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A resource - consumer model applied to the leafminer (*Tuta absoluta*) - tomato (*Solanum lycopersicum*) system: consequences of agronomic practices and environmental temperature

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Abstract

The South American tomato leaf miner, *Tuta absoluta* (Meyrick) (Lepidoptera: Gelechiidae), is a devastating leaf-mining pest, and one of the key pests for tomato, *Solanum lycopersicum*. Originating from South America, in the last fifteen years *T. absoluta* was able to expand in most of European and African countries, and current estimates all indicate the potential spread to all key tomato-growing regions.

Despite the major importance of this pest at a global level, its population dynamics is very poorly studied, with the vast majority of scientific literature focusing on the pest biology at the individual level. Very few studies concerned population dynamics, even fewer attempted a mathematical process-based modelization, and none considered the coupled dynamics of plant and pest. The aim of this thesis is to conceive the first coupled *T. absoluta* - tomato plant model, developed within the framework of the ecological process-based models. The model is a particular case of a general ecological system composed by an herbivorous insect and the plant it feeds on. The model, calibrated using data and empirical evidences found in literarure, is able to reproduce several observed patterns. Eventually, the model has been used for studying the behaviour of the *T. absoluta* - tomato system under the combined effect of temperature, irrigation, fertilization and bio-control.

Sommario

La minatrice fogliare *Tuta absoluta* (Meyrick) (Lepidoptera: Gelechiidae), è un infestante della pianta di pomodoro, *Solanum lycopersicum* . Specie originaria del Sud America, negli ultimi quindici anni *T. absoluta* è stata in grado di invadere la maggior parte dei paesi di Europa ed Africa, e le previsioni indicano una potenziale diffusione a tutte le maggiori aree di produzione del pomodoro a livello globale. Nonostante il pericolo rappresentato da *T. absoluta*, la maggior parte delle pubblicazioni scientifiche ne studia la biologia a livello individuale, e la sua dinamica di popolazione rimane poco studiata. Pochi studi hanno considerato la dinamica di popolazione, ancora meno ne hanno dato una rappresentazione matematica, e nessuno ha considerato l' interazione con l' accrescimento della pianta. Lo scopo di questo lavoro è realizzare il primo modello dinamico del sistema *T. absoluta* - pomodoro, nel contesto dei modelli ecologici consumatore - risorsa. Questo modello descrive un caso particolare di un sistema ecologico generale costituito da un insetto erbivoro e dalla pianta di cui si nutre. Il modello, parametrizzato utilizzando dati ed evidenze empiriche disponibili in letteratura, è in grado di riprodurre diversi pattern osservati. Infine, il modello è stato utilizzato per studiare il comportamento del sistema *T. absoluta* - pomodoro sotto l'effetto combinato di temperatura, irrigazione, fertilizzazione e bio-controllo.

Chapter 1

Introduction

1.1 Tomato pinworm *Tuta absoluta* : a global agricoltural pest of tomato

The International union for the conservation of nature (IUCN) defines Invasive alien species (IAS) as “ animals, plants or other organisms that are introduced into places outside their natural range, negatively impacting native biodiversity, ecosystem services or human well-being” (Iucn 2018). IAS , whose emergence and spread can be facilitated both by increasing globalization and climate change, represent a main cause of biodiversity loss and species extinctions, and are also a global threat to food security (Biondi, Guedes, et al. 2018). The relationship between food security and IAS is particularly concerning when these act as agricultural pests, therefore leading to harvest reduction, increased control costs and reliance on pesticides in the Agro – Ecosystems.

T. absoluta makes no exception: this species origins from the Peruvian highlands, but subsequently expanded throughout several Latin American countries during the 1960s, where it was addressed as a key pest for tomato, causing drastic harvest losses due to its leaf-mining activity and through fruit infestation in solanaceous vegetables (Han, Desneux, et al. 2019). A key step in the process of becoming a major threat to global tomato production is represented by its introduction in Europe: it was firstly detected in 2006 in Spain, and it quickly spread across the Afro-Eurasian supercontinent, with an average speed of 800 km/year both southwards and eastwards. Despite accidental, human-induced, transport is the main reason of *T. absoluta* diffusion, climate change could favor its establishment in areas not specifically suitable in the past, thus worsening the overall situation (Santana et al. 2019). The rapid spread of *T. absoluta* and its detrimental effect on tomato crop fields is particularly concerning, since Tomato is one of the most widely cultivated commodities, with 5 million hectares (ha) planted worldwide and 170 million tons produced yearly (Biondi, Guedes, et al. 2018).

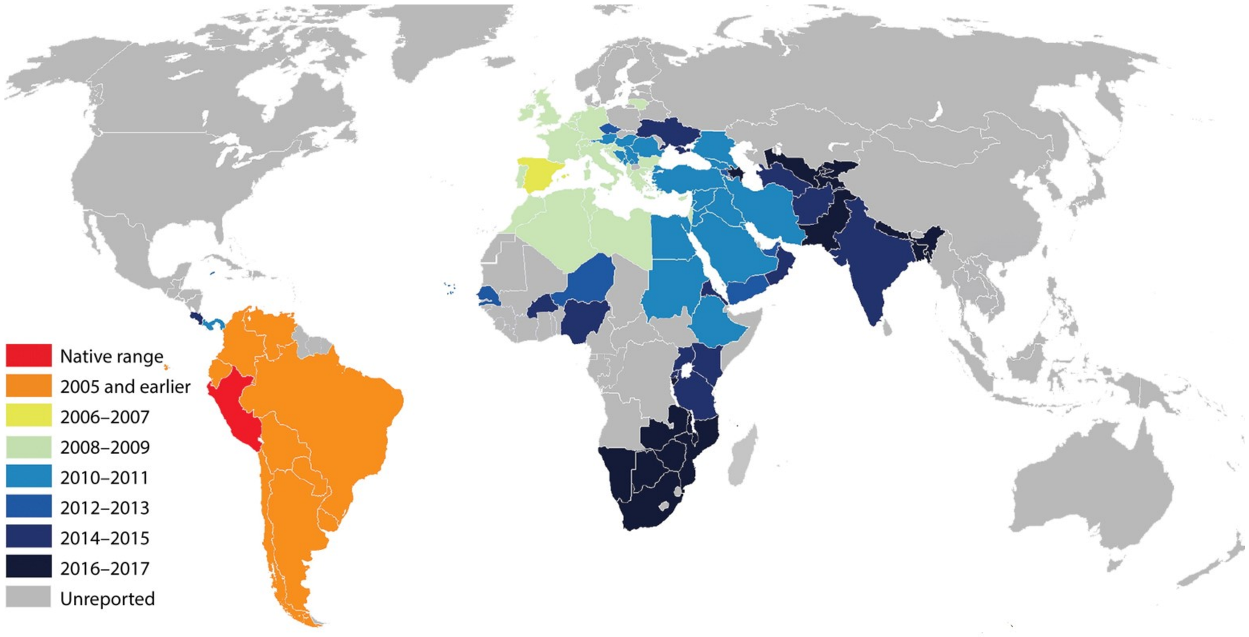
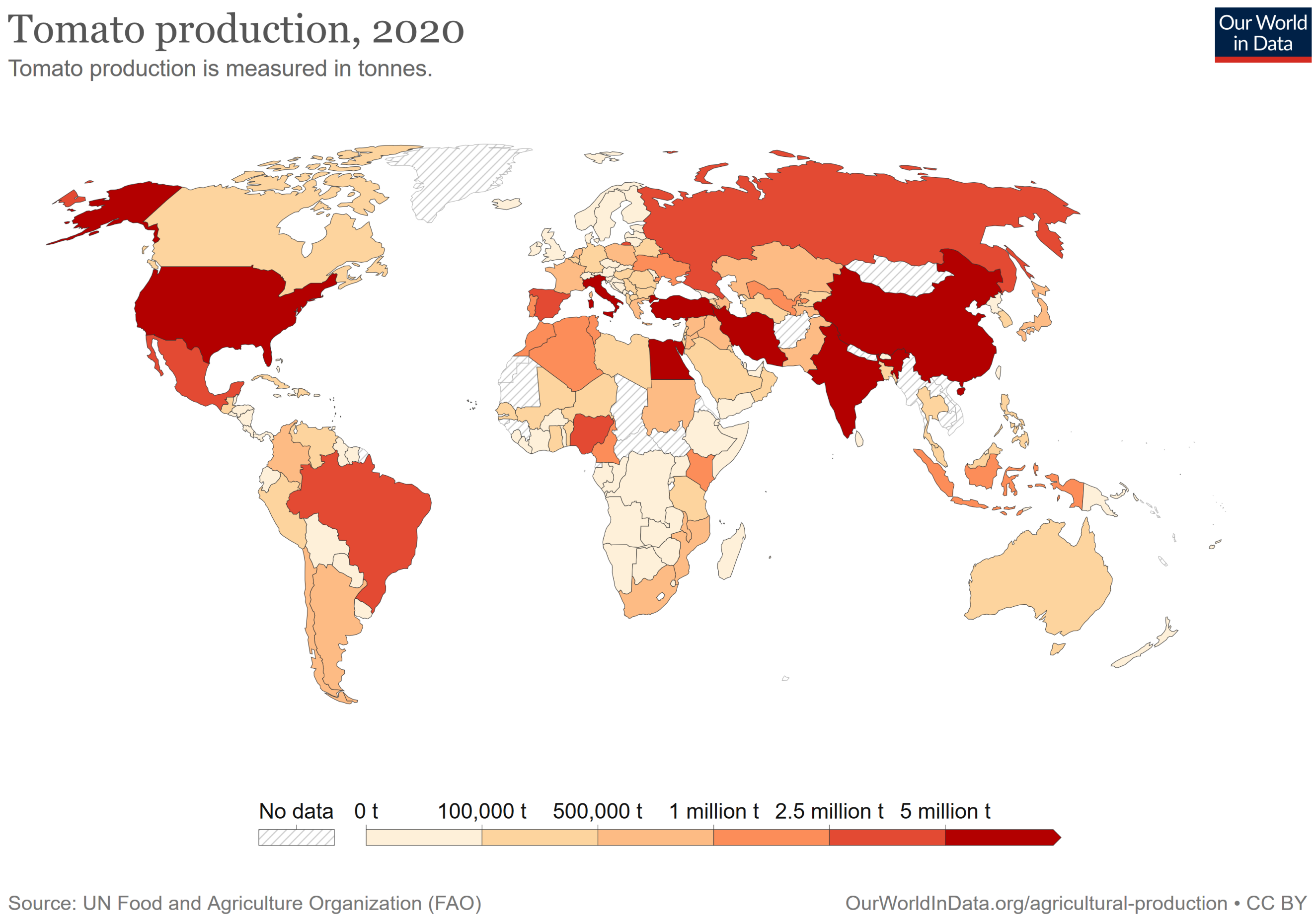


Figure 1.1: *T. absoluta* worldwide spread, updated at year 2018. figure taken by (Biondi, Guedes, et al. 2018)



Tomato production, 2020

Tomato production is measured in tonnes.

Source: UN Food and Agriculture Organization (FAO)

OurWorldInData.org/agricultural-production • CC BY

Figure 1.2: Global tomato production per county

1.1.1 *T. absoluta biology*

T. absoluta (Meyrick) (Lepidoptera: Gelechiidae), targets all solenaceus plants, but has a strong preference for cultivated tomato, *S. lycopersicum* (Han, A.-V. Lavoir, et al. 2022).

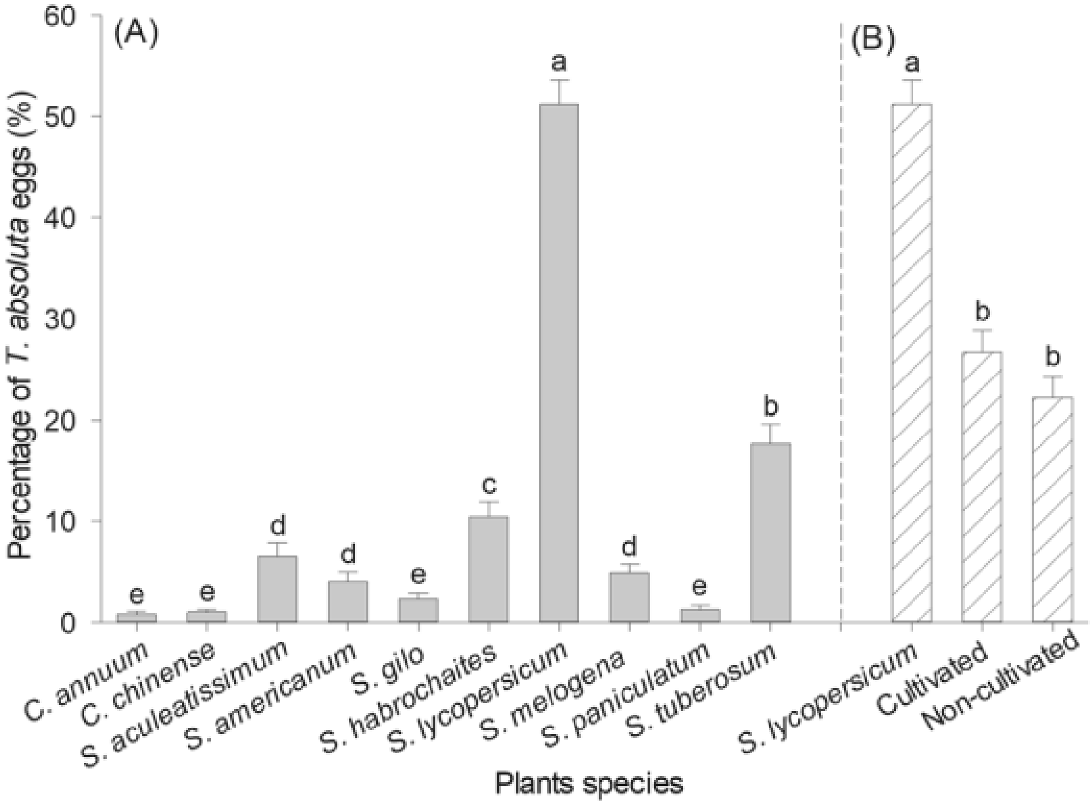


Figure 1.3: Oviposition preferences of *T. absoluta*, when offered different solenaceous plants, figure taken from (Silva et al. 2021)

T. absoluta spread and persistence in the environment is greatly facilitated by the fact that this pest has many potential target plants, since it can oviposit and develop on several wild species, also outide Solanaceous family, such as the Amaranthaceae, Convolvulaceae, Fabaceae, and Malvaceae (Bawin et al. 2016). This ability of targeting multiple plant species make *T. absoluta* virtually impossible to eradicate: even if the infested cropfields are destroyed, the pest will persist in the environmental reservoir, moving to the new crops as soon as these are planted again.

Even considering only the plants that are philogenetically closest to tomato , *i.e.* the one belonging to the Solanum genus, it is clear that *T. absoluta* have potential wild host plants in vast majority of the newly invaded regions (Figure 1.4).

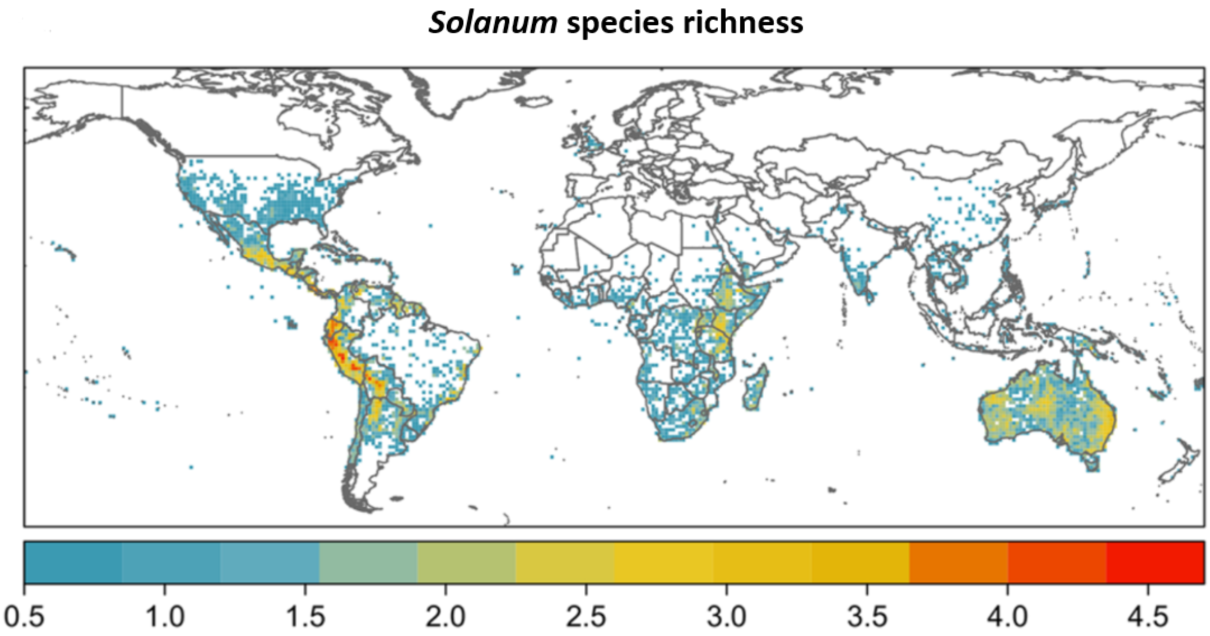


Figure 1.4: Solanum species distribution at global level, edited from Echeverría-Londoño et al. 2020

T. absoluta is a multivoltine insect, and its life cycle its composed by four different stages of development: egg, larva, pupa and adult. The eggs are laid by mature females on the upper parts host plants (leaves, stems and sepals), individuated thanks to the plant chemical volatile compounds. After hatching, the larvae penetrates within the leaf, and start feeding on the leaf mesophyll, thus producing a thin leaf mine. Mature larvae usually drop to the soil where they produce a thin, silky cocoon and transform into pupae. Adults are crepuscular, and both genders are sexually active by the first day of emergence; both sexes are polygamous and show almost no refractory period. Mate communication relies on female sexual pheromones, and mating lasts from a few minutes up to six hours (Biondi, Guedes, et al. 2018). Interestingly, virgin females from French and Tunisian populations can exhibit deuterotoky parthenogenesis, owing to *Wolbachia* infection (Caparros Megido, Haubruge, and Verheggen 2012), even if such phenomena have never been described in the native range.

(a) Eggs

(b) Larva

(c) Pupa

(d) Adult

Figure 1.5: *Tuta absoluta* development stages

The pest affects tomatoes produced for both fresh and processed markets, with larvae causing up to 100 % losses when no management methods are efficiently implemented . The feeding habits of *T. absoluta* make its presence difficult to detect in the early infestation period, resulting in severe damage on young plants. In addition, feeding activity on fruits directly affects the visual appeal of harvested products and increases costs for fruit post harvest selection before marketing (Biondi, Narciso, et al. 2018).


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Figure 1.6: Tomato plants damaged by *T. absoluta*

1.1.2 Tomato plants and cultivation

The berries of tomato plant, *S. lycopersicum*, represents one of the most consumed food commodities at global level. In terms of worldwide production, tomato is the seventh most important crop species after maize, rice, wheat, potatoes, soybeans and cassava (Bergougnoux 2014).

The tomato belongs to the family of Solanaceae (also known as the nightshade family), a family that contains more than 3000 species, including important vegetable crops such as potato (*Solanum tuberosum*), aubergine (*Solanum melongena*), pepper (*Capsicum annuum*), tomatillo (*Physalis ixocarpa*) and tobacco (*Nicotiana tabacum*) as well as many wild plants producing poisonous or medicinal compounds (Bergougnoux 2014)

The word tomato does not refer only to the commonly known tomato crop (*S. lycopersicum*), but it is a term that contains many other tomato wild species, herbaceous perennials native of the western South America. Obviously, the tomato crop *S. lycopersicum* is a result of the domestication process of another species, *lycopersicum* var. cerasiforme, that started in South America, presumably during the Pre-colombian era.

Tomato crop is a perennial herbaceous plant but it is commonly grown as an annual crop, even if biennial and perennial forms exist, especially on the native range. This crop is largely cultivated both in open field (typically in tropical and temperate climates) and in greenhouses (typically in temperate climates and in contexts of large-scale production). ("Tomato (Solanum lycopersicum)" 2017) The growth habit of the plant along the cropping season significantly varies among cultivars, but in general terms the Leaf area index, LAI (defined as the m^2 of leaf surface per m^2 of field) grows from 0.5 to 3 in 120 days, (Heuvelink, 1999) and the plant can reach up to three meters high. Tomato crop leaves have an average density of 35 g / m^2: this implies that, in a single square meter of crop field, the total leaf mass will grow on average from 17.5 g to 105 g along the cropping season.

Quite interestingly, Solanaceae are a plant family rich of dangerous species, and tomato plants (belonging to the Solanum genus) are able to produce chemical substances that have a detrimental effect on a wide range of animals (Pomilio, Falzoni, and Vitale 2008). Thus, the interaction between *T. absoluta* and the tomato plants is obviously not one-sided: as the larvae start eating the leaves, the plants starts to exert a defensive action, trying to get rid of the infestation. (Coqueret et al. 2017; Han, Desneux, et al. 2019). In particular, the defensive action is generated by the combination of three types of resistance traits:

- Constitutive resistance traits: these traits are naturally present in the plant before the infestation, and mostly found in wild varieties of tomato. These traits include the presence and the density of plant trichomes and the chemical compounds found inside them. These compounds, such as methyl-ketones and acyl sugar have an antixenotic and antibiotic action, *i.e.* they interfere with eggs laying and larval feeding, and affect larval survival and growth.

- Induced resistance traits: These traits regards defence mechanisms that emerge upon the pest infestation, and they comprehend:
  - Production of a particular blend of Volatile Organic Compounds (VOC), aimed at attracting *T. absoluta* natural enemies and/or reducing plant attractiveness for the pest (Han, Desneux, et al. 2019).
  - Increased production of defensive allelochemicals and defensive enzimes.
- Introduced resistance traits: These traits are introduced into the plant via genetic modification. Even if this research branch may lead to interesting potential innovation, e.g. by modifying the tomato genome in order to enable the plant to produce insecticidal proteins, it is not within the domain of the present study and will not be discussed further.

The well-known devastating effect of *T. absoluta* shows how the defense mechanisms of the tomato crop *S.lycopersicum* are not sufficiently effective. However, since the plant can rely on a finite amount of resources; it can be safe to assume that, upon infestation, the plant will divert a certain amount of resources from ”growth” to ”defence”.

1.2 Integrated management of *T. absoluta*

1.2.1 Traditional management practicies

Insecticide use, negative effects and the EU directive

The use of Insecticide has been, historically, the first and most used tool to manage *T. absoluta* (as well as many other invasive arthropods) both in South America and in the newly-invaded areas, also as a consequence of the apparent lack of other strategies (Desneux et al. 2022).

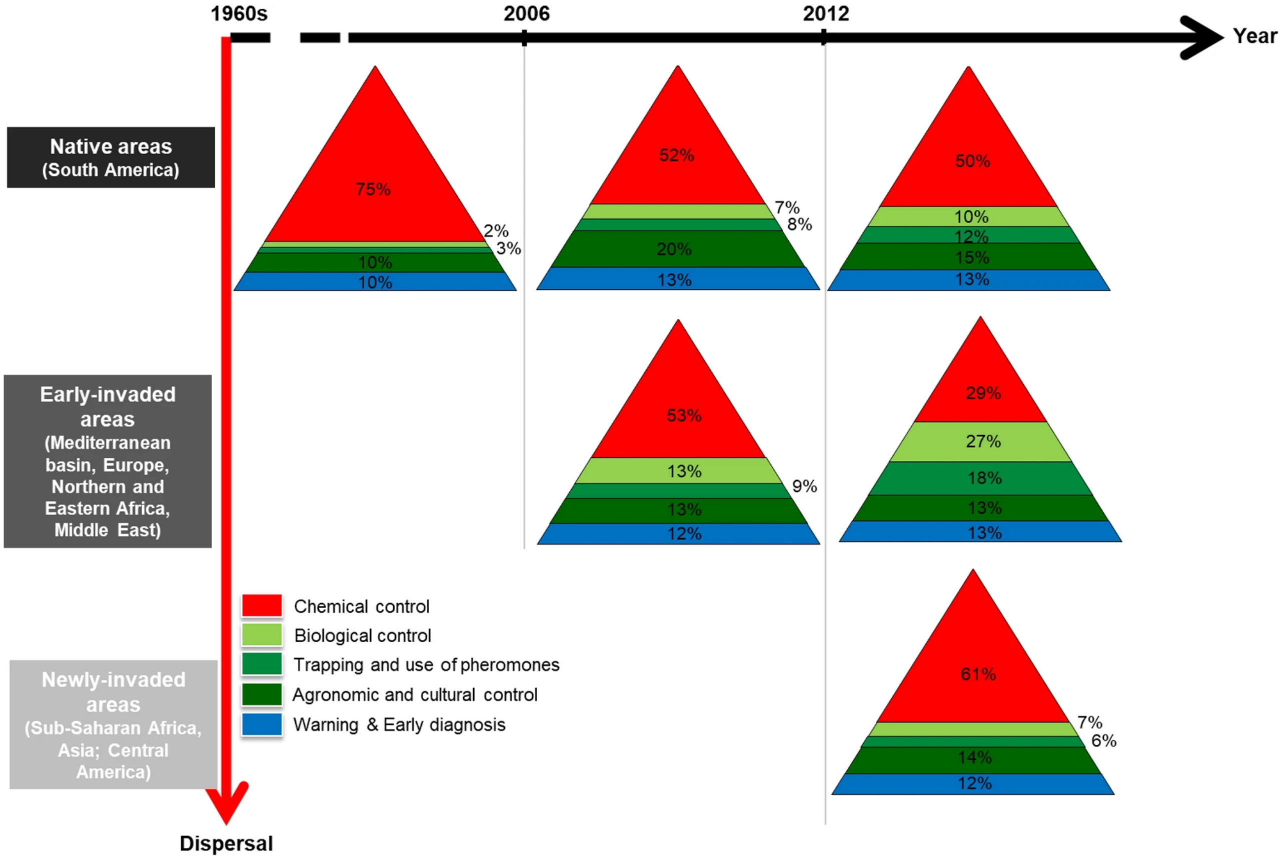


Figure 1.7: The temporal trends of different control strategies against *T. absoluta*, in native, early invaded and recently invaded areas, figure taken from Desneux et al. 2022

The management of *T. absoluta* via the application of chemical substances is complex, often ineffective, and presents several drawbacks: the intensive insecticide use triggered a rapid insurgence of pesticide-resistance traits in many *T. absoluta* populations; Moreover, broad-range insecticides have a negative effect on many other insect species, including the pest natural predators, thus contributing to the disruption of the ecological community of the Agro-Ecosystem (Desneux et al. 2022).

The European Union Directive 2009/128/EC aims at tackling this problem and achieving a sustainable use of pesticides in the EU by reducing the risks and impacts of pesticide use. Integrated Pest management (IPM) is one of the primary tools for achieving this goal, and it is defined as the ”consideration of all available plant protection methods and subsequent integration of appropriate measures that discourage the development of populations of harmful organisms and keep the use of plant protection products and other forms of intervention to levels that are economically and ecologically justified and reduce or minimise risks to human health and the environment. ’Integrated pest management’ emphasises the growth of a healthy crop with the least possible disruption to agro-ecosystems and encourages natural pest control mechanisms” (EU, Integrated Pest Management).

Pheromone-based strategies

In order to reduce the use of pesticides, also pheromone-based strategies were evaluated to control *T. absoluta* populations, including mass trapping (*i.e.* the use of pheromone traps to capture and kill the adult males) and mating disruption, a technique that consists in saturating the area with pheromones in order to prevent female localization and mating. Anyway, pheromone based strategies are based on the assumption that breeding happens via sexual reproduction: this is not always true for *T. absoluta*, since some strains are able to reproduce via deuteroky parthenogenensis, as a consequence of an infection by the endosymbiontic bacteria *Wolbachia* . Therefore, this peculiar reproductive behaviour may endanger the effectiveness of pheromone based trapping (Biondi, Guedes, et al. 2018).

1.2.2 Emerging practices

Within this context, two main, complementary and promising lines of action emerge from the ongoing studies:

Biological control (Top-Down effect)

Bio-control constitutes one of the most promising elements of the IPM package: numerous species, spanning over 160 different taxa, were found to exert a predatory action on this pest, both in the Neotropical and Paleartic regions (Biondi, Guedes, et al. 2018). In particular, omnivorous mirids were successfully used as a sustainable control tool, and it is interesting to underline that one of the most used species for this purpose, *Macrolophus pygmaeus*, it is a native species in Europe and it is commonly found in several E.U. countries (De Backer et al. 2014)

Figure 1.8: An adult indivudual of *M. pygmaeus* on a tomato leaf

Resource input manipulation (Bottom-up effect)

A reduction of abiotic resources availability, mostly water and nitrogen, not only has the obvious effect of reducing plant development, but has strong, plant-mediated effects also on the associated herbivorous insects, including *T. absoluta.* Recent studies (Han, A. V. Lavoir, et al. 2014) showed how a reduced input of water and nitrogen is associated with a reduced survival and a longer development time. In other words, *T. absoluta* was found to develop faster and with a lower mortality on plants that were optimally watered and fertilized. This finding suggest that *T. absoluta* behaves coherently with the " Plant vigor hypothesis" (Price 1991), according to which some herbivorous insect may be favoured (*i.e.* developing faster and better) by vigorous plants, since these provides a higher quality food resource.

The " Plant vigor hypothesis" is strictly intertwined with the "Nitrogen limitation hypothesis": Nitrogen represent the limiting factor for the development of Lepidoctera larvae (including *T. absoluta*) (Han, Desneux, et al. 2019). In order to reach a sufficient body weight and transform into pupae, the larvae need to ingest and process a certain amount of nitrogen and, since the consumption rate is independent of nitrogen content (Coqueret et al. 2017), a more nutritious, nitrogen-loaded plant will allow the larvae to intake more nitrogen per unit of time, thus resulting in a shorter development time.

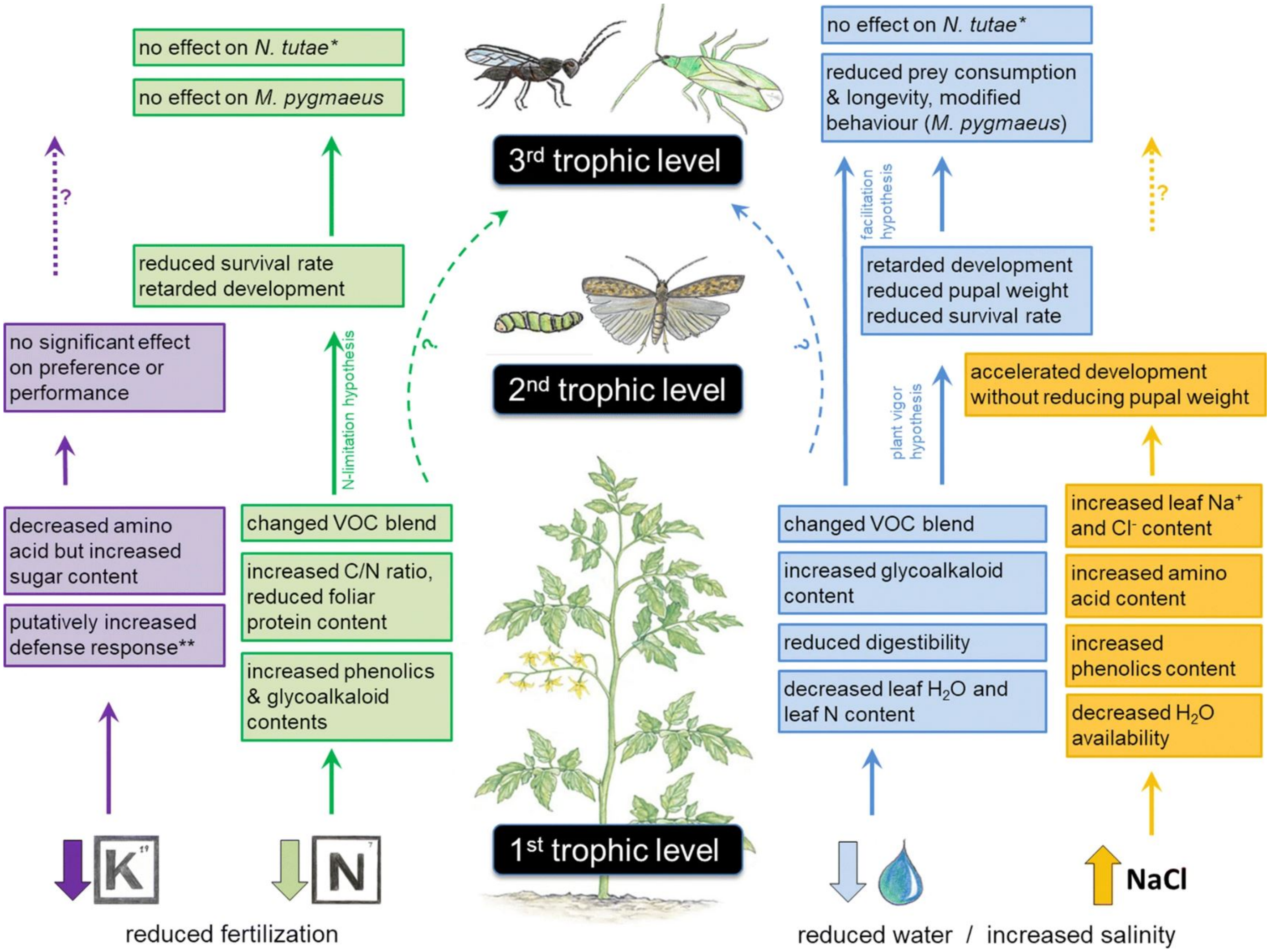


Figure 1.9: Bottom up effects propagation on the tri-trophic system formed by the tomato plant, the pest and the arthropod predator. Source: Han, Desneux, et al. 2019

1.3 Use and potential of mathematical models

A mathematical model can be defined as either a physical representation of mathematical concepts or a mathematical representation of reality (Brittanica Online encyclopedia). In simpler terms, a model ”is a set of assumptions on how nature works, together with an algorithm for calculating the consequences” (Murdoch, Briggs, and Nisbet 2003). Mathematical model represents an extremely useful tools in almost every branch of science, including ecology, where they can be used for:

- System understating: the realization and the analysis of a well built model allows the testing of hypothesis, thus bringing to a better comprehension of the physical and/or biological mechanisms underpinning the observed behaviours (Tilman 1994).
- Forecasting: given the input, state and output values up to time t (the time when the forecast is made), the model can predict the state and output values from t to t+h, (where h =lead time).
- Simulation: given the initial state and the trajectory of the input, simulate the trajectory of the state and output. This allows to simulate the behaviour of the system in hypothetical, ’what-if’ scenarios that could be very expensive or dangerous to be reproduced in experiments.
- Decision making: the results coming from the application of a model can significantly improve the decision making process. In particular, forecasting can lead to better decision making because it allows an earlier detection of the risk and the implementation of an anticipatory action. Instead simulation provides information on how the system could behave in possible alternative of future scenarios (*e.g.* the ones induced by climate change), thus representing a useful tool to evaluate different decisions and management practices.

1.4 Aim of the thesis

As for other invasive insect pests, the rapid spread of *T. absoluta* was made possible by competitive biological traits, such as high reproduction potential and high selection pressure, causing a rapid evolution of high resistance to pesticides (Desneux et al. 2022). For these reasons, ecologically-based rather than chemical-based control options can be a tool of utmost importance in pest management (Han, Desneux, et al. 2019). In this work , we present a novel ecological, process-based model, built within the framework of the resource-consumer models, with the aim of describing the combined, coupled dynamics of both the plant and the pest. This model was subsequently calibrated for the Tomato – *T. absoluta* system, and used with the goal of increasing system understanding and knowledge, also aimed at informing decision making. This task was done exploring the effects of different Integrated Pest Management (IPM) practices, both in terms of resource inputs (bottom-up effects) and control strategies , with a special focus on bio-control (top-down effects). Long term, inter annual dynamics and temperature dependence were also explored.

Chapter 2

The model

2.1 Resource-Consumer models: context and framework

Charles Elton, one of the founders of animal ecology, wrote that ”The primary driving force of all animals is the necessity of finding food and enough of it. Food is the burning question of animal society, and the whole structure and activities of the community are dependant upon questions of food supply” (Elton 1927) . In other words, the interaction between a consumer and a resource is perhaps the fundamental unit of each ecological community (Murdoch, Briggs, and Nisbet 2003), and it is possible to identify different types of resource consumer interaction: Predation, herbivory, parasitism and so on.

Every single species is involved in a consumer-resource interaction, with the role of consumer, resource, or both; and even a simple ecosystem contains hundreds of different resource consumer interactions, that together constitute the trophic web. The fundamental importance of this topic in Ecology is well-represented by the vast amount of models aimed at describing this interaction: there have been about 1000 host-parasitoid, 3000 parasite-host, and 5000 predator-prey modeling studies (Lafferty et al. 2015). However, it is possible to state that all these different models stems from the Lotka - Volterra model, commonly recognized as the first resource consumer model.

The Lotka - Volterra model is based on a series of assumptions:

- In absence of consumers, the resource shows a density-dependent dynamics, so it does not grow exponentially but tends to an equilibrium value. If the resource is a population, this value represents the carrying capacity.
- In absence of resource, the consumer populations goes extinct, since the resource modelled is the only one the consumer feeds on.
- resource transfer is the only interaction between consumer and resource. .

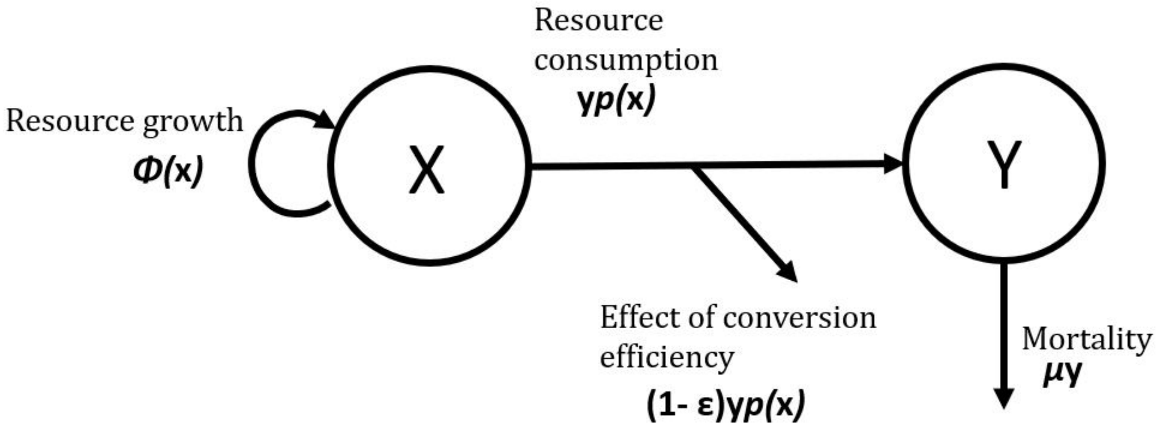


Figure 2.1: Schematic representation of the Lotka - Volterra model

The Lotka - Volterra model, in its most general form, is described by the following equations.

$$\begin{cases} \frac{dx}{dt} = \phi(x) - yp(x) \\ \frac{dy}{dt} = -\mu y + \epsilon yp(x) \end{cases} . \tag{2.1}$$

Where

- x is the biomass of the population that constitutes the resource

- y is the biomass of the consumer's population
- $\phi(x)$ is the resource density dependence growth function, that takes place in absence of consumers.
- μ is the mortality rate of the consumer in absence of resource
- $p(x)$ is the consumer functional response, linking the consumption rate of a single unity of resource by a single consumer to the resource abundance
- ϵ is the gross conversion efficiency of the consumers, not all the biomass ingested by the consumer is transformed into consumer's biomass.

2.2 Plant-herbivorous insect model

The model presented in this work (from now on referred to as "the model") aims at describing the coupled dynamics of the resource (the crop) and the consumer (the pest).

The model belongs to the category of conceptual models, aims at describing only the main dynamics occurring in the system and it is built starting from *a priori* knowledge and inference from available data. The fact that it describes the dynamics occurring in the system, and that all the parameters have a biological sense makes it a process-based model.

All the life stages of the consumer are explicitly modelled in a stage-structured approach, and the herbivorous insect is assumed to consume the resource with a type two functional response. A logistic growth function is used for the crop in absence of pest.

The state variables that represent the density of individuals at egg (E), larval (L), pupal (P), and adult (A) stage are expressed in individuals/m^2.
The crop leaf biomass (the resource) is represented by the state variable F, expressed in g/m^2.

All the parameters of the models depend on the biology of the two species and on the considered "agronomic scenario". The scenario defines Temperature, Irrigation and fertilization.

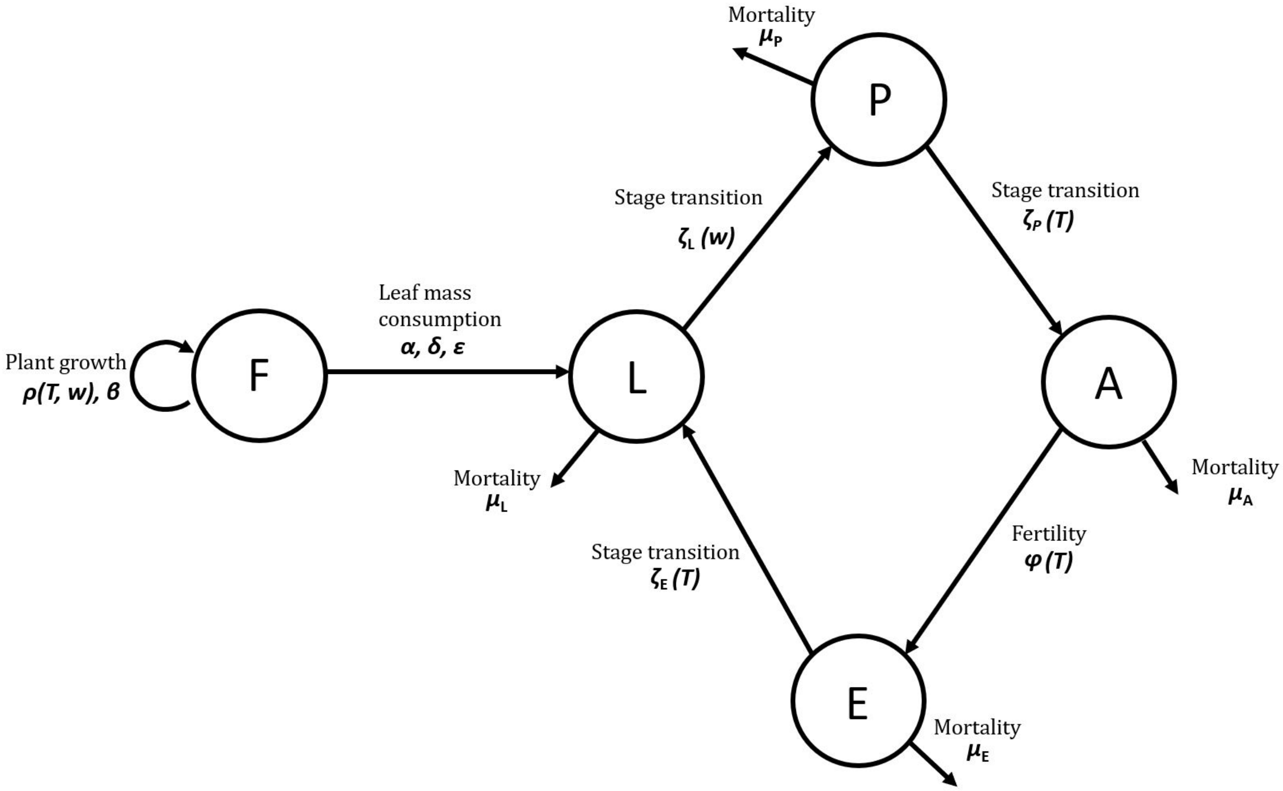


Figure 2.2: Schematic representation of the presented model, below each arrow are reported the parameters and the functions associated with the corresponding process, T represents environmental temperature [°C] and$w$is an adimensional parameter describing irrigation and fertilization.

2.2.1 Herbivore density dependence

As the model explicitly describes the interaction between the consumer and the resource, no consumer density-dependence element is introduced *a priori* in the relation between the adults and the eggs produced. Instead, the pest population growth is regulated by the resource in a simple way : a larva needs to occupy a certain leaf surface; as a consequence, at each instant there is only room for a finite number of larvae (*i.e.* a finite number of spots). This number of spots depends on the total leaf surface, which varies in time.

$$\text{number of spots} = \frac{\text{total leaf surface}}{\text{spot dimension}} \tag{2.2}$$

Therefore, at each time instant, the number of new larvae entering the leaf is the minimum between the number off eggs that are ready to hatch and the number of ”free spots” on the leaf surface.

$$\text{number of free spots} = \text{number of spots} - \text{number of larvae} \tag{2.3}$$

$$\text{new larvae} = \min[\text{ eggs hatching, number of free spots}] \tag{2.4}$$

The herbivorous insect affect the growth of the plant both directly (by consuming leaf-mass) and indirectly : it is clearly acknowledged (Coqueret et al. 2017) that the larvae presence triggers defensive mechanism in the plant (Han, Desneux, et al. 2019), thus causing a re-allocation of the plant resources, from ”growth” to ”defence”.

2.2.2 The role of temperature, water and mineral nutrients

The processes described by the model depends on temperature, fertilizer and water inputs, as these elements can influence some of the biological traits both of the pest and the plant. There are numerous evidence that ambient temperature has an effect on plant growth rate, and on the insect biology, affecting the duration of the various stages and its fertility(Mateus Ribeiro de Campos et al. 2021). In particular, egg and pupal stage duration are modelled as inversely proportional to environmental temperature.

Instead, the larval stage duration depends on the availability and quality of the resource; Therefore, the temperature effects on larval stage duration is considered to be plant mediated and not explicitly modelled. Larval stage duration depends on irrigation and fertilization: a more healthy and nutrient-rich plant is a more nutritious food source for the larvae (Han, Desneux, et al. 2019), larvae feeding on nutrient rich leaves will process the food with an higher conversion efficiency, thus gaining weight faster and shortening the stage duration.

Irrigation and fertilization also influences both the plant growth rate, since a higher input of nutrients has beneficial effects on growth. For these reason, many of the model parameters are described as a function of temperature, irrigation and fertilization, or both. Fertilization and Irrigation are introduced into the model through the parameter w, representing a 'fertigation scenario'. This parameters range is [0,1] where 0 is the total lack of water and nutrients and 1 is the maximum.

2.2.3 Third trophic level and biological control

A third species , a predator of the herbivorous insect, can be introduced in the model in order to simulate the effectiveness of eventual bio-control strategies. This "predator" species is assumed to prey on the pest with a type two functional response, have constant abundance in time and its presence have the effect of adding an extra mortality factor to pest immature stages

2.3 Model equations

2.3.1 Ordinary differential equation system

The core of the model is composed by five differential equations: one for the resource and one for each of the pest's stages.

$$\begin{cases} \frac{dF}{dt} = \rho F - \beta F^2 - \alpha \frac{FL}{F+\delta} \\ \frac{dE}{dt} = \phi A - \frac{E}{\zeta_E} - \mu_E E - z\frac{E}{\iota+E} \\ \frac{dL}{dt} = min(\frac{E}{\zeta_E}, \frac{F\Omega}{\nu} - L) - \frac{L}{\zeta_L} - \mu_L L \\ \frac{dP}{dt} = \frac{L}{\zeta_L} - \frac{P}{\zeta_P} - \mu_P P \\ \frac{dA}{dt} = \frac{P}{\zeta_P} - \mu_A A \end{cases} \quad . \tag{2.5}$$

Where ρ represents the actual plant growth rate (d^{-1}) which is given by a potential growth rate ρ_F, possibly depending on environmental temperature T and water and nutrient availability (represented by the parameter w) and its reduction due to density of larvae over the leaf surface $\frac{L}{F}$

$$\rho = \rho_F e^{-\sigma \frac{L}{F}} \tag{2.6}$$

Where σ takes into account the indirect damage to the plant growth, caused by the damage to the mesophyll and the photosynthetic capacity and by the re-allocation of plant's resources, from growth to defence.

Where:

$$\rho_F = \rho_T w \tag{2.7}$$

and

$$\rho_T = \rho_{max}(\frac{T - T_{mc}}{T_{opt} - T_{mc}})(\frac{T_{Mc} - T}{T_{Mc} - T_{opt}})^{\frac{T_{Mc}-T_{opt}}{T_{opt}-T_{mc}}} \tag{2.8}$$

Where the parameter ρ_{max} is peculiar of the crop variety, and represents the maximum achievable growth rate; it is reach with optimal temperature and optimal fertilization and irrigation. The parameter ρ_T is the maximum achievable growth rate at a certain temperature, as reported in Eq.(2.8), where here T represents the environmental temperature [° C], T_{mc} and T_{Mc} represent the minimum and maximum temperatures that allow crop growth [° C], T_{opt} is the optimal temperature for the considered crop. When $T = T_{opt}, \quad \rho_T = \rho_{max}$. ρ_T is then multiplied by w in order to obtain the parameter ρ_F that is the actual growth rate (in absence of pest) and takes into account the effect of both temperature and fertigation.

Consequently:

$$\rho = \rho_{max} w (\frac{T - T_{mc}}{T_{opt} - T_{mc}})(\frac{T_{Mc} - T}{T_{Mc} - T_{opt}})^{\frac{T_{Mc} - T_{opt}}{T_{opt} - T_{mc}}} e^{-\sigma \frac{L}{F}} \tag{2.9}$$

Parameter β accounts for density dependent plant growth($d^{-1}\ g^{-1}$),
$\alpha \frac{FL}{F+\delta}$ represents the overall leaf mass consumption rate, where α and δ are the two parameters of the larvae type two functional response, respectively the maximum *per - capita* consumption rate ($g\ d^{-1}$) and the semi-saturation constant ($g\ m^{-2}$).

Parameter ϕ represents the adult fertility (eggs adult^{-1} d^{-1}), and it is derived from Ψ, the total fertility rate, defined as the average number of eggs that are laid by a female over the duration of its adult stage.

Parameter Ψ is linked to the temperature by Eq. (2.11). where T represents the environmental temperature [° C], T_{mp} and T_{Mp} represent the minimum and maximum temperature compatible with pest survival [° C] a is a scale factor, c is lower than the optimal temperature and b gives the skewness

$$\phi = \frac{\Psi}{2\zeta_a} \tag{2.10}$$

$$\boldsymbol{\Psi} = \frac{a_1(T - T_{mp})^{b_1}(T_{Mp} - t)}{(c_1 - T_{mp})^{b_1}(T_{Mp} - T_{mp})} \tag{2.11}$$

μ_i represents the mortality rate(d^{-1}) at $i-th$ stage and ζ_i the average duration(d) of $i-th$ stage, thus $\frac{1}{\zeta_i}$ is the rate of transition from $i-th$ stage to the following one. Both the egg and pupal stage duration is temperature dependent, as described by a simple exponential law.

$$\zeta_e = a_2 e^{-b_2 T} \tag{2.12}$$

$$\zeta_p = a_3 e^{-b_3 T} \tag{2.13}$$

Starting from the assumptions listed in Par. 2.2.2, it is possible to describe the duration of larval stage (ζ_L) as a function of larvae functional response ($p(F)$), the mass gain required to trigger the transition to pupa (χ) and the conversion efficiency (ϵ)

Starting from larvae functional response: $p(F)$ is the resource consumption rate by a single larva, equal to

$$p(F) = \alpha \frac{F}{F + \delta} \tag{2.14}$$

$\chi/\ \epsilon$ is the amount of resource that should be consumed by a larva in order to reach the mass required to become a pupa.

Consequently, larval stage duration can be expressed as:

$$\zeta_L = \frac{\chi/\epsilon}{p(F)} = \frac{\chi}{\epsilon\alpha\frac{F}{F+\delta}} \tag{2.15}$$

Where ϵ_{max} is the maximum value of larvae conversion efficiency [/], corresponding to an optimally irrigated and fertilized crop.

$$\epsilon = \epsilon_{max} w \tag{2.16}$$

The term $z\frac{E}{\iota+E}$is the number of eggs eaten by the predators in the unit of time. it is a type two functional response, where z represents predatory pressure, and parameter ι the semi-saturation constant of the functional response of the predator$(\frac{eggs}{m^2})$. While $\frac{E}{\zeta_E}$ represents the number of eggs that will hatch in the unit of time, Ω represents the conversion factor from leaf mass to leaf surface (m^2 g^-1) and ν is the surface needed by a single larva (m^2); Thus, $\frac{F\Omega}{\nu}$ represents the maximum number of larvae that can simultaneously feed on a plant of leaf mass F, $\frac{F\Omega}{\nu} - L$ the number of larvae that could enter within the plant leaves at time t, and $min(\frac{E}{\zeta_E}, \frac{F\Omega}{\nu} - L)$ is the actual inflow of individuals into the larval stage.

Chapter 3

Application to the leaf miner *T. absoluta* - tomato *S. lycopersicum* system

3.1 Model Calibration

The model has been then calibrated for the *T. absoluta*-*S. lycopersicum* system. All the parameters were calibrated with an offline approach, using the experimental data contained in several different scientific publications.

Plant growth rate ρ

All the parameters concerning the plant growth were estimated starting from the data of a single study (Coqueret et al. 2017), showing the dry mass of a two plant leaflets, at several time steps, both in optimal fertigation conditions, one with no *T. absoluta* larvae (acting as a control) and the other one infested by 12 larvae.

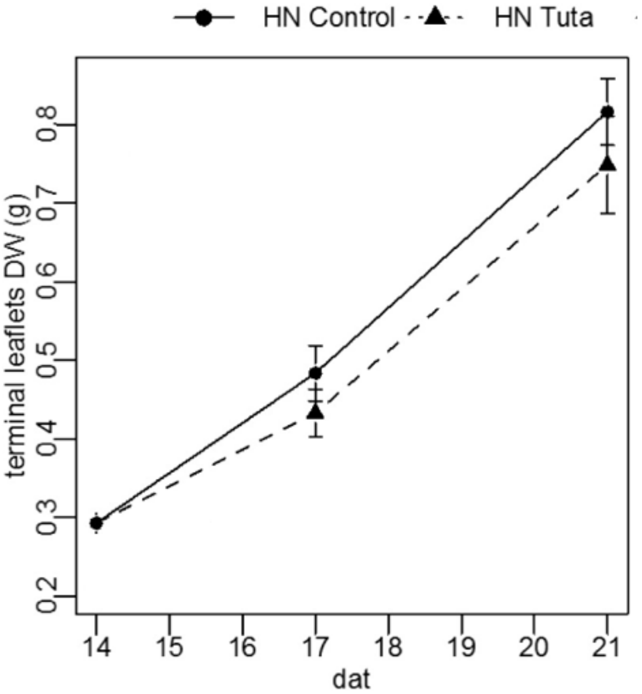


Figure 3.1: Terminal leaflet growth and expansion, in high nitrogen conditions, with and without *T. absoluta* larvae. Source : Coqueret et al. 2017

The first step for obtaining the function linking temperature, fertilization, irrigation and larvae density to plan growth rate is calibrating ρ_{max}, *i.e.* the growth rate that is obtained in conditions of optimal temperature, fertilization, irrigation and absence of pest.

Coqueret et al. reported the growth of a leaflet under the above mentioned optimal conditions; therefore, these values were used for calibrating the maximum achievable plant growth rate ρ_{max}.

plant age [days]	plant dry weight [g]
25	0.30
28	0.49
32	0.81

Table 3.1: Observed plant growth

Since the experiment take place in the very fist stage of plant growth, the logistic growth function has been simplified to an exponential.

$$\frac{dF}{dt} = \rho_{max} F \tag{3.1}$$

and, consequently:

$$F(t) = a \exp \rho_{max}(t) \tag{3.2}$$

$$F(t) = 0.3 \exp \rho_{max}(t - 25) \tag{3.3}$$

The function 3.3 has been linearized and fitted to the data presented in Tab.1 with the least squares method, thus obtaining $\rho_{max} = 0.144\, d^{-1}$

parameter	value [°C]
optimal temperature	12
minimum temperature	22
maximal temperature	30

Table 3.2: Optimal, minimum and temperature for tomato crops

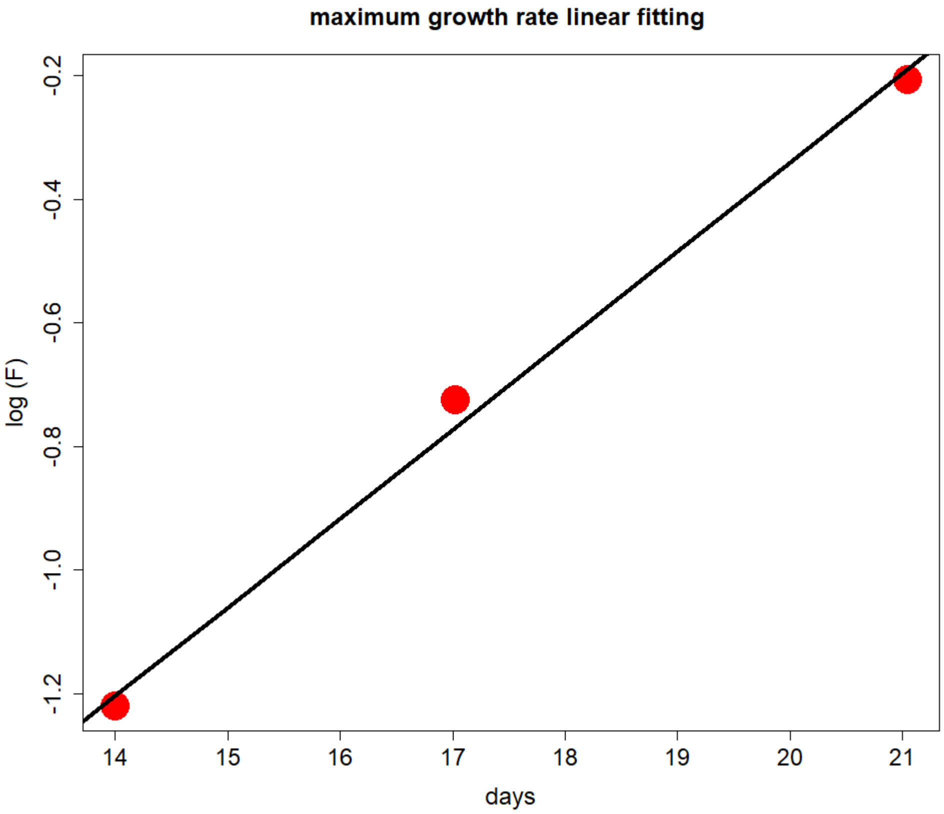


Figure 3.2: ρ_{max} linear calibration

Once ρ_{max} is calibrated,the parameters of function ρ_T needs to be calibrated, in order to allow the computation of the maximum plant growth rate for a generic temperature T. All the parameters of function 2.9 have a physical meaning, being respectively the minimum,maximum and optimal temperature for the tomato plant, and a value was assigned to them according to Shamshiri et al. 2018

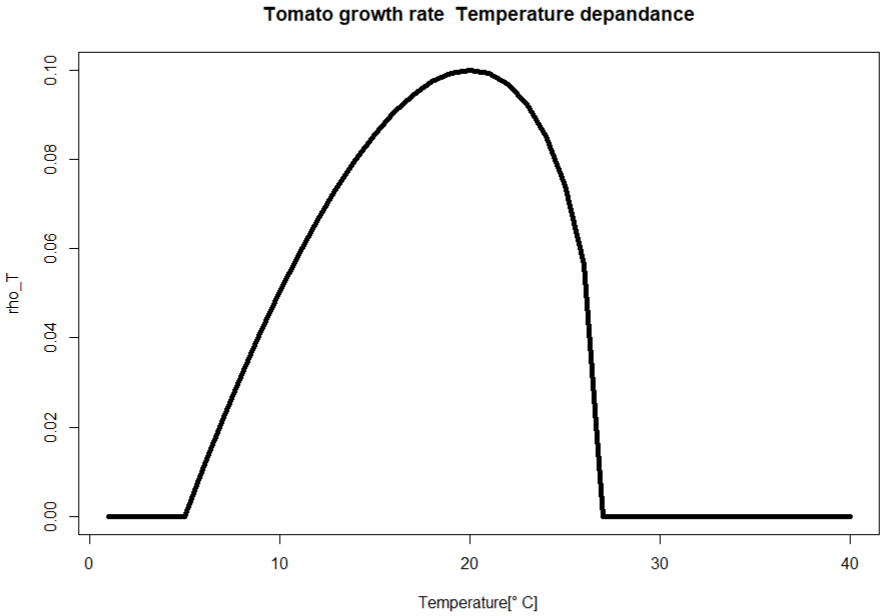


Figure 3.3: Temperature effect on tomato growth rate

Stages duration ζ_E, ζ_L, ζ_A

Multiple studies (Mateus R. Campos et al. 2021 ,Martins et al. 2016 and Rostami et al. 2017) published results showing the egg and pupal stage duration at different temperatures. In particular, Rostami et al. observed the stage duration at a constant temperature, equal to 25 °C, but on three different tomato cultivars: Falkato, Grandella and Isabella. The data from the three datasets were merged and a different non-linear exponential function was fitted for each stage.

For adult stage duration, no evidence temperature dependence is found in scientific literature, and therefore it is assumed constant. This assumption can be justified by the fact that , while juvenile stages have a very limited ability to move and have to endure and adapt to the temperature of their position (leaves for eggs and larvae, soil for pupae), the adults may be capable of regulating their temperature by actively moving around, looking for warmer or colder spots. The value of ζ_A was obtained as the average between three values observed by Rostami et al. 2017 on different tomato cultivars. Therefore $\zeta_A = 10.28\ d$

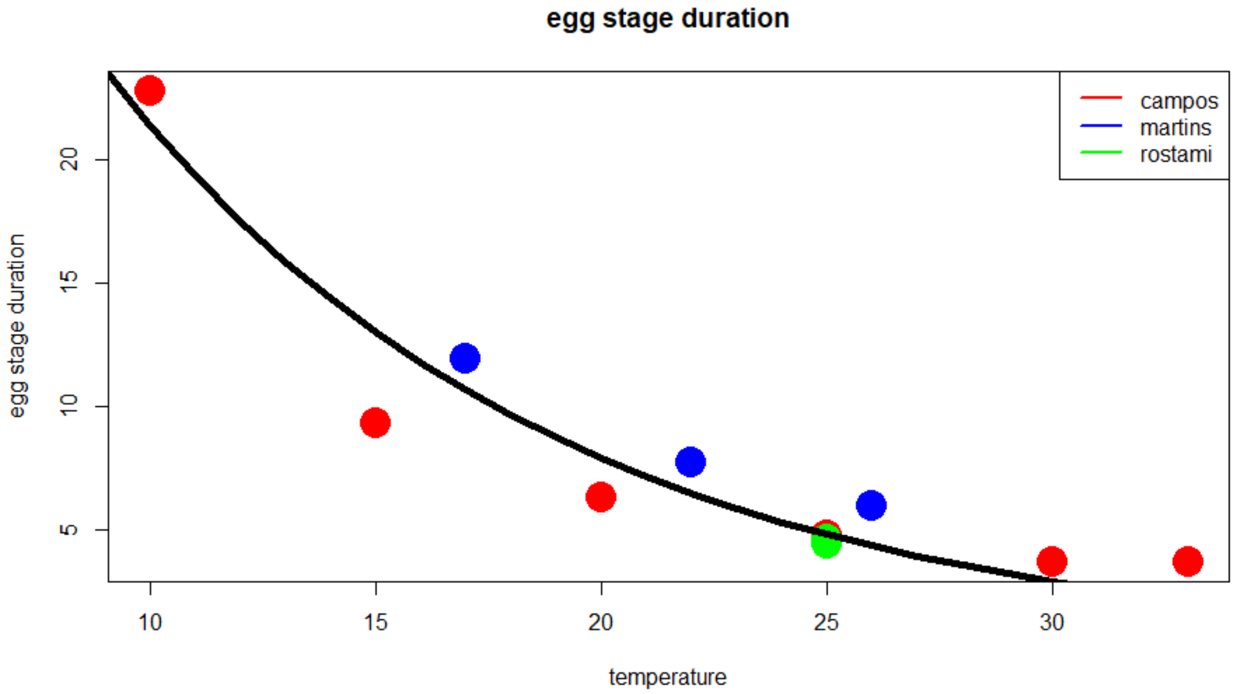


Figure 3.4: Experimental data and fitted function

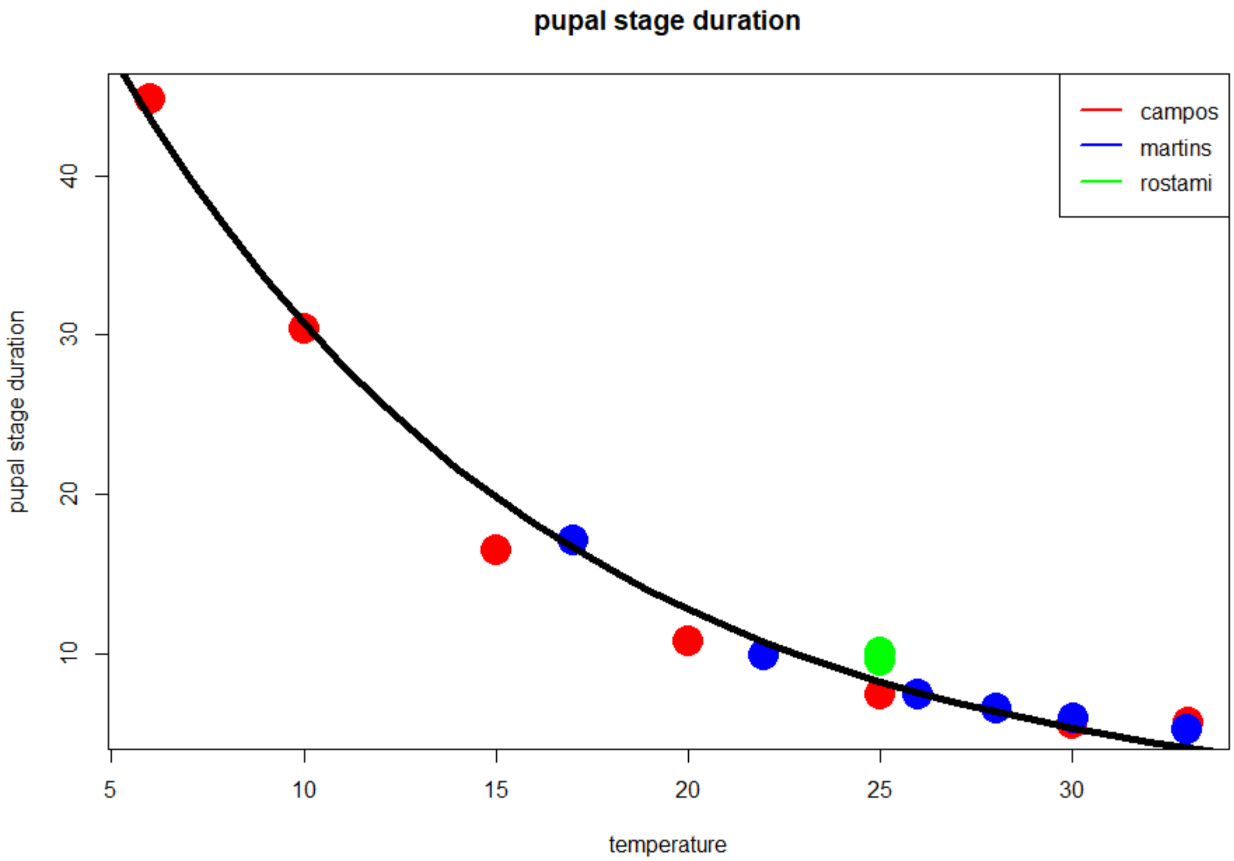


Figure 3.5: Experimental data and fitted function

So, the two calibrated functions for egg and pupal stage duration are :

$$t_e(T) = 57.72e^{-0.10T} \tag{3.4}$$

$$t_p(T) = 73.78e^{-0.09T} \tag{3.5}$$

where T is the environmental temperature, expressed in [°C].

Adults fertility ϕ

Campos et al observed the total fertility rate at different temperatures. Also in this case, the selected non-linear function $\boldsymbol{\Psi}(T)$ (Equation 2.11) was fitted to the observed data, obtaining the following values of the parameters

parameter	value
a	290.58
b	1.57
c	20.64
minimum temperature	4.90
maximum temperature	32.7

Table 3.3: Calibrated parameters of $\boldsymbol{\Psi}(T)$

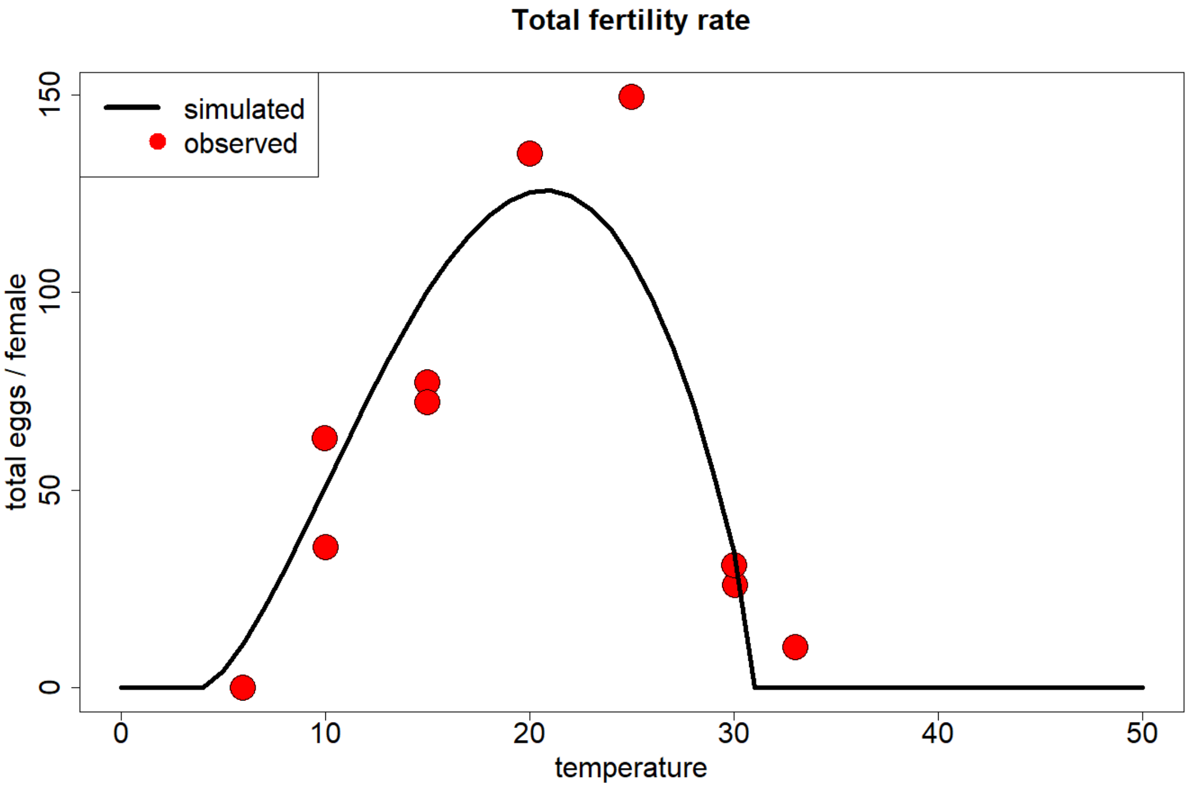


Figure 3.6: Adult fertility : Experimental data and fitted function

Pest mortality rates μ_i

Rostami et al. 2017 computed mortality rates μ_i for each of the i-stages of *T. absoluta*, on three different cultivars.

For each stage, the value mortality rate was simply defined as equal to the average of the three different values observed in the three different cultivars.

parameter	value
μ_E	0.24
μ_L	0.22
μ_P	0.041
μ_A	0.27

Table 3.4: Mortality rates for each $T.absoluta$ stage

These mortality rates are supposed to be temperature independent: by increasing or decreasing the stage duration, temperature already plays an important role into total mortality M_i , since

$$M_i = e^{-\mu_i \tau_i} \tag{3.6}$$

Larvae consumption rate α

The leafmass consumption activity by the larvae is hypothesized to happen with a type two functional response. Coqueret et al. 2017 observed the expansion in time of the mine area produced by 12 larvae feeding on a terminal leaflet. A tomato leaflet offer an amount of resource that is much higher than the one needed by 12 larvae, so it can be safe to assume that these larvae are eating the resource with rate α

These values of surface were converted in leafmass, and alpha was computed diving the total eaten leafmass by the number of larvae by the time interval, thus obtaining $\alpha = 6.5 \times 10^{-4}$ g

Larvae maximum gross conversion efficiency ϵ_{max}

This parameter was calibrated starting from a set of larval gross conversion efficiency values of many insect species belonging to the lepidoctera family (**Schroeder1980**), the highest value reported was set equal to the maximum conversion efficiency, therefore $\epsilon_{max} = 0.55$.

This is the value associated with optimal fertigation (w= 1).

Larvae indirect damage to the plant σ

Coqueret et al. also gathered data on a leaf growth in presence of larvae (Figure 3.1) When L is not equal to zero, but the plant is still in the very initial growth phase (*i.e.* the intraspecific competition in negligible) the leafmass differential equation can be written as :

$$\frac{dF}{dt} = \rho_{max}e^{-\sigma\frac{L}{F}} \tag{3.7}$$

That, once integrated, becomes:

$$F(t) = ae^{\rho_{m}axe^{-\sigma\frac{L}{F}}t} \tag{3.8}$$

Using the available data, it is possible to write:

$$F(t) = 0.3e^{0.144e^{-\sigma\frac{12}{F}}t} \tag{3.9}$$

Since three couples of values (F,t) are known , σ is the only unknown, and can be estimated via a non linear optimization thus obtaining $\sigma = 0.1$.

In order to allow the calibration procedure,the leafmass consumed by the larvae was neglected, and only the indirect damage due to their presence was taken into account.

This assumption can be justified by the fact that,in a 7 days time span, 12 larvae could eat at most α times the number of larvae (12) times the number of days (7), equal to 0.05 mg, that is one order of magnitude smaller than the leaflet mass.

Larvae functional response semisaturation constant δ

Unfortunately, no experimental data linking the larvae consumption rate and the leafmass abundance are available. A feasible ,average value, of the semisaturation constant could be assumed as equal to 1/3 of the carrying capacity value of the resource. Since the values of leafmass has a maximum of around 100 g/m^2 ,the parameter δ value was defined as $\delta = 30\ g$.

Conversion factor to leafmass to leaf surface Ω

This the only parameter whose value was taken directly from scientific literature: according to (Bertin and Gary, 1998), $\Omega = 35\ \ g/m2$

Surface occupied by a single larva ν

According to experiments led in the INRAE unit *Plantes et Systèmes de culture Horticoles*, in high infested plants the larvae density on a leaf can be up to 20 $\frac{\text{larvae}}{dm^2}$ (Unpublished data). Therefore, a feasible value of parameter ν was obtained as the ratio between leaf surface and number of larvae, equal to $\nu = 5 \times 10^{-4}\ \ m^2$

Larvae mass increase required for the metamorphosis to pupa χ

Coqueret et al. also measured the mean weight of the pupae, on plants with both high and low nitrogen content.

nitrogen content	Pupal weight [mg]
HN	4.43
LN	3.63

Table 3.5: Mean pupal weights with different leaf nitrogen contents

Authors hypothesize that the final weight of the pupae depends on the leaf nitrogen content: individuals that consume a plant will reach a higher pupal (and presumably adult) weight, with possible consequences in terms of survival probabilities and fertility. Anyway, this model does not aim at describing differences among individuals; moreover, the leaf nitrogen content, even if strongly influenced on fertilization, it is expected to change along the cropping season, due to the evolution between the different phenological stages of the plant (Schroeder and Malmer 1980). Consequently, the pupal weight is assumed as a constant value for all individuals, equal to the average between the values observed at two different nitrogen concentration. (reported in Table 3.4).

The average dimension of a *T.absoluta individual* at larval stage (4.15 mm of length) is on order of magnitude bigger than its dimension at egg stage (0.41 mm of length) (Chavan et al. 2020). It is safe to assume that this rate is maintained also in mass terms, so that the weight at the very beginning of the larval stage (equal to the egg weight) is negligible with respect to the weight at the end of the larval stage (equal to pupal and adult weight).

Under all this assumptions, it is possible to set $\chi = 4 \times 10^{-3} \;\; g$

Plant coefficient of intraspecific competition β

The logistic growth function tend to an asymptotic value, known as carrying capacity.

$$\frac{dF}{dt} = \rho F - \beta F^2 \tag{3.10}$$

The value of carrying capacity K can be obtained by putting eq. 3.10 equal to zero, thus obtaining:

$$K = \frac{\rho}{\beta} \tag{3.11}$$

In optimal conditions, ρ is known an K can be safely assumed as equal to 120 g/ m^2 (Heuvelink,1999). Consequently, β can be simply obtained by inverting eq. 3.11, obtaining $\beta = 0.0012\, g^{-1}\, d^{-1}$

Predator response function semi-saturation constant ι

Once again, dedicated experiments and data gathering should be carried out in order to define this parameter. In lack of data, the semisaturation constant in was hypothesized as close to 1/3 of the maximum amount of T.absoluta juvenile stages present in a fully infested crop, *i.e.* 3000 individuals. Consequently $\iota = 3000\; ind\; \mathrm{m}^{-2}$

3.1.1 Parameters summary table

In following table is reported the full set of calibrated parameters,for an ambient temperature of 25 °C, along with the units of measure and the corresponding references.

parameter	description	value	units
ϕ	adult fertility	5.6	$eggs\ d^{-1}\ adult^{-1}$
μ_E	egg mortality rate	0.24	d^{-1}
μ_L	larvae mortality rate	0.22	d^{-1}
μ_P	pupae mortality rate	0.04	d^{-1}
μ_A	adult mortality rate	0.27	d^{-1}
ζ_E	egg stage duration	4.9	d
ζ_P	pupal stage duration	8.4	d
ζ_A	adult stage duration	10.28	d
α	max consumption rate	6.5×10^{-4}	$g\,d^{-1}$
β	Plant density dependence	0.012	$g^{-1}\,d^{-1}$
δ	Larvae semisaturation constant	35	$g\,m^{-2}$
ϵ	Conversion efficiency	0.55	/
χ	critical mass gain	4×10^{-3}	g
σ	indirect damage	0.1	/
Ω	conversion factor from leafmass to surface	1/35	$m^2\,g^{-1}$
υ	surface needed per larva	5×10^{-4}	m^2
ρ_{max}	crop max growth rate	0.144	d^{-1}
ι	Predator semisaturation constant	3000	eggs m^{-2}

Table 3.6: Parameters summary table, containing a set of parameters coherent with a 25 °C temperature.

3.2 Performance indicators

In order to be able to evaluate and compare the performance of the system, two simple and straightforward indicators were introduced.

- Harvest: Given a cropping season of 120 days, the leafmass at the end of the cropping season, at time t_h is taken as a proxy of the harvest, and therefore is an indicator that has to be maximized. The underlying assumption are that high value of leafmass (close to the carrying capacity values) describes a situation were the plant was poorly damaged by the pest, and that leafmass and fruit production are proportional.

$$i_h = F(t_h) \tag{3.12}$$

- Infestation magnitude: the indicator chosen to represent the severity of the infestation is the total number of adults generated along the cropping season.

$$i_p = \int_0^{t_h} \frac{P}{\zeta_P} \, dt \tag{3.13}$$

The associated objective are obtained simply specifying the direction of optimization of the two indicators: quite intuitively, the harvest indicator has to be maximized, while the infestation indicator has to be minimized. Therefore, the objectives can be written as:

$$J_h = \max_u i_h \tag{3.14}$$

$$J_p = \min_u i_p \tag{3.15}$$

Where u is a two-dimensional vector containing the two possible control variables : fertigation(w) and bio control (z)

$$u = \begin{bmatrix} \mathrm{w} \\ z \end{bmatrix}$$

Chapter 4

Results and Discussion

4.1 Pattern oriented model validation

Despite the devastating effect of *T. absoluta* on the tomato crops and its worldwide spread, little to no data on the population dynamics exist in literature. These lack of data impairs the possibility of a traditional validation procedure and, as a consequence, a 'pattern - oriented' validation approach was implemented.

4.1.1 Pattern oriented modelling

A pattern can be defined as characteristic and clearly identifiable structures in nature(Grimm, Franka, et al. 1996). Patterns are the visible outcome of several "hidden" phenomena of the system, deriving from the interaction between internal processes and external factors (such as environmental conditions)(Gallagher et al. 2021).

Concerning ecology, it is possible to identify patterns that span across each level of the ecological hierarchy and it is possible to classify them in seven distinct categories: behaviour, energetics, movement, genetics and evolution, structure, dynamics, and distributions.

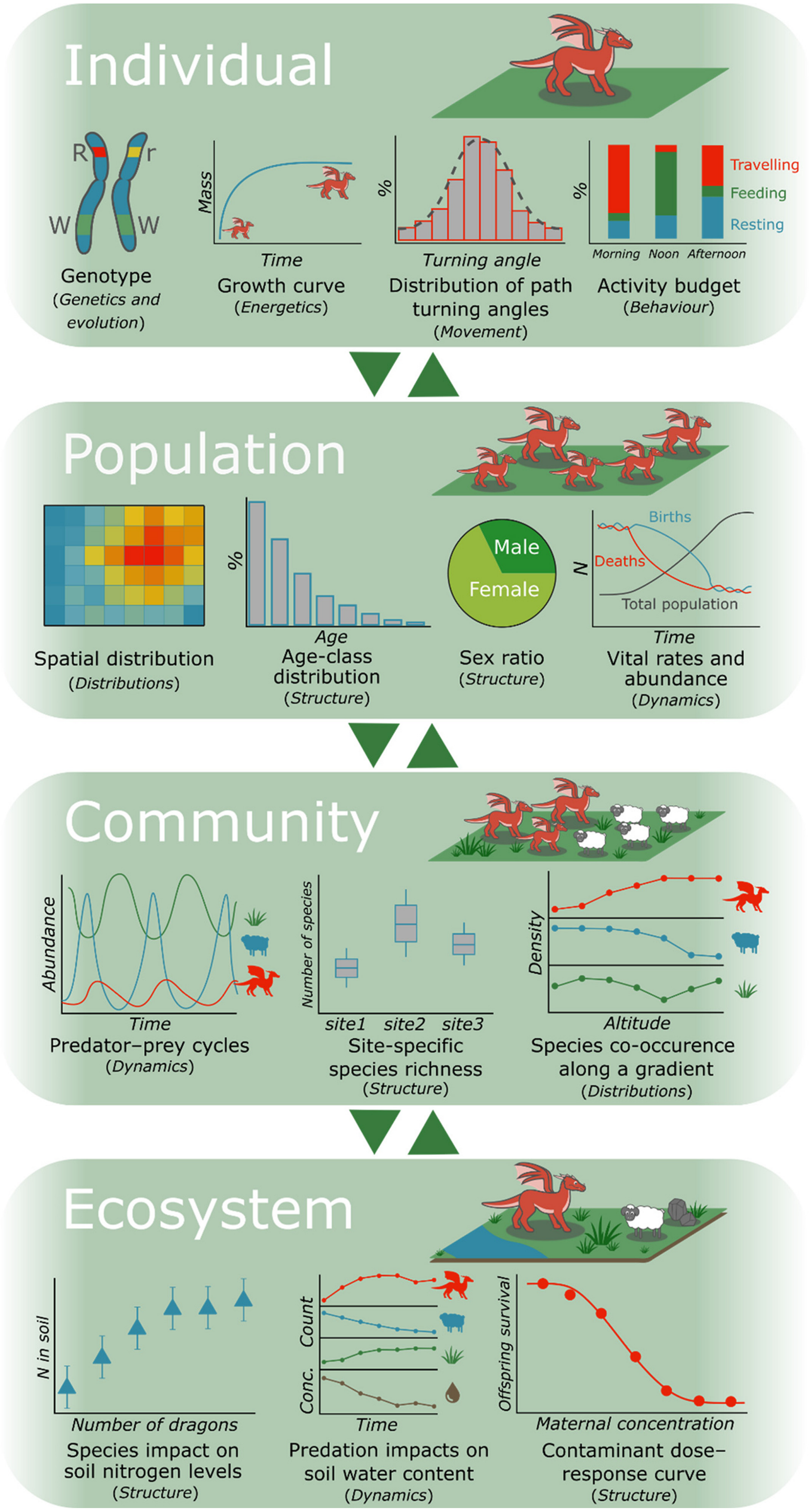


Figure 4.1: An overview of possible types of pattern that can be observed in ecology, derived according to type and hierarchical level , figure taken by (Gallagher et al. 2021)

Among patterns, strong patterns are particularly relevant, as they are the ones that provide a strong indication of the underlying processes in a system and are typically described quantitatively (Grimm and Railsback 2012).

Patterns provide useful information, that can be used to allow or enhance the process of model realization: Pattern oriented modelling (POM) is a technique that employs the confrontation of empirical patterns and model output in order to enable the model of capturing the processes in the system necessary for the model purpose.

4.1.2 Selected Patterns

Regarding the interaction between *T. absoluta* and the tomato plant, two strong empirically observed patterns, belonging to different hierarchical levels, emerge from the scientific literature. Therefore, the model was used to simulate the same conditions and the model output was then compared with the observed phenomena.

The effect of water and nitrogen availability on larval development time

This first pattern emerges at individual level, and, referring to larval growth rate (and implicitly to larval feeding activity) is both an energetics and behaviour pattern. As presented before, larval development time is affected by nitrogen and water availability (Coqueret et al. 2017) and (Han et al, 2014) and (Han et al, 2017).

In particular, Han, A. V. Lavoir, et al. 2014 reported the values of the development times from egg to pupa under different conditions of water and nitrogen availability (Figure 4.2)

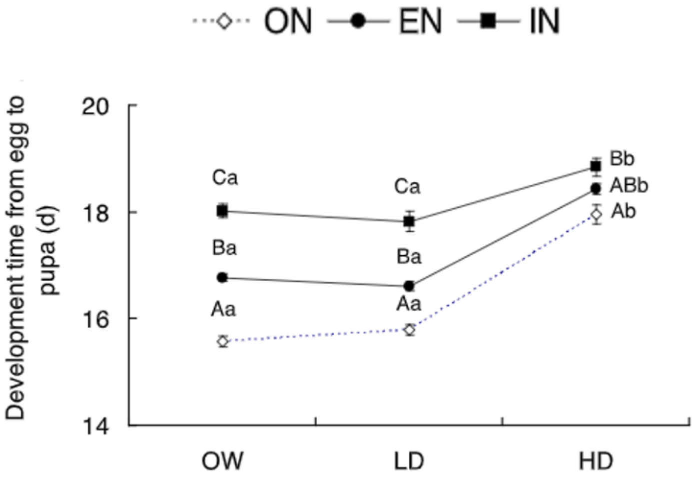


Figure 4.2: Experimental data, measured on plants with different regimes of irrigation and fertilization, source Han, A. V. Lavoir, et al. 2014

Since in our model, water and nitrogen are coupled in one single parameter (w, fertigation), the information regarding the different regimes of irrigation and fertilization was re-arranged as shown in Table 4.1.

irrigation regime	fertilization regime	plant stress level	w value
OW	ON	null	1
LD	IN	medium	0.85
HD	ON	medium	0.85
HD	IN	high	0.7

Table 4.1: Different combinations of irrigation and fertlization regimes, and the correspondant w value

In order to check if the model is able to grasp this significant aspect of the system, 100 simulation were run, each of them with a different value of w, covering the whole range of possible values [0, 1]. For each simulation, average larval stage duration was obtained using Eq. 2.17 , and the results were compared with the values found by Han, A. V. Lavoir, et al.

2014.

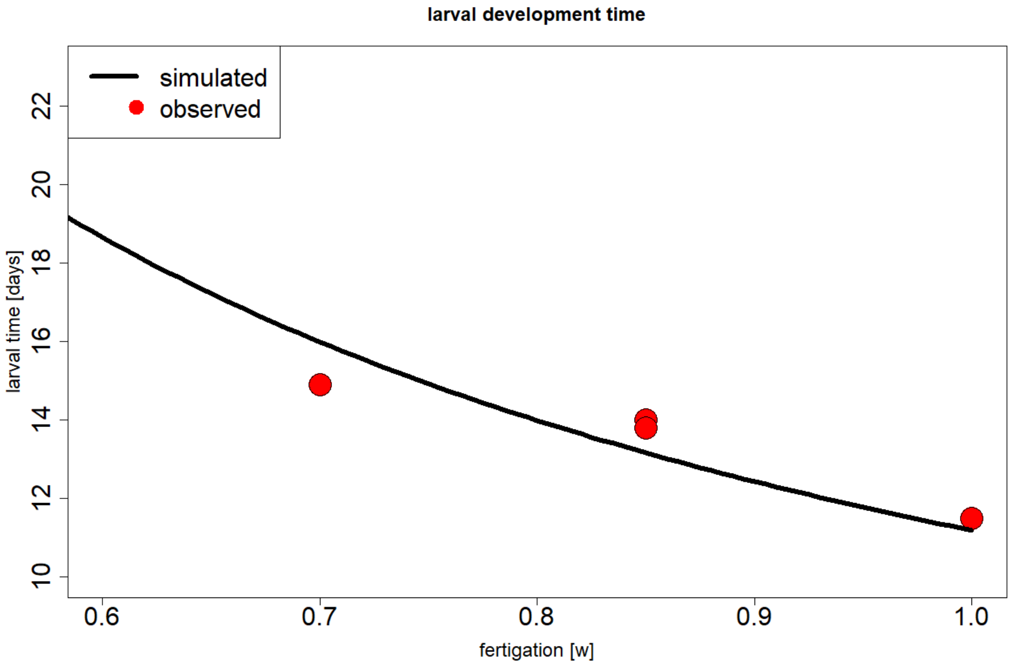


Figure 4.3: Experimental data of LDT, measured on plants with different regimes of irrigation and fertilization, corresponding to different values of w

Tomato plant destruction by *T. absoluta*

The tomato plants can be strongly damaged when infested, leading to harvest losses up to 100 % (Biondi, Guedes, et al. 2018). Despite uniform agreement on this, very few recordings of the infestation process have been documented.

In a recent study (Bompard et al. 2013) it is shown how, even in presence of another pest (Toacco whitefly, *Bemisia tabaci*), *T. absoluta* population grew exponentially, causing the destruction of the host tomato plants and the consequential local extinction of both *T. absoluta* and B. tabaci, due to absence of resource. This whole process ends within 9 weeks.

This second pattern is a dynamics-type pattern, belonging to the community ecological level. The model have been used to simulate the experiment led in the study, setting initial conditions as close as possible to the ones of the experiment. A comparison between the experiment's results and the simulation output is shown in Figure 4.5.

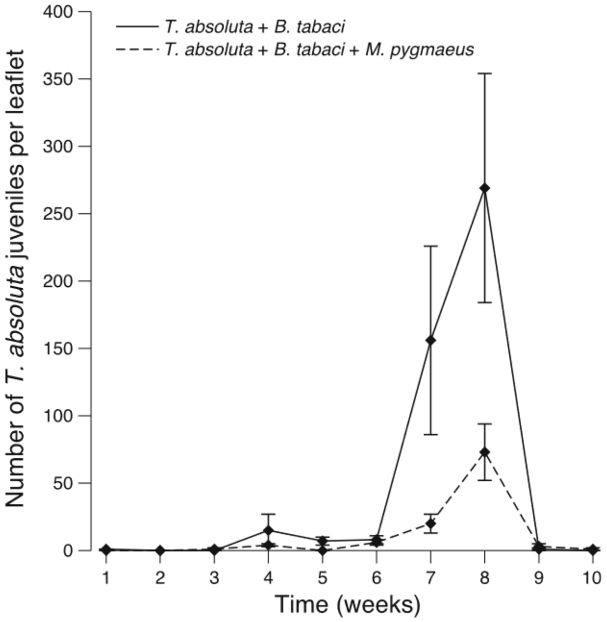


Figure 4.4: Experimental data on *T. absoluta* dynamics, in presence of onother tomato pest, B.Tabaci

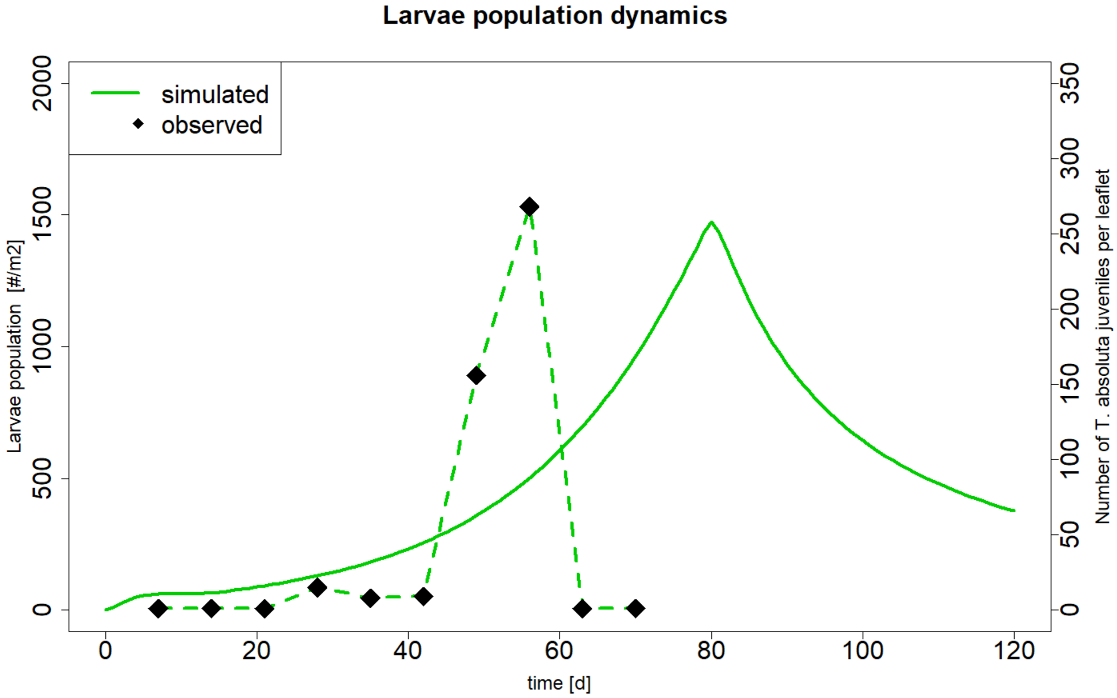
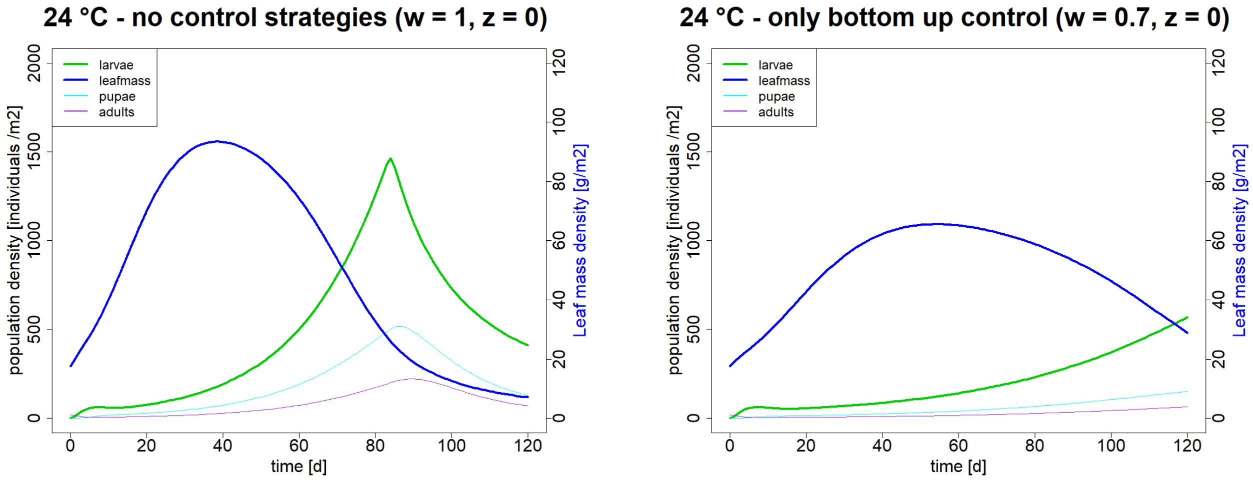


Figure 4.5: Crop-Pest dynamics simulated by the model, in the same condition of the experiment

The differences between the simulated and observed larvae dynamics may be attributed to the presence of a second pest in the experiment (*B. tabaci*), that causes an earlier destruction of the tomato plant. Nevertheless, the model is able to reproduce the qualitative behaviour of the population dynamics: a slow growth during the first weeks, followed by a peak and an abrupt decline.

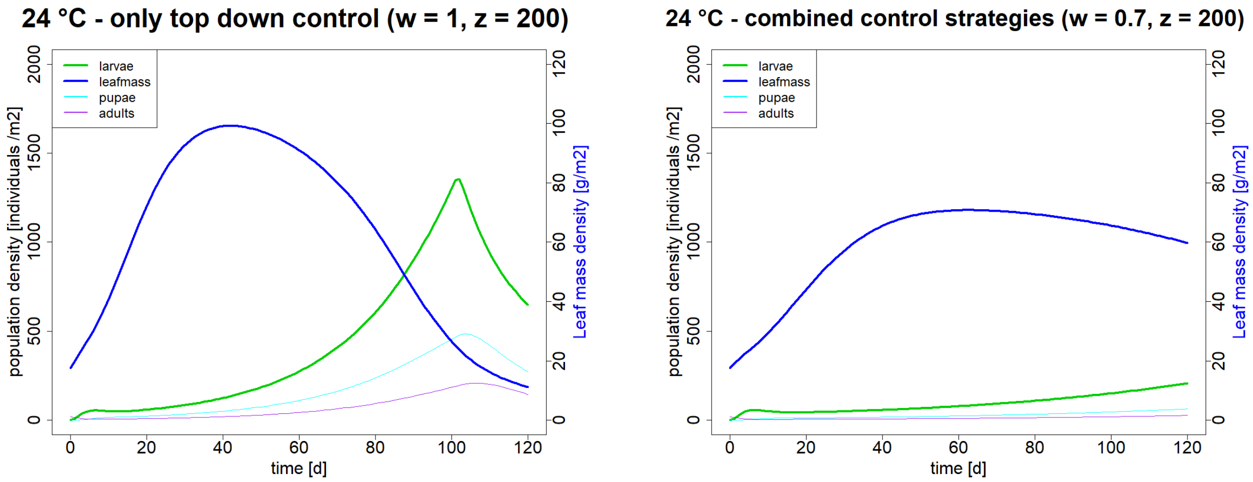
4.2 System trajectories: effect of temperature, irrigation, fertilization and biocontrol

After having assessed the ability of the model to reproduce the observed patterns, the ”validated” model was used to simulated the coupled crop pest dynamics under an average temperature (24 °C) and different fertigation and biocontrol conditions. The results are shown in Figure 4.6. The hypothesis of constant is temperature quite reasonable in the case of greenhouse conditions, while it introduces an greater approximation in the case of open field conditions. It is possible to note how the reduction of water and nutrients inputs to the plant (decreasing the value of w) has a considerable effect on the pest dynamics. This is coherent with the findings of a recent study (Han, A.-V. Lavoir, et al. 2022), according to which the effects of this kind of bottom - up control strategies propagates and amplifies thought the trophic chain. Instead, even a high value of bio-control is not particularly effective when used alone, but can be useful if used in combination with a reduction of fertigation. Even when no control strategies are implemented, the system behaviour is markedly temperature dependant: as can be seen in Figures 4.7 and 4.8, the leafmass trejectories in presence and absence of pest are quite similar for 12 °C, 18 °C and 30 °C (showing a typical logistic growth); instead, at intermediate temperatures (22 °C and 24 °C) the presence of the pest leads to an unimodal function, with a significative reduction of the leaf mass in the final period of the cropping season.



(a) No control

(b) Only bottom up control



(c) Only top down control

(d) Combined control

Figure 4.6: Crop-pest dynamics at 24 °C, under different combination of biocontrol and fertigation

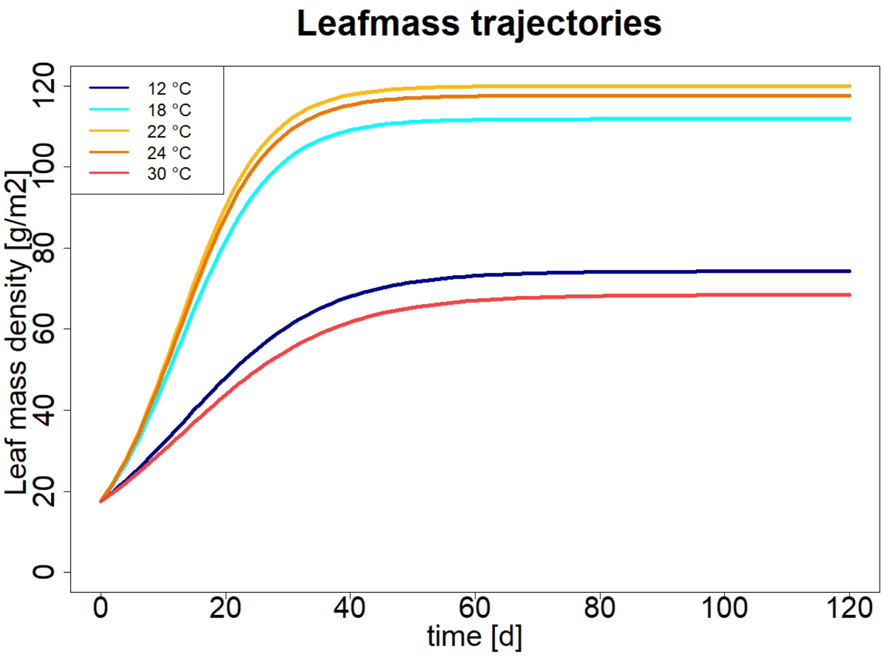


Figure 4.7: Leafmass dynamics in absence of pest

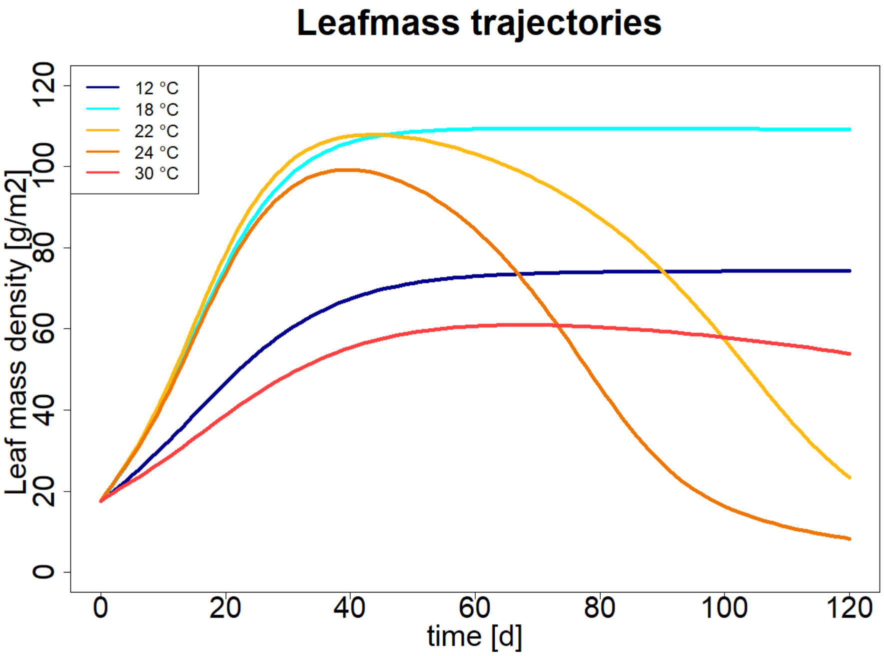


Figure 4.8: Leafmass dynamics with pest

4.3 System performance: harvest and infestation magnitude

4.3.1 Sensitivity analysis

A sensitivity analysis was led in order to find out which biological traits of *T. absoluta* are more responsible of the devastating effect on host plant when no control strategies are implemented. This was done by perturbing one parameter at a time, while all the other parameters are kept constant and refers to an optimally irrigated and fertilized crop at an ambient temperature of 24 °C. The results are shown in Figures 4.9 and 4.10.

The sensitivity analysis shows how, for almost every parameter, a relatively small variation in the parameter's value (+- 20 %) can significantly change the performance of the system. Quite intuitively, parameters values responsible of high infestation magnitudes are also linked to low harvest values, and vice-versa. Moreover, the sensitivity analysis may allow to observe that shorter development times, lower moralities and higher fertility parameter's value are linked with higher infestation densities and low harvest values. In particular, the system is specially sensible to the *T. absoluta* adult fertility ϕ.

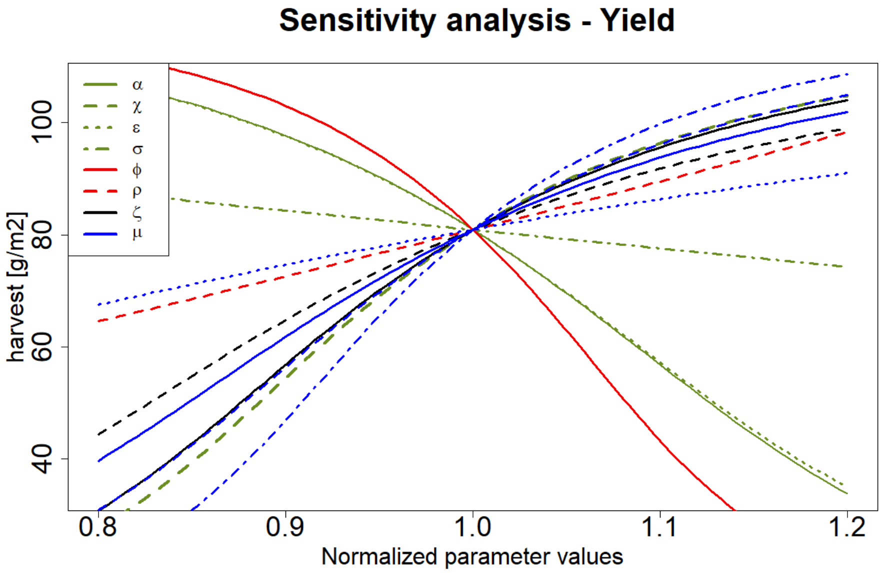


Figure 4.9: Simulated variation of the harvest in response to changes in the parameters value. For mortality and stage duration parameters, continuous line refers to eggs, dashed line to larvae, dotted lines to pupae, dotdash lines to adults

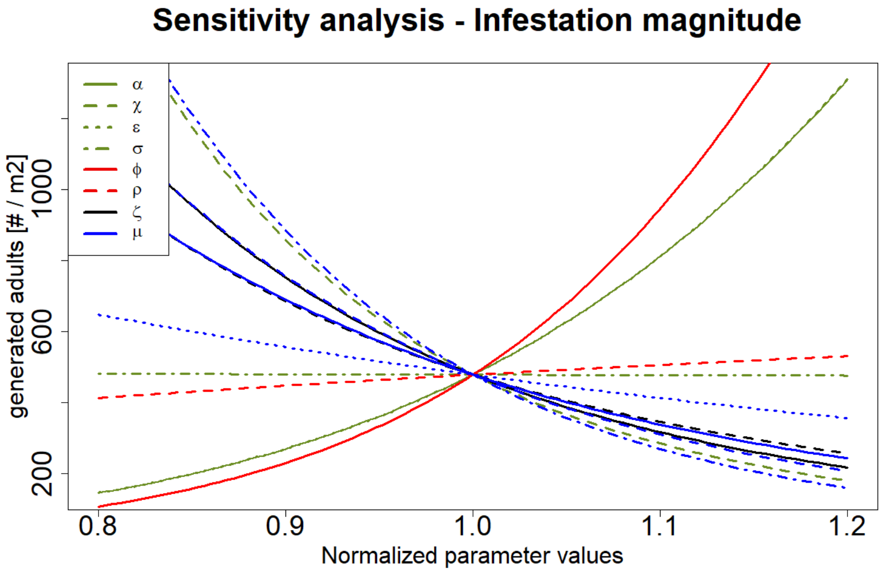


Figure 4.10: Simulated variation of the infestation magnitude in response to changes in the parameters value. For mortality and stage duration parameters, continuous line refers to eggs, dashed line to larvae, dotted lines to pupae, dotdash lines to adults

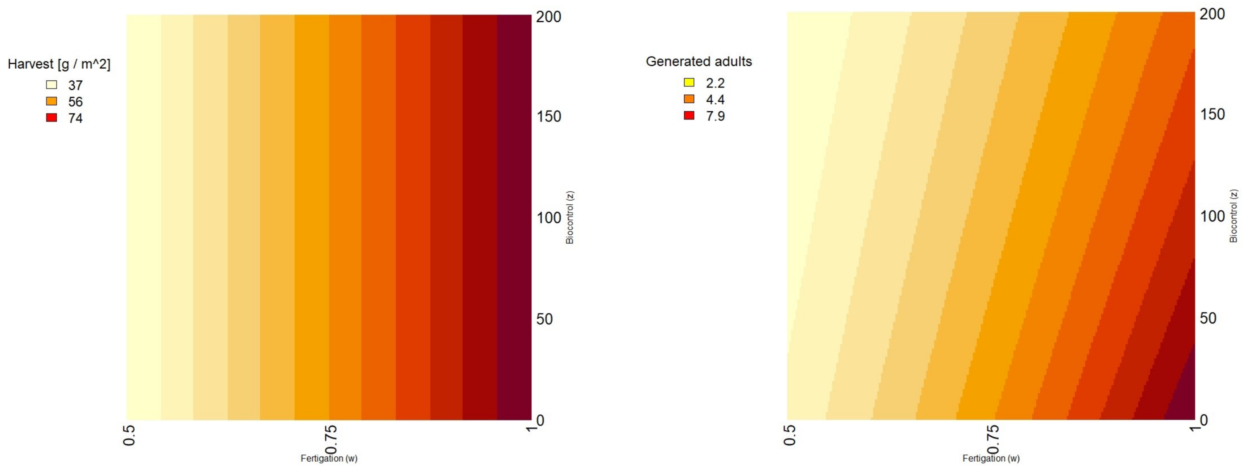
4.3.2 Combined effect of fertilization, irrigation and bio-control at different temperatures

As presented in Figures 4.7 and 4.8, the system behaviour is significantly temperature dependant. This variability is further explored thought a series of heat maps, each of them referring to a different temperature, showing the value of a performance indicator for different combinations of bio-control and fertigation. A second series of heatmaps was obtained with the same procedure, but instead of the harvest, the explored model outcome is the total numbers of adults generated along the cropping season. The results are presented in Figure 4.11.

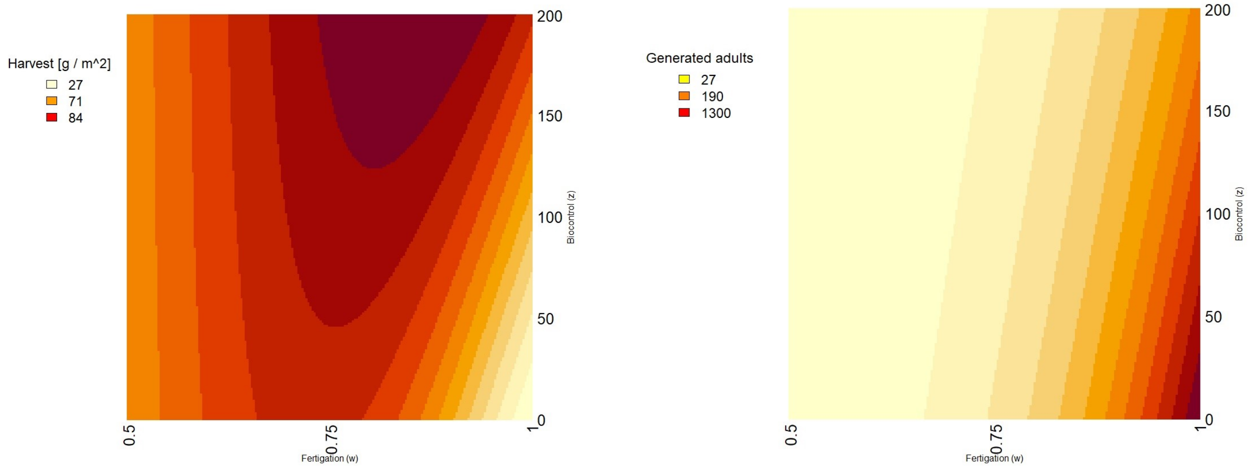
The heatmap referring to "extreme values"(12 °C and 30 °C) are qualitatively very similar: since the temperature doesn't allow the pest population to reach damaging concentrations, the harvest is basically independent from the bio-control. Instead, the peculiar patterns that emerge at medium range temperature are quite informative:

- Plant in high stress conditions: $0.5 < w < 0.75$ the plant has a low nutritional value for the larvae, that consequently have a low conversion efficiency and need to ingest more food (requiring more days) in order to reach a sufficient mass gain for the metamorphosis. Here is possible to see the effect of the mechanism underlying the "Nitrogen Limitation hypothesis". This longer larval stage duration prevent a fast pest population growth and the pest induced harvest reduction is contained. Consequently, the harvest is scarcely dependant from biocontrol.
- Plant in mild stress/ optimal conditions: ($w > 0.75$): with this level of fertigation, larval stage duration is short enough to allow a rapid population build-up and a drastic harvest reduction. It can be noted how, for a fixed value of fertigation, increasing biocontrol always leads to an increase in harvest. At the same time, a reduction in fertigation creates a delay of the larval stage duration, hindering the pest population build-up and allowing to get the same harvest with a lower biocontrol. In synthesis

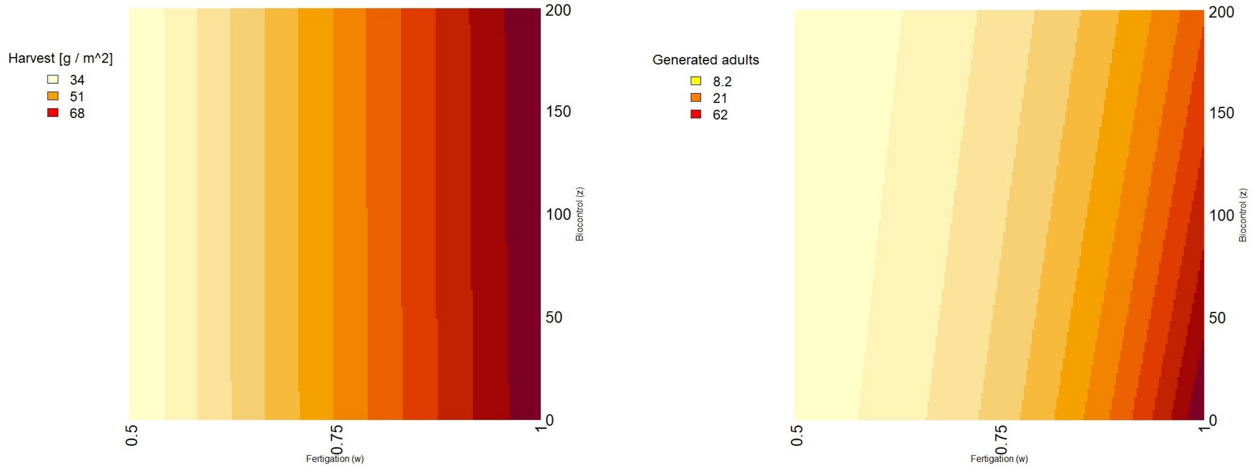
there there is an optimal value of fertigation, that is different from the maximum achievable one; the plants provide the best harvest under a certain level of stress. This is a finding of particular importance for agronomic management: in presence of pest, and for intermediates level of bio-control, the water and fertilizers input should be controlled with great care, as the best harvest is obtained at an ”optimal level” of plant stress.



(a) Harvest at 12 °C (b) Infestation magnitude at 12 °C



(c) Harvest at 25 °C (d) Infestation magnitude at 25 °C

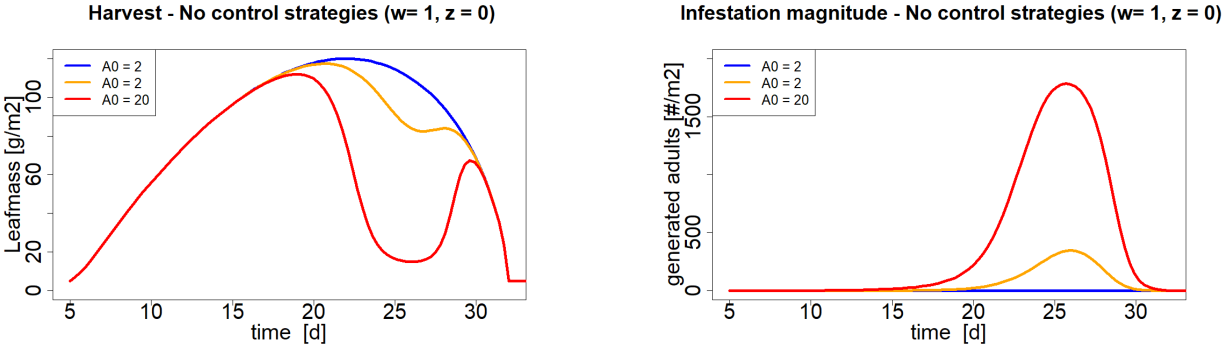


(e) Harvest at 30 °C (f) Infestation magnitude at 30 °C

Figure 4.11: System performance indicators at 12 °C, 25 °C and 30 °C, under different combinations of bio-control and fertigation. The values shown at the left of each heatmap shows respectively the minimum, the median and the maximum value

The effect of ambient temperature, fertigation and bio-control on the Harvest is also explored in another series of graphs, showing the value of the performance indicators when no control is implemented (Figure 4.12) and under different control strategies (Figure 4.13), with an initial condition at the beginning of the cropping season of no pest (blue line), two adults (orange line), twenty adults (red line). In particular, it can be observed how, for temperatures lower than approximately 18 °C, the infestation magnitude is very low and, consequently, the presence of *T. absoluta* as an irrelevant effect on the harvest. Instead, in the range between 20 °C and 30 °C, *T. absoluta* is able to reach notable densities, thus causing a strong harvest reduction. In addiction, the system performance within this temperature range depends from the initial conditions, as an initial values of twenty adults will cause a much worse system performance than an initial value of only two adults. For temperatures higher than 30 °C, the pest life cycle is shortened, but also the adult fertility is strongly reduced (as shown in Figures 3.4, 3.5, 3.6). This impairs the population growth of *T. absoluta*, whose densities remain at low values. As a consequence, the pest presence as a negligible effect on the harvest.

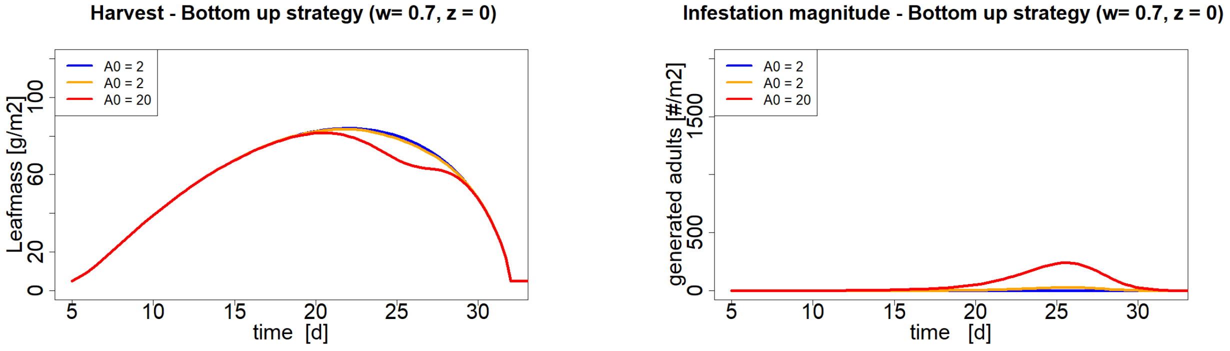
These results seems to suggest that the optimal temperature range for this pest is between 20 °C and 30°C, apparently because this range provides the most favorable combinations of life - cycle speed and adult fertility, with a value of optimal temperature equal to 25 °C.



(a) Harvest

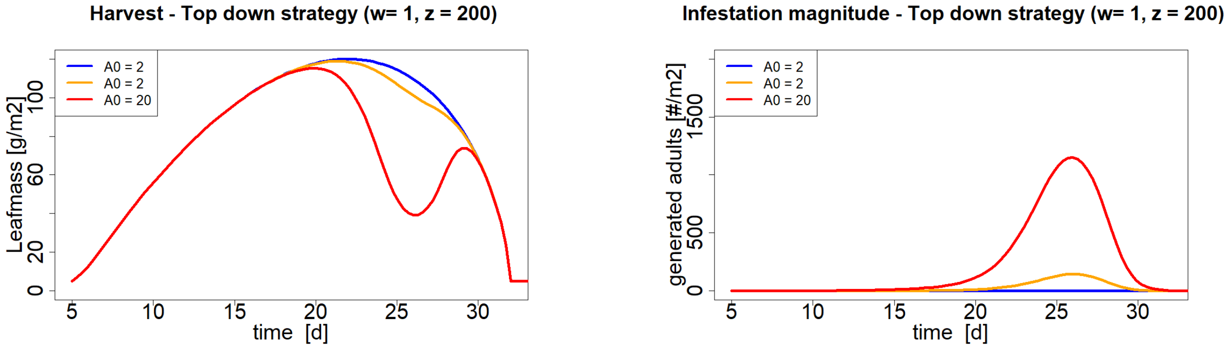
(b) Infestation magnitude

Figure 4.12: Harvest and infestation at different temperatures when no control strategies are implemented



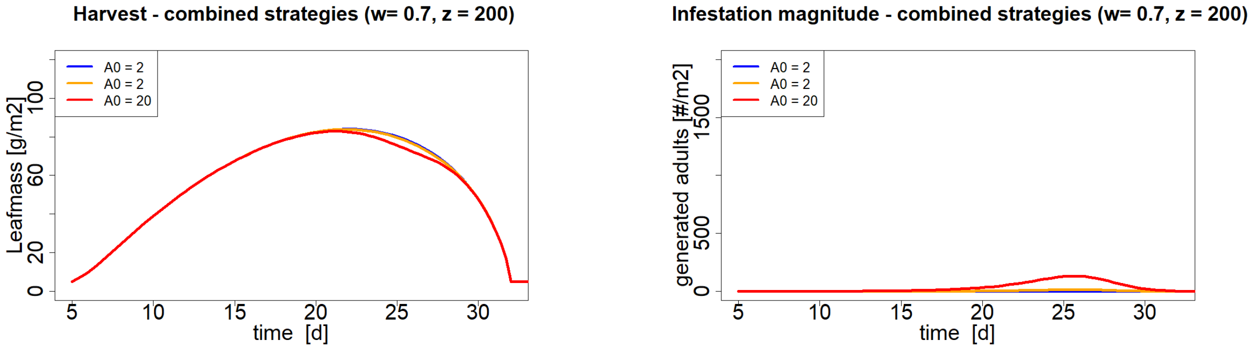
(a) Only input nutrients limitation

(b) Only input nutrients limitation



(c) Only bio-control

(d) Only bio-control



(e) Combined control strategies

(f) Combined control strategies

Figure 4.13: System performance indicators at different temperatures, under different combination of control practices

4.4 System trajectories under Northern Mediterranean temperatures

Aiming at a more realistic simulation of the processes occurring in the crops in open-field conditions, time varying temperature simulations were performed.

4.4.1 Seasonal dynamics

A very simplified temperature trajectory was built, starting from data of the average daily temperatures in Avignon (France),throughout the year. The model was then initialized with values corresponding first of April

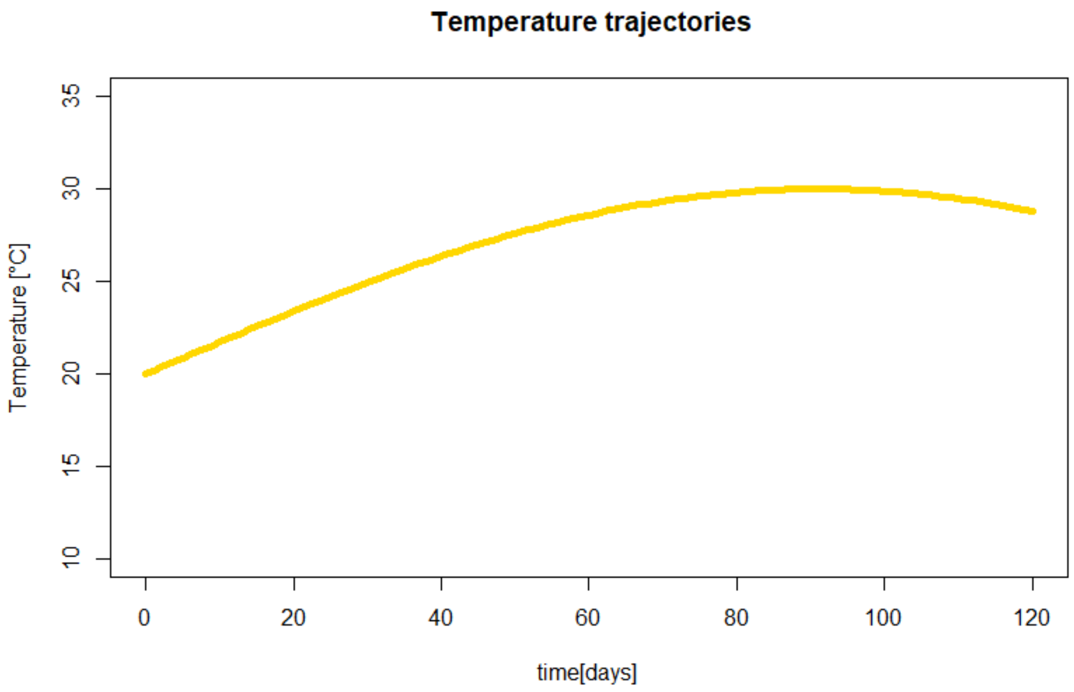


Figure 4.14: Temperature values from 1st April to 31 July

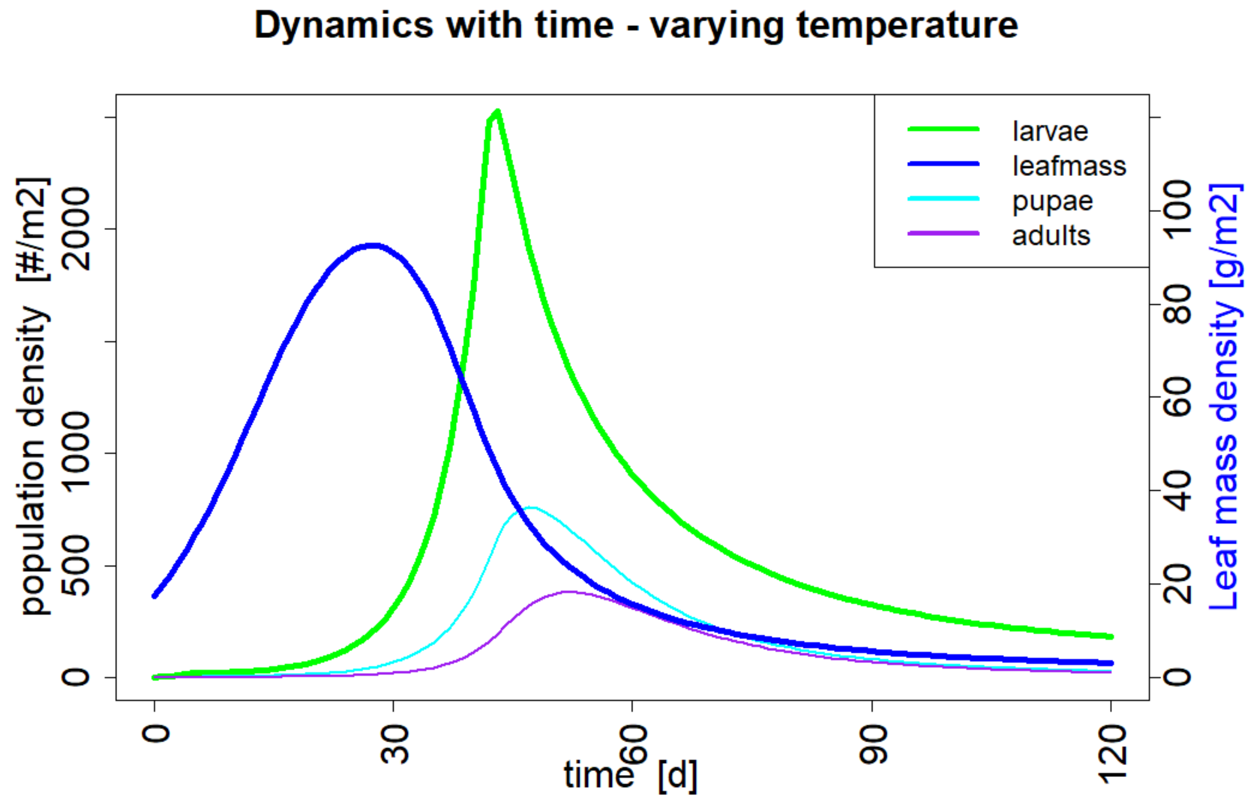


Figure 4.15: Simulation for a tomato crop open-field in Avignon

It can be noted how the introduction of a time varying temperature doesn't change the trajectories in a qualitative way. Anyhow, a growing temperature along the cropping season allows a faster development of *T. absoluta* from egg to pupa, resulting in an earlier population build-up and an earlier destruction of the tomato crop.

4.4.2 Inter annual dynamics

The model also allowed to perform simulations with a time horizon longer than the 120 days of the tomato cropping season. At a first look, it may seem that this ”long term” simulation is of limited interest, as the tomato is, in the vast majority of cases, an annual crop that is replanted after every season. Despite this, these simulation should not be overlook for the following reasons:

- They may reproduce the behaviour of *T. absoluta* in the environmental reservoir. As discussed before, this pest does not attack only cultliveted crops, but also many other wild plants (Bergougnoux 2014). Naturally, the interaction with different plants will be characterized by different parameters than the ones associated to the domestic tomato, but even the current parametrization could provide a qualitative, but informative, description of the phenomena.
- They provide information about which periods of the year is more likely to trigger an exponential growth of the pest population.

As can be observed in Figure 4.17, the pest remain at low density values for the vast majority of the year, until the combination between resource abundance and favorable environmental temperature triggers a rapid growth of the population. This abrupt growth almost bring to extinction the host plant, thus causing an equally abrupt decline of pest population. These kind of simulation may bring useful information regarding the times of the year in which pest monitoring should be reinforced, because *T. absoluta* is more likely to reach high densities, and, consequently, more likely to attack cultivated fields.

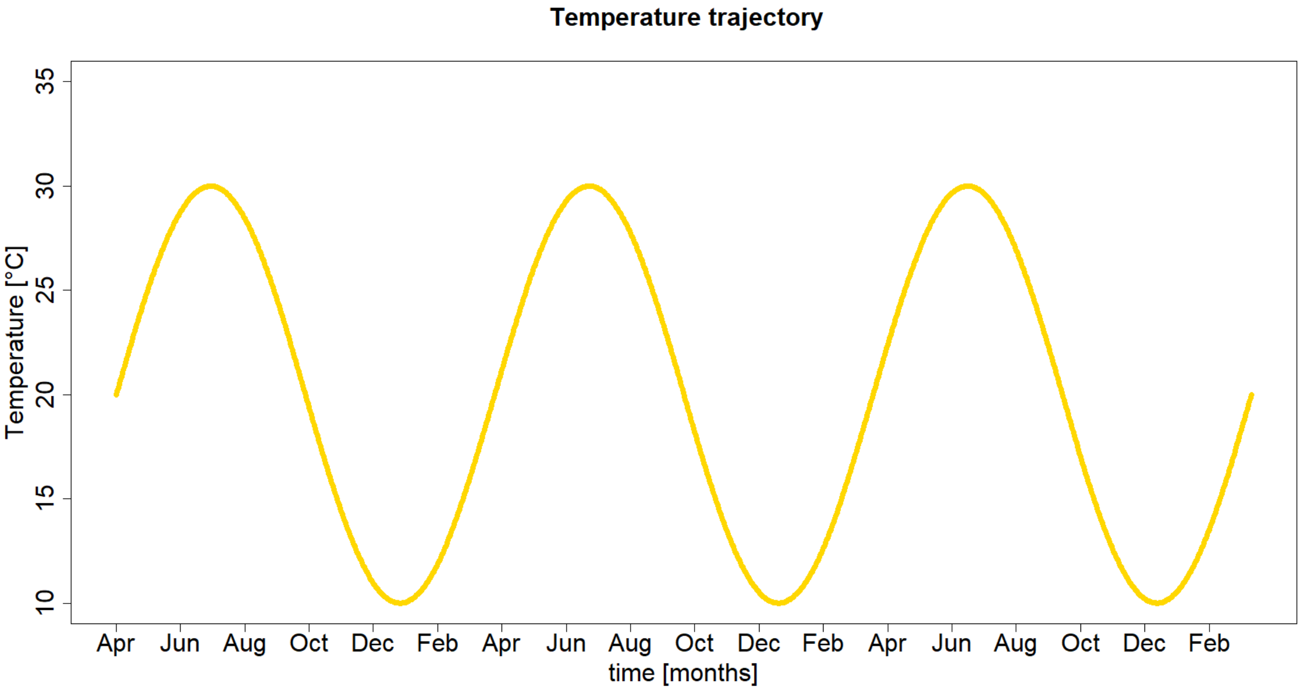


Figure 4.16: A simplified daily temperature trajectory for Avignon, France

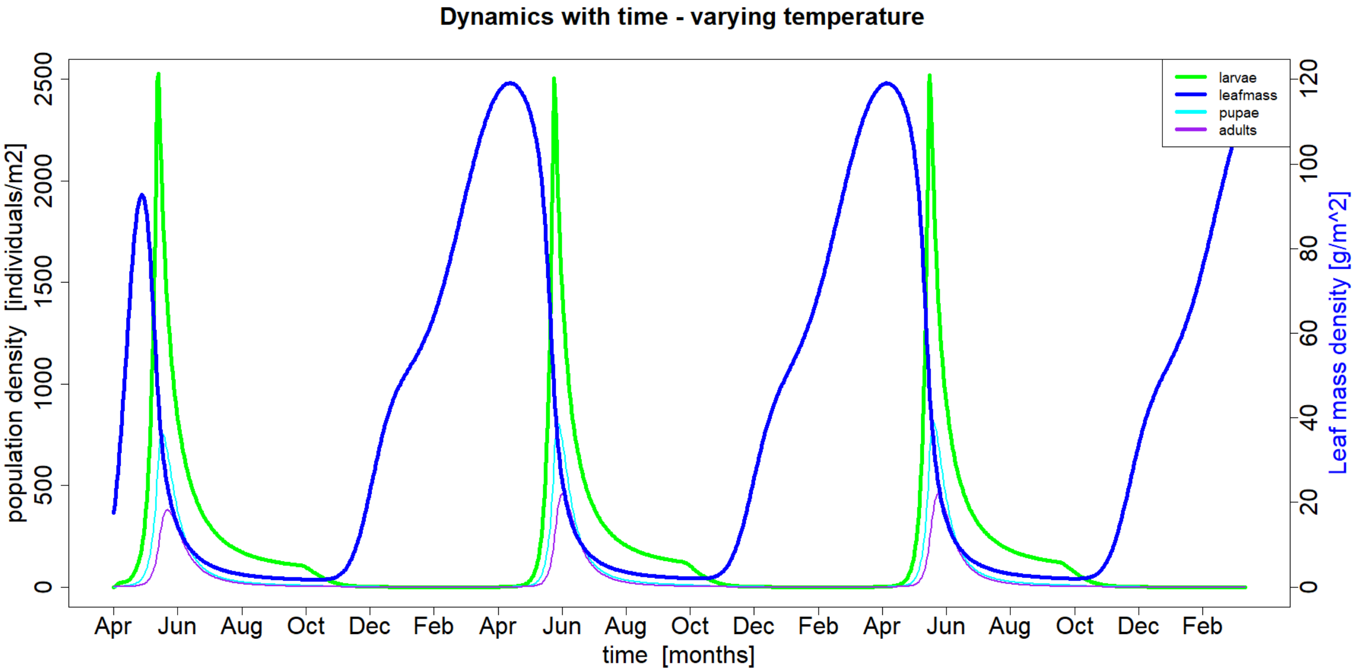


Figure 4.17: Inter annual Crop-Pest dynamics

4.4.3 Possible effects of climate change

The introduction of temperature dependence also allows to get a first, preliminary, understanding of how climate change could influence the plant growth, the magnitude of infestations and the resulting harvest. Since it is not the focus of the present work, this assessment was led with an extremely simplified approach, but it allows to show how small changes in the temperature trajectories can alter the behaviour of the system.

In order to lead the analysis,the simplified temperature annual trajectory is used as a starting point to generate synthetic trajectories, via the technique of additive perturbation.

$$T' = T^H + \gamma \tag{4.1}$$

Additive perturbation schemes allows to compute scenarios that capture changes in mean, but does not modify the historical value of variance, *i.e.*, in the generated scenarios, variability is not expanding.

A proper climate change impact assessment is beyond the scope of this study; for this reason, just two temperature trajectories were generated, in coherence with the expected temperature increase in the Mediterranean basin. In particular, each temperature trajectory is associated with a value of γ, and these values were chosen in accordance with the estimated increase in annual mean temperature for the Mediterranean basin in 2080, according to RCP 4.5 and RCP8.5, respectively +1.9 °C and +3.8°C (JRC 2017).

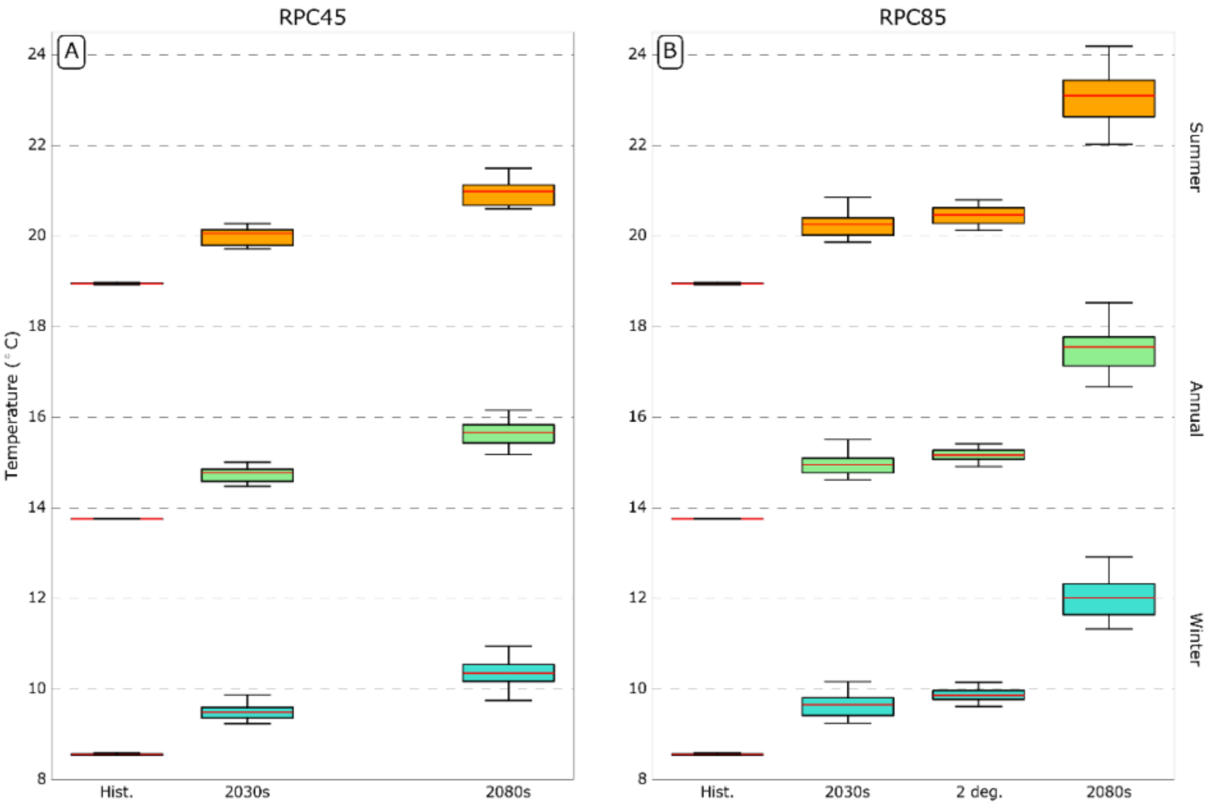


Figure 4.18: Mean annual temperature, mean summer temperature and mean winter temperature values for the Mediterranean climate domain, at current conditions, in 2030s and 2080s. The future temperatures are the result of the simulation of 11 different simulation, each with a different Regional Climate model (RCM). (JRC 2017)

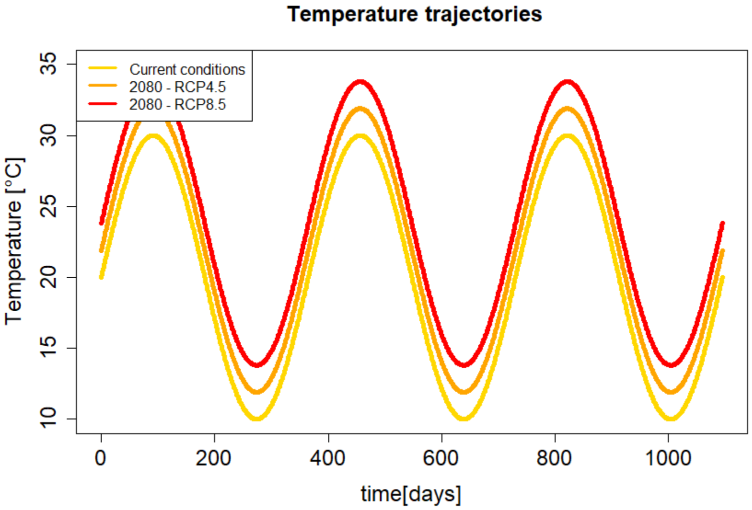


Figure 4.19: An ensemble of two synthetic trajectories generated via Additive Perturbation and current conditions, plotted on a three years interval.

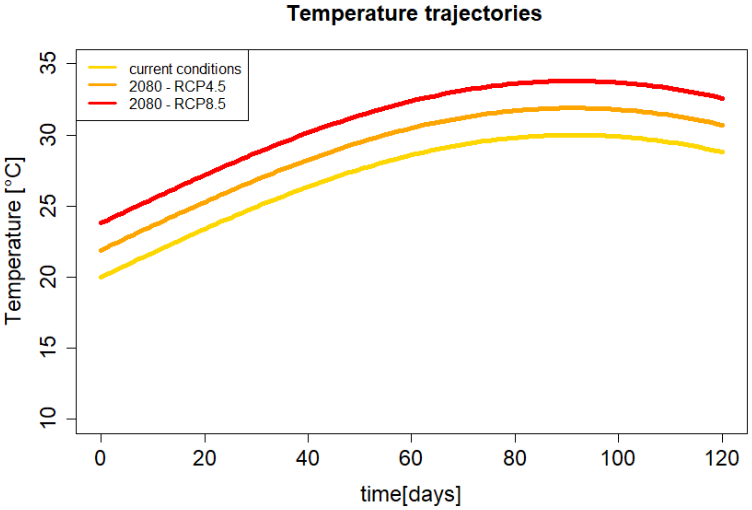


Figure 4.20: An ensemble of two synthetic trajectories generated via Additive Perturbation and current conditions, plotted for the cropping season (on a three months interval).

The system dynamics were then simulated for these two simplified temperature trajectories, and compared with the results of a simulation running under the current temperature conditions.

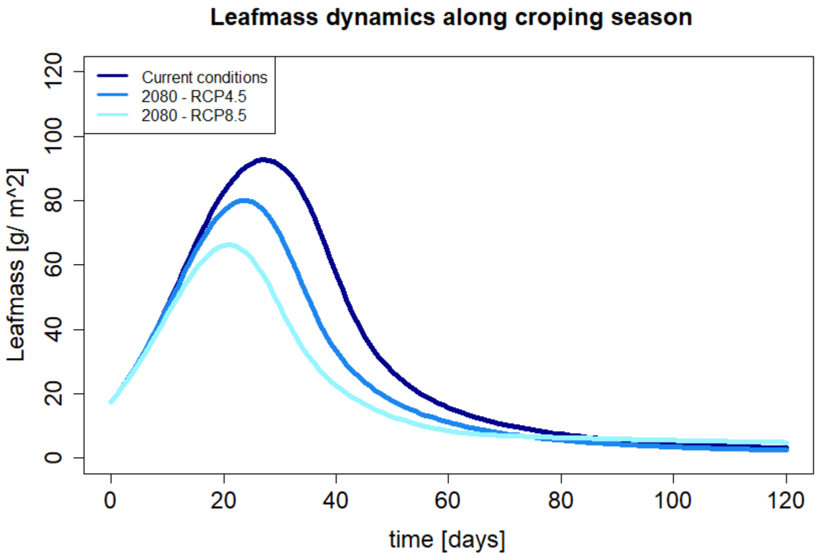


Figure 4.21: simulated leafmass dynamics along cropping season, in current condition, under RCP4.5 and under RCP8.5

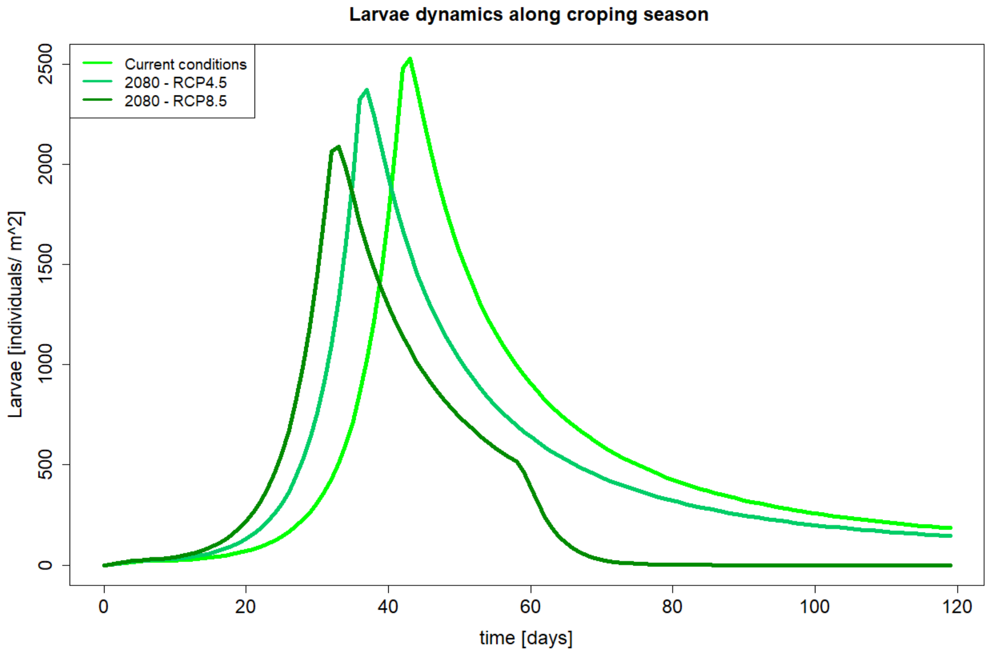


Figure 4.22: simulated larvae population dynamics along cropping season, in current condition, under RCP4.5 and under RCP8.5

Interestingly, climate change is expected to negatively affect *T. absoluta* in northern mediterranean areas: as can be observed in Figure 4.22, temperature increase is inversely proportional to the larvae population maximum. This results may appear in contrast with other studies (Martins et al. 2016), that recognize 30 °C as the optimal temperature for *T. absoluta*. Therefore, one could expect that temperature trajectories closer to 30 °C would imply higher pest densities, while the model simulation shows the exact opposite.

The reason behind this disagreement can be identified in the fact that the experiment led by Martins et al. is, once again, focused on the individual level : 20 eggs were laid on a tomato leaf, and the development times were observed, in an environment kept at constant temperature. This procedure was repeated for different values of temperature. This kind of experiment doesn't allow to capture the full effect of the interaction between plant and pest, of the "coupled dynamics". At higher temperatures, the pest will have a shorter development time and will be able to grow more rapidly, but this cause a earlier destruction of the tomato plant, thus putting a lower limit to the *T. absoluta* population growth.

Moreover, also the tomato plant will be affected negatively by higher temperature trajectories, that cause a reduction in its growth rate, thus providing a lower amount of resource for *T. absoluta*. For these reasons, even if 30 °C is the temperature that cause the shortest development time,it should not be addressed as the "optimal temperature" in a broad sense.

Chapter 5

Conclusions

5.1 What makes *T. absoluta* so devastating ?

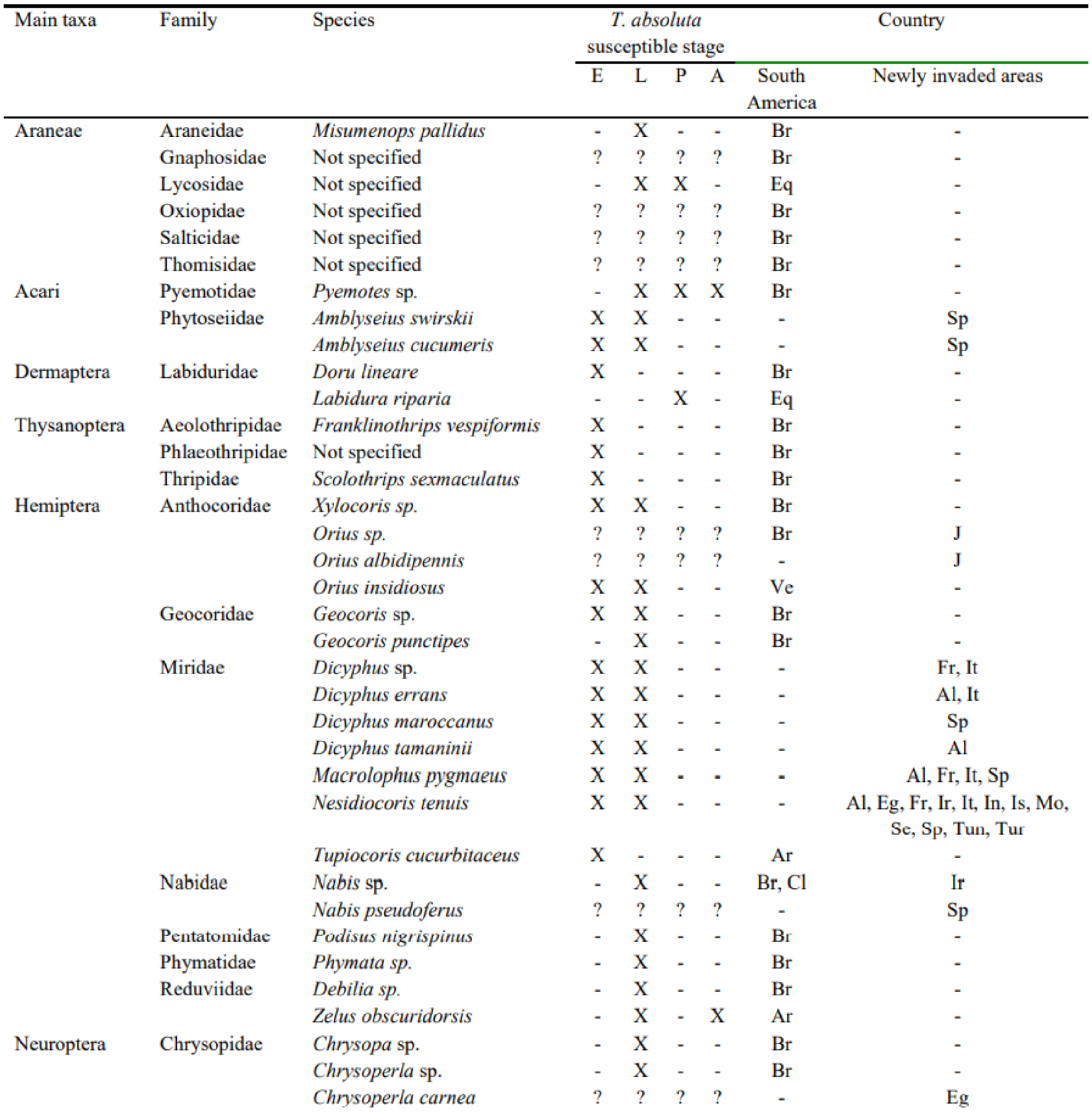
In a sense, the case of *T. absoluta* is not a typical, paradigmatic case of an IAS, *i.e.* a species that is damaging for the ecosystem because it finds himself interacting with species which did not co-evolve with it. *T. absoluta* it is surely an allochthonous species in the paleoartic region, but so is tomato: in fact, both species share the same native range. And yet, *T. absoluta* is known for destroying the crop and subsequently facing local extinction for lack for resource (Bompard et al. 2013). So, the key question is: how it's possible that two species, that presumably co-evolved, have such an ”unbalanced” and ”unregulated” interaction, that leads to the extinction of both the resource and the consumer ?

This question is linked to one of the key challenges of population ecology: the search for an explanation to the persistence of species. Some influential ecologists suggested that species extinction is (relatively) rare in nature because most populations are regulated at some spatial scale; Consequently, they define the study of population dynamics as the search for regulatory mechanisms and their effects (Murdoch, Briggs, and Nisbet 2003).

Within this context, the previous question could be rephrased as: What regulatory mechanisms have gone missing, moving from the original *T. absoluta* - wild tomato system in the native range to the *T. absoluta*- tomato crop system in the newly invaded regions?

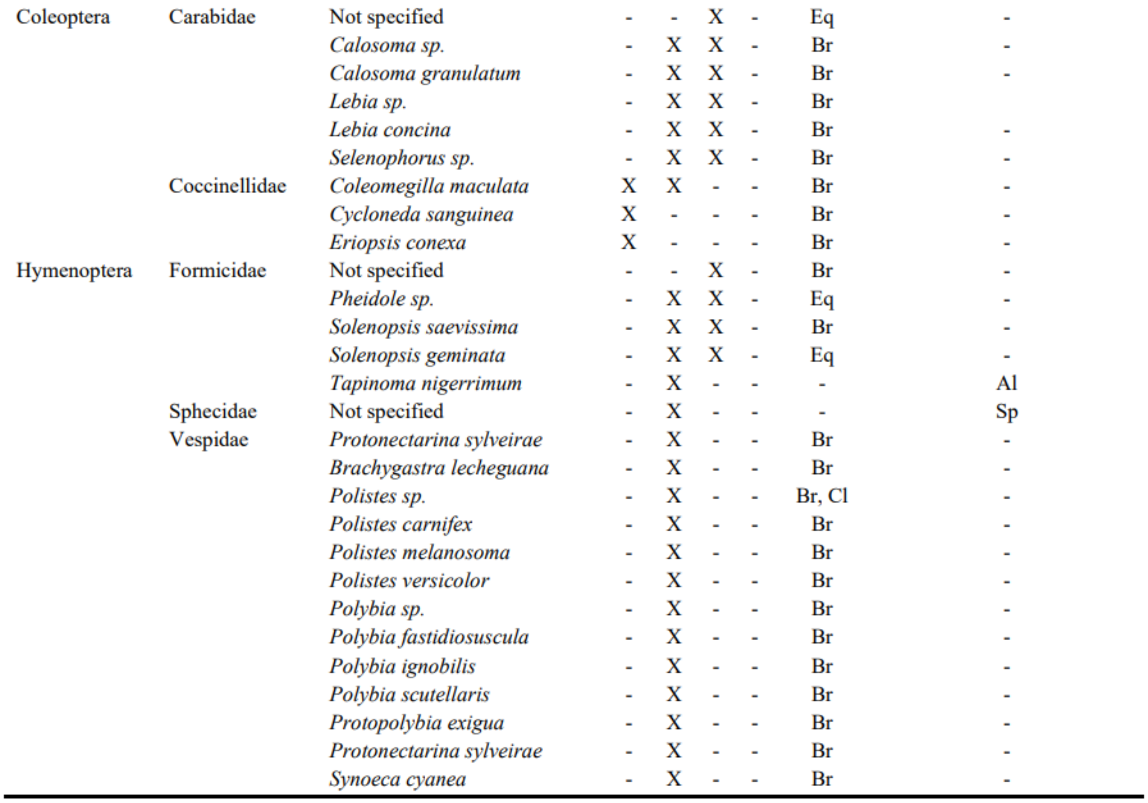
A study of this agronomic problem under a more ecology-based perspective may suggest three possible regulation mechanisms ,three possible explanations , for this phenomena:

- As presented in Figures 5.1 and 5.2 , In the newly invaded areas, there is a smaller number of predator and parasitoids, that cause an additional mortality in *T. absoluta* and can therefore exert an action of demographic regulation.



Main taxa	Family	Species	*T. absoluta* susceptible stage				Country	
			E	L	P	A	South America	Newly invaded areas
Araneae	Araneidae	*Misumenops pallidus*	-	X	-	-	Br	-
	Gnaphosidae	Not specified	?	?	?	?	Br	-
	Lycosidae	Not specified	-	X	X	-	Eq	-
	Oxiopidae	Not specified	?	?	?	?	Br	-
	Salticidae	Not specified	?	?	?	?	Br	-
	Thomisidae	Not specified	?	?	?	?	Br	-
Acari	Pyemotidae	*Pyemotes* sp.	-	X	X	X	Br	-
	Phytoseiidae	*Amblyseius swirskii*	X	X	-	-	-	Sp
		Amblyseius cucumeris	X	X	-	-	-	Sp
Dermaptera	Labiduridae	*Doru lineare*	X	-	-	-	Br	-
		Labidura riparia	-	-	X	-	Eq	-
Thysanoptera	Aeolothripidae	*Franklinothrips vespiformis*	X	-	-	-	Br	-
	Phlaeothripidae	Not specified	X	-	-	-	Br	-
	Thripidae	*Scolothrips sexmaculatus*	X	-	-	-	Br	-
Hemiptera	Anthocoridae	*Xylocoris sp.*	X	X	-	-	Br	-
		Orius sp.	?	?	?	?	Br	J
		Orius albidipennis	?	?	?	?	-	J
		Orius insidiosus	X	X	-	-	Ve	-
	Geocoridae	*Geocoris* sp.	X	X	-	-	Br	-
		Geocoris punctipes	-	X	-	-	Br	-
	Miridae	*Dicyphus* sp.	X	X	-	-	-	Fr, It
		Dicyphus errans	X	X	-	-	-	Al, It
		Dicyphus maroccanus	X	X	-	-	-	Sp
		Dicyphus tamaninii	X	X	-	-	-	Al
		Macrolophus pygmaeus	X	X	-	-	-	Al, Fr, It, Sp
		Nesidiocoris tenuis	X	X	-	-	-	Al, Eg, Fr, Ir, It, In, Is, Mo, Se, Sp, Tun, Tur
		Tupiocoris cucurbitaceus	X	-	-	-	Ar	-
	Nabidae	*Nabis* sp.	-	X	-	-	Br, Cl	Ir
		Nabis pseudoferus	?	?	?	?	-	Sp
	Pentatomidae	*Podisus nigrispinus*	-	X	-	-	Br	-
	Phymatidae	*Phymata sp.*	-	X	-	-	Br	-
	Reduviidae	*Debilia sp.*	-	X	-	-	Br	-
		Zelus obscuridorsis	-	X	-	X	Ar	-
Neuroptera	Chrysopidae	*Chrysopa* sp.	-	X	-	-	Br	-
		Chrysoperla sp.	-	X	-	-	Br	-
		Chrysoperla carnea	?	?	?	?	-	Eg

Figure 5.1: List of *T. absoluta* predators, recorded both in the Native areas and newly-invaded ones - part one. Source : Biondi, Guedes, et al. 2018



Coleoptera	Carabidae	Not specified	-	-	X	-	Eq	-
		Calosoma sp.	-	X	X	-	Br	-
		Calosoma granulatum	-	X	X	-	Br	-
		Lebia sp.	-	X	X	-	Br	
		Lebia concina	-	X	X	-	Br	-
		Selenophorus sp.	-	X	X	-	Br	-
	Coccinellidae	*Coleomegilla maculata*	X	X	-	-	Br	-
		Cycloneda sanguinea	X	-	-	-	Br	-
		Eriopsis conexa	X	-	-	-	Br	-
Hymenoptera	Formicidae	Not specified	-	-	X	-	Br	-
		Pheidole sp.	-	X	X	-	Eq	-
		Solenopsis saevissima	-	X	X	-	Br	-
		Solenopsis geminata	-	X	X	-	Eq	-
		Tapinoma nigerrimum	-	X	-	-	-	Al
	Sphecidae	Not specified	-	X	-	-	-	Sp
	Vespidae	*Protonectarina sylveirae*	-	X	-	-	Br	-
		Brachygastra lecheguana	-	X	-	-	Br	-
		Polistes sp.	-	X	-	-	Br, Cl	-
		Polistes carnifex	-	X	-	-	Br	-
		Polistes melanosoma	-	X	-	-	Br	-
		Polistes versicolor	-	X	-	-	Br	-
		Polybia sp.	-	X	-	-	Br	-
		Polybia fastidiosuscula	-	X	-	-	Br	-
		Polybia ignobilis	-	X	-	-	Br	-
		Polybia scutellaris	-	X	-	-	Br	-
		Protopolybia exigua	-	X	-	-	Br	-
		Protonectarina sylveirae	-	X	-	-	Br	-
		Synoeca cyanea	-	X	-	-	Br	-

Figure 5.2: List of *T. absoluta* predators, recorded both in the Native areas and newly-invaded ones - part two. Source : Biondi, Guedes, et al. 2018

- The sensitivity analysis reported in Figures 4.9,4.10 showed that the shorter pest development times lead to infestations of higher magnitude. An artificially irrigated and fertilized tomato crop has a nutritious value for the larvae much higher than the one that presumably characterize the wild tomato varieties,that face intraspecific and interspecific competition for a finite amount of abiotic resources. As reported in Figure 4.2, and assessed in recent studies (Coqueret et al. 2017) this brings to a shortening of the larval development time, thus causing a considerable effect in the *T. absoluta* population increase.

- Since current tomato cultivars are derived from original wild varieties, it's possible that this selection process brought to plants characterized by a less abundant fruit production, in exchange for lower defense abilities against pest. This is also hinted by the fact that *T. absoluta* immature stages have a lower mortality when feeding on *S. lycopersicum* than on any other Solanum plant, as shown in Figure 5.3.

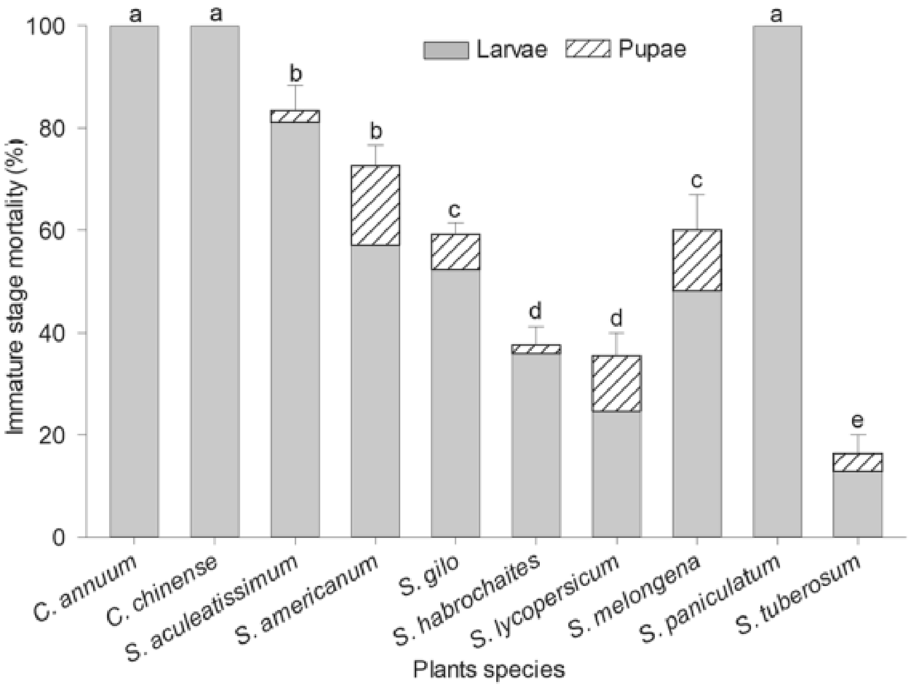


Figure 5.3: Larvae and pupae mortality on different plants belonging to the Solanum genus source: Silva et al. 2021

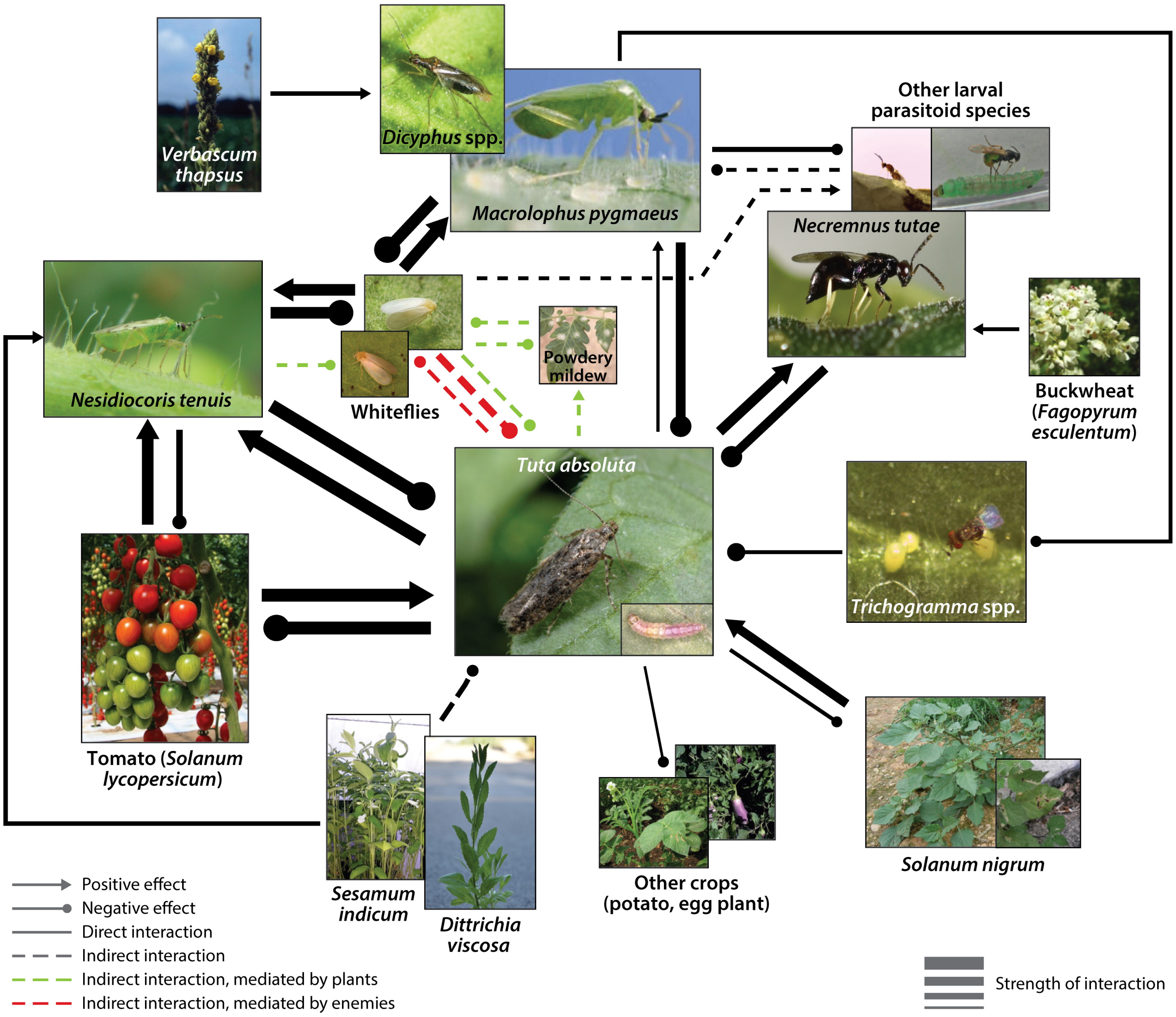
The model's simulation seems to confirm the first two hypothesis: as can be seen in Figure 4.11, at each considered temperature, the infestation magnitude is considerably lowered by bio-control (that introduces an additional mortality factor) and by a reduction of the water and fertilizers input to the plant (that slows down the insect development time). This analysis straightens the the findings of previous studies, that have highlighted potential for reducing fertilizers and water inputs in greenhouse productions (Bot and Adamowicz 2005). This hints at the existence of a a win–win situation, where a strengthening in pest management is achieved by reducing resource input for cultivation, with all the consequent ecological and economic benefits.

5.2 Further developement

The quality of the presented model is unavoidably constrained by the lack of knowledge about the system: much more experiments and field data are needed to create more detailed, reliable and effective models. Moreover, considering a system only formed by three species(one crop, one pest and one predator) implies a strong simplification. In fact, these three species are part of an Agro-Ecosystem, whose biological community is formed by crops, wild plants and dozens (if not hundreds) of other animal species. Some of the Biotic interactions concerning *T. absoluta* and the tomato plant are reported in Fig. 5.4. Neglecting the vast majority of these interaction and inter dependencies may result in an excessive simplification, that could not enable the model to effectively reach its purpose.

Another source of approximation can be found within the defined harvest indicator : As already presented in paragraph 3.2, the value of leaf mass at the end of the cropping season is chosen as a proxy of the final harvest. This is a strong assumption, as no actual relationship between leaf area and tomato harvest was found in scientific literature.

For all these reason, the present model should be perceived as a starting point, or starting framework, to be developed according to future experimental findings. Nevertheless, the obtained results are promising, as they hint at the presence of a possible trade off between crop harvest and pest management.



Biondi A, et al. 2018.
Annu. Rev. Entomol. 63:239–58

Figure 5.4:

Biotic interaction between *T. absoluta* and other species present in the agro-ecosystem. Lines with circles represent negative effects in the direction of the circles, lines with arrows represents positive interaction in the direction of the arrow. Continuous lines represent direct interactions, while dashed lines represent interactions mediated by another species. Lines thickness is proportional to the strength of the interaction. from (Biondi, Guedes, et al. 2018)

5.2.1 Simulating a possible outcome of *Wolbachia* infection

A simple,flexible yet process-based model can be useful also for a " perspective study", regarding one aspect that is quite neglected but could have significant implications : the infection of a *T. absoluta* population by *Wolbachia* bacteria. *Wolbachia* is one of the most diffused reproductive parasites worldwide, and it is thought to infect approximately 16 % of neotropical insects. This bacteria can indice profound alteration in the reproductive capabilities of their host, and four different phenotypes have been recorded: male killing, feminization, parthenogenesis and Cytoplasmic incompatibility (Werren, Baldo, and Clark 2008).

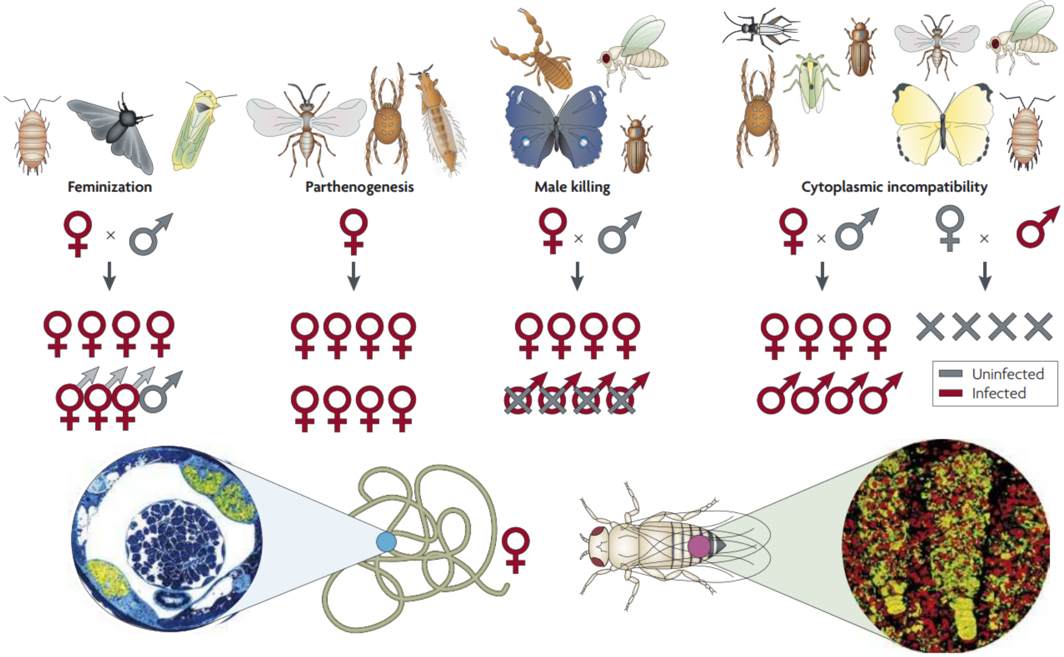


Figure 5.5: *Wolbachia*-induced phenotypes, figure taken from (Werren, Baldo, and Clark 2008)

Feminization results in genetic males that develop as females (in the Hemiptera, Isopoda and Lepidoptera orders), parthenogenesis induction eliminates males from reproduction (in the Acari, Hymenoptera and Thysanoptera orders), Male killing eliminates infected males to the advantage of surviving infected female siblings (in the Coleoptera, Diptera, Lepidoptera and Pseudoscorpiones orders) and cytoplasmic incompatibility prevents infected males from successfully mating with females that lack the same *Wolbachia* types (in the Acari, Coleoptera, Diptera, Hemiptera, Hymenoptera, Isopoda, Lepidoptera and Orthoptera orders)

As reported by (Caparros Megido, Haubruge, and Verheggen 2012), there are evidences that strains of *Wolbachia* bacteria infected some *T. absoluta* population in the mediterranean basin, inducing deuteroky parthenogenesis. It is particularly interesting to underline that this phenomena is a consequence of the accidental introduction of *T. absoluta* in Europe, as it has never been observed in the native range (Biondi, Guedes, et al. 2018)

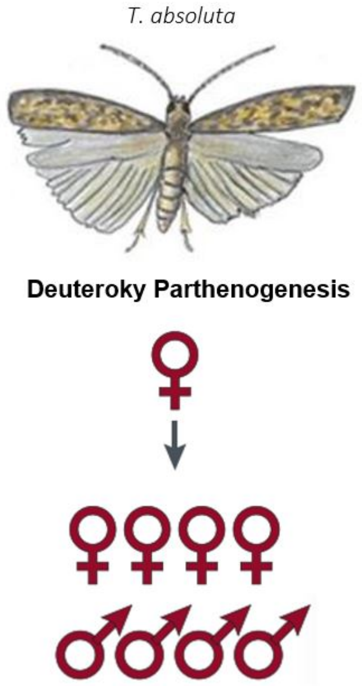


Figure 5.6: *T. absoluta* can exhibit deuteroky parthenogenesis when infected by *Wolbachia*

Among Lepidoptera, the wolbachia induced phenotype emerges as a result of the interaction between a particular species and a particular wolbachia strain; a single *Wolbachia* strain can infect multiple species, and cause a different phenotype in each of them (Fujii et al. 2001).

A *Wolbachia* - induced increase in the female/male ratio reduces (or deletes) the efficacy of pheromone-based control practices, since these targets only males. Beside this, *Wolbachia* infection can be concerning for another reason: thelithoky parthenogenesis (where only female offspring is generated) or the combination of deuteroky parthenogenesis and adult feminization has non-trivial effects on the population dynamics, because it has the effect of significantly increasing the daily fertility rate ϕ. An appropriate simulation highlighted how these increase in the fertility contributes in making the pest even more destructive, as can be seen in Figure 5.7. The fact that even a low increase in the level of *T. absoluta* fertility implies strong reduction in the harvest can also be seen in the results of the sensitivity analysis.

This suggest that the utmost attention should be payed in monitoring the evolution of *Wolbachia* infections on *T. absoluta*.

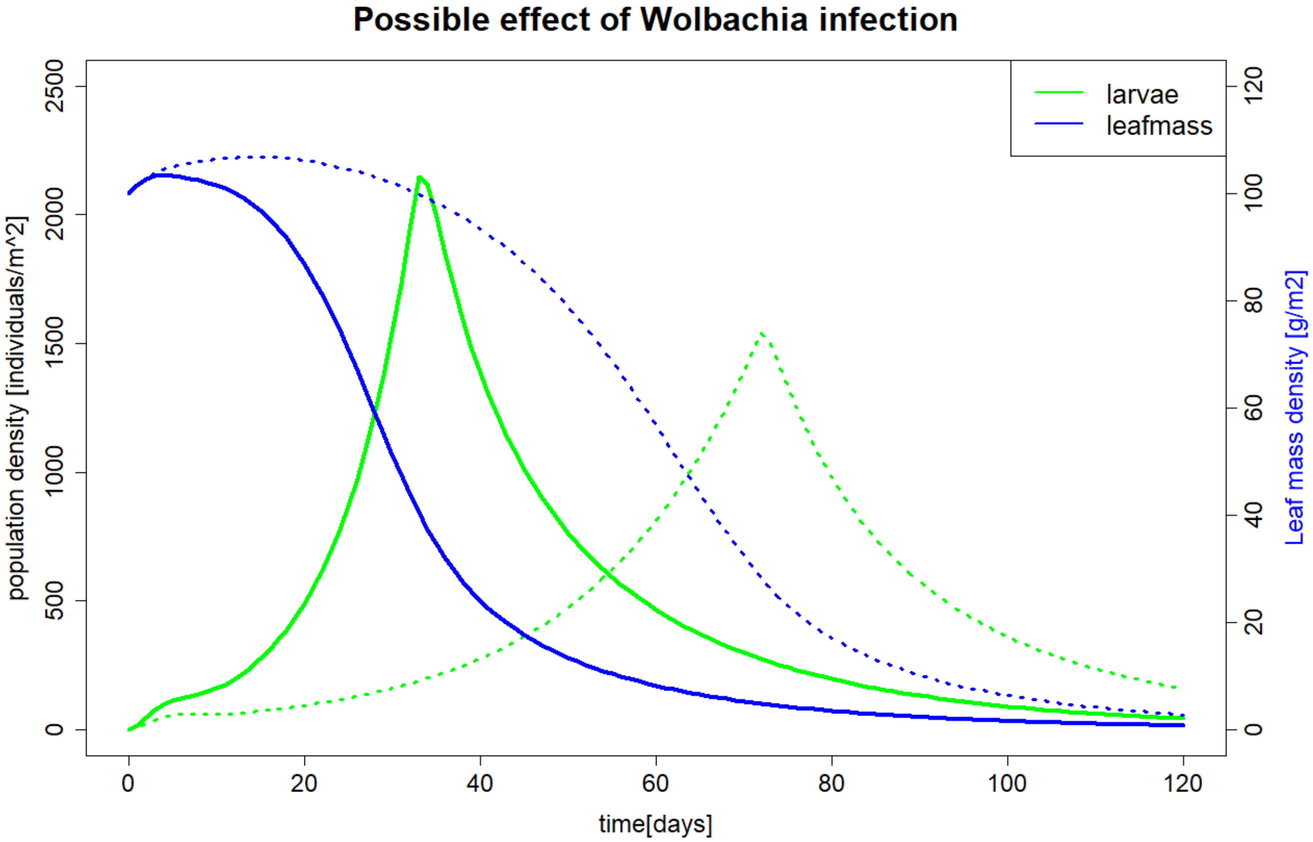


Figure 5.7: The possible effects of a *Wolbachia*-infected population on larvae and leafmass dynamics(in continuous line) compared with the situation without *Wolbachia* (dashed line)

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