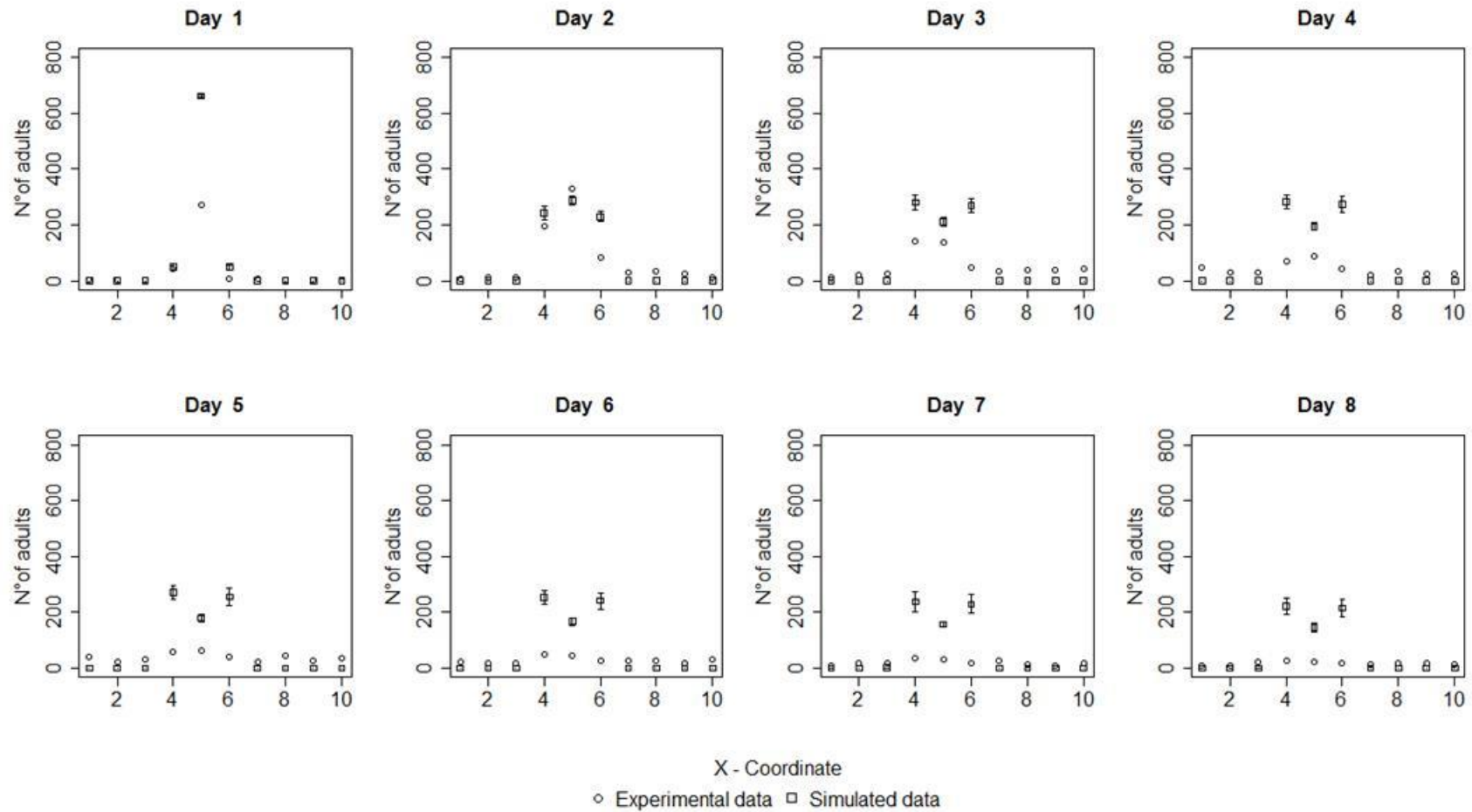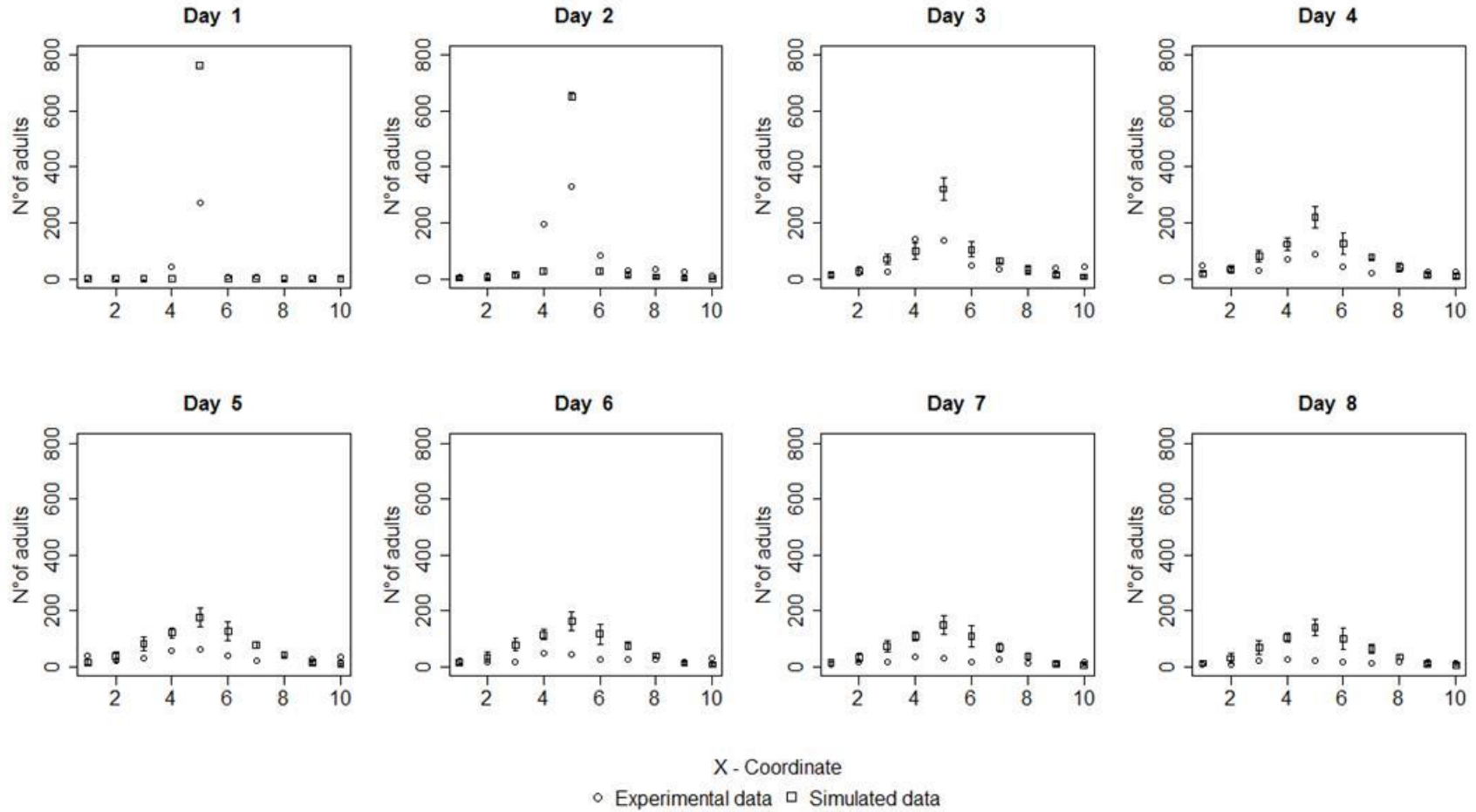
Figure 5. Distribution of whitefly adults for the eight nearest neighbor plants dispersal behavior under density-independent option (Experiment number 2, Table 3) in an experiment of 10 x 10 plants and 762 adults in the central plant at time zero.

Figure 6. Distribution of whitefly adults for the empirical negative exponential function for the dispersal behavior under density-independent option (Experiment number 3, Table 3) in an experiment of 10 x 10 plants and 762 adults in the central plant at time zero.
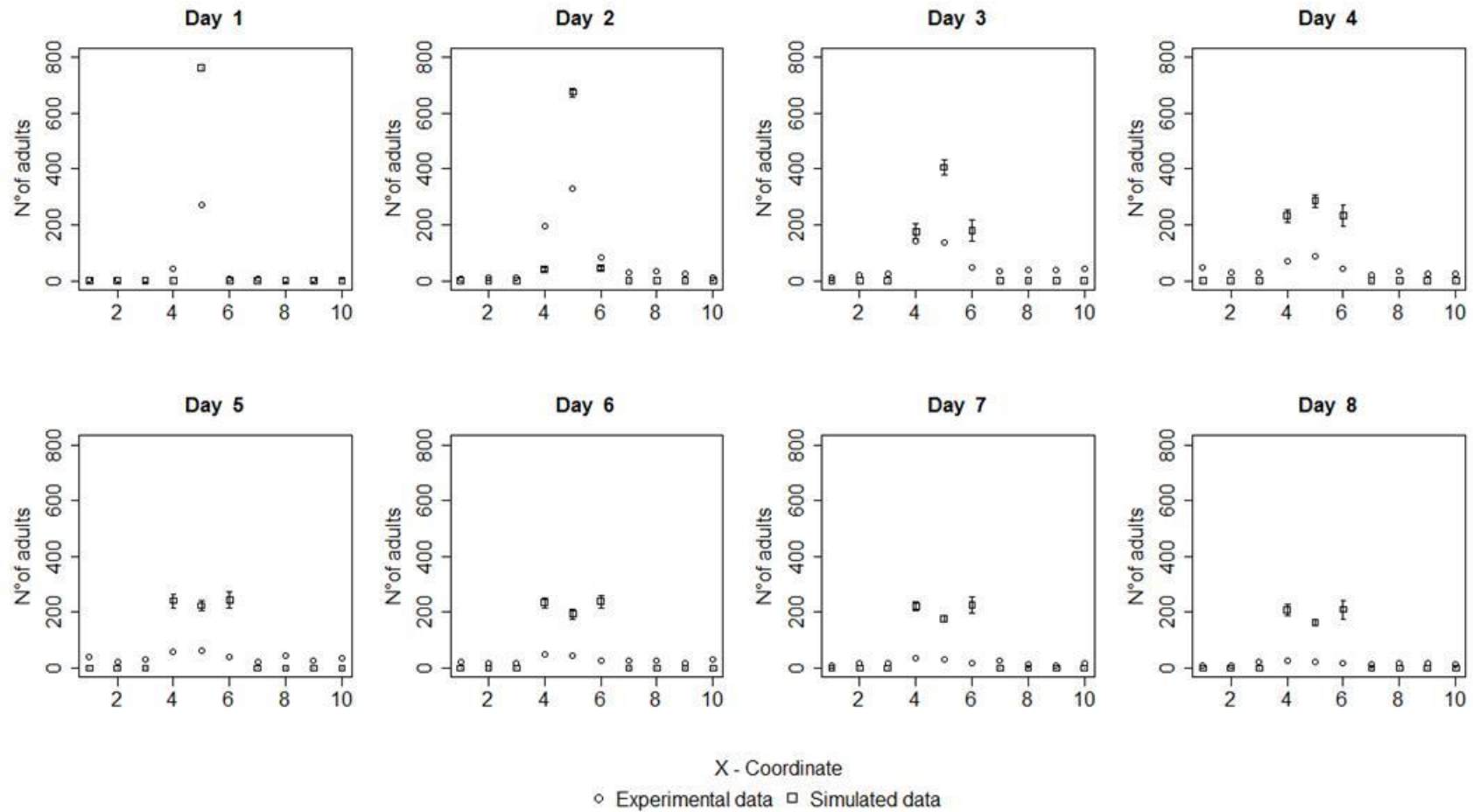
Figure 7. Distribution of whitefly adults, for the following cues dispersal behavior under density-independent option (Experiment number 4, Table 3) in an experiment of 10 x 10 plants and 762 adults in the central plant at time zero.

Figure 8. Distribution of whitefly adults for the random uniform dispersal behavior under density-dependent option (Experiment number 5, Table 3), in an experiment of 10 x 10 plants and 762 adults in the central plant at time zero.

Figure 9. Distribution of whitefly adults for the eight nearest neighbors dispersal behavior under density-dependent option (Experiment number 6, Table 3), in an experiment of 10 x 10 plants and 762 adults in the central plant at time zero.

Figure 10. Distribution of whitefly adults for the negative exponential dispersal behavior under density-dependent option (Experiment number 7, Table 3), in an experiment of 10 x 10 plants and 762 adults in the central plant at time zero.

Figure 11. Distribution of whitefly adults for the following cues dispersal behavior under density-dependent option (Experiment number 7, Table 3), in an experiment of 10 x 10 plants and 762 adults in the central plant at time zero.
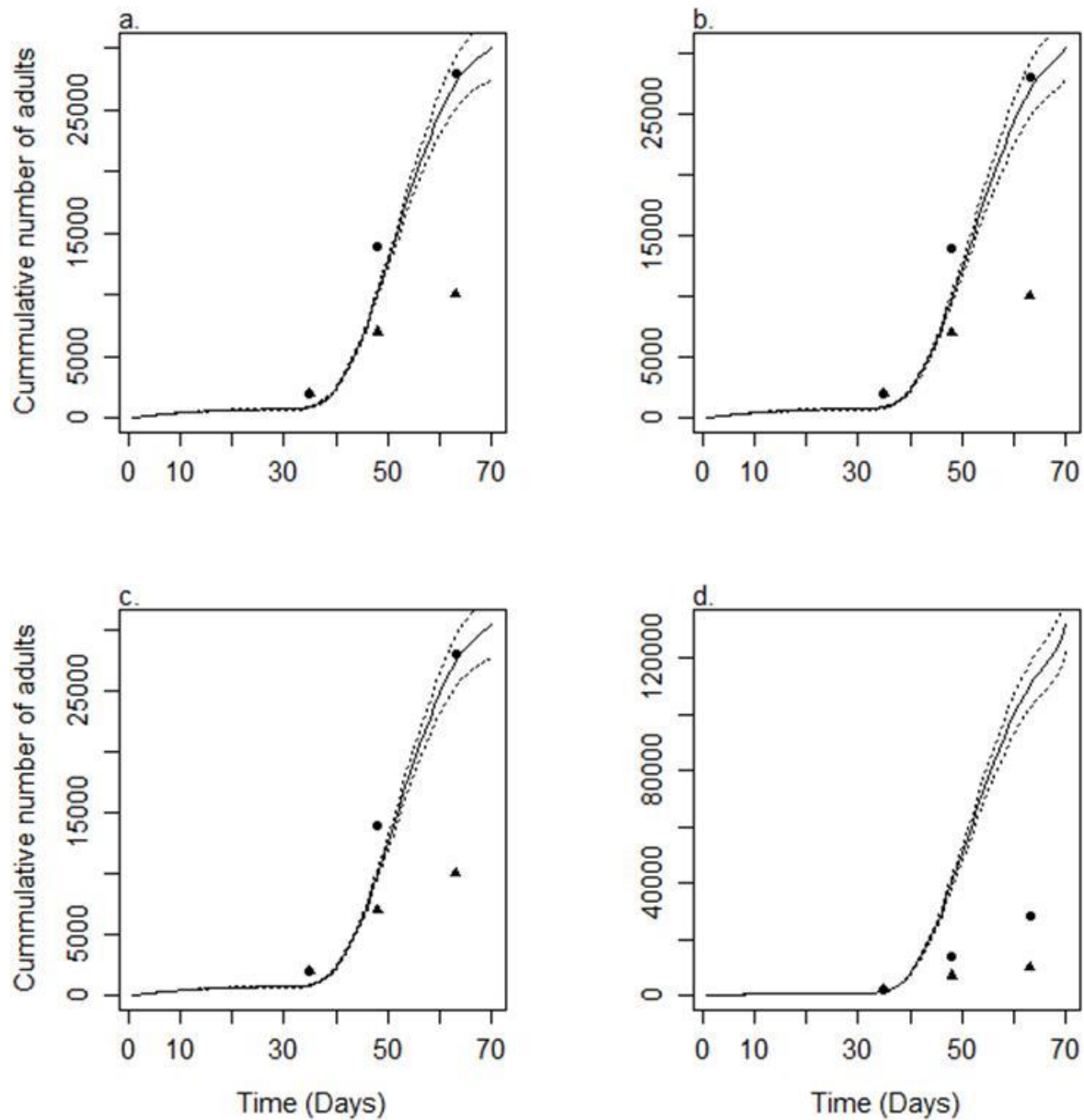
Figure 12. Population growth of whiteflies (mean +/- s.d. of five runs) in five plants infested with 50 females at day zero. The dispersal behaviors were: eight nearest neighbors (a and b) and negative exponential function (c and d), in density-independent (a and c) and density-dependent (b and d) decision option (see table 2). Circles and triangles represent two experimental data sets from Joosten and Elings (1985)
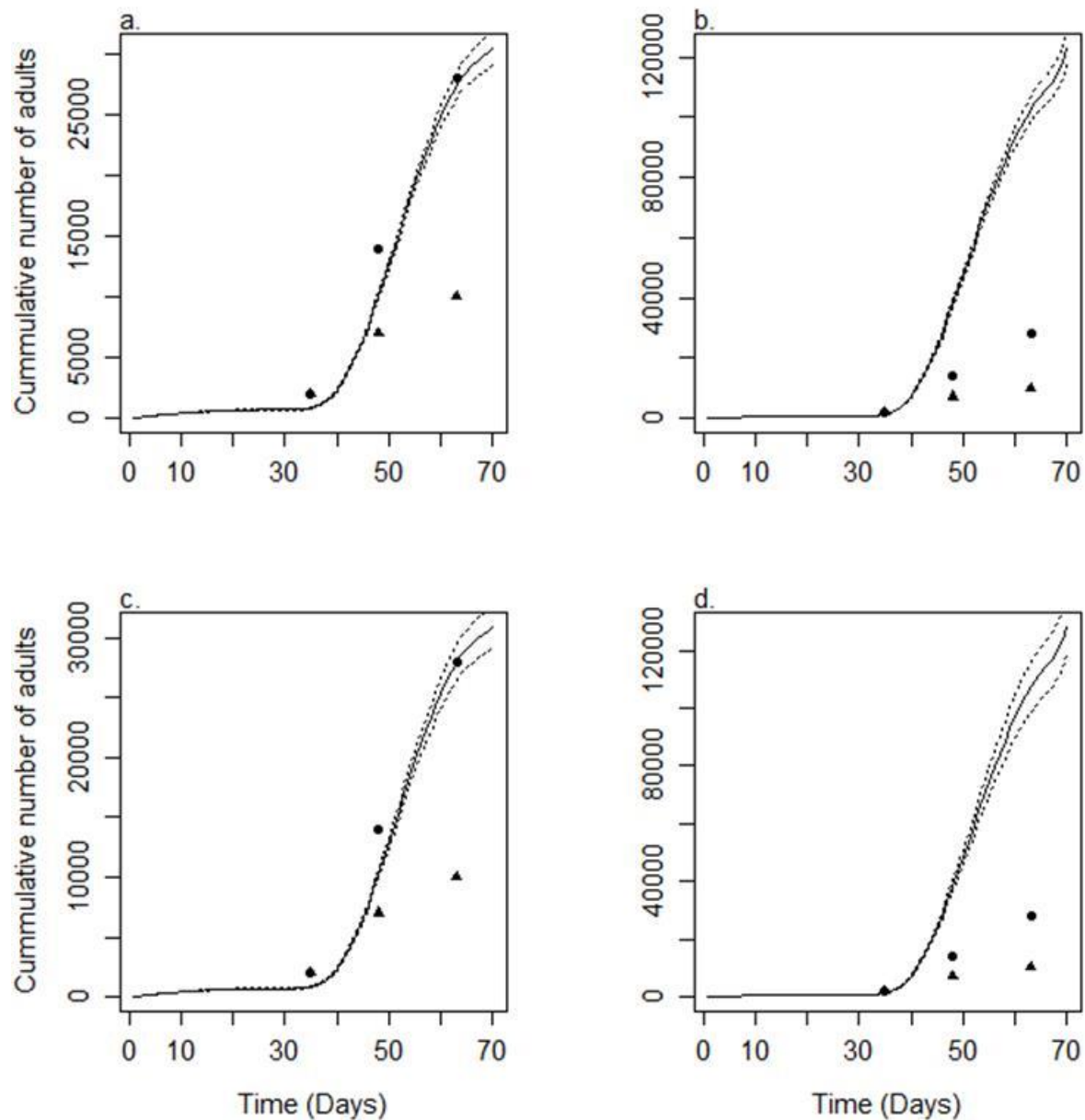
Figure 13. Population growth of whiteflies (mean +/- s.d. of five runs) in five plants infested with 50 females at day zero. The dispersal behaviors were: random uniform (a and b) and following cues (c and d), in density-independent (a and c) and density-dependent (b and d) decision option (see table 2). Circles and triangles represent two experimental data sets from Joosten and Elings (1985).
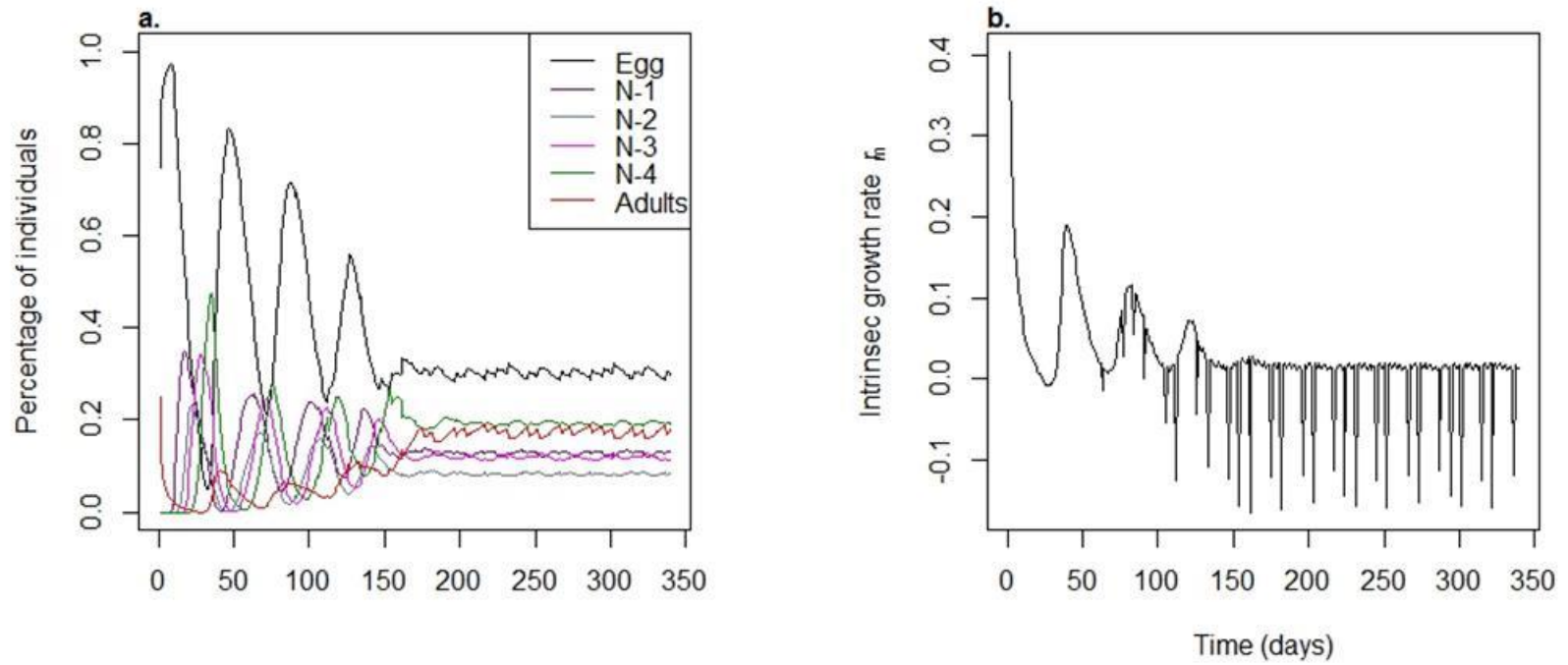
Figure 14. Whitefly population growth in an arrangement of 10 by 10 plants infested with 10 females at time zero, when the adults move to the eight nearest neighbor plants daily.
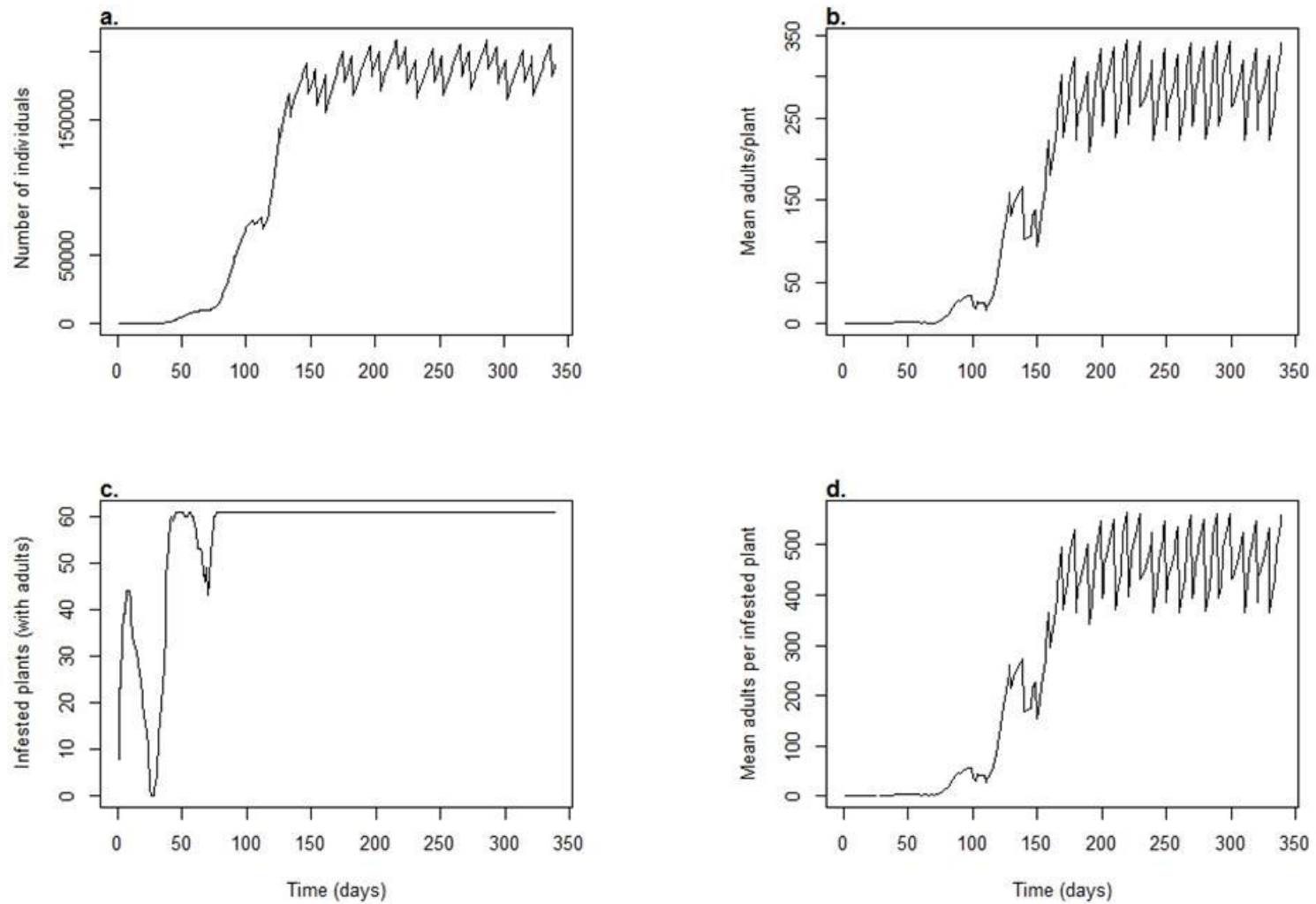
Figure 15. Example results showing the pest population (adults only) in time. Density-independent eight nearest neighbor plants dispersal behavior.

Small experiments are not suitable to describe the insects' dispersal since the only limited place to move is available unlike in the real systems. Studies in the wind tunnel, contribute to elucidate the possible cues involved in the foraging behavior of chemicals emitted by host plants (Bleeker et al., 2009). However, the presence of other factors like different plants, or insects can affect the behavior at some point (Inbar and Gerling, 2008) changing the dispersal pattern. For example, the small scale experiments following population growth cannot be extrapolated to a higher number of plants or to a crop due to the difference in the conditions available for the population to grow and disperse.

The foraging behaviors tested here show the important effect of the density-dependent decision rules for the increasing population size (Figures 4-7 and Figures 8-11). Many of the field studies show difficulties in following the numerous flights of the small size individuals 10 hours a day (Bonsignore, 2014). Therefore, simulation studies on the dispersal process can help to understand and predict the dispersion patterns of the insects in crops, using the individual-based approach.

4 Extension of the model: Pest - Parasitoid

The dynamics of the pest populations can be affected by abiotic and biotic factors like temperature, humidity, and natural enemies. To take into account such case, in this model the introduction of the parasitoid Encarsia Formosa was implemented. The parasitoid development follows a similar stage structure based on the accumulation of degree days. This model extension allows testing the dispersal patterns of the parasitoid and the effects of parasitoid spread on pest population dynamics.

The foraging behavior of the parasitoid *E. formosa* on leaves is well documented. Times for landing, walking and handling host until the parasitoid leaves the leaf are described in tomato (Roermund and Lenteren, 1995) and Gerbera (Sutterlin and Lenteren, 1999). A simulation model of the parasitoid behavior shows that the parasitoid searches and encounters the host randomly, and also that the walking activity affects the oviposition in low densities of pest (Van Roermund et al., 1996).

Studies on the long distance search for the host by *E. formosa* show no response when the plants are infested with whiteflies but a positive response to the green light transmitted through the tobacco leaves. In a short distance search study a non-volatile contact kairomone from honeydew of nymph 3 and 4 causes longer searching times (Romeis and Zebitz, 1997). In contrast, the study of (Guerrieri, 1997) shows the increase in oriented long distance flights when the host is present on the plant and in short distance flights the importance of visual and chemical cues.

(Roermund et al., 1997) conducted a simulation study of the pest-parasitoid dynamics where they assumed no preference for the foraging behavior of *E. formosa* and used an exponential function to let the individuals of pest and parasitoid select the next plant to visit. Later studies suggested that the parasitoid is more likely to leave the pest´ patch with the increase of time from the last encounter despite the host distribution (Burger et al., 2006).

4.1 Model description:

Only the new elements for this extension are described below, for the main model description see chapter X.

4.1.1 Purpose:

The purpose of this extension is to test if the foraging options used for whiteflies could be applied to parasitoid *E. Formosa.*

4.1.2 Entities, state variables, and scales:

The parasitoid is a mobile individual with state variables for location (x, y and z coordinates), age, stage and number of eggs per day (Figure 4.1). The scales of the model are the same as for the pest model (Section 2.3.2.3).

4.1.3 Process overview and scheduling:

The process of parasitoid is scheduled to happen after the pest processes.

Parasitoids' growth. The ageing process is modeled by changing the "stage variable" when a number of necessary degree-days for the stage is reached (Table 4).

Parasitoids´ dispersal. Only adults execute dispersal and follow the same rules as the pest.

Parasitoids´ host feeding. Parasitoid feeds up to three nymphs stage 2 per day.

Parasitoids´parasitization. The reproduction for the parasitoid is the parasitization process and implies the death of a host-pest and immediately a new parasitoid in the system**.**
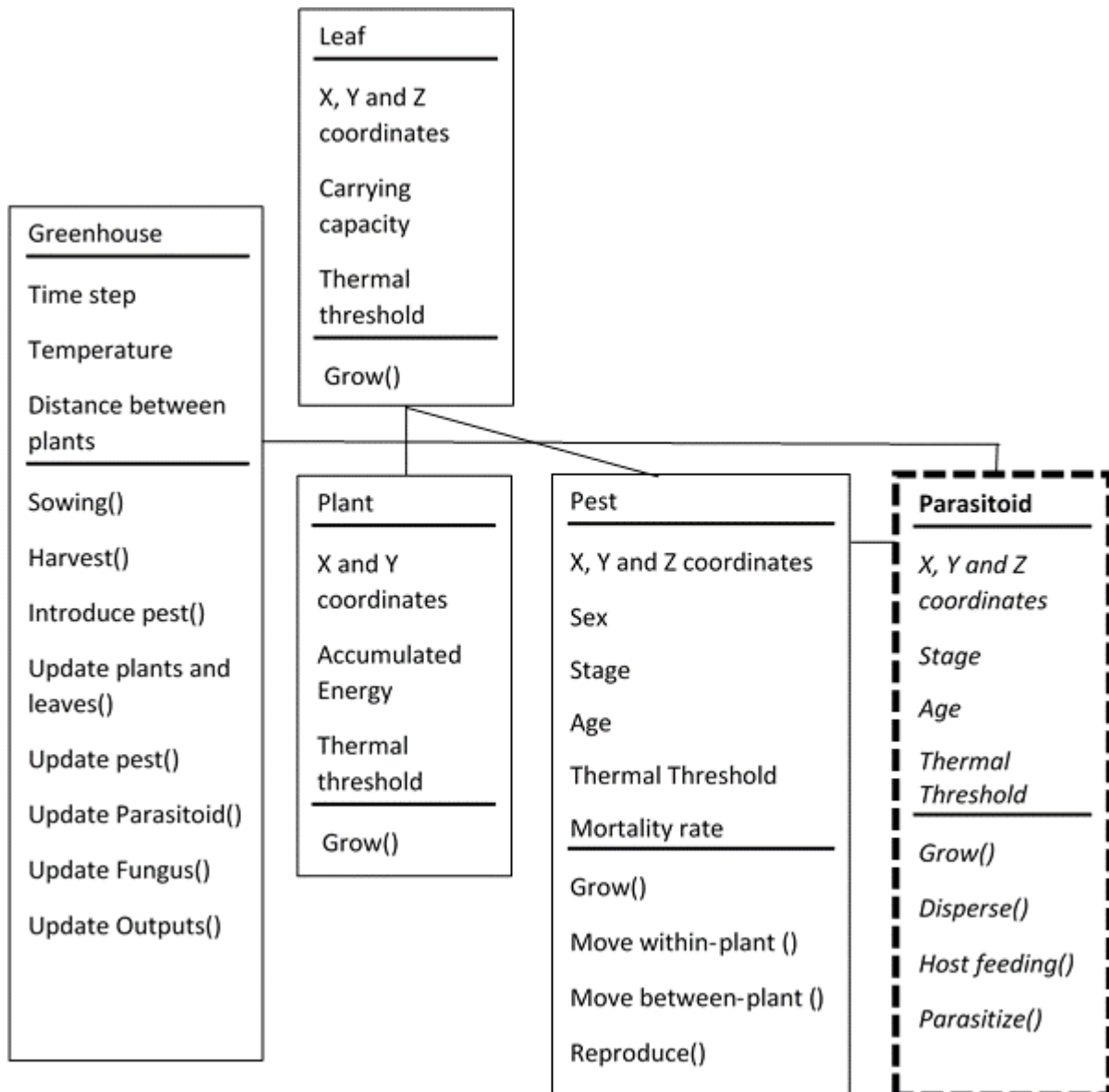
Figure 16. Static scheme of the model extension of whitefly and *E. formosa* dispersion (Chapter 2, Figure 17) with the parasitoid extension (discontinuous lines).

4.1.4 Design concepts

Basic principles: The same four alternative dispersal rules used for the pest were tested for the parasitoid in order to elucidate the foraging behavior.

Emergence: The population size of pest and parasitoid emerge from the combination of dispersal behaviors and plants growth in the model.

Adaptation: Parasitoids adults decide to feed the host or to parasitize depending on the stage of development of the host. Otherwise, they move to look for another patch of pest.

Stochasticity: Stochasticity is included in stages duration variability and in the direction of adults´ dispersal behavior.

Observation. Summary statistics for the parasitoid population in time and space are saved each time step.

Table 4. Parameters for the parasitoid extension of the model.

Parameter	Value		
	Initial	Minimum	Maximum
Parasitoid			
Lower Thermal Threshold (Roermund and Lenteren, 1992)		10.5 °C	-
Stages (number of degree-days)(Osborne, 1982)			
Egg – black scale	assigned	80.8	93.0
Black scale - Adult	randomly within the	93.7	105.7
Adult	range	178.0	199.8
Oviposition (Aragón et al., 2008)		13	-
Host feeding		3	-
Attempts	6		

4.1.5 Initialization.

The number, location and time to introduce the parasitoids are assigned according to each experiment (Table 5).

4.1.6 Submodels

4.1.6.1 Parasitoids´ growth.

The parasitoids have three stages 1) egg, 2) black scale and 3) adult. The duration of each stage is assigned randomly within a range of values (Table 4). The parasitoids grow in the same way as pest (See section 2.3.6.3).

4.1.6.2 Parasitoids dispersal.

The dispersal process happens daily up to six attempts per time step. The between-plants movement follows the random uniform, eight nearest neighbor and exponential function rules as for pest (See section 2.3.6.4), the only difference is that the parameter alfa for the exponential function was changed to 0.95 as was reported by Roermund et al. (1997). The cues option was not used parasitoids as there are different studies showing no evidence of chemical cues to find plants with suitable host and the color attraction from plants is the only cue used (Roermund et al., 1997; Romeis and Zebitz, 1997), but is not explicitly model here as all plants have the same characteristics.

4.1.6.3 Parasitoids´ host feeding.

The parasitoid senses the availability of host nymph stage 2 and can eat up to 3 individuals per day.

4.1.6.4 **Parasitoids´ parasitization**.

In order to use the most realistic data the value of the number of hosts parasitized is taken from the greenhouse experiments (Aragón et al., 2008)(Table 4). Maximum 6 attempts per time step and the parasitization number in one leaf can be a number between zero and five where zero means cases where even with available host the parasitoid is not parasitizing. The stages to parasitize are nymph 3 and nymph 4 of whiteflies. In this model 50% of the time they choose nymph stage 3, otherwise, the stage 4 is selected to parasitize.

4.1.6.5 **Degree days**.

The thermal units for development of parasitoids are calculated in the same way as for the pest and plants but with the lower thermal threshold (Table 4).

4.2 Simulation procedures

In order to test the behavior of the parasitoids and its effect on the whiteflies population dynamics the following simulation was run:

Table 5. Initial conditions of pest – parasitoid simulation experiment.

Parameter	Value
Experiment (Section)	*Small patch (section 4.2.1)*
Simulation time (days)	112
Number of plants	1344
Initial number of pest (♀)	18
Time of infestation	0
Pest initial spatial distribution	Aggregated (18 central plants)
Parasitoid initial spatial distribution	Central plant
Leaf carrying capacity	21862
Pest dispersal rule	Eight nearest neighbor plant
Parasitoid dispersal rule	(See section 4.1.6.2)
Initial number of adult parasitoids (Time of release)	1304 (23 days)
	3629 (37 days)
	6048 (51 days)
	3333 (65 days)
Reference	(Eggenkamp-Rotteveel et al., 1982b)

4.2.1 Field patch experiment

A virtual experiment of a patch of 1344 plants infested with whiteflies in a tomato greenhouse with four releases of the parasitoids (Eggenkamp-Rotteveel et al., 1982b) was run. The initial conditions are given in table 5.

4.3   Results and discussion

4.3.1 Patch experiment

The experiment in the greenhouse patch with 1344 plants show a clear effect of the parasitoids by host feeding on nymph 2, the parasitization on nymph 3 and 4 and the consequences of the parasitoid control on the whitefly adult population (Figure 17). The three behaviors tested (random, eight nearest and exponential) to find the next plant were effective to reduce the pest population. The random search and the exponential show similar tendency but the eight nearest seems to be extremely effective and let the parasitoids to use almost all the host nymphs available in the plants (Figure 18). The number of individuals of nymph 2 is higher than the number of stage 3 and 4 which is explained by the less host feeding effect compare with the effect of parasitism. However, the host feeding seems to be important for the control of pest population (Figure 17a).
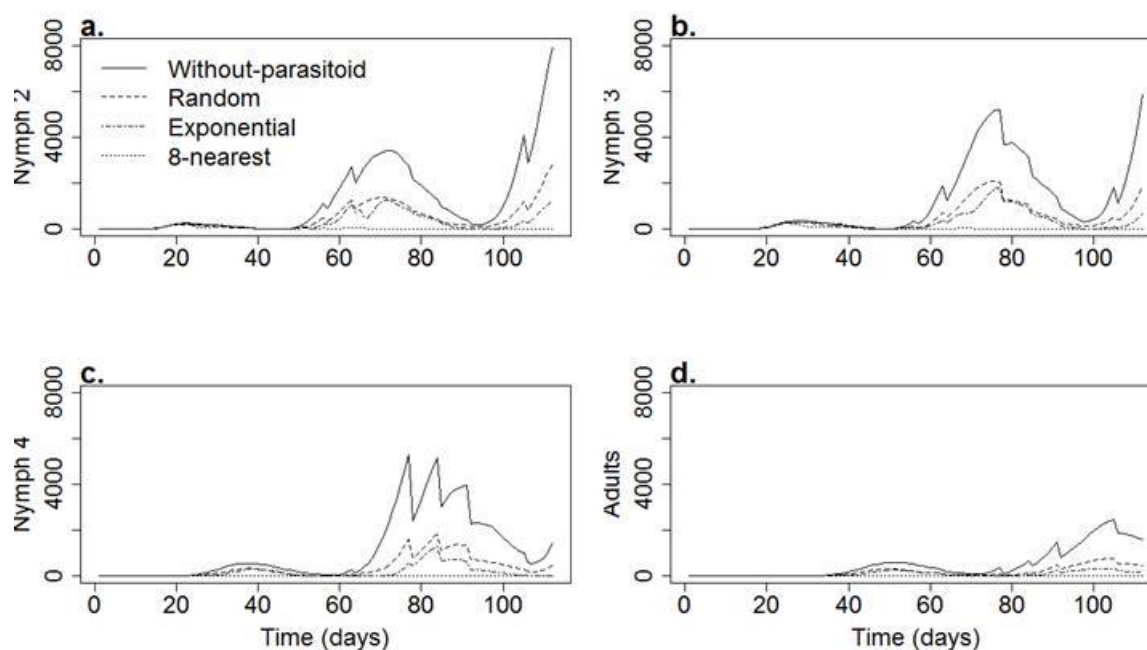
Figure 17. Simulated number of individuals, of different stages of whiteflies in treatments without parasitoids, and with four releases of parasitoids (See table 5) using three different dispersal rules.

The number of nymphs 4 fluctuate below 300 and 700 individuals in the field data, while in the simulations produce two clear increases at 40 and 80 days corresponding to the first and second generation of the whiteflies. The maximum simulated value for the first generation was approximately 400 individuals and for the observed data was 600 individuals. After that, the simulations and field data agree, but the simulations predict a high number of individuals at around 85 days and then a faster decrease explained by the natural dynamics of the population that is going to be new adults, which start to emerge at this time (Figure 17d).

The exponential function seems to be the most realistic representation of the parasitoid behavior of the three tested. However, the differences between field data and simulations suggest that some other details must be taken into account to understand and predict the parasitoid efficacy in crops. The effect of other factors that affect the pest population can be also affect directly or indirectly the parasitoid behavior (Inbar and Gerling, 2008). The lack of evidence of cues used by parasitoids to localize their host pest from distance (Romeis and Zebitz, 1997) seems to explain to some degree the whitefly population dynamics under

biocontrol of the parasitoids in crops. Nevertheless, the fact that the exponential function behavior reproduces a lower number of whiteflies closer to field data, suggest that probably other factors apart from randomness are involved in this parasitoid foraging behavior. Experiments on gerbera plants found more parasitoids on plants already infested with whiteflies than in plants not infested (Sütterlin and Lenteren, 2000), as well the parasitoids were reported more attracted by infested plants to orient their flights (Guerrieri, 1997).

The underestimation of the population size at 40 days and the overestimation at 80 days can be explained by an adaptable behavior proposed for the parasitoid in which at low host densities the individuals tend to leave the searching patch and with high host densities increases the probability to stay in the same searching patch (Burger et al., 2006). This flexible condition for the parasitoids was not included in this simulations as the parasitoids behavior works independently of the host density for all simulations, but also independent of the spatial distribution of the whiteflies in the leaf. This makes the parasitoid efficiency similar under any host density and dependent only on the presence or absence of then pest in the leaf.

The behavior of parasitoids in the leaves is already well and detailed studied (Roermund and Lenteren, 1995) and here the number of leaves visited per day were used as a summary of the behavior daily behavior.

The number of adults per plant was higher in the random dispersal, followed by exponential and eight nearest (Annex 1, Figures 5a, 6a, and 7a). The exponential behavior agrees with the values reported in the study of van Roermund et al. (1997). For this experiment, the maximum number of plants with adults was 15 with about 25 (Annex 1, Figure 7 c) individuals per infested plant. In this plants, where they emerge on the lower leaves and then move up to the middle and upper part of the plant (Annex 1, Figures 5d, 6d, and 7d). However, the population tends to be placed in the middle and lower part because as the plants produce new leaves the adults move there to get fresh resources but the lower leaves are pruned by crop managers changing the relative position of the individuals. This vertical spatial distribution that emerges from the behavior of the insects and the management of the crop reproduce well the vertical spatial distribution reported in different studies (Eggenkamp-Rotteveel et al., 1982a; Manzano and van Lenteren, 2009; Noldus et al., 1985; Pérez et al., 2011b)
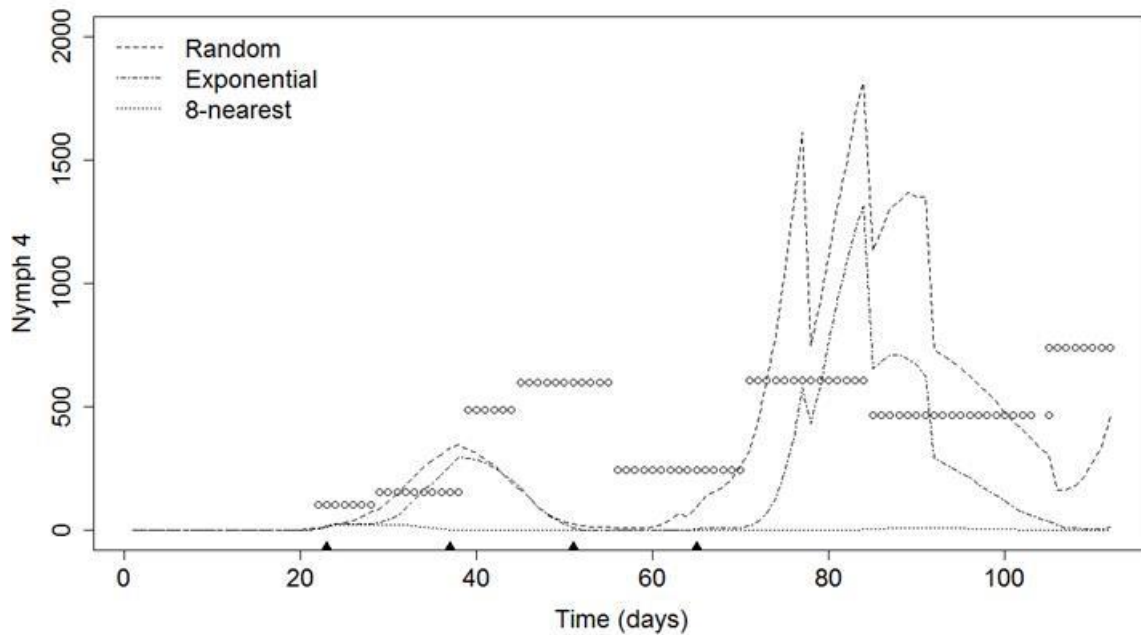
Figure 18. Number of nymphs stage 4 in the three parasitoid foraging behavior scenarios. Empty point are field data counts (Eggenkamp-Rotteveel et al., 1982b) and the black triangles represent the releases of the parasitoid(see Table 5).

5   Powdery mildew – *Oidium neolycopersici*

There is evidence of the effect of mildew presence on the behavior of the parasitoid, where the parasitization rate was reduced by 25% in laboratory experiments (Focke, 2000). However, there is not conclusive information about the quantities of mildew to affect the insects. Therefore, here is considered just the presence in the leave to change the behavior and the aim is to test if there is an effect on the biological control of the pest population when mildew is present.

5.1 Simulation procedures

The experimental design of small patch used for the pest- parasitoid (Table 5) was used here with the only difference that 1% of the leaves are randomly infected by mildew at the beginning of the experiment. Not growth or quantity of the pathogen in the leaves is simulated.

The same dispersal rules for parasitoids were tested except that when the insect land on a leaf infected with mildew, the parasitoid chooses to move to another leaf and not parasitization or host feeding happen in an infected leaf.

5.2 Results and discussion

The sole presence of mildew in 1% of the leaves, produce an effect on the parasitoids biocontrol activity. A decrease in the parasitoids biocontrol activity given more nymphs stage 4 present in the crop for the random and eight nearest neighbor parasitoids dispersal behaviors (Figure 19 a and b) but for the exponential function the effect was the opposite resulting in an increase in the biocontrol effect (Figure 19c). In this experiment, the whitefly initial population was placed in the central plants and the parasitoid start from the central plant as well. As the two different insects used the same rules to disperse the probability of the parasitoid to find its host insect is higher in exponential than in the other two behaviors (random and eight nearest). The presence of mildew makes the parasitoid search for another leaf which may increase the probability to parasitize, as the number of attempts per day to parasitize can be higher than in cases where there is no mildew.

The effect of mildew on the parasitization was also observed in nymph 3, especially after 60 days where the population size is increasing (Figure 20). An opposite effect happens in the exponential behavior where the number of individuals is lower in the presence of mildew than in its absence, similar to the results for nymph 4.

The presence of mildew in the leaves change also the spatial distribution of the adults increasing the number of adults in the random dispersal rule experiment but reducing the number for the eight nearest and exponential dispersal experiments (Annex 1, Figures 8c, 9c, and 10c). This results must be evaluated in real experiments, because as was shown in the last two chapters the exponential or eight nearest rules can reproduce well the population growth and distribution of whiteflies, and the experiments in this chapter indicate that the presence of the mildew in crops can increase the dispersion of whitefly adults indirectly by the change in the parasitoid foraging behavior who avoid leaves infected with mildew. The vertical spatial distribution of whiteflies was not affected by the presence of mildew (Annex 1, Figures 8-10), therefore the distribution in the plant can be explained by the interaction between the pest and the plant dynamics but the horizontal distribution can be affected by other factors like the presence of a disease.
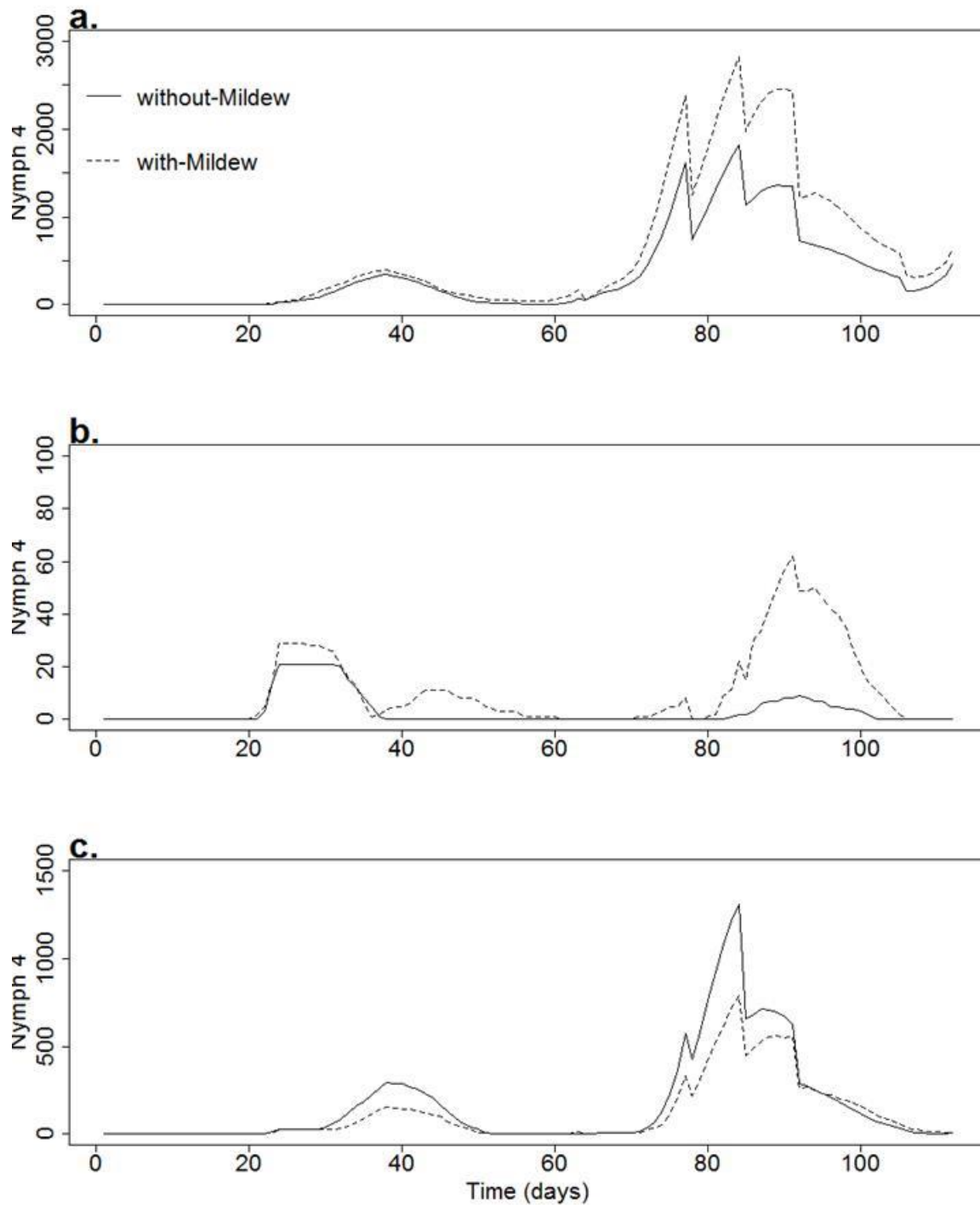
Figure 19. Effect of mildew presence on the population size of nymph stage 4 of whiteflies on 1344 plants (see Table 5), for the parasitoid dispersal behaviors: a) Random, b) Eight nearest neighbor and c) Exponential function.
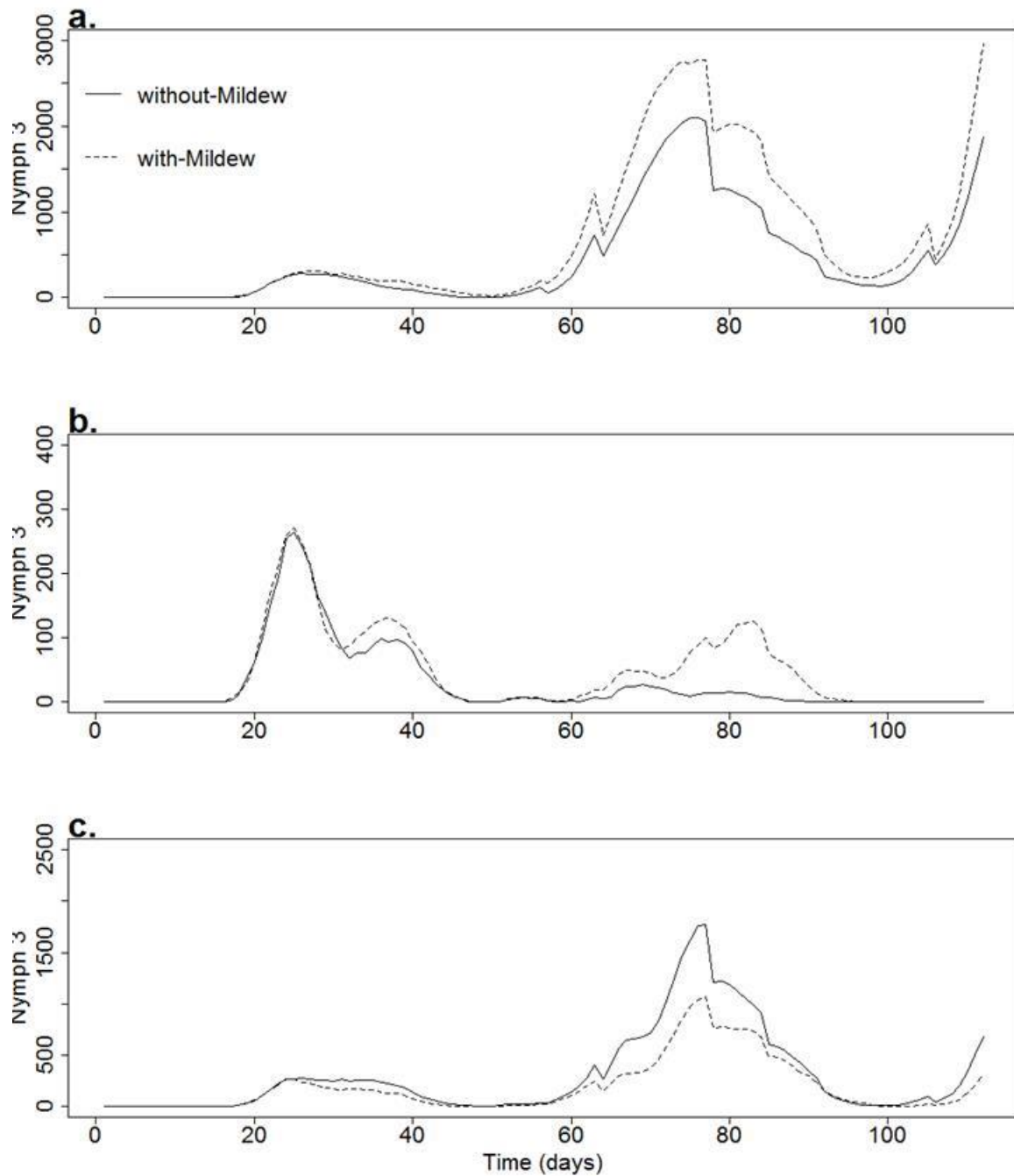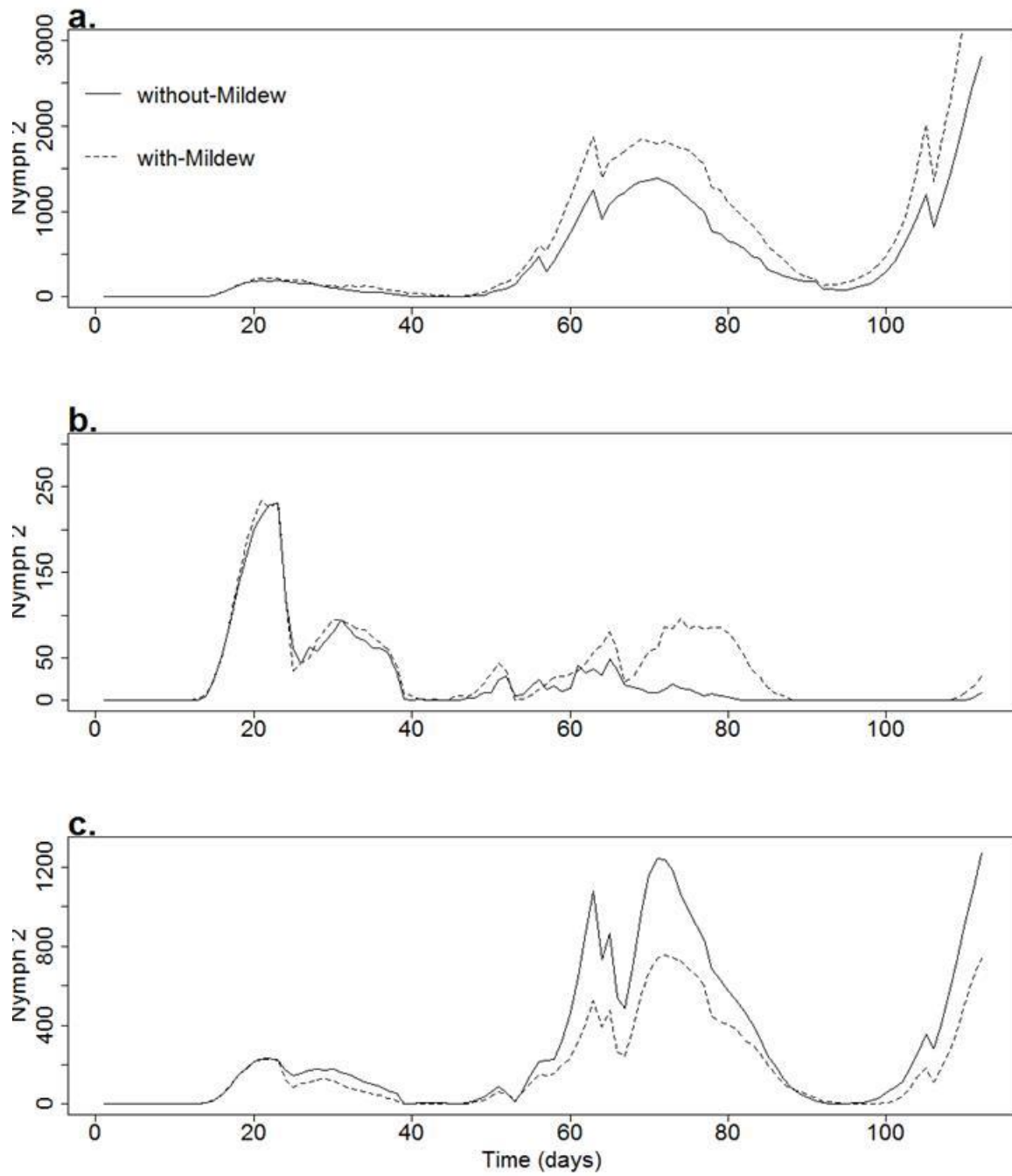
Figure 20. Effect of mildew presence on the population size of nymph stage 3 of whiteflies on 1344 plants (see Table 5), for the parasitoid dispersal behaviors: a,) Random, b) Eight nearest neighbor and c) Exponential function.

Figure 21. Effect of mildew presence on the population size of nymph stage 2 of whiteflies on 1344 plants (see Table 5), for the parasitoid dispersal behaviors: a,) Random, b) Eight nearest neighbor and c) Exponential function.

6   General conclusions

- To my knowledge, this is the first simulation approach validated for spatial distribution and population size in time. This characteristic makes the model robust enough to reproduce real experiments in small scale (less than 20 plants) and in crop patches (more than 1000 plants).

- The foraging behavior of whiteflies seems to be non-random and some rules are followed by the insects probably related with chemical or visual cues from the plants as the cues following dispersal rule can reproduce well the population behavior of field data. The empirical exponential function also works well to reproduce the population distribution and growth but as a statistical empirical model based on the field distribution, it is expected to reproduce the distribution without explanations of the causes of the distribution or movement.

- The whitefly population can spend more than 150 days in crop simulations to reach the stable stages distribution where the population intrinsic rate is close to zero. However, this a more theoretical than a practical conclusion as the real populations are affected by different abiotic and biotic factors that can change its dynamics, for example, the natural enemies or a phytopathogen.

- The presence of mildew on the system can affect the effectivity of the parasitoid as a biocontrol agent by reducing its parasitization rate. The increase in the parasitization rate and host feeding when parasitoid uses the exponential function can be explained by the use of a more exhaustive search per day. However, this increase result also in an increase in the whitefly adults' dispersion as the parasitoid foraging activity takes place in the mildew-free leaves.

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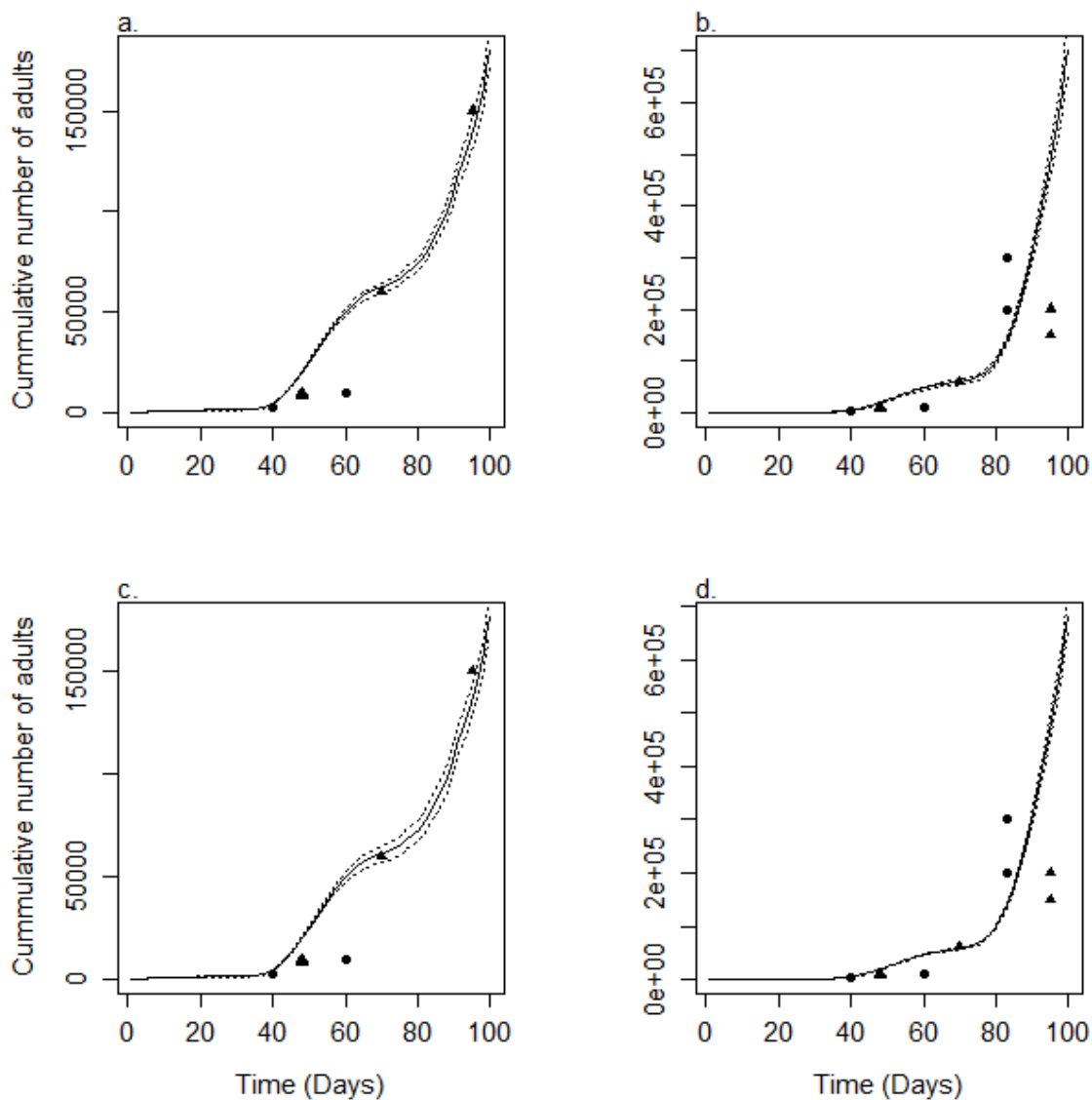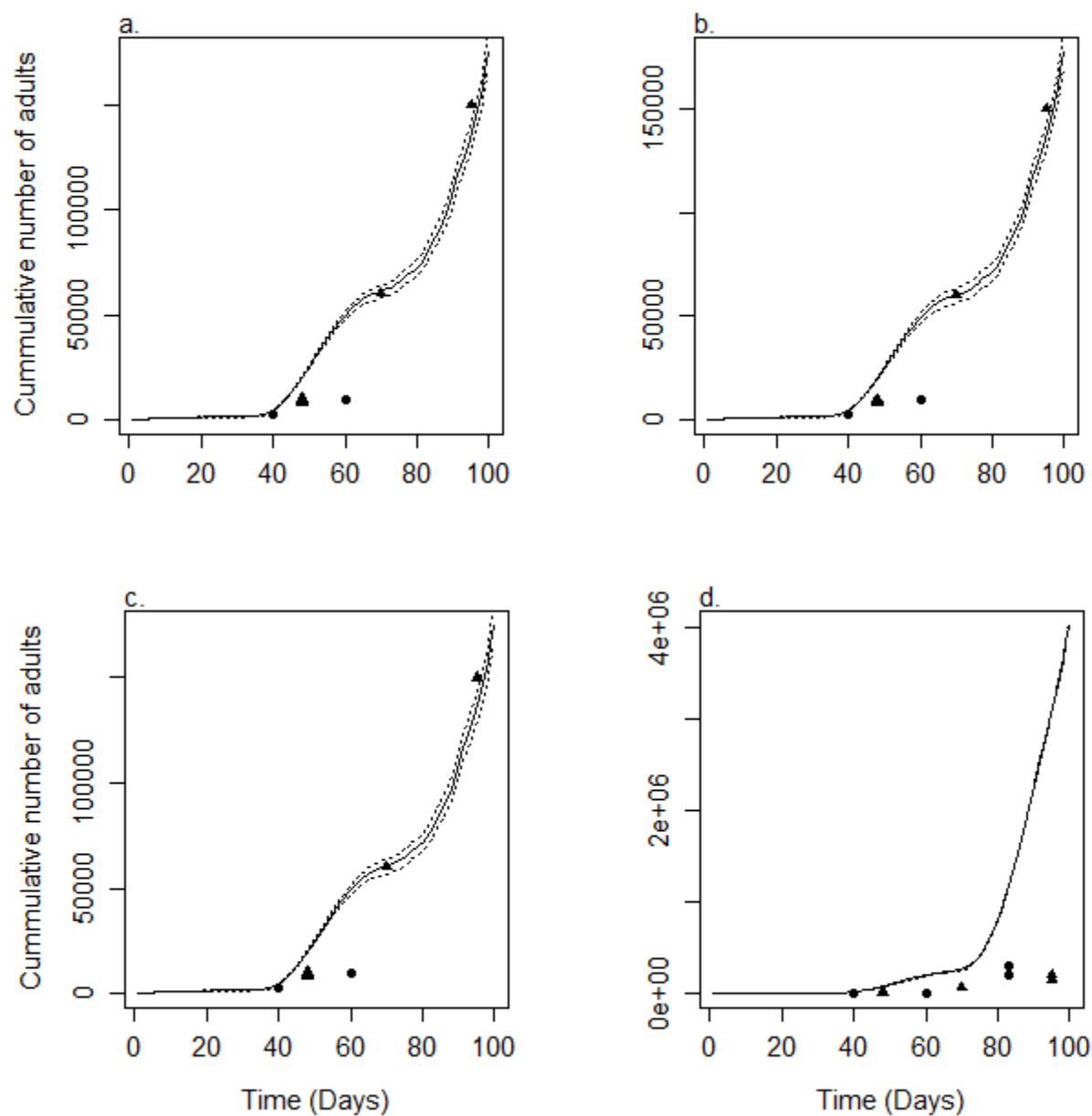# 8   Annex 1 Complementary plots of different simulation experiments

Figure 1. Population growth of whiteflies (mean +/- s.d. of five runs), in 10 plants infested with 100 females at day zero. The dispersal behaviors were: Eight nearest neighbors (a and b) and Exponential function (c and d), in density independent (a and c) and density dependent (b and
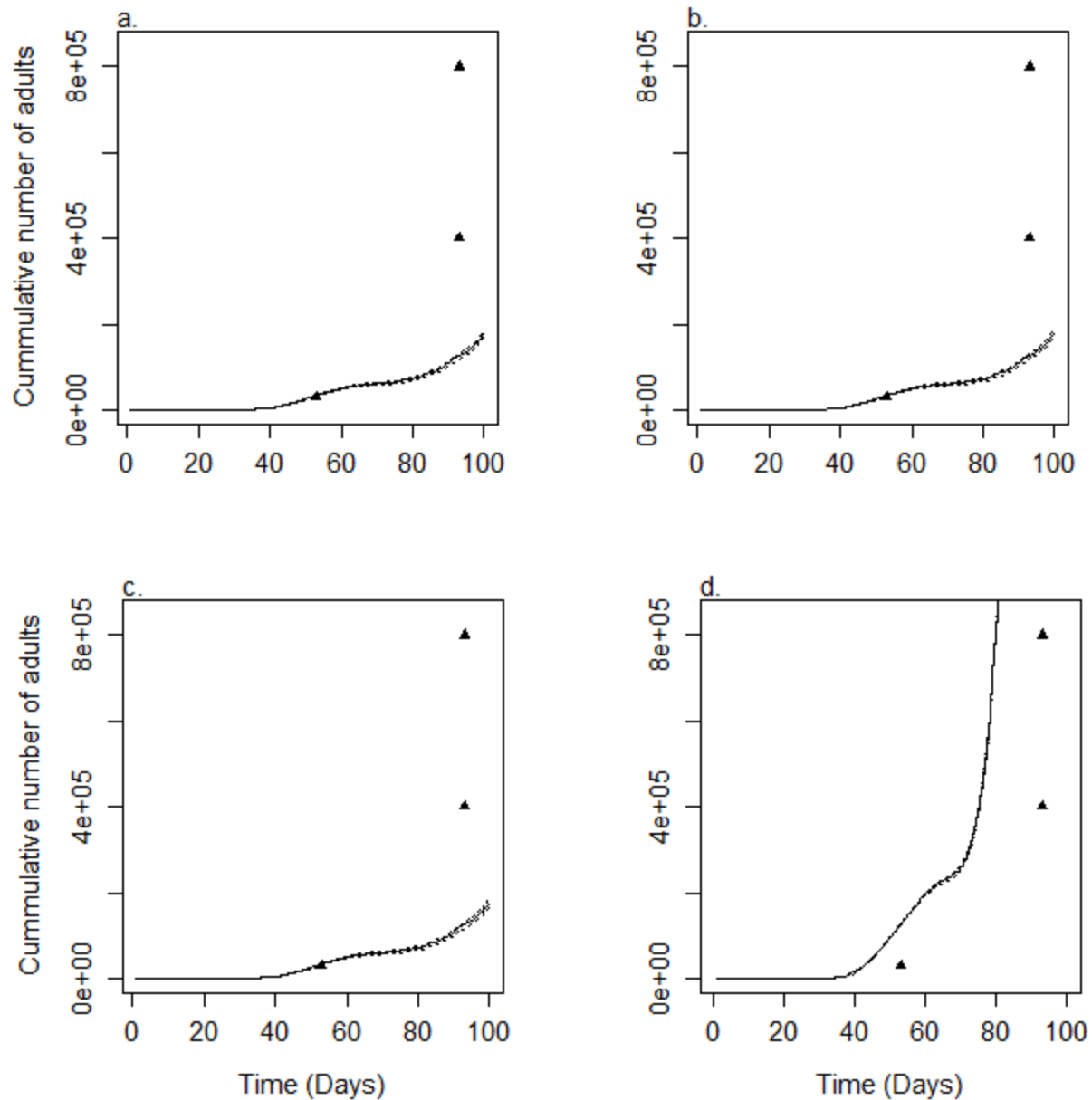
d) decision option (see table 2). Data points of experimental data comes from literature


(Elzinga, 1982; Joosten and Elings, 1985)

Figure 2. Population growth of whiteflies (mean +/- s.d. of five runs), in 10 plants infested with 100 females at day zero. The dispersal behaviors were: Random uniform (a and b) and Cues (c

and d), in density independent (a and c) and density dependent (b and d) decision option (see
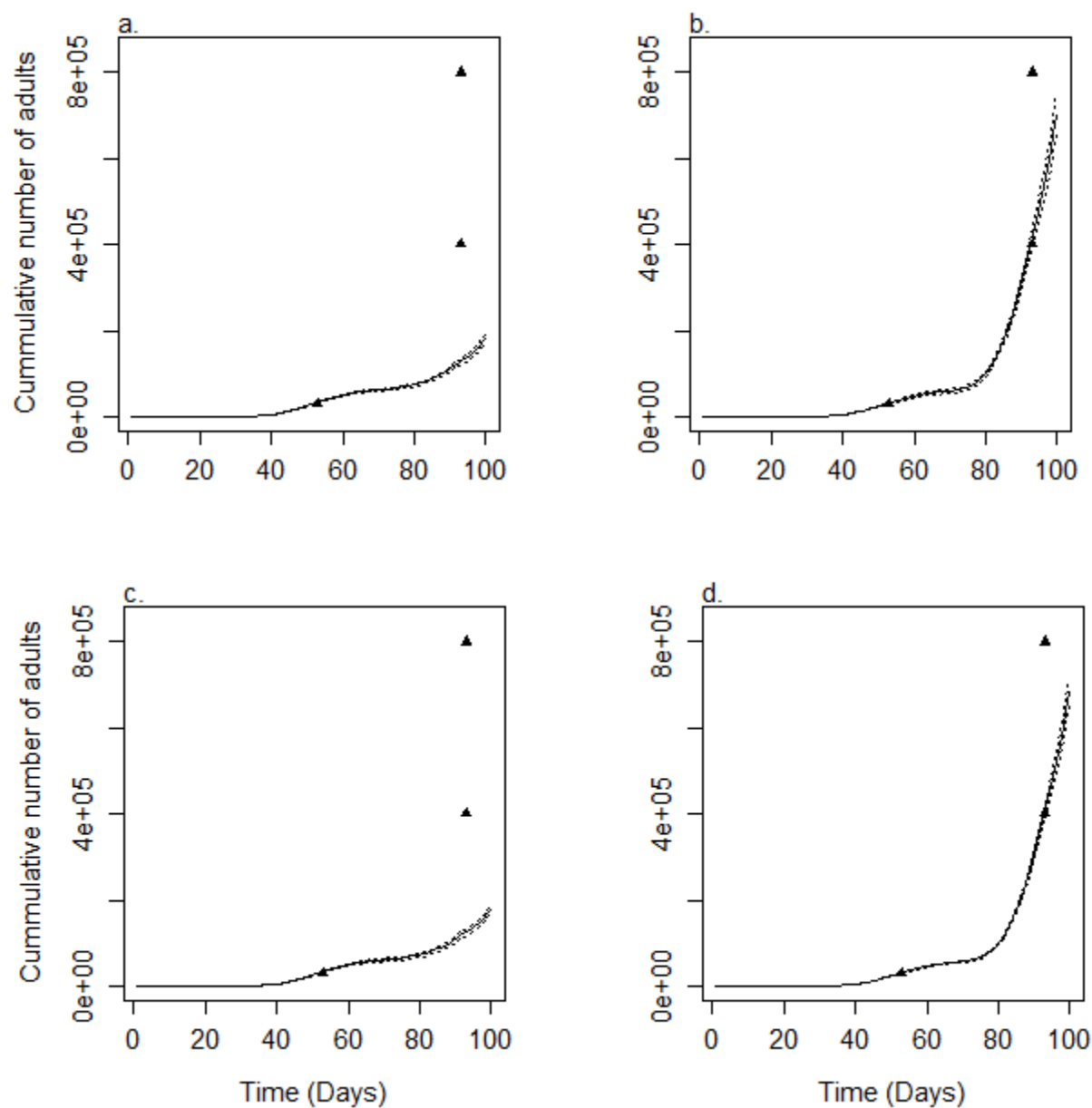
table 2). Data points of experimental data comes from literature (Elzinga, 1982; Joosten and Elings, 1985)

Figure 3. Population growth of whiteflies (mean +/- s.d. of five runs), in 15 plants infested with 300 females at day zero. The dispersal behaviors were: Eight nearest neighbors (a and b) and Exponential function (c and d), in density independent (a and c) and density dependent (b and d) decision option (see table 2). Data points of experimental data come from literature (De Ponti and Steenhuis, Unpublish).

Figure 4. Population growth of whiteflies (mean +/- s.d. of five runs), in 15 plants infested with 300 females at day zero. The dispersal behaviors were: Random uniform (a and b) and Cues (c and d), in density independent (a and c) and density dependent (b and d) decision option (see table 2). Data points of experimental data come from literature (De Ponti and Steenhuis, Unpublish).
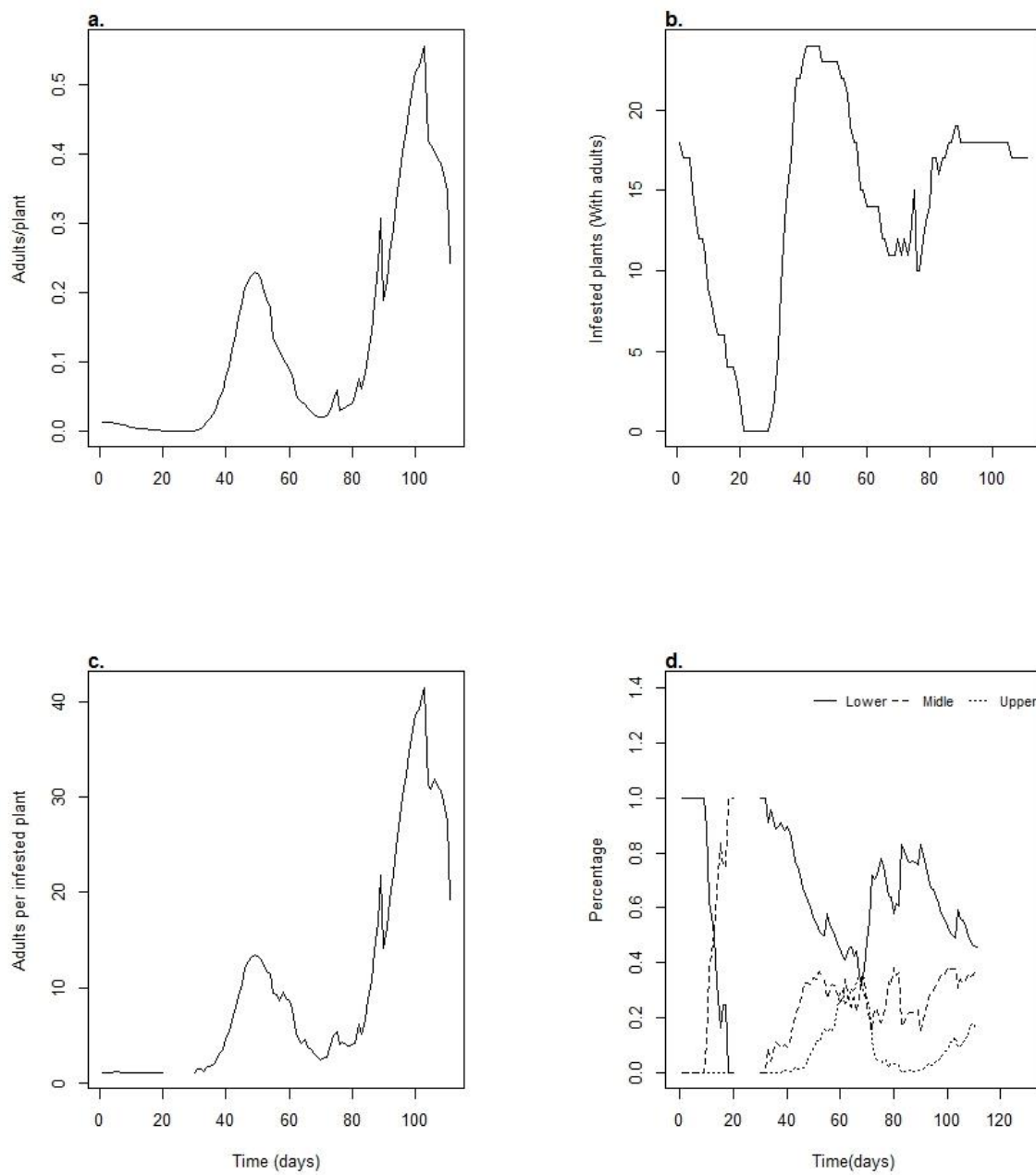
Figure 5. Adult population in the random dispersal rule for parasitoids.
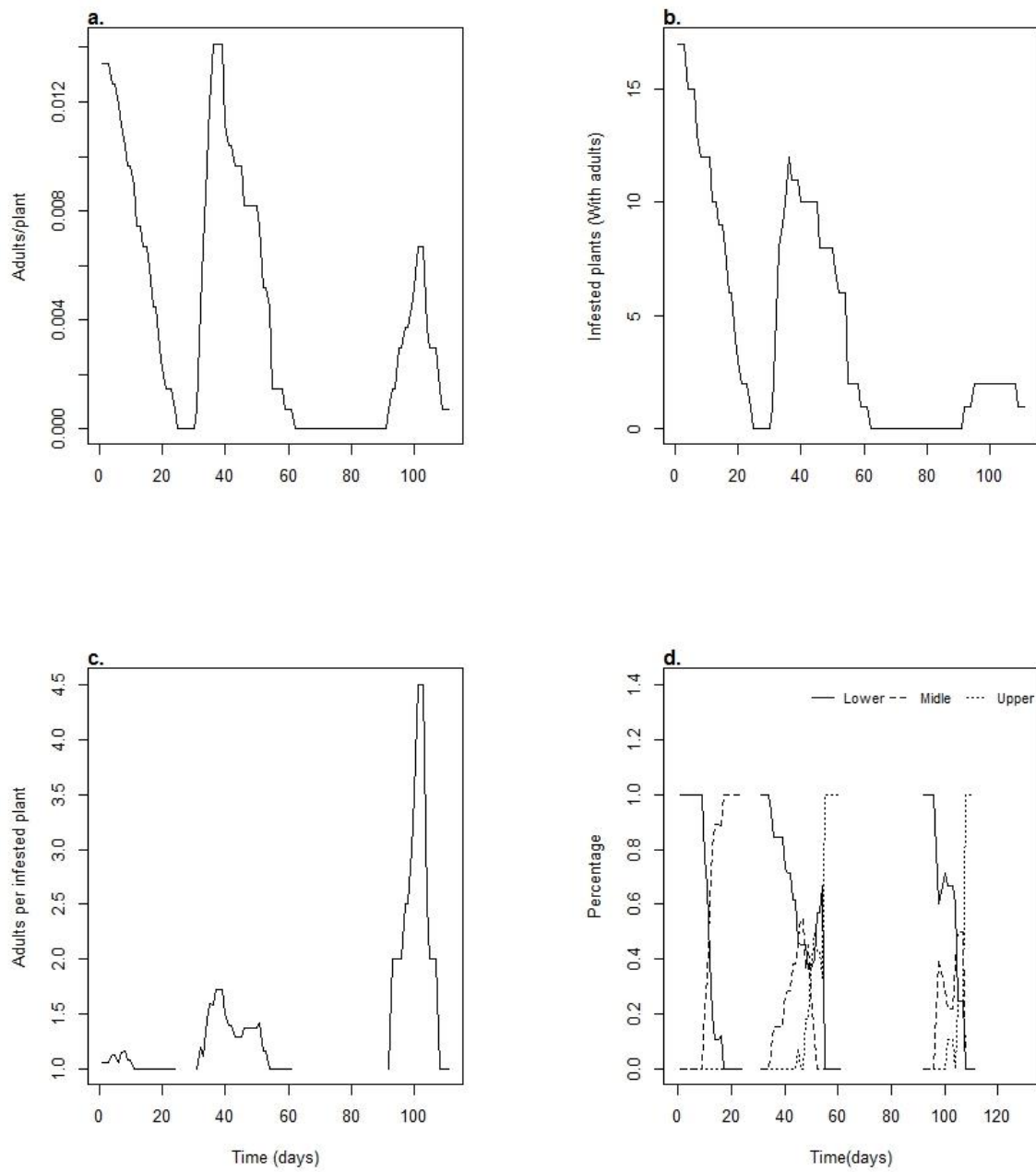
Figure 6. Adult population in the eight nearest dispersal rule for parasitoids.
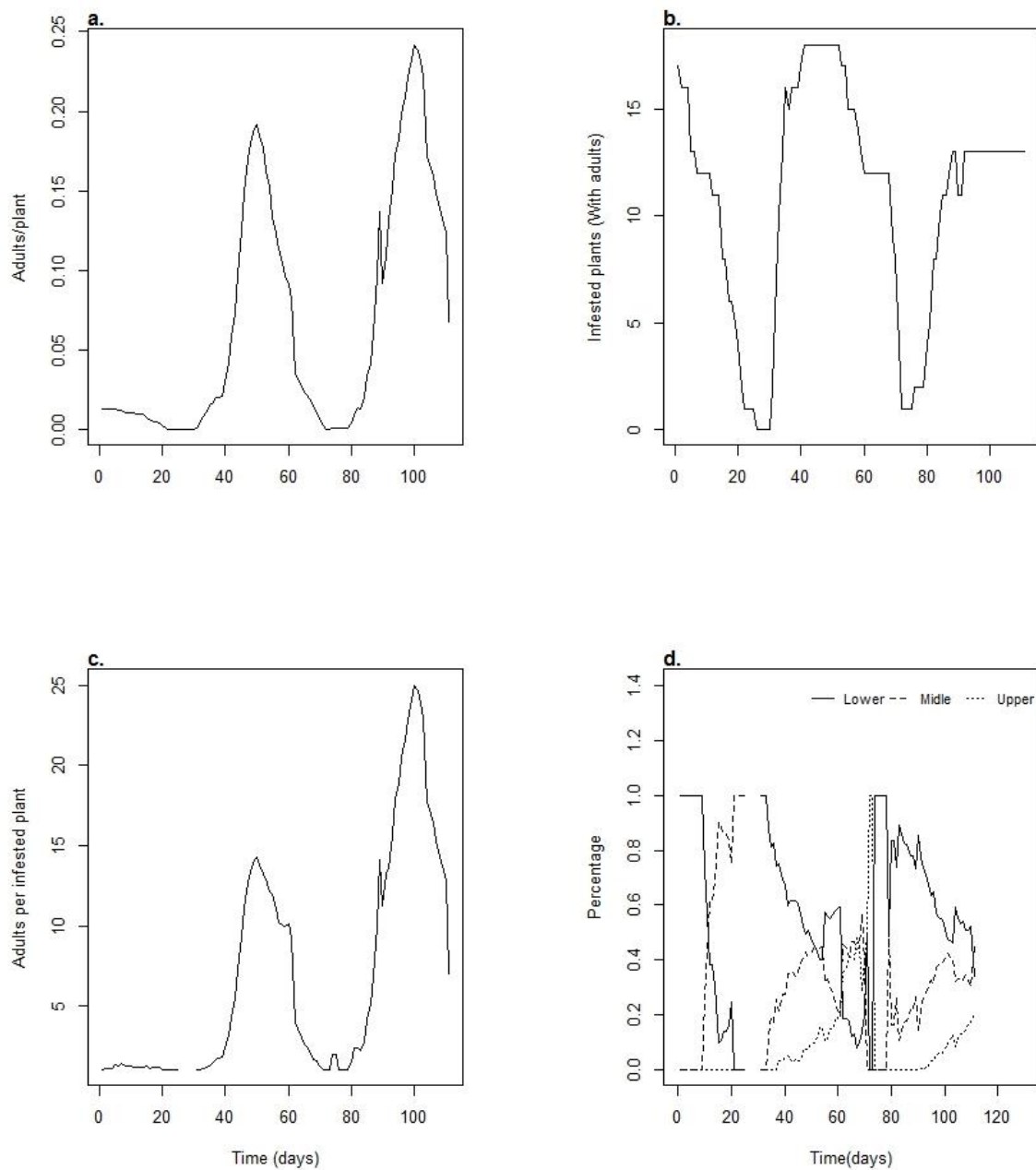
Figure 7. Adult population in the exponential function dispersal rule for parasitoids.
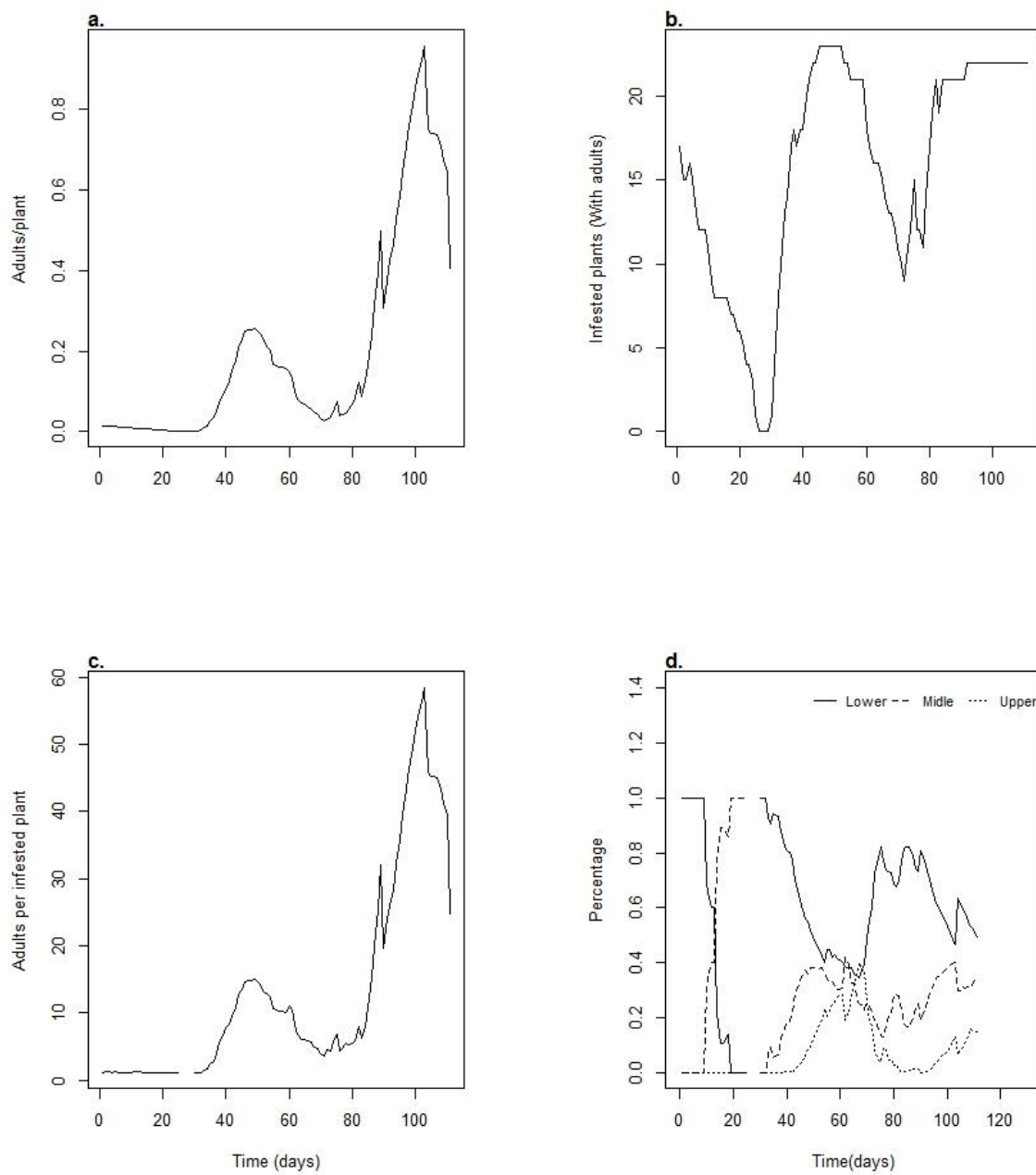
Figure 8. Adult population in the random dispersal rule for parasitoids with mildew presence in leaves.
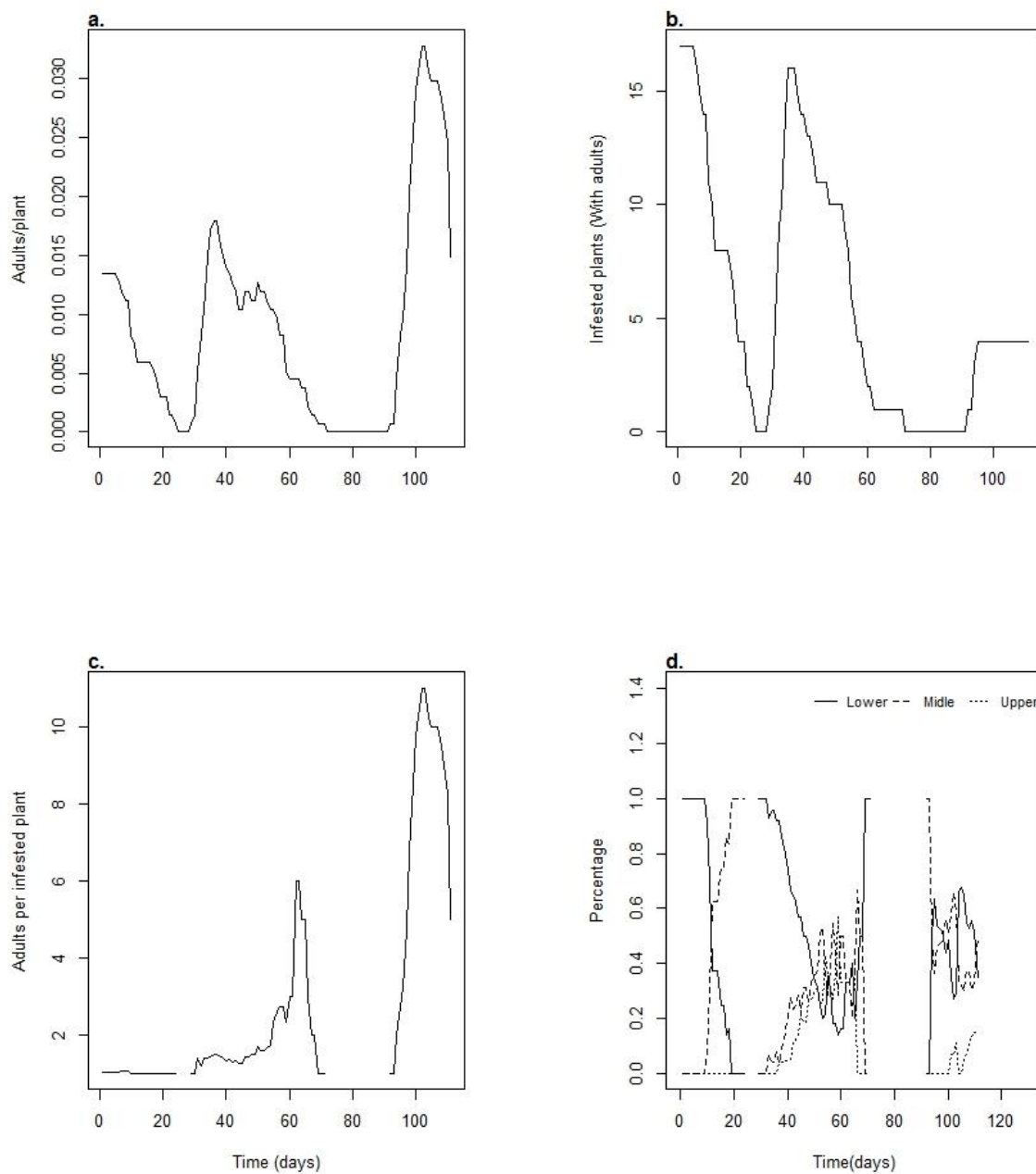
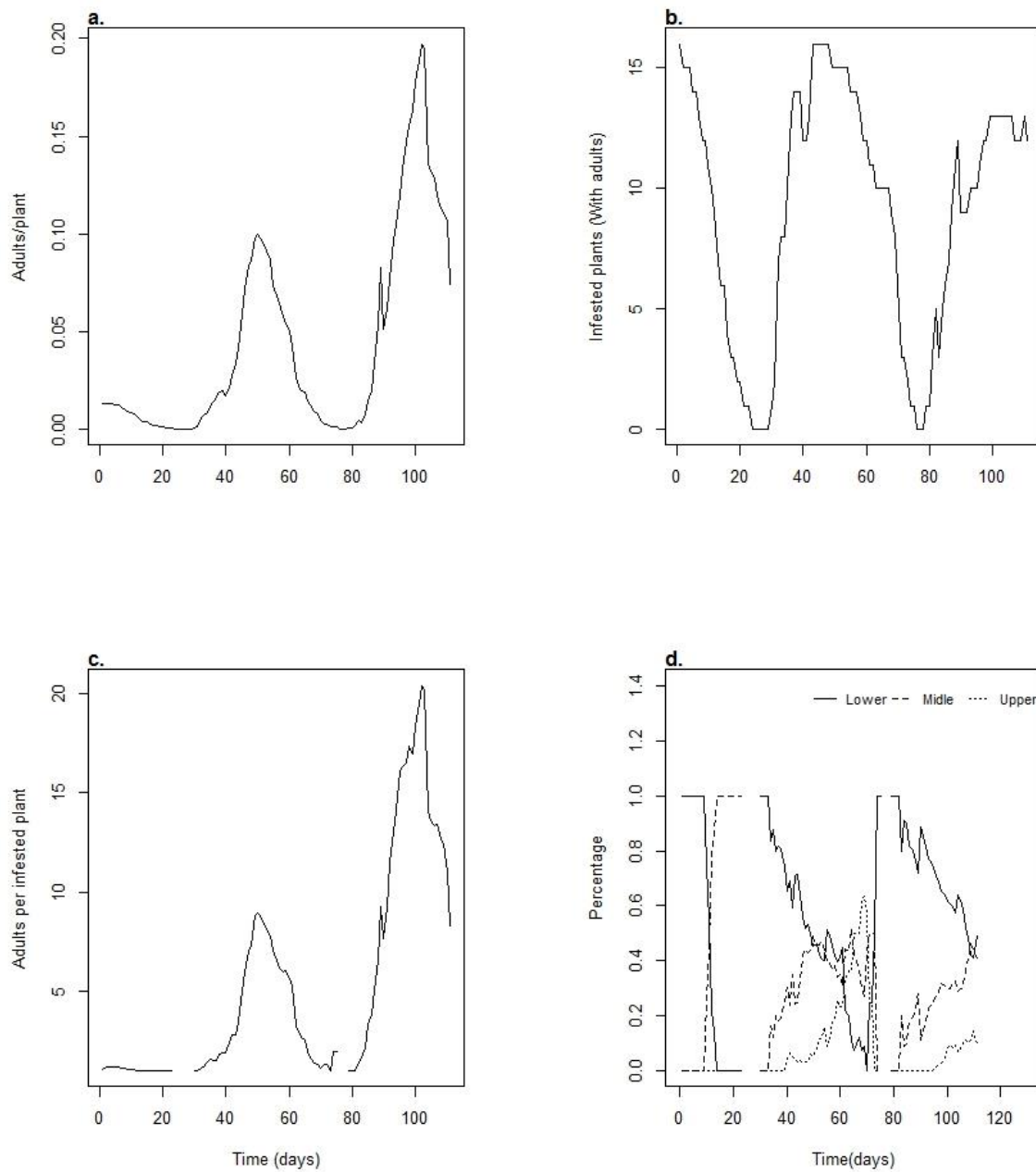**Figure 9.** Adult population in the eight nearest dispersal rule for parasitoids with mildew presence in leaves.

Figure 10. Adult population in the exponential function dispersal rule for parasitoids with mildew presence in leaves.

9   Acknowledgements

10   Curriculum Vitae

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WORK EXPERIENCE

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2005 – 2007	Young researcher Universidad Militar Nueva Granada, Colombia ▪ Mass rearing insects, writing scientific proposals, guidance of bachelor students Education
2007 – 2010	Research Assistant CENIFLORES ▪ Implementation of integrated strategies for pest management in rose crops. Floriculture

EDUCATION AND TRAINING

2012 - 2016	Ph.D. Agricultural Sciences University of Göttingen, Germany ▪ Development of individual-based models in applied ecology, programming languages.
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| 1999 - 2004 | B.Sc. Biology
Universidad Militar Nueva Granada, Colombia
▪ Standardization of a mass rearing of crop pests. |

PERSONAL SKILLS

Mother tongue(s)	Spanish
Other language(s)	English

	Listening (B1)
	    Reading (B1)
	    Spoken interaction (B1)
	    Spoken production (B1)
	    Writing (B1)

Communication skills	▪ Good scientific communication skills acquired during the Master and Ph.D. Studies.
Organizational / managerial skills	▪ Leadership responsible for a team of 8 professionals in Biology in the context of a project in rose crops.
Job-related skills	▪ Good as a project manager acquired during the project with farmers and scientist
Digital competence	▪ good command of the office suite (word processor, spreadsheet, presentation software) ▪ good command of C++ and Netlogo for programming, and R for statistical analysis.
Driving licence	International licence

PUBLICATIONS

| 1 | **Bustos, A.**, Rodríguez, D., Cure, J.R., Cantor, F., A Simulation Model of the Mass Rearing of Tetranychus urticae Koch (Acari: Tetranychidae) on Beans. Neotrop. Entomol.2016 |
| 2 | Arguelles Angélica, Natali Plazas, **Henry Alexander Bustos Rodríguez**, Rodríguez Daniel, Fernando Cantor. "Interacción entre dos ácaros depredadores de Tetranychus urticae koch (Acariformes: Tetranychidae) en laboratorio". Acta Biológica Colombiana ISSN: 0120-548X ed: Facultad De Ciencias Universidad Nacional v.18 fasc.1 p.137 - 148, 2013. |

3   Stephanie Johana Numa Vergel, **Henry Alexander Bustos Rodríguez**, Daniel Rodríguez Caicedo, Fernando Cantor, "Laboratory and greenhouse evaluation of the entomopathogenic fungi and garlic pepper extract on the predatory mites, Phytoseiulus persimilis and Neoseiulus californicus and their effect on the spider mite Tetranychus urticae" . Biological Control ISSN: 1049-9644 ed: Academic Press v.57 fasc. p.143 - 149, 2011.

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AWARDS

2011	Scholarship "Francisco José de Caldas" for Doctoral studies