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An eco-physiological model coupling plant growth and aphid population dynamics

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Abstract

Aphids alter plant development and can transmit viruses, thus representing a major threat for crops. Aphids may be controlled through cultural practices, however classical agronomic and ecological models are not suitable to explore their effects on plant pest interaction. Generally, the former do not explicitly consider the dynamics of pest, the latter have a too simplistic representation of the plant. In the present work, we extended a classical plant growth model, describing carbon and nitrogen assimilation and allocation, by integrating the population dynamics of an aphid population and the development of plant defences. We calibrate the model against data of peach *Prunus persica* subjected to different fertilization and irrigation regimes, infested by the aphid *Myzus persicae*. Our results suggest that aphid infestation induces the plant to produce defensive compounds that impair aphid ingestion and fecundity. Our model, parametrized for the peach-green aphid system, shows that all these apparently contrasting empirical evidences can emerge from

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the same biological principles governing plant-pest dynamics and that both plant vigour and plant stress hypotheses can find support when observing a plant-pest system.

Introduction

Aphids are specialized herbivores that feed on the phloem of vascular plants. They are responsible for the depletion of the plant's yield, which affects plant growth and reproduction and eventually impacts crop production (Goggin, 2007; Zvereva et al., 2010). Moreover, aphids can transmit viruses with detrimental effects on the plant and on the yield (Zust and Agrawal, 2016). In agriculture, aphids control mostly relies on the use of chemical pesticides with inherent environmental costs and whose efficacy decays in time due to the emergence of resistant strains (Matson et al., 1997).

In the last decades, **agroecology** developed as discipline to provide alternatives to the use of chemicals in agronomy. The rationale is that ecological concepts and principles can be applied to control pest populations while reducing the use of pesticides (Gliessman, 2007). The concept of **"bottom-up" control**, on the basis of which population dynamics are driven by resources quantity and quality, is particularly interesting in agroecology. In fact, there exist a number of agricultural practices that can affect plant physiology and alter the level of resource offered by plants to pests (Gonthier et al., 2013; Kytö et al., 1996; Awmack and Leather, 2002; Coley and Bryant, 1985). For example, fertilization modifies nutrient balance in plants, enhancing plant tissue nutritional status, and influences the synthesis of defences

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compounds (Awmack and Leather, 2002; Sauge et al., 2010). Similarly, irrigation controls plant vigour, phloem nutritional quality and viscosity, possibly regulating aphid abundance (Sevanto, 2014; Girousse et al., 1996). However, the way a pest is affected by the plant status is not obvious and empirical evidences provided support to different hypotheses. On the one hand, the **Plant Vigour Hypothesis** PVH (Price, 1991) argues that pest populations increase on vigorously growing plants (or organs), hence providing more resources for the pest. In support to this hypotheses, some authors observed that practices such as fertilization and irrigation, or favourable conditions for plant growth as organic soil fertility, were associated to abundant pest populations (Inbar et al., 2001; Huberty and Denno, 2006; Tamburini et al., 2018; Rousselin et al., 2016). On the other hand, the **Plant Stress Hypothesis** PSH (White, 1984) argues that pests better perform on stressed plants that would not have resources to deploy defences and whose nutritional quality might be enhanced in certain stressful conditions. This is the case for some aphid species feeding on plants subjected to controlled irrigation deficit (Tariq et al., 2012; Oswald and Brewer, 1997). In order to efficiently use the concepts of bottom-up control in agroecology, it is necessary to shed light on the mechanisms that are responsible for the observed patterns and ideally derive a **unified conceptual framework keeping together the different hypotheses**. This should imply both **field experiments** and mathematical modelling. The first are necessary to test the validity of theoretical hypotheses, but they can be extremely costly and time consuming. The latter, particularly **mechanistic models**, represent a useful tool to investigate which processes can be responsible of the observed patterns and

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to explore the consequences of different agricultural practices (Thornley and Johnson, 1990).

Modelling approaches commonly used **in agronomy** empirically parametrize in the plant vital rates the detrimental effect of pests and they neglect the dynamical interaction between the plant (or some of its component parts) and the pest (see Aggarwal et al., 2006; Willocquet et al., 2008; Dietze and Matthes, 2014). That is, the impact of a pest on the plant is modelled by varying one or more plant parameters, according to the pest disturbance level. For instance, the presence of a defoliator herbivore have been modelled through a reduction in the net growth rate of the leaves; while the presence of a root rot have been modelled through an increase of root turnover rate (Dietze and Matthes, 2014). On the other hand, **in ecology**, a broad literature of models on interactions (e.g. predation, consumption, competition etc.) between different species exists. These models have been widely used to study temporal and spatial dynamics also in plant-pest systems (see Bewick et al., 2016; Levins and Schultz, 1996; Lebon et al., 2014), yet they usually present a simplistic description of the plant, that limits the possibility to consider the effects of agronomic practices.

With the aim to **bridge the gap** between the classical agronomic and the ecological modelling approach, here we couple a plant growth model, that describes carbon and nitrogen assimilation and allocation to shoot and root compartments of a plant, with an aphid population model. With regard to **the plant**, we use the modelling framework proposed by Thornley in the early 70s (Thornley, 1972b,a), and refined in the following decades (Reynolds and Thornley, 1982; Thornley, 1996, 1998; Thornley and Cannel,

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2000), which represents a cornerstone in plant and crop modelling (Thornley and Johnson, 1990). With regard to **the aphid**, we propose a population model with scramble competition where birth and mortality rates depend on the pest per-capita resource availability and quality. Moreover, we assume that the presence of the aphid can induce the plant to produce **defensive compounds** intended to decrease the aphid feeding and/or birth rate.

We **demonstrate the model** by applying it to a peach *Prunus persica* - green aphid *Myzus persicae* system, we **calibrate** model parameters and select model assumptions against field data obtained under different conditions of irrigation and fertilization. The resulting model has the ability to reproduce different system properties observed in field studies and provides insights to conceive new experiments and rethink the control of plant-aphid systems.

The model

Model outline and assumptions

The model, which describes the temporal variation, during a growing season, of plant dry mass (partitioned into shoots and roots, in turn composed by structural dry mass, carbon and nitrogen substrates), its defensive compounds and the aphid population dwelling on the plant is schematically represented in Fig.1

According to **Thornely et al's** seminal works (Thornley, 1972a; Thornley and Johnson, 1990; Thornley, 1998, 1996), carbon is assimilated from

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the atmosphere via photosynthesis and stored in shoots, as **shoot carbon substrate ($\mathbf{C_S}$)**, or transported and then stored in roots as **root carbon substrate ($\mathbf{C_R}$)**. Similarly, nitrogen is assimilated from the soil, stored in roots as **root nitrogen substrate ($\mathbf{N_R}$)**, or transported and then stored in shoots as **shoot nitrogen substrate ($\mathbf{N_S}$)**. Carbon and nitrogen substrates are utilized, in a fixed ratio, to constitute **structural shoot (S) and root (R) dry mass**. The assimilation of substrate (C_S or N_R) per unit of plant organ (S or R) decreases with organ mass due to shoot self-shading and root competition for nitrogen and it is inhibited by substrate concentration in the organ (Thornley, 1998).

We coupled the model of carbon and nitrogen assimilation and partitioning in a plant with an aphid population model by assuming that **aphids**, which penetrate growing shoots of the host plant with a stylet and feed on the phloem (Zust and Agrawal, 2016), **intercept** a fraction of the substrates ($\mathrm{C_S}$ and $\mathrm{N_S}$) directed towards the shoot structural mass compartment (S) to support their growth (Goggin, 2007). We assume that aphids act in a **scramble competition** context (Dixon, 1998) and therefore any aphid ingests its maximum daily amount of food when the per-capita available resource is enough, otherwise the available resource is evenly shared among all the individuals. The intrinsic aphid **birth rate** depends on the per-capita ingested food (Dixon, 1985) while the **mortality rate** is constant (Müller et al., 2001). Eventually, crowding can induce aphids to leave the system (Müller et al., 2001).

We assume that the plant can be induced by the aphid presence to produce **defensive compounds** which can reduce aphid **accessibility** to the

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resource (e.g. by phloem sealing) (Medina-Ortega and Walker, 2013; Will et al., 2013; van Velzen and Etienne, 2015) and/or decrease aphid **reproduction** rate (e.g. by release toxic components in the sieve) (Lebon et al., 2014; Zust and Agrawal, 2016). The plant is assumed to implement both carbon (*e.g.* terpenes, phenolics) and nitrogen (*e.g.* alkaloids, non-protein amino acids, cyanogenic compounds, proteinase inhibitors) based defences (Herms and Mattson, 1992), with the latter being more effective (Schoonhoven et al., 2005). In fact, after having detected aphids saliva, plants can produce defensive compounds from the same substrates used for growth (Herms and Mattson, 1992; Will et al., 2013; Lebon et al., 2014; Zust and Agrawal, 2016).

Model equations

In quantitative terms, we describe the temporal variation of the eight variables composing the plant-aphid system with the following system of ordinary differential equations.

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$$
\begin{cases}
\dot{C}_S = \sigma_{\mathrm{C}} S[(1+\frac{S}{\nu})(1+\frac{C_S}{S\iota_{\mathrm{C}}})]^{-1} - \varphi_{\mathrm{C}}\kappa\frac{C_S}{S}\frac{N_S}{S}S - (\frac{C_S}{S}-\frac{C_R}{R})(SR)^q\cdot(S^q+R^q)^{-1} - \alpha\frac{C_S}{S}A & (1a)\\
\dot{N}_S = (\frac{N_R}{R}-\frac{N_S}{S})(SR)^q\cdot(S^q+R^q)^{-1} - \varphi_{\mathrm{N}}\kappa\frac{C_S}{S}\frac{N_S}{S}S - \alpha\frac{N_S}{S}A & (1b)\\
\dot{S} = \begin{cases} \Phi\kappa\frac{C_S}{S}\frac{N_S}{S}S(1-\frac{\theta_{max}A}{\Phi\kappa\frac{C_S}{S}\frac{N_S}{S}S}) & \text{if } \theta_{max}\cdot A \leq \Phi\kappa\frac{C_S}{S}\frac{N_S}{S}S\frac{\beta\pi_1^{\delta_1}}{\pi_1^{\delta_1}+(\frac{D}{S})^{\delta_1}}\\ \Phi\kappa\frac{C_S}{S}\frac{N_S}{S}S(1-\frac{\beta\pi_1^{\delta_1}}{\pi_1^{\delta_1}+(\frac{D}{S})^{\delta_1}}) & \text{otherwise}\end{cases} & (1c)\\
\dot{C}_R = (\frac{C_S}{S}-\frac{C_R}{R})(SR)^q\cdot(S^q+R^q)^{-1} - \varphi_{\mathrm{C}}\kappa\frac{C_R}{R}\frac{N_R}{R}R & (1d)\\
\dot{N}_R = \sigma_{\mathrm{N}} R[(1+\frac{R}{\nu})(1+\frac{N_R}{R\iota_{\mathrm{N}}})]^{-1} - \varphi_{\mathrm{N}}\kappa\frac{C_S}{S}\frac{N_S}{S}S - (\frac{N_R}{R}-\frac{N_S}{S})(SR)^q(S^q+R^q)^{-1} & (1e)\\
\dot{R} = \Phi\kappa\frac{C_R}{R}\frac{N_R}{R}R & (1f)\\
\dot{D} = (\varepsilon_{\mathrm{C}}\alpha\frac{C_S}{S} + \varepsilon_{\mathrm{N}}\alpha\frac{N_S}{S})A & (1g)\\
\dot{A} = \begin{cases} (\xi\theta_{max}(1-(\delta_2\frac{D}{S})^{\pi_2}) - \mu - \omega\frac{A}{S})A & \text{if } \theta_{max}\cdot A \leq \Phi\kappa\frac{C_S}{S}\frac{N_S}{S}S\frac{\beta\pi_1^{\delta_1}}{\pi_1^{\delta_1}+(\frac{D}{S})^{\delta_1}}\\ (\xi\Phi\kappa\frac{C_S}{S}\frac{N_S}{S}S\frac{\beta\pi_1^{\delta_1}}{\pi_1^{\delta_1}+(\frac{D}{S})^{\delta_1}}\frac{1}{A}(1-(\delta_2\frac{D}{S})^{\pi_2}) - \mu - \omega\frac{A}{S})A & \text{otherwhise}\end{cases} & (1h)
\end{cases}
\tag{1}
$$

where C_S, N_S, S, C_R,N_R and R are expressed in grams (g); D is expressed in an arbitrary defence unit (DU) and A in individuals (ind.); t represents the number of days (d) that have passed since the 1st of January of the year of the considered growing season; $\Phi = \frac{\lambda^\eta}{\lambda^\eta + t^\eta}$ is a **time variant parameter** that we introduced to simulate the fact that perennial plants in temperate regions address substrates to reserves rather than to vegetative growth at the end of the growing season, when the day length starts decreasing (Heide, 2008; Petterle et al., 2013).

In **equation 1a**, $\sigma_{\mathrm{C}} S[(1+\frac{S}{\nu})(1+\frac{C_S}{S\iota_{\mathrm{C}}})]^{-1}$ is the **carbon substrate assimilated in shoots**, $\varphi_{\mathrm{C}}\kappa\frac{C_S}{S}\frac{N_S}{S}S$ is the shoot carbon substrate **allocated** to shoot growth or reserves, $(\frac{C_S}{S}-\frac{C_R}{R})(SR)^q\cdot(S^q+R^q)^{-1}$ is the shoot carbon substrate **transported** toward roots and $\alpha\frac{C_S}{S}A$ is the shoot carbon substrate

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diverted to defensive compounds, in a unit of time.

In **equation 1b**, $(\frac{N_R}{R} - \frac{N_S}{S})(SR)^q \cdot (S^q + R^q)^{-1}$ is the nitrogen substrate transported from roots towards shoots; $\varphi_{\mathrm{N}}\kappa\frac{C_S}{S}\frac{N_S}{S}S$ is the shoot nitrogen substrate allocated to shoot growth or reserves, and $\alpha\frac{N_S}{S}A$ is the shoot nitrogen substrate diverted to defensive compounds, in a unit of time.

In **equation 1c**, $\Phi\kappa\frac{C_S}{S}\frac{N_S}{S}S$ is the increase in structural shoot dry mass in the absence of any phloem withdrawal by the aphids. The term $\theta_{max}A$ (or $\Phi\kappa\frac{C_S}{S}\frac{N_S}{S}S\frac{\beta\pi_1^{\delta_1}}{\pi_1^{\delta_1}+(\frac{D}{S})^{\delta_1}}$) represents the amount of phloem diverted from allocation to plant growth because ingested by aphids. By definition, it cannot exceed the mass increase that would have occurred in absence of aphids (i.e. for $A = 0$) and it is a function of i) the maximum aphid ingestion capacity θ_{max}, ii) the flux of substrates that the plant allocates to shoot growth $\Phi\kappa\frac{C_S}{S}\frac{N_S}{S}S$ and iii) the concentration of defensive compounds in the shoots $\frac{D}{S}$. The term $\frac{\beta\pi_1^{\delta_1}}{\pi_1^{\delta_1}+(\frac{D}{S})^{\delta_1}}$ is the fraction of substrates allocated to shoot growth that can be intercepted by the aphids that is assumed to possibly decrease with the concentration of defensive compounds $\frac{D}{S}$.

The dynamics of the variables in the root compartments (C_R, N_R, R) follow similar rules for substrates assimilation, transport and allocation to root growth and we assumed that they are not directly affected by the presence of aphids.

In **equation 1h**, we assume that the aphid birth rate is proportional to the per-capita ingested resource mass and that it can decrease, even attaining negative values if the defensive compounds turn to be lethal to the aphid, due to a possible chemical action of the defensive compounds. The parameter ω indicated the aphid sensitivity to crowding and hence their migration rate

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induced by crowding.

Details on the model variables and parameters are reported in Table 1.

Material and Methods

Study case and available data

We apply the model to the peach-green aphid system. **Peach** is a cultivar of economic importance over all temperate regions (FAO, 2016) whose growth (and fruit production) has been extensively modelled in the last decades (Grossman and DeJong, 1994; Lescourret et al., 1998) and the **green aphid** is a main pest of fruit crops, it is responsible for decreased plant growth (Bevacqua et al., 2016) and transmission of lethal viruses (e.g. Plum Pox Virus) causing up to 100% of yield losses (Rimbaud et al., 2015). Observed data come from a **greenhouse experiment** where 44 peach plants were subjected to different levels of fertilization and irrigation and infested by green aphids. The plant growth and the abundance of the resident aphid population was then weekly recorded on every plant from the beginning of May to beginning of July corresponding to the end of the plant growing season. Details on the experiment are reported in Rousselin et al. (2016) and in the Supplementary Information (**SI.1**).

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Model calibration and selection

Model calibration

According to the available data, we set **initial conditions** of the system at the first observation date (i.e. May 6th, 126th day of the year 2013) (see Supplementary Information **SI.2**).

We set the value of model **parameters** according to information available from **peer-reviewed literature** whenever possible (See Table 1). On the other hand, **no information** was available to *a priori* derive reliable estimates for parameters σ_{N} (net N assimilation rate) and k (allocation of substrates to plant growth), which depend on environmental conditions that were varied in the considered experiment; parameter q, affecting substrates transport within the plant and depending on the plant architecture (Thornley, 1998), and five parameters relevant to the production of defensive compounds (*i.e.* α) and their efficacy ($\pi_1, \delta_1, \pi_2, \delta_2$). We estimated these unknown parameters by minimizing a **cost function** L expressed as the sum of two negative log-likelihood functions, computed with respect to observations of shoot dry mass and all aphids abundance:

$$\begin{cases} L = -(ln(L_y) + ln(L_x)) & (2a) \\ ln(L_y) = -N_y ln(\sqrt{2\pi {\sigma_y}^2}) - \frac{1}{2{\sigma_y}^2} \sum_{P=1}^{P=n_P} \sum_{i=1}^{n_i} (y_{i,P} - \hat{y_i})^2 & (2b) \\ ln(L_x) = -N_x ln(\sqrt{2\pi {\sigma_x}^2}) - \frac{1}{2{\sigma_x}^2} \sum_{P=1}^{P=n_P} \sum_{j=1}^{n_j} (x_{j,P} - \hat{x_j})^2 & (2c) \end{cases} \tag{2}$$

Where $y_{i,P}$ and $x_{j,P}$ are the values of the variables y and x observed on

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the plant P at time i and j, respectively (total samples size equal to N_y and N_x, respectively), $\hat{y}_i$ and $\hat{x}_j$ are the corresponding values simulated by the model. We assumed that the errors between each observation and the corresponding value estimated by the model follow a Gaussian distribution with mean 0 and unknown variance ${\sigma_y}^2$ or ${\sigma_x}^2$. To derive the log-likelihood functions, we assumed that the error structure is additive. This is equivalent to pay attention to errors at bigger values of the variable which makes sense for agronomic applications. In our case, y is the average shoot dry mass of a plant and x is the average aphid abundance per shoot. Minimization of the of the cost function was performed using the Matlab function "fminsearch" (Nelder-Mead algorithm).

We assessed the empirical **probability distributions** of calibrated parameters by making use of the moving block bootstrap, recommended to reconstruct time series of the observed variables (Kreiss and Lahiri, 2012). Namely, we reconstructed bootstrapped time series for each of the observed variable and we assessed the values of the unknown parameters. We repeated this process 1,000 times and we generated the 90% confidence intervals for each parameter via the percentile methods (Efron, 1979).

We examined the **sensitivity** of the predicted shoot production and aphid population peak to variation in model parameter estimates by varying each model parameter within the 90% confidence interval (CI) of its estimate (Table 1).

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Model selection

The way a plant reacts to aphid infestation and the effect that such a reaction has on the aphid performance is likely to vary with plant and aphid species (Zust and Agrawal, 2016). In a given plant-aphid system, the plant can be induced to produce defences compounds or not. Also, defences compounds might affect the feeding rate of the aphid, its birth rate or have no effect (Herms and Mattson, 1992; Royer et al., 2013; Zust and Agrawal, 2017). To account for possible different **mechanisms regarding the plant reaction to infestation and the effect of defensive compounds**, we contrasted a **full version of the model** with a set of reduced models with less parameters. Namely, the full model considers that the plant diverts substrates from growth toward defences ($\alpha \neq 0$) which reduce both aphid ingestion ($\delta_1 \neq 0$, $\beta = 1$) and birth ($\delta_2 \neq 0$) rate. Three **reduced models** consider defences production ($\alpha \neq 0$), but with different consequences on the aphid i.e. no effect ($\delta_1 = 0$, $\beta = 2$ and $\delta_2 = 0$), reduction of the aphid ingestion rate ($\delta_1 \neq 0$, $\beta = 1$ and $\delta_2 = 0$), reduction of the aphid birth rate ($\delta_1 = 0$, $\beta = 2$ and $\delta_2 \neq 1$). Eventually, the most reduced model does not consider the production and therefore the presence of defences in the system ($\alpha = 0$).

Although some authors suggest that crowding might induce aphid to abandon the host plant, there is no unanimous consensus (Müller et al., 2001). Thus, we also tested if **crowding** promotes ($\omega \neq 0$) or not ($\omega = 0$) aphid migration from the plant.

Also, we tested if the effect of **irrigation and fertilization** can be represented in the model thorough a variation in those parameters representing

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allocation of substrates to plant growth k, which is expected to increase with irrigation (Muller et al., 2011; Sevanto, 2014), and nitrogen assimilation rate σ_{N}, which is expected to increase with fertilization (Connor et al., 2011; Thornley and Parsons, 2014). We then contrasted different versions of each model assuming that *i)* κ and σ_{N} respectively vary with irrigation and fertilization treatments; *ii)* κ varies with irrigation and σ_{N} does not vary with fertilization; *iii)* κ does not vary with irrigation and σ_{N} varies with fertilization; *iv)* neither σ_{N} nor κ vary with fertilization and irrigation. Therefore, we calibrated two values for nitrogen assimilation rate per unit of root (σ_{N}^{+}, σ_{N}^{-}) in cases *i* and *iii* and a unique value ($\sigma_{\mathrm{N}}^{\pm}$) in cases *ii* and *iv*. Analogously, we calibrated two values for the allocation of substrates to plant growth (κ^{+} and κ^{-}) in cases *i* and *ii* and a unique value ($\kappa^{\pm}$) in cases *iii* and *iv*.

Overall, we compared 40 different models, obtained by incorporating five hypotheses on plant defences, two hypotheses on aphids migration, and four hypotheses on the effect of irrigation and fertilization, to one another by evaluating the relative support in the observed data for each model. We selected the best model as the one that assured the best compromise between goodness of fit (estimated by the sum of the negative log-likelihood functions L, eq. 2), and parsimony (estimated by the number of calibrated parameters n_p), according to Akaike information criterion (Akaike, 1974):

$$AIC = 2L + 2n_p \tag{3}$$

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The role played by fertilization and irrigation

After having ascertained that parameters σ_{N} and k are likely to vary with fertilization and irrigation practices, respectively, we used the selected model to **simulate the temporal dynamics** of the system for different values of these parameters and to perform an ***in silico*** experiment to verify if the model was able to reproduce the observed empirical patterns that claimed support for the plant vigour or plant stress hypotheses. The *in silico* experiment is intended to test if the aphid abundance dwelling on an infested plant is affected by the fertilization (or irrigation) treatment. We considered five levels for the fertilization treatment (i.e. σ_{N} equals to **0.0014, 0.003, 0.014, 0.07 and 0.14** d^{-1}) and five levels for the irrigation treatment (i.e. k equals to **21, 41, 205, 1025 and 2050** d^{-1}) corresponding to very low - low - average - high - very high levels of fertilization (or irrigation). We varied the level of one treatment while keeping the other to its average value. To simulate the fact that in factorial experiments there are replicates (i.e. different plant individuals) for each scenario, we considered, *in silico*, 10 replicate trajectories of the system variables by running the model 10 times with the 10 estimated parameters value drawn from the empirical distribution obtained in the estimation process.

Eventually, we compared pairwise differences of aphid abundances (i.e. variable A of the model) and aphid density (i.e. ratio A/S in the model) between scenarios using the Mann-Whitney U test, at different times (i.e. 1th June and 15th June).

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Results

Model calibration and selection

The ranking of the forty candidate models is reported in Table 2: the best model ("the model", hereinafter) assumes that *i*) the aphid presence induces the plant to divert resources from growth to defences, which reduce both aphid feeding and reproduction rates, *ii*) migration due to crowding can be neglected, *iii*) nitrogen assimilation (σ_{N}) and plant growth (κ) rates differ for different levels of fertilisation and irrigation, respectively. The modelled responses of aphid feeding and reproduction rates to an augment of the concentration of defensive compounds are reported in **Figure 2**. The defensive mechanism that impair aphids fecundity starts being effective for value of defence concentration higher than 0.045 and it rapidly decreases aphids fecundity.

The model reproduces observed temporal variation of shoot mass, with plants growing more in the N^+ treatments and with employed considered water treatments having little effect in the N^- cases. On the other hand, the negative effect of the employed lower watering on plant growth becomes visible in the N^+ treatments. The model simulates this negative effect of lower irrigation over plant growth but it still overestimates plant growth in the N^+H^- case **(Figure 3A)**. The model reproduces the temporal dynamics of aphid abundance, which peak in mid-June, are higher in the N^+ cases and maximized in the case N^+H^+. The latest corresponding to the scenario with the highest shoot growth (Figure 3B). At the beginning of July, aphids abundance drops to zero for all the treatments, this is probably due to defensive

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mechanism that impairs aphid fecundity.

The role played by fertilization and irrigation

Shoot growth follows a sigmoid pattern and it increases with fertilization and irrigation (Figure 4A-B). Concentration of **carbon** substrates vary between 5-20 % during the growing season with peaks at the beginning, when the plant growth is limited by the nitrogen supply, and at the end, when plant growth is arrested in response to daylight shortening, but carbon assimilation continues. Carbon concentration is enhanced in the considered stressful conditions that limit plant growth rather than carbon assimilation (Figure 4C-D). Concentration of **nitrogen** substrates vary between 0.1-1 % during the growing season (Figure 4E-F). It decreases in the first weeks of growth, but, in the case of very high/high fertilization, or very low/low watering, it increases. In fact, for high fertilization, nitrogen is not initially consumed by plant growth which is limited by carbon supply and, for low watering, nitrogen concentration increases as plant growth is impaired while N assimilation is not. Defences concentration peak is delayed in time with fertilization and irrigation (Figure 4 G-H). **Aphid abundance** peaks at the mid of June when plant growth is maximum. Interestingly, when plant is well watered, the time of aphid peak is delayed in time. This is due to the fact that defensive compounds need more time to reach significant concentrations in bigger plants (Figure **4I-J**). The positive effect of fertilization and irrigation over aphid abundance becomes evident in the end of May, a couple of weeks after the beginning of simulations. Similarly, **aphid density** peaks in

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the mid of June and is delayed for high levels of fertilization (or irrigation). On the other hand, in the first part of the season, aphid density is enhanced by a low/average value of fertilization (or irrigation) while later in the season aphid density is higher in a well fertilized (irrigated) plant (Figure **4K-L**).

The results of our **virtual experiment** show that one could draw very different conclusions depending on *i)* the observed variable (i.e. total aphid abundance or aphid density), *ii)* the considered factor levels and *iii)* the time of observations. For instance, one could infer that **fertilization enhances** aphid populations by observing aphid abundances in the mid-late part of the season (Figure 5-C-E); **decreases** them, by observing aphid density in the mid season for average and high values of fertilization (Figure 6-C); **has no effect**, by observing aphid abundance early in the season, for low to very high values of fertilization (Figure 5-A). Similarly, different conclusions can be drawn regarding the effect of irrigation: positive (Figure 5-D-F), negative (Figure 6-B) or null (Figure 5-B).

Discussion

Model calibration and selection

Zust and Agrawal (2016) report that infested plants can put in place phloem-sealing mechanisms to interfere with aphids access to plant resources and produce a number of secondary metabolites (e.g. cardenolides, glucosinolates and benzoxazinoids) which, if ingested, impair aphid fecundity. Our results suggest that both **defensive mechanisms** are likely to act in the peach-

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green aphid system. According to our model calibration the one impairing phloem accessibility is the most effective at low defence concentration, while the one impairing aphids fecundity is most effective at high defence concentration.

The model application to a real system subjected to different irrigation×fertilization treatments indicates that parameters relevant to **plant nitrogen assimilation (σ_{N}) and plant growth rate (κ)**, originally proposed within a theoretical framework (Thornley, 1972b,a) can be linked to agronomic practices. Particularly, the former increases with fertilization and the latter with irrigation. Although the model on the whole fitted experimental data (Fig. 3), it overestimated peach growth in the N^+H^- treatment and underestimated aphid abundance in the N^+H^+ treatment. The **overestimate**, might be due to the fact that nitrogen uptake, even if the soil is rich in nitrogen, is impaired by low water availability (Le Deunff and Malagoli, 2014). If true, it means that the irrigation treatment should affect also the nitrogen assimilation rate σ_{N}, and not only the plant growth rate k, as we assumed. However, in absence of any quantitative evidence, we could not test this assumption. **Aphid underestimate** might be due to the fact that aphid feeding rate is increased in well irrigated plants (Hale et al., 2003) due to a facilitated accessibility to a less viscose sap (Sevanto, 2014). If quantitatively measured, such a mechanisms would translate in an higher parameter θ_{max} in those treatments with higher irrigation. yet, also in this case, we had no data to test this hypothesis. The drop in aphids abundance simulated at the beginning of July can be linked to high defence concentration (Fig 4 G-H-I-J). This is in accordance with Kim and Jander (2007); Kim et al. (2008); Mewis et al.

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(2005) works on Arabidopsis-*Myzus persicae* system, which report reductions of aphids fecundity, up to 100%, in response to high concentration of some plant defensive compound.

Finding **correct numerical values for parameters** of biological models is virtually impossible because many parameters cannot be directly measured. On the other hand, good fitting does not guarantee unique parameter estimation, due to possible correlations among the parameters (Li and Vu, 2013) and model identifiability problems can arise due to an imbalance between model complexity and available data (De Pauw et al., 2008). **Overparameterized models** are characterized by the fact that the **information content of the measured data is too low** to provide accurate estimates for all model parameters. Our simulations indicate that predicted plant growth and aphid population peaks are particularly **sensitive** to uncertainty in the estimate of parameters q, α**,** π_1 **and** δ_2 (Fig. S1 in the Supplementary Information) (see the model description for details on the meaning of these parameters). The proposed modelling framework would therefore enormously benefit from experimental works dedicated to the measure, or at least the assessment, of these four parameters. Interestingly, despite the importance of the parameter q in Thornley's models, we found no studies on the assessment of this parameter. Similarly, although it is well known that a plant can divert resources from primary to secondary compounds (Herms and Mattson, 1992), we found no quantitative relationships relevant to the cost of making defences, in terms of growth loss, neither between the presence of secondary compounds and pest performances. We believe that our work could inspire future field experiments which are necessary to confirm our findings, deny

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them and/or address to new hypotheses adding mechanisms responsible to the system functioning.

The role played by fertilization and irrigation

Variations in plant growth, and in the concentration of C and N substrates in plant tissues, for different levels of fertilization and/or irrigation are well acknowledged, from seminal to most recent works (White, 1937; Jia and Gray, 2004; Muller et al., 2011) and they have already been shown to be **emerging properties** of the original model for plant growth used in this work (Thornley, 1972b,a). Our **pest-plant model** maintains these properties regarding the plant component (fig. 4 A-B-C-D-E-F) and sheds some light on the variations observed in aphid population.

Such an issue has been mostly dealt with in empirical works not providing a straightforward picture. Some authors observed no effect of fertilization and a negative effect of irrigation on aphid populations in the wheat-*Diuraphis noxia* and in the cotton-*Aphis gossypii* systems, respectively (Archer et al. (1995) and Matis et al. (2008)). Others observed the highest aphid abundance at an average level of fertilization and no effect of irrigation, in the chrysanthemum-*Aphis gossypii* system (Bethke et al. (1998)). Hale et al. (2003) reported that, for three grass species, irrigation had a positive effect on the aphid intrinsic rate of increase. On the other hand, aphid population was observed to be maximum for moderate water stress in the systems cabbage-*Myzus persicae* and cabbage-*Brevicoryne brassicae* (Tariq et al., 2012), and in one out of three genotypes tested for the poplar-*Phloemomyzus passerinii*

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system (Dardeau et al., 2015).

Our model, parametrized for the peach-green aphid system, shows that all these apparently contrasting empirical evidences can emerge from the same biological principles governing plant-pest dynamics and that both plant vigour and plant stress hypotheses can find support when observing a plant-pest system evolving in time and subject to different changes in environment conditions. The aphid population dynamics reproduced by our model (Fig. 5-6) indicate that the **effect of fertilization and irrigation on the pest population cannot be simply reduced as "positive" or "negative"**.

In fact, its sign and strength depends on the considered levels of fertilization/irrigation, the date of observation along the growing season and the observed variables.

Conclusions

In this work we demonstrated that embedding a mechanistic plant growth model, widely acknowledged in agronomy, in a consumer-resource modelling framework, widely studied in ecology is a promising approach for agroecology. We used this novel approach to study the consequences of irrigation and fertilization treatments in the peach-green aphid system. Yet, the proposed model has the ambition of being physiologically rigorous and general enough to be applied to **different plant-pest systems** and to incorporate the description of other **agronomic practices**.

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FIGURES

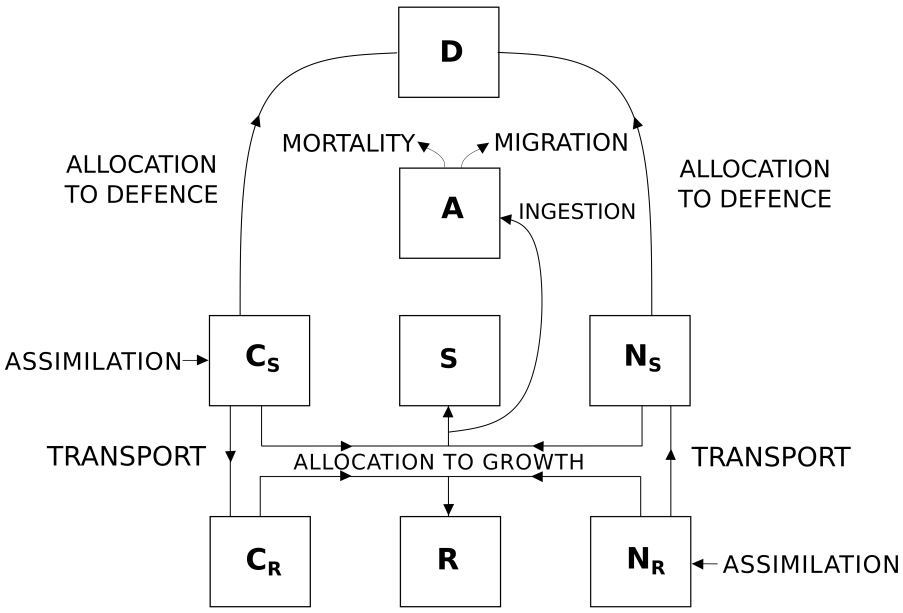

Figure 1: Schematic representation of the plant-aphid model where the plant is constituted by shoot (S) and root (R) structural dry mass, carbon (C_i) and nitrogen (N_i) substrates in shoots (i=S) and roots (i=R). The aphid population (A) intercepts a fraction of substrates allocated to constitute shoot structural mass and the plant diverts shoot substrates (carbon and nitrogen) to produce defences compounds (D). More details are given in the main text.

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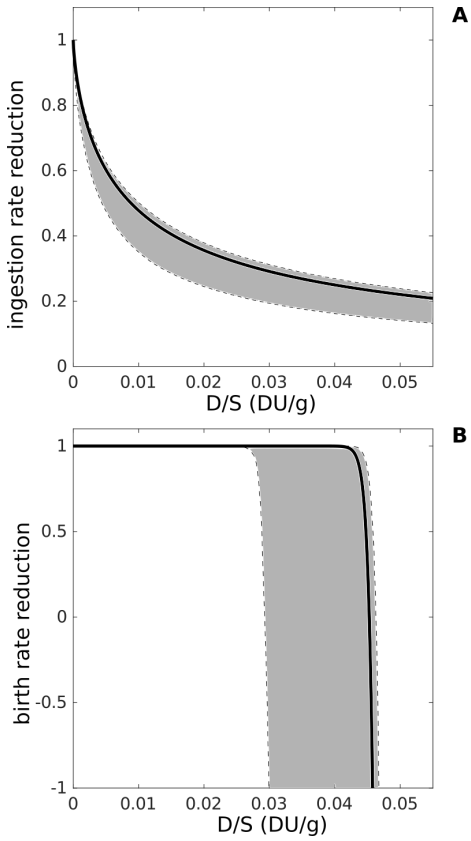

Figure 2: Regulation of the aphid ingestion rate (A) as a function of concentration of defensive compounds and its 90% C.I. due to the uncertainty in the estimate of parameters π_1 and δ_1. Regulation of the aphid conversion rate (B) as a function of concentration of defensive compounds and its 90% C.I. due to the uncertainty in the estimate of parameters δ_2 and π_2.

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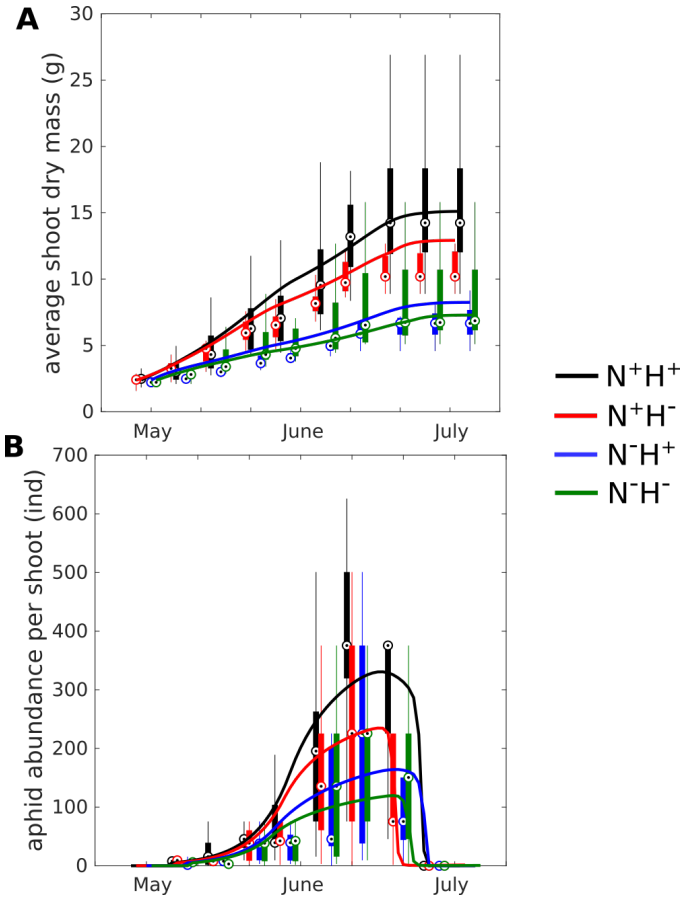

Figure 3: Temporal dynamics of A) average shoot dry mass and B) average aphid abundance per shoot. Circles and bars represent the median and the 50% CI of observed values, whiskers extend to the most extreme data points and continuous lines represent the simulated values. Colours (for both bars and lines) identify a treatment scenario (see legend)

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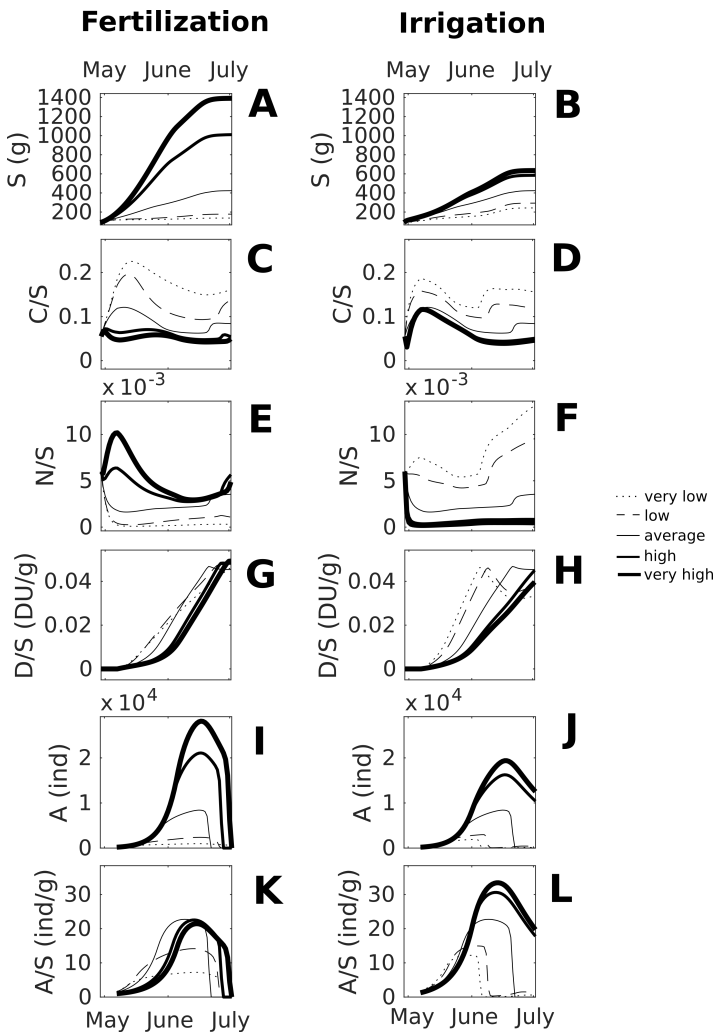

Figure 4: Simulated effect of fertilization (A-C-E-G-I-K) and irrigation (B-D-F-H-J-L) on the plant-aphid system: average shoot dry mass (A-B), carbon (C-D) and nitrogen (E-F) substrate concentration in shoots, defence (G-H) concentration in shoot, aphid abundance (I-J) and density (K-L). Lines style identify fertilization or irrigation level (see legend).

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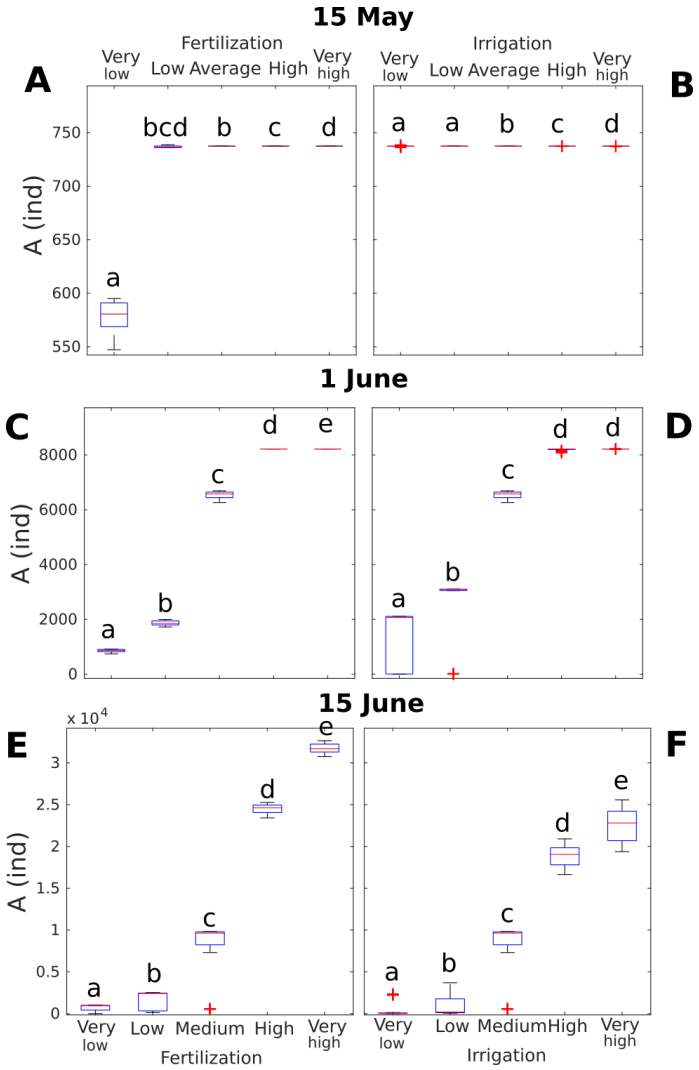

Figure 5: Simulated effect of fertilization (A-C-E) and irrigation (B-D-F) on aphids abundance on 15 May, 1 June and 15 June. Box represents the medians, lower and upper quartiles [25% and 75%] of 20 "virtual" replicates of each fertilization/irrigation treatments, whiskers extend to the most extreme values and outliers are plotted individually using the '+' symbol. Treatments with different letters are significantly different (P<0.05). For fertilization, $\sigma_N = 0.0014, 0.003, 0.014, 0.07, 0.14$. For irrigation, $\kappa = 21, 41, 205, 1025, 2050$

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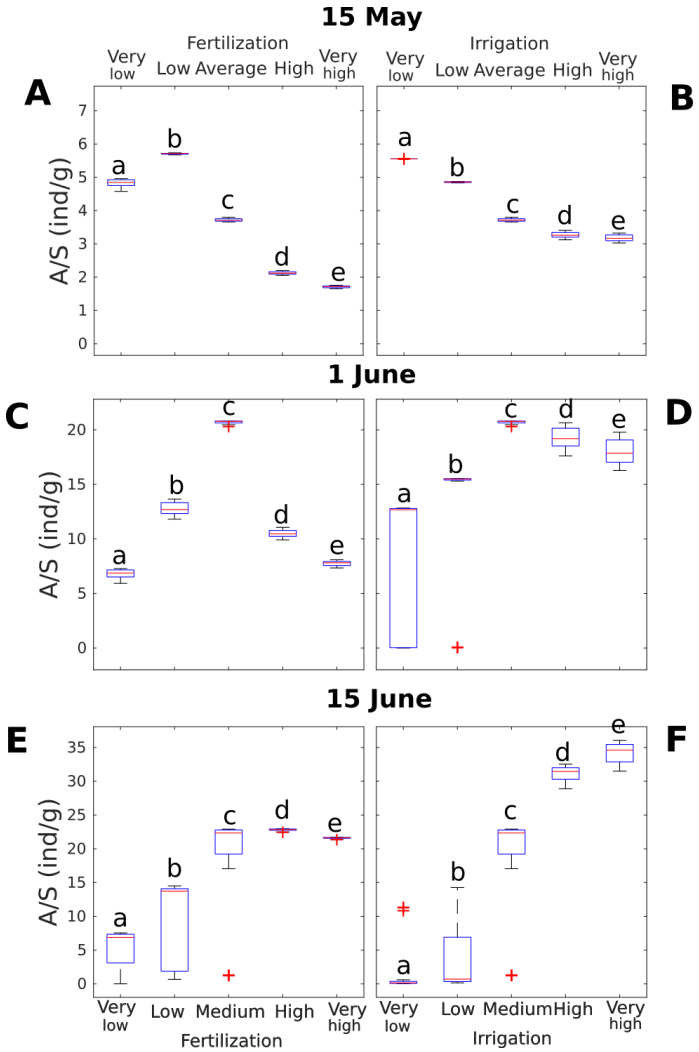

Figure 6: Simulated effect of fertilization (A-C-E) and irrigation (B-D-F) on aphids abundance on 15 May, 1 June and 15 June. Box represents the medians, lower and upper quartiles [25% and 75%] of 10 "virtual" replicates of each fertilization/irrigation treatments, whiskers extend to the most extreme values and outliers are plotted individually using the '+' symbol. Treatments with different letters are significantly different (P<0.05). For fertilization, $\sigma_N = 0.0014, 0.003, 0.014, 0.07, 0.14$. For irrigation, $\kappa = 21, 41, 205, 1025, 2050$

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Figure 7: Empirical probability distributions and correlations of parameters σ_N^+, σ_N^-, κ^+, κ^-, q, α, π_1, δ_1, δ_2, π_2.

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Tables

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Table 1: Model variables and parameters descriptions, values and sources. Variables initial values are reported in the Supplementary Information (SI.3). For those parameters calibrated in the present work, values are reported (in bold), along with a confidence interval of 90% (in brackets).

Variable		**Dim.**	**Description**	
S		g	Shoot structural dry mass	
R		g	Root structural dry mass	
C_S		g	Shoot carbon substrate	
C_R		g	Root carbon substrate	
N_S		g	Shoot nitrogen substrate	
N_R		g	Root nitrogen substrate	
D		DU	Plant induced defence	
A		ind	Aphid population	
Parameter	**Value**	**Dim.**	**Description**	**Source** [a]
C and N assimilation				
σ_C	0.1	d^{-1}	Net C assimilation rate	(1)
σ_N	**0.007 - 0.02** [0.005-0.013] [0.014-0.03] [b]	d^{-1}	Net N assimilation rate	(6)
ν	1000	g	Self shading semi-saturation value	(1)
ι_C	0.1	/	Photosynthesis product inhibition semi-saturation value	(1)
ι_N	0.01	/	N assimilation product inhibition semi-saturation value	(1)
C and N allocation				
φ_C	0.5	/	Fraction of structural C in structural dry matter	(1)
φ_N	0.025	/	Fraction of structural N in structural dry matter	(1)
κ	**142 - 268** [88-241] [162-474] [c]	d^{-1}	Allocation of substrates to plant growth	(6)
η	111	d^{-1}	Allocation of substrates to plant growth sensitivity to time	(6)
λ	165.5	d	Time of equal allocation to growth and reserves	(6)
Transport				
q	**0.79** [0.78-0.86]	/	Plant architecture scaling parameter	(7)
defenses				
ϵ_C	$5\ 10^{-2}$	DU g^{-1}	Conversion efficiency of C substrate in defenses	(2)
ϵ_N	1	DU g^{-1}	Conversion efficiency of N substrate in defenses	(2)
α	$\mathbf{1.7\ 10^{-2}}$ [1.1-1.7] 10^{-2}	g d^{-1} ind^{-1}	Allocation of substrates to defences per unit of aphid	(6)
Aphid				
Θ_{max}	$1.12\ 10^{-3}$	g d^{-1} ind^{-1}	Maximum substrate uptake per unit of aphid	(3)
ξ	171	ind g^{-1}	Maximum conversion efficiency of ingested substrates into descendants	(4)
π_1	$\mathbf{9.0\ 10^{-3}}$ [4.4-10] 10^{-2}	DU g^{-1}	Midpoint of feeding defences concentration	(6)
δ_1	**0.73** [0.71-0.76]	/	Sensitivity to feeding defences concentration	(6)
δ_2	**22.6** [21.6-34.2]	g DU^{-1}	Efficacy of reproduction defences concentration	(6)
π_2	**66.2** [38.6-105]	/	Sensitivity to reproduction defences concentration	(6)
μ	0.04	d^{-1}	Aphid mortality rate	(5)

[a](1) Thornley (1998); (2)Schoonhoven et al. (2005); (3)Day and Irzykiewicz (1953); (4)Saguez et al. (2005); (5)Gange et al. (1999);(6) Calibrated in the present work.

[b]values refer to N = 2 g/plant σ_N^- and N = 22.2 g/plant σ_N^+ supply, respectively.

[c]values refer to halved (κ^-) and full (κ^+) irrigation treatments, respectively.

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Table 2: Comparison among candidate models for the plant-aphid system. Each model is based on different hypotheses about induced plant defences allocation ($\alpha = 0$ if there is no induction to make defences, $\alpha \neq 0$ otherwise); defences effects on aphid feeding ($\delta_1 \neq 0$ if it is reduced, $\delta_1 = 0$ if it is not affected) and reproduction rate ($\delta_2 \neq 0$ if it is reduced, $\delta_2 = 0$ if it is not affected); and dependence of model parameters to agronomic practices (σ_N varies between considered fertilization treatments or not; k varied between considered irrigation treatments or not). Model complexity is given by the number of calibrated parameters n_p; L is the minimized value of the cost function; AIC is the Akaike score; Δ_{AIC} is distance from the best model.

Model	def.alloc.	def. effect	migration	σ_N	κ	n_p	L	AIC	Δ_{AIC}
M5d	$\alpha \neq 0$	$\delta_1 \neq 0, \delta_2 \neq 0$	$\omega = 0$	${\sigma_N}^+ > {\sigma_N}^-$	$\kappa^+ > \kappa^-$	12	3253	6529	0
M5dm	$\alpha \neq 0$	$\delta_1 \neq 0, \delta_2 \neq 0$	$\omega \neq 0$	${\sigma_N}^+ > {\sigma_N}^-$	$\kappa^+ > \kappa^-$	13	3252	6531	2
M4d	$\alpha \neq 0$	$\delta_1 = 0, \delta_2 \neq 0$	$\omega = 0$	${\sigma_N}^+ > {\sigma_N}^-$	$\kappa^+ > \kappa^-$	10	3268	6556	26
M4dm	$\alpha \neq 0$	$\delta_1 = 0, \delta_2 \neq 0$	$\omega \neq 0$	${\sigma_N}^+ > {\sigma_N}^-$	$\kappa^+ > \kappa^-$	11	3268	6557	28
M3dm	$\alpha \neq 0$	$\delta_1 \neq 0, \delta_2 = 0$	$\omega \neq 0$	${\sigma_N}^+ > {\sigma_N}^-$	$\kappa^+ > \kappa^-$	11	3274	6571	41
M5cm	$\alpha \neq 0$	$\delta_1 \neq 0, \delta_2 \neq 0$	$\omega \neq 0$	${\sigma_N}^+ > {\sigma_N}^-$	$\kappa^+ = \kappa^-$	12	3275	6574	45
M4c	$\alpha \neq 0$	$\delta_1 = 0, \delta_2 \neq 0$	$\omega = 0$	${\sigma_N}^+ > {\sigma_N}^-$	$\kappa^+ = \kappa^-$	9	3283	6584	55
M4cm	$\alpha \neq 0$	$\delta_1 = 0, \delta_2 \neq 0$	$\omega \neq 0$	${\sigma_N}^+ > {\sigma_N}^-$	$\kappa^+ = \kappa^-$	10	3283	6587	57
M3d	$\alpha \neq 0$	$\delta_1 \neq 0, \delta_2 = 0$	$\omega = 0$	${\sigma_N}^+ > {\sigma_N}^-$	$\kappa^+ > \kappa^-$	10	3302	6625	95
M5c	$\alpha \neq 0$	$\delta_1 \neq 0, \delta_2 \neq 0$	$\omega = 0$	${\sigma_N}^+ > {\sigma_N}^-$	$\kappa^+ = \kappa^-$	11	3303	6628	98
M2dm	$\alpha \neq 0$	$\delta_1 = \delta_2 = 0$	$\omega \neq 0$	${\sigma_N}^+ > {\sigma_N}^-$	$\kappa^+ > \kappa^-$	9	3305	6628	99
M1dm	$\alpha = 0$	$\delta_1 = \delta_2 = 0$	$\omega \neq 0$	${\sigma_N}^+ > {\sigma_N}^-$	$\kappa^+ > \kappa^-$	8	3308	6632	103
M3c	$\alpha \neq 0$	$\delta_1 \neq 0, \delta_2 = 0$	$\omega = 0$	${\sigma_N}^+ > {\sigma_N}^-$	$\kappa^+ = \kappa^-$	9	3312	6641	112
M3cm	$\alpha \neq 0$	$\delta_1 \neq 0, \delta_2 = 0$	$\omega \neq 0$	${\sigma_N}^+ > {\sigma_N}^-$	$\kappa^+ = \kappa^-$	10	3311	6642	113

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Model	def.alloc.	def. effect	migration	σ_N	κ	n_p	L	AIC	Δ_{AIC}
M2cm	$\alpha \neq 0$	$\delta_1 = \delta_2 = 0$	$\omega \neq 0$	${\sigma_N}^+ > {\sigma_N}^-$	$\kappa^+ = \kappa^-$	8	3315	6646	117
M1cm	$\alpha = 0$	$\delta_1 = \delta_2 = 0$	$\omega \neq 0$	${\sigma_N}^+ > {\sigma_N}^-$	$\kappa^+ = \kappa^-$	7	3341	6696	167
M4bm	$\alpha \neq 0$	$\delta_1 = 0, \delta_2 \neq 0$	$\omega \neq 0$	${\sigma_N}^+ = {\sigma_N}^-$	$\kappa^+ > \kappa^-$	10	3349	6718	189
M4b	$\alpha \neq 0$	$\delta_1 = 0, \delta_2 \neq 0$	$\omega = 0$	${\sigma_N}^+ = {\sigma_N}^-$	$\kappa^+ > \kappa^-$	9	3351	6719	190
M3bm	$\alpha \neq 0$	$\delta_1 \neq 0, \delta_2 = 0$	$\omega \neq 0$	${\sigma_N}^+ = {\sigma_N}^-$	$\kappa^+ > \kappa^-$	10	3351	6722	192
M5bm	$\alpha \neq 0$	$\delta_1 \neq 0, \delta_2 \neq 0$	$\omega \neq 0$	${\sigma_N}^+ = {\sigma_N}^-$	$\kappa^+ > \kappa^-$	12	3349	6722	193
M5b	$\alpha \neq 0$	$\delta_1 \neq 0, \delta_2 \neq 0$	$\omega = 0$	${\sigma_N}^+ = {\sigma_N}^-$	$\kappa^+ > \kappa^-$	11	3357	6735	206
M5a	$\alpha \neq 0$	$\delta_1 \neq 0, \delta_2 \neq 0$	$\omega = 0$	${\sigma_N}^+ = {\sigma_N}^-$	$\kappa^+ = \kappa^-$	10	3365	6751	222
M3am	$\alpha \neq 0$	$\delta_1 \neq 0, \delta_2 = 0$	$\omega \neq 0$	${\sigma_N}^+ = {\sigma_N}^-$	$\kappa^+ = \kappa^-$	9	3367	6752	222
M5am	$\alpha \neq 0$	$\delta_1 \neq 0, \delta_2 \neq 0$	$\omega \neq 0$	${\sigma_N}^+ = {\sigma_N}^-$	$\kappa^+ = \kappa^-$	11	3365	6753	223
M2d	$\alpha \neq 0$	$\delta_1 = \delta_2 = 0$	$\omega = 0$	${\sigma_N}^+ > {\sigma_N}^-$	$\kappa^+ > \kappa^-$	8	3370	6756	227
M3b	$\alpha \neq 0$	$\delta_1 \neq 0, \delta_2 = 0$	$\omega = 0$	${\sigma_N}^+ = {\sigma_N}^-$	$\kappa^+ > \kappa^-$	9	3378	6773	244
M2c	$\alpha \neq 0$	$\delta_1 = \delta_2 = 0$	$\omega = 0$	${\sigma_N}^+ > {\sigma_N}^-$	$\kappa^+ = \kappa^-$	7	3381	6775	246
M3a	$\alpha \neq 0$	$\delta_1 \neq 0, \delta_2 = 0$	$\omega = 0$	${\sigma_N}^+ = {\sigma_N}^-$	$\kappa^+ = \kappa^-$	8	3385	6787	257

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Model	def.alloc.	def. effect	migration	σ_N	κ	n_p	L	AIC	Δ_{AIC}
M4am	$\alpha \neq 0$	$\delta_1 = 0, \delta_2 \neq 0$	$\omega \neq 0$	${\sigma_N}^+ = {\sigma_N}^-$	$\kappa^+ = \kappa^-$	9	3388	6794	264
M1bm	$\alpha = 0$	$\delta_1 = \delta_2 = 0$	$\omega \neq 0$	${\sigma_N}^+ = {\sigma_N}^-$	$\kappa^+ > \kappa^-$	7	3390	6794	265
M2bm	$\alpha \neq 0$	$\delta_1 = \delta_2 = 0$	$\omega \neq 0$	${\sigma_N}^+ = {\sigma_N}^-$	$\kappa^+ > \kappa^-$	8	3390	6796	266
M1am	$\alpha = 0$	$\delta_1 = \delta_2 = 0$	$\omega \neq 0$	${\sigma_N}^+ = {\sigma_N}^-$	$\kappa^+ = \kappa^-$	6	3393	6798	269
M2am	$\alpha \neq 0$	$\delta_1 = \delta_2 = 0$	$\omega \neq 0$	${\sigma_N}^+ = {\sigma_N}^-$	$\kappa^+ = \kappa^-$	7	3393	6800	271
M4a	$\alpha \neq 0$	$\delta_1 = 0, \delta_2 \neq 0$	$\omega = 0$	${\sigma_N}^+ = {\sigma_N}^-$	$\kappa^+ = \kappa^-$	8	3423	6863	333
M2b	$\alpha \neq 0$	$\delta_1 = \delta_2 = 0$	$\omega = 0$	${\sigma_N}^+ = {\sigma_N}^-$	$\kappa^+ > \kappa^-$	7	3426	6865	336
M2a	$\alpha \neq 0$	$\delta_1 = \delta_2 = 0$	$\omega = 0$	${\sigma_N}^+ = {\sigma_N}^-$	$\kappa^+ = \kappa^-$	6	3430	6872	343
M1c	$\alpha = 0$	$\delta_1 = \delta_2 = 0$	$\omega = 0$	${\sigma_N}^+ > {\sigma_N}^-$	$\kappa^+ = \kappa^-$	6	3602	7216	687
M1d	$\alpha = 0$	$\delta_1 = \delta_2 = 0$	$\omega = 0$	${\sigma_N}^+ > {\sigma_N}^-$	$\kappa^+ > \kappa^-$	7	3607	7228	699
M1a	$\alpha = 0$	$\delta_1 = \delta_2 = 0$	$\omega = 0$	${\sigma_N}^+ = {\sigma_N}^-$	$\kappa^+ = \kappa^-$	5	3616	7242	712
M1b	$\alpha = 0$	$\delta_1 = \delta_2 = 0$	$\omega = 0$	${\sigma_N}^+ = {\sigma_N}^-$	$\kappa^+ > \kappa^-$	6	3625	7262	733