Evaluating the banker plant system for biologically controlling the cotton aphid, *Aphis gossypii*, with larvae of the gall midge, *Aphidoletes aphidomyza*, with a mathematical model

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The cotton aphid, *Aphis gossypii*, is a major pest in eggplant crops grown in greenhouses throughout Japan. This species easily becomes resistant against insecticides. A promising way to control these aphids biologically is with banker plants. Then, the alternative prey, *Rhopalosiphum padi*, on these plants should guarantee a permanent production of the general predator, larvae of the gall midge *Aphidoletes aphidomyza* which prefer to eat the pest insect. When the pest in the crop is scarce the banker plant should serve as a refuge for the general predator. With a differential equation model we show under which conditions biological control in this specific system can be called successful. We discuss whether the mathematical conclusions are biologically feasible.

Keywords: open rearing system, eggplant, mathematical model

Since the early seventies of the twentieth century a lot of pest species in greenhouses have been controlled with biological control agents like parasitoids or predators (van Lenteren & Godfray 2005). For the control of the whitefly *Trialeurodes vaporariorum* Westwood, the parasitoid *Encarsia formosa* Gahan has been used successfully (van Lenteren *et al.* 1996). For some pest species like aphids chemical pesticides were used intensively. Currently, however, some aphid species like the cotton aphid, *Aphis gossypii* Glover, have become resistant against pyrethroid insecticides in some parts of the world (Sun *et al.* 1994). Therefore a search has started for a new strategy to control these resistant aphids. For aphids in glasshouses natural enemies like parasitoids and predators are both available. Usually, these were introduced with massive inoculations. Recently, one of the promising ways to control these aphids is by means of the banker plant system.

In such systems non-crop plants are brought into the greenhouse for controlling pests. These plants are allowed to develop pest infestations that do not harm the crop plants. The natural enemies of the pest developed on the so-called banker plants are released onto these plants. These released natural enemies are polyphagous and act as biological control agents for the pest in the crop: as these reproduce and increase in numbers, they spread out into the whole greenhouse. It is like a mini-rearing system for the biocontrol agents.

This strategy has become popular in recent years (see *e.g.* van der Linden & van der Staaij 2001). In addition, the banker plant system is, particularly for aphid control, introduced by producers of biological control agents (Franks 2010). In the most commonly used situation, a cereal grass (wheat, oats, barley) is sold in rockwool cubes, pre-infested with an aphid that is very specific to feeding on these types of grasses. The rockwool cube is potted up into a larger pot size or hanging basket and grows along with the rest of the crop. Aphid parasitic wasps or predators are released onto these banker plants and as new adults emerge they fly out into the main crop. The system can give excellent control of aphids and has the advantage of continuous introduction of newly emerging wasps or predators that have not had to undergo the trauma of being shipped half-way around the world before they reach their final destination. In this way, the predators or parasitoids stay longer around because the alternative prey or host on which they are reared is still present on the banker plant. Moreover, in the practice of biological control the banker plants are replaced regularly by fresh ones to guarantee a permanent inflow of predators or parasitoids into the crop.

In this paper, we concentrate on one particular system where *A. gossypii* is biologically controlled by larvae of the gall midge, *A. aphidomyza*. This aphid species occurs worldwide and is a primary pest on cucumbers, melons and eggplants in greenhouses. To reduce the numbers of these aphids in Japanese greenhouses with eggplant as crop, biological control is preferred, when other pests are also controlled biologically (Yano 2006). With a simplified two-compartment model we are investigating the population dynamics of the cotton aphid and its predator, just after the adult gall midges can disperse from the banker plant compartment into the full greenhouse. We are especially interested in the questions: (1) whether pest control is possible at different initial densities of pest, and (2) what is the timing of the control: from which time does the decline start?

MATERIAL AND METHODS

The system

In Japanese greenhouses, *A. gossypii* is frequently discovered as a pest species on eggplants. Biological control of this aphid species is preferred and therefore, the banker plant system has been introduced some years ago (Yano 2006, Franks 2010). In this kind of biological control a general predatory species of aphids is reared on an alternative prey species, here the bird cherry aphid, *Rhopalosiphum padi* (L.) on the banker plant. This aphid species can primarily be found on its primary host the bird cherry (*Prunus padus*). For rearing, secondary host plant species can be used, namely members of the family Gramineae, especially maize, barley, oats and wheat. In Japan, the bird cherry aphid is reared mostly on barley. The general predators considered are larvae of the gall midge *A. aphidomyza*. These voracious larval predators of aphids are used successfully on herbs to biologically control aphids in general and especially the cotton aphid (Franks 2010). In the banker plant compartment all stages of the gall midge can be present on the barley and the bird cherry aphid sub-system. As adult gall midges emerge from pupae, the females fly to find aphid colonies amongst which they lay eggs. The small orange-red eggs hatch in a few days and the yellow/orange maggot-like larvae (up to 2.5 mm long) kill and feed on the aphids. The larvae drop from the plants to pupate.

The model

For the purpose of suppressing the pest density of the cotton aphid in the crop compartment (see Figure 1) we start with neglecting the banker plant compartment and built the model of the interaction between the prey and predator from first principles. This one prey and one predator system is governed by the growth of the cotton aphid, its consumption by the predator, the production of the predators and the natural death of the predator (see eqn. 1). The dynamics of the state variables C the density of the cotton aphid and P_C the density of the predaceous larvae and their change in time are given in eqn. 1.

$$\begin{aligned} \frac{dC(t)}{dt} &= \begin{bmatrix} \text{growth rate} \\ \text{of prey} \end{bmatrix} - \begin{bmatrix} \text{consumption rate of prey} \\ \text{by predator} \end{bmatrix} \\ \frac{dP_C(t)}{dt} &= \begin{bmatrix} \text{growth rate of predator} \\ \text{due to prey consumption} \end{bmatrix} - \begin{bmatrix} \text{death rate} \\ \text{of predator} \end{bmatrix} \end{aligned} \tag{1}$$

For the growth rate of the cotton aphid we assume exponential growth in the absence of the predator. The consumption by the predator is modelled with a Holling type two functional response (see *e.g.* Turchin 2003), which is a saturat-

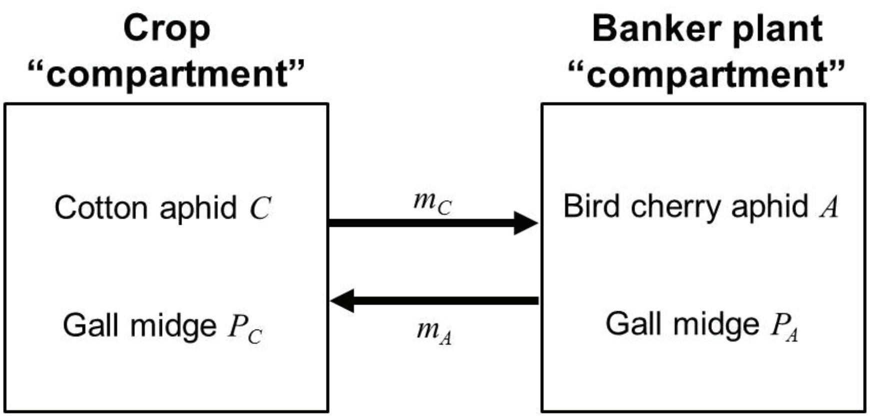

Figure 1. Schematic figure for the description of the banker plant system with a two compartments model. The migration rates to and from the banker plant are m_C and m_A, respectively.

ing function with increasing prey density. Predators are produced from the consumption of the prey with an efficiency e_C. The predator is assumed to have a constant per capita death rate q. With these assumptions the interaction between prey and predator in the crop compartment is given by eqn. 2. For simplicity we give an overview of the state variables and parameters of the full (two compartment) model in Table 1.

$$\begin{aligned} \frac{dC(t)}{dt} &= r_C C(t) - \frac{f_C C(t)}{h_C + C(t)} P_C(t) \\ \frac{dP_C(t)}{dt} &= e_C \frac{f_C C(t)}{h_C + C(t)} P_C(t) - q P_C(t) \end{aligned} \tag{2}$$

In essence, the same kind of predator-prey interaction (eqn. 2) takes place in the banker plant compartment. Here, A is the density of the alternative prey, the bird cherry aphid and P_A is the density of the predaceous larvae in this compartment (although it is the same species). Up to now the two predator-prey interactions in the two compartments are modelled separately. However, the two compartments are connected by the migration of the predators between crop and banker plants (see Figure 1). We assume that the predators migrate with a constant probability per time unit m_A from the banker plant compartment into the crop and vice versa (m_C). Therefore, the term $m_A P_A(t)$ is added to the second line and subtracted from the fourth line in eqn. 3, $m_C P_C(t)$ is subtracted from the second line and added to the fourth line in eqn. 3.

$$\begin{aligned} \frac{dC(t)}{dt} &= r_C C(t) - \frac{f_C C(t)}{h_C + C(t)} P_C(t) \\ \frac{dP_C(t)}{dt} &= e_C \frac{f_C C(t)}{h_C + C(t)} P_C(t) - q P_C(t) - m_C P_C(t) + m_A P_A(t) \\ \frac{dA(t)}{dt} &= r_A A(t) - \frac{f_A A(t)}{h_A + A(t)} P_A(t) \\ \frac{dP_A(t)}{dt} &= e_A \frac{f_A A(t)}{h_A + A(t)} P_A(t) - q P_A(t) + m_C P_C(t) - m_A P_A(t) \end{aligned} \tag{3}$$

If (i) in the banker plant compartment the production rate of the predator is maximum $e_A f_A P_A(t)$ because a lot of alternative prey is available, and (ii) the migration rate for the predator to the crop is much higher than migration from the crop to the banker plant ($m_A >> m_C$), because the cotton aphid is the preferred prey item, then the system of differential equations reduces to

Table 1. Description of the parameters and state variables. For each of these we give the (pseudo)units and the default value if appropriate.

State variables	Description	Unit	Initial value
C	Density of pest insect (cotton aphid)	[#prey] [plant] $^{-1}$	varying
P_C	Density of predator (larvae of gall midge) in crop compartment	[#pred] [plant] $^{-1}$	varying
P_A	Density of predator (larvae of gall midge) in banker plant compartment	[#pred] [plant] $^{-1}$	varying
A	Density of alternative prey (bird cherry aphid)	[#prey] [plant] $^{-1}$	varying

Parameters	Description	Unit	Default value
r_C	Relative growth rate of C	Time $^{-1}$	0.37
f_C	Maximum rate of prey C intake per predator	[#pred] $^{-1}$ day $^{-1}$	0.878
e_C	Conversion factor for prey C into predator	[#pred] [#prey] $^{-1}$	0.167
h_C	Density of prey C at which the predator obtains half of its maximum intake rate	[#prey] [plant] $^{-1}$	50
r_A	Relative growth rate of A	day $^{-1}$	-
f_A	Maximum rate of prey A intake per predator	[#pred] $^{-1}$ day $^{-1}$	0.581
e_A	Conversion factor for prey A into predator	[#pred] [#prey] $^{-1}$	0.198
h_A	Density of prey A at which the predator obtains half of its maximum intake rate	[#prey] [plant] $^{-1}$	-
m_C	Migration rate of predator from crop to banker plants	day $^{-1}$	-
m_A	Migration rate of predator from banker plants to crop	day $^{-1}$	0.1
q	Death rate of predator	day $^{-1}$	0.25

$$
\begin{aligned}
\frac{dC(t)}{dt} &= r_C C(t) - \frac{f_C C(t)}{h_C + C(t)} P_C(t) \\
\frac{dP_C(t)}{dt} &= e_C \frac{f_C C(t)}{h_C + C(t)} P_C(t) - qP_C(t) + m_A P_A(t) \\
\frac{dA(t)}{dt} &= r_A A(t) - f_A P_A(t) \\
\frac{dP_A(t)}{dt} &= e_A f_A P_A(t) - qP_A(t) - m_A P_A(t)
\end{aligned}
\qquad (4)
$$

From now on we simplify system 4: (1) The alternative prey A is assumed to stay on the banker plant and is also kept at a high level by the glasshouse owner. Therefore, we are not considering the dynamics of the alternative prey. (2) The simplified differential equations for the predator (P_A) in the banker plant compartment is a simple exponential model. It has the solution $P_A(t) = P_A(0)\exp[(e_A f_A - q - m_A)t]$ (see derivation in eqn 5).

$$
\begin{aligned}
\frac{dP_A(t)}{dt} &= \frac{d}{dt}P_A(0)exp\left[(e_A f_A - q - m_A)t\right] \\
&= (e_A f_A - q - m_A)P_A(0)exp\left[(e_A f_A - q - m_A)t\right] \Leftrightarrow \\
\frac{dP_A(t)}{dt} &= (e_A f_A - q - m_A)P_A(t)
\end{aligned}
\tag{5}
$$

q.e.d.

In equilibrium, the aphid population population in the banker plant compartment is $A(t) = f_A\, P_A(t) / r_A$. Thus the simplified model based on assumptions (1) and (2) is given in eqn. 6.

$$
\begin{aligned}
\frac{dC(t)}{dt} &= r_C C(t) - \frac{f_C C(t)}{h_C + C(t)} P_C(t) \\
\frac{dP_C(t)}{dt} &= e_C \frac{f_C C(t)}{h_C + C(t)} P_C(t) - qP_C(t) + m_A P_A(0) exp\left[(e_A f_A - q - m_A)t\right]
\end{aligned}
\tag{6}
$$

After we have parameterized the model in eqn. 6 simulations were done with Grind for Matlab developed by E.H. van Nes (http://www.aew.wur.nl/UK/GRIND) in MatLab 7.8.0.

Parametrization of the simplified model

The relative growth rate (r_C) for *A. gossypii* (on cucumber) is reported by van Steenis (1993) as 0.37–0.45 per day (at 24 °C). In addition, we know (Nishikawa *et al.*, unpubl.) the relative growth rate of the predatory stage of *A. aphidomyza* on the cotton aphid (r_{PC}) as 0.147 per day (at 25 °C) and on the bird cherry aphid (r_{PA}) as 0.115 per day. Because we know approximate values of the maximum daily predation of *A. aphidomyza* larvae on cotton aphids and bird cherry aphids as 6.92 and 5.67 aphids per day (Junichiro Abe, pers. comm.), we can calculate e_C as (the number produced) / (the number consumed) = exp(0.147) / 6.92 r_{PC} / f_C and e_A = exp(0.115) / 5.67 (see Table 1). Moreover, $f_C = r_{PC} / e_C$ and $f_A = r_{PA} / e_A$ The migration rate from banker plant to crop is set to 0.1 per day, meaning that it takes on average 10 days to migrate. The larvae live on average 4 days and therefore the value of q is set to 0.25.

RESULTS

The system of two differential equations (eqn. 5) is non-autonomous, because time is explicitly used in the last term in the differential equation for the predator. Therefore, a stable equilibrium point cannot be calculated and a stability analysis is not appropriate. With simulations at different initial densities of aphids per plant in the crop $C(0)$, initially no predators in the crop $P_C(0) = 0$ and different initial densities of the predator $P_A(0)$ in banker plant compartment we determine whether control is achieved within a time span of two weeks, the timing of the control is denoted and the maximum number of aphids per plant in the crop is investigated.

As can be seen in Figure 2a the pest can in principle be controlled at any initial number of aphids per plant, but these initial numbers should be above a certain threshold, which is higher if initial numbers are higher. The time of the decline of the number of cotton aphids per plant decreases with higher introduced numbers of predators in the banker plant compartment (Figure 2b). Moreover, the maximum number of aphids at which the decline starts is higher as the decline starts later (Figure 2c). Because the predator has a short lifespan the control in this system is not long-lasting as can be seen in the two typical dynamics that show no control and temporarily control (Figures 3a and 3b, respectively).

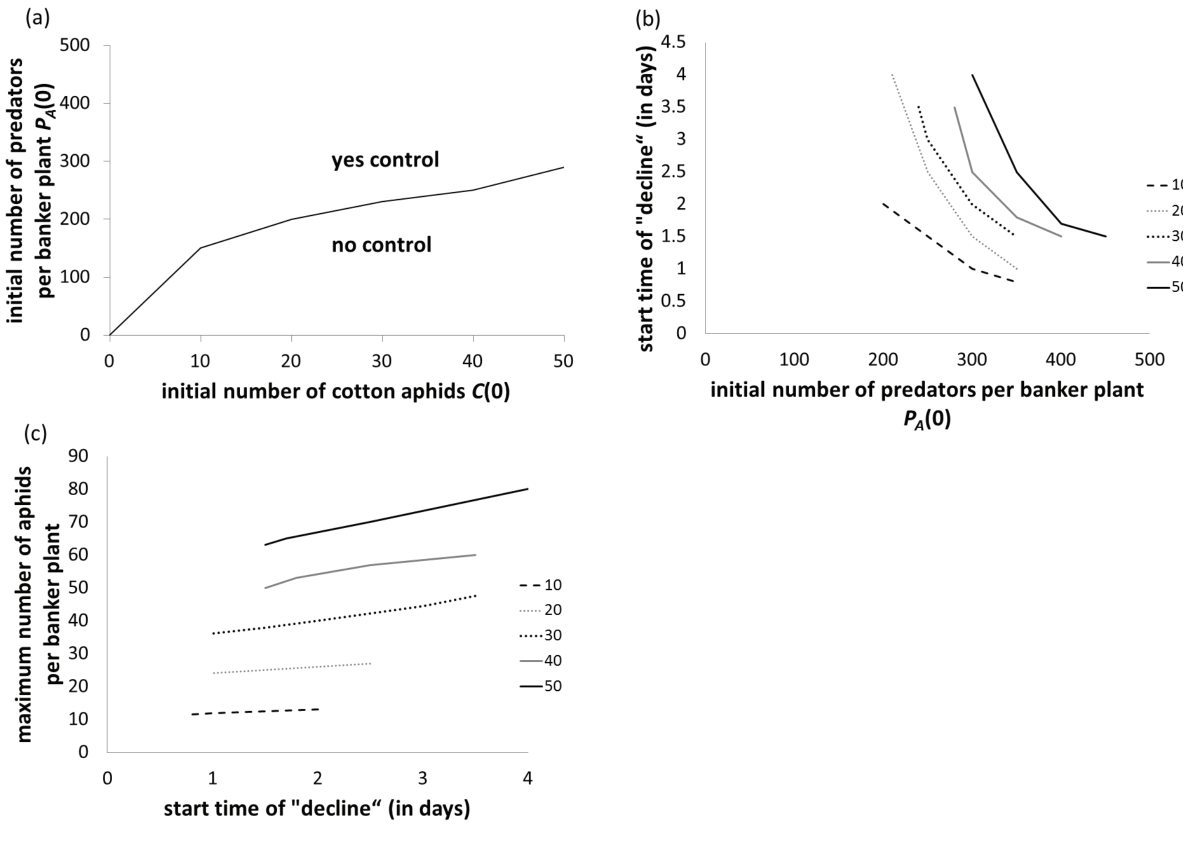

Figure 2. The simulations were done with the parameter values from Table 1. (a) The relation between initial number of cotton aphids per plant and the initial numbers of predators per plant in the banker plant compartment is shown. Only for numbers of introduced predators above the drawn line the pest insect in the crop can, according to the model, be controlled. (b) For the initial aphid number per plant as shown in the legend the relation between the initial number of predators in the banker plant compartment and the start time of the 'decline' is given. (c) For the initial aphid number per plant (shown in the legend) the relation between the start time of the 'decline' and the maximum number of aphids per plant at the start time of the 'decline' is plotted.

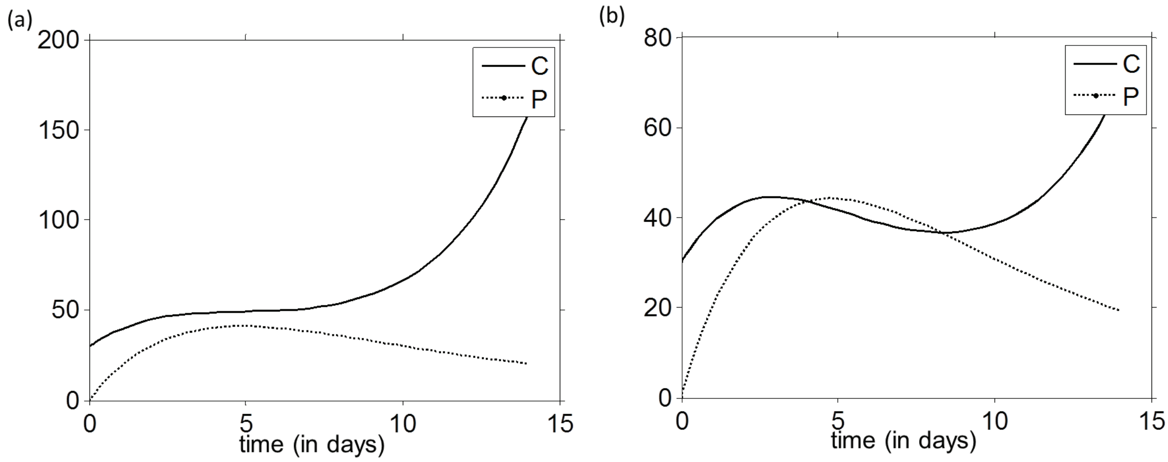

Figure 3. The development of the cotton aphid numbers per plant and the predators per plant in the crop compartment. (a) The aphid population growth is slowed down [$C(0) = 30$; $P_A(0) = 230$]. (b) The aphid population temporarily decreases [$C(0) = 30$; $P_A(0) = 250$].

Conclusion

It pays to be early with introduction of predators: introduce predators already at low aphid infestations. Less predators are needed for a decline in the pest population to happen.

From Figures 3a and 3b we can conclude that the predator population is unable to guarantee biological control in the long term; Figure 3b suggests that more introductions of predators are necessary for continued control

The timing of the decline can be relevant for assessing the damage of the commercially harvested plant fruits. If data are available about losses due to damage of the eggplant fruit, then an optimal introduction strategy for the predator might be determined with the help of the model.

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