



Combining banker plants to achieve long-term pest control in multi-pest and multi-natural enemy cropping systems

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Abstract

Banker plants increase biological pest control by supporting populations of non-pest arthropod species, used as alternative hosts or prey by natural enemies. Due to the specificity of trophic interactions, banker plants may not efficiently promote natural enemies with different ecologies. Yet in most cropping systems, different pest species are present together and require different biocontrol agents to efficiently control them. In the present study, we tested the combined use of two banker plants and their associated prey/host to enhance populations of the specialist parasitoid *Encarsia formosa* targeting the main tomato pest *Bemisia tabaci*, and a polyphagous ladybird *Propylea japonica* targeting the secondary pest *Myzus persicae* in tomato crops. In a laboratory and a greenhouse experiment, we measured the abundances of these four species using the *Ricinus communis*—*Trialeurodes ricini* banker plant system alone, in combination with the *Glycines max*—*Megoura japonica* system, or in absence of banker plants. We found that the first banker plant system enhanced populations of *E. formosa*, resulting in increased suppression of *B. tabaci* populations and the suppression of their outbreak in both our laboratory and greenhouse experiment. Conversely, abundances of *P. japonica* were not affected by this first system, but were significantly increased when the second was present. This resulted in increased control of *M. persicae* populations and the suppression of their early and late outbreaks. Our study demonstrates the potential for combined banker plants to provide long-term, sustainable control of multiple pests by their target natural enemies in complex agroecosystems.

Keywords Alternative prey · *Bemisia tabaci* · Biocontrol agent · Competition · *Encarsia formosa* · Functional plant · *Myzus persicae* · *Propylea japonica* · Secondary pest

Key message

- Multiple pest species are present simultaneously in cropping systems, requiring multiple natural enemies.
- Multiple banker plants are needed to support populations of biocontrol agents with contrasted ecologies.

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- We tested the combined use of two banker plants, targeting two biocontrol agents to control two tomato pests.
- Combined banker plants enhanced the control of both main and secondary pests in laboratory and greenhouse.
- Pest outbreaks were suppressed on the long term only when banker plants were present.

Introduction

With the rise of integrated pest management (IPM), practical applications of biological control agents releases have become increasingly complex to improve pest control with reduced used of chemical pesticides (Desneux et al. 2007; Naranjo et al. 2015; Huang et al. 2020; Zang et al. 2021). To achieve sustainable long-term control of multiple pest populations simultaneously, different biocontrol agents can be released together (Barbosa 1998; Heimpel and Mills 2008), involving natural enemy species with limited niche competition (Liu et al. 2012; Chailleux et al. 2014a; Liang et al. 2021; Sanchez-Hernandez et al. 2021), but with complementary ecologies to regulate different pest populations or over different time periods and spatial scales (Hall 2011; Chailleux et al. 2017). Most often, a specialist natural enemy (e.g., a parasitoid wasp) is combined with a generalist natural enemy (Tan et al. 2016; Perez-Valencia et al. 2019): the specialist targets the dominant pest species and prevents its outbreaks, while the generalist regulates populations of secondary pests (Chailleux et al. 2013, 2017; Dainese et al. 2017; Aparicio et al. 2020). In such complex agroecosystems, the successful colonization of crops and the establishment of stable populations by released biocontrol agents is challenging, and may heavily rely on means to support populations (Bianchi et al. 2006). This is especially true since biocontrol agents are most often released before pest populations reach high densities to prevent pest outbreak (Albajes et al. 2000). Therefore, the development of strategies supporting biocontrol agent populations could be useful in extending the adoption and efficacy of multi-species releases.

The use of banker plants has been increasingly investigated and developed in the context of conservation biological control (Frank 2010). Banker plants are non-crop plants, supporting populations of herbivorous arthropod species, which do not attack adjacent crops (Parolin et al. 2012), and which may be used as alternative prey or hosts by natural enemies attacking target pest species in cropping systems. By providing shelter and alternative prey/hosts, banker plants can enable the early colonization of adjacent crops by natural enemies (Franck 2010; Parolin et al. 2012) and the establishment of their populations when main prey are scarce (Yano et al. 2018). Hence, banker plants can be used in combination with crops as an

entry point for the inoculative release of biocontrol agents. Plant species supporting populations of alternative prey/hosts in the same functional group as the target pest species are well suited to be used as banker plants (Laurenz and Meyhofer 2021). For instance, the non-crop oat species *Avena sativa* Linnaeus supporting populations of the alternative aphid species *Metopolophium dirhodum* Walker resulted in an increased suppression of the target aphid pest *Myzus persicae* Sulzer by its parasitoid *Aphidoletes aphidimyza* Rondani in chilly crop (*Capsicum annum* Linnaeus; Hansen 1983). Similarly, the non-crop papaya banker plant *Carica papaya* Linnaeus supporting populations of the alternative whitefly species *Trialeurodes variabilis* Quaintance successfully increased the suppression of the *Bemisia tabaci* Gennadius by the ladybird *Delphastus pusillus* LeConte in many vegetable crops (Osborne et al. 1990). Banker plants may also support populations of biocontrol agents after the suppression of the target pest populations, and thereby avoid their escape from the agroecosystem, which is common in practical biological control applications and may result in late pest outbreaks (Huang et al. 2011). Maintaining natural enemies within the agroecosystem could limit secondary outbreaks of pest populations (Zheng et al. 2017).

One key aspect in assessing the suitability of a plant species as a banker plant, is the high fitness of the alternative herbivorous prey/host developing on the banker plant, versus a low fitness on crop plants (Huang et al. 2011; Perovic et al. 2018; Damien et al. 2020; Wang et al. 2020). Theoretically, the alternative prey/host on banker plants and the target prey/host on crops form an apparent competition system by sharing a natural enemy (Chailleux et al. 2014b; Desneux et al. 2019; Monticelli et al. 2021). Most studies investigating the suitability of plant species as banker plants focused on a single plant species supporting a single alternative herbivorous prey species (Andorno and Lopez 2014). Conversely in practical applications with multiple biocontrol agents, functional plants were used to provide alternative food resources and shelter to multiple natural enemies but have seldom been evaluated as banker plants. A single functional plant species providing alternative food resources is likely to support populations of natural enemy species with similar ecological niches (Xu et al. 2020), unless they jointly provide alternative food (floral) resources (Wäckers and van Rijn 2012; Zhao et al. 2017; Perovic et al. 2018; Jaworski et al. 2019) and support alternative host/prey populations. However, the simultaneous use of multiple resources in a single banker plant system by different natural enemies may induce competition and/or behavioural disturbances (Bianchi et al. 2006; Chailleux 2013). To avoid this, combining various banker plant species to enhance populations of multiple natural enemy species could create a spatial separation and

help achieve long-term sustainable pest control in multi-pest cropping systems.

Tomato is a major vegetable greenhouse crop in China, attacked by several major insect pest species including the main pest species, the whitefly *B. tabaci* and a secondary pest, the aphid *M. persicae*; both pests are most often present simultaneously and it is necessary to control them together to avoid outbreaks of either species (Lange & Bronson 1981; Hullé et al. 2020). *Encarsia formosa* Gahan (Hymenoptera: Aphelinidae) is a parasitoid wasp specialized on whiteflies and commonly used as a biocontrol agent to suppress *B. tabaci* populations (Enkegaard 2011; Tao et al. 2018). In particular, *E. formosa* can prey and develop on *Trialeurodes ricini* Misra (Hemiptera: Aleyrodidae), a whitefly mainly using the castor bean host plant *Ricinus communis* Linnaeus (Wang et al. 2016): it prefers *R. communis* over other host plants (Huang et al. 2014) and cannot survive on tomato (Shishehbor & Brennan 1996). *Propylea japonica* Thunberg (Coleoptera: Coccinellidae) is a predatory ladybird attacking a variety of prey species, and often used in biocontrol programmes especially to control aphids (Kuroda & Miura 2003; Yang et al. 2014). In particular, *P. japonica* preys and develops on the aphid *Megoura japonica* Matsumura (Hemiptera: Aphididae) (Li et al. 2011). This aphid species develops well on soybean *Glycines max* Merr, or *Vicia faba* Linnaeus (Wang et al. 2013), but has a reduced fitness on tomato crops (Liang Y, unpublished data). Besides, both *R. communis*—*T. ricini* and *G. max*—*M. japonica* have been used as banker plant systems in commercial greenhouses, most often introduced as infested potted plants between cropped plants (Liang Y, unpublished data). Predatory ladybirds often engage in intraguild predation (Ovchinnikov et al. 2019; Liang et al. 2021) and may especially prey on parasitoid wasps developing inside their host (Chacón & Heimpel 2010; Tan et al. 2016; Aparicio et al. 2020). However, ladybirds have limited predation on whiteflies (Tan et al. 2016). This reduces the potential for intraguild predation by *P. japonica* on *E. formosa*, as well as the potential for apparent competition between *M. persicae* and *B. tabaci* mediated by *P. japonica*. Using distinct banker plant systems to support *E. formosa* and *P. japonica* could further enhance such trophic niche partitioning, and hence further reduce the risk for intraguild predation and help enhance the control of the *B. tabaci*—*M. persicae* pest complex in greenhouse tomato crops.

In the present study, we tested the role of combined banker plant systems in enhancing pest control in a commercially realistic multi-pest, multi-biocontrol agent system in a laboratory and greenhouse experiments. Using tomato crops, we measured the abundance of the main pest *B. tabaci* and of the secondary pest *M. persicae*, as well as of their respective introduced biocontrol agents *E. formosa* and *P. japonica*. We evaluated the potential of the two banker plant systems in combination: (1) *R. communis* supporting populations of the whitefly *T. ricini*, itself parasitized by *E. formosa* and (2) *G. max* supporting populations of the aphid *M. japonica*, itself preyed upon by *P. japonica* (Table 1). We investigated the long-term control efficiency of the two pest populations by the two natural enemies (i) in absence of banker plants, (ii) when only one banker plant system targeting the main pest was provided, and (iii) when two banker plant systems in combination were provided. Because of the niche separation of the two biocontrol agents, and the need to control both pest species, we expected that the combination of banker plant systems would be necessary to obtain long-term sustainable pest control in this multi-pest tomato cropping system.

Material and methods

Plants and insects

Plants

Tomato *Solanum lycopersicum* cv. Baofeng and soybean *G. max* cv. YY-1 plants were provided by the Noah Organic Farm (Ping'gu, Beijing, China, N40°09', E116°99'), while castor bean *R. communis* cv. ZB plants were provided by the Jingnan Horticulture Company, Beijing, China, all free of pesticides. All plants were grown in pots (diameter 10 cm, height 10 cm) with a mixed nutrition soil (Miracle-GRO, Ohio, USA) and a hydroponic nutrient solution in a nursery garden free of pathogens and pests at the Institute of Plant and Environment Protection (IPEP), Beijing Academy of Agricultural and Forestry Sciences (BAAFS), Beijing, China, until they developed five true leaves (tomato and *R. communis*) or 20–25 cm height (soybean) to be used for insect rearing or in the laboratory and greenhouse experiments.

Table 1 The banker plant systems used and their targeted natural enemy and apparent pest competitor.

Banker plant system	Banker plant	Target tomato pest	Alternative prey / host	Natural enemy
BPS1	<i>Ricinus communis</i>	<i>Bemisia tabaci</i>	<i>Trialeurodes ricini</i>	<i>Encarsia formosa</i>
BPS2	<i>Glycines max</i>	<i>Myzus persicae</i>	<i>Megoura japonica</i>	<i>Propylea japonica</i>

Pest species

All insects were reared in the insectary of the IPEP. Environmental conditions were automatically regulated (L-100, Suntech, Beijing, China; 25 ± 1 °C, $65 \pm 5\%$ RH, photoperiod: 16 h L: 8 h D and a light intensity of 650 lx). Over 500 *B. tabaci* adults were collected in tomato greenhouses in the Noah Organic Farm and 730 *T. ricini* adults were collected from horticultural *R. communis* plants in the nursery garden of the Jingnan Horticulture Company during May 2019. The *B. tabaci* strain was identified as MEAM1 based on molecular tests from 100 randomly selected individuals (Zhang et al. 2013). Both whitefly species were reared in separate cages with 100 pairs of whiteflies per cage (40 × 40 × 35 cm, made of aluminium frames and 40-mesh fabric net walls). Four tomato plants and four *R. communis* plants were provided as host plants in every cage of *B. tabaci* and *T. ricini* whiteflies, respectively. We produced over 30,000 adults of *B. tabaci* and *T. ricini* each for the experiments.

Over 1000 nymphs of *M. persicae* and 1200 nymphs of *M. japonica* were collected in tomato greenhouses and soybean fields, respectively, in the Noah Organic Farm during May 2019. Up to 300 *M. persicae* or *M. japonica* aphids were placed in a separate cage as previously described with five tomato plants or soybean plants, respectively. Over 30,000 aphids of each species were produced for the experiments.

All colonies were maintained for a year (from May 2019 to June 2020) and had a mixed population structure with both adults and nymphs present simultaneously. Plants were replaced every 5–7 days when needed. About 3–4 and 12–15 generations were completed before the 2019 laboratory experiment and the 2020 greenhouse experiment, respectively.

Natural enemies

Encarsia formosa and *P. japonica* were bought from Hengshui Tianyi Biocontrol Co., Ltd, Hengshui, Hebei, China. Commercial *E. formosa* were provided at the pupal stage parasitizing *B. tabaci* whiteflies at the 3rd–4th nymphal stage and with a single parasitoid wasp per nymph, as evidenced by one visible black dot inside the nymph. Whiteflies were packaged in groups of 1000 nymphs on one tomato leaf. The newly emerged viable *E. formosa* females were collected with a vacuum pipe and maintained in Petri dishes at 10–15 wasps per dish, in which honey was provided for feeding. Wasps were used in the experiments about 1–2 days later. Commercial *P. japonica* were provided as 4th instar larvae, packaged in groups of 30 larvae in a tetrahedron shape paper container filled with sawdust to reduce cannibalism. The larvae were kept in plastic boxes (30 per box, 15 × 15 × 20 cm)

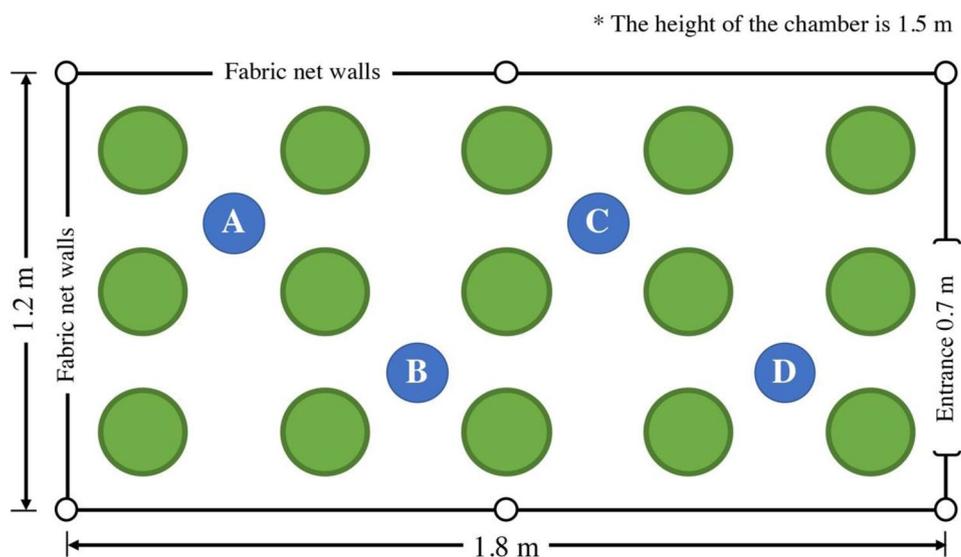
in the insectary and fed artificial diet microcapsules (Tan et al. 2015) daily over the course of the experiments.

Laboratory experiment

In 2019 in a laboratory experiment, we evaluated the potential for the combined use of the *R. communis*—*B. tabaci* and the *G. max*—*M. japonica* banker plant systems to sustainably enhance biological pest control by the combination of the specialist *E. formosa* and the generalist *P. japonica* biocontrol agents (Table 1). We tested four treatments: (a) control with the two pest species *B. tabaci* and *M. persicae* on tomato plants, but no biocontrol agents and no banker plant system; (b) control with the two pest species and the two biocontrol agents but no banker plant system; (c) one-banker plant system with the two pest species and the two biocontrol agents and with the *R. communis*—*B. tabaci* banker plant system; and (d) two-banker plant system with the two pest species, the two biocontrol agents, and the two banker plant systems (*R. communis*—*B. tabaci* and *G. max*—*M. japonica*). Because both *B. tabaci* and *M. persicae* are always present simultaneously in commercial greenhouses, it would be unrealistic to test each pest system in isolation (and besides, this has been tested elsewhere, see eg Chailleux et al. 2014a, 2017). Therefore we did not include a treatment with *B. tabaci*—*E. formosa* or *M. persicae*—*P. japonica* only. Also, *B. tabaci* is the main target of IPM in commercial tomato greenhouses and requires efficient control, most often through releases of *E. formosa*. For this reason, we sought to improve its control by adding a first banker plant system targeting *E. formosa*, but we did not test the second banker plant system (*G. max*—*M. japonica*) alone because it would be unrealistic relative to IPM programmes.

In a cage in the insectary (made of hollow aluminium pipes of diameter 1.5 cm and 40-mesh fabric net walls; 1.8 × 1.2 × 1.5 m; Fig. 1), we placed 15 tomato plants and four banker plants infested with their respective alternative host/prey beforehand. In each cage, two *R. communis* banker plants were placed in A and C. In the two-banker plant system cages, two *G. max* plants were also added in B and D (Fig. 1), while in control cages no banker plant was provided. Ten days before the start of the experiment, tomato and *R. communis* plants were infested with *B. tabaci* and *T. ricini* whiteflies, respectively: 10 pairs of adults were enclosed on each of the five plant leaves with a 40-mesh net. The adults were removed after a two-day egg laying period. Then, eight days later the number of 3rd–4th instar nymphs was adjusted to 100 *B. tabaci* nymphs per tomato plant and 200 *T. ricini* nymphs per *R. communis* plant by gently removing excess nymphs with a brush. Tomato plants were further infested with 30 *M. persicae* 3rd–4th instar aphid nymphs per tomato plant (taken directly from rearing cages) while *G. max* were infested with 250 *M. japonica* 3rd–4th

Fig. 1 Description of the laboratory experiment. Green dots: position of the potted tomato plants and blue dots: position of the infested potted banker plants, in one experimental cage



instar aphid nymphs each. Finally, one day after aphid infestation, 20 parasitoid female adults were introduced on each *R. communis* plant and five ladybird 4th instar larvae on each *G. max* plant if present, or per cage if the banker plants were absent and except in the control—no natural enemy treatment. Ten replicates per treatment (control, no biocontrol agent/control with biocontrol agents/one-banker plant system/two-banker plant system) were produced, with a total of 40 cages. The densities of insects were chosen based on a pilot experiment, and populations of alternative hosts/prey on banker plants were large enough throughout the 14-week duration of the experiment to efficiently sustain natural enemies. We visually observed and counted the number of individuals of each species (*B. tabaci*, *M. japonica*, *E. formosa* and *P. japonica*) of all developmental stages (except eggs) on six randomly selected tomato plants per cage, starting one week after the release of biocontrol agents and every Monday from June 3rd to September 30th, 2019. We calculated the total number of insects of each species per six plants by summing numbers counted in each of the six plants, so as to obtain one value per cage and per week. Environmental conditions were the same as for insect rearing (see “Plants and insects” section).

Greenhouse experiment

In 2020, we performed a greenhouse experiment to estimate the potential for the combined banker plant systems to be used in practical biocontrol greenhouse applications, involving multiple pest and biocontrol agent species. We tested the same four treatments as in our 2019 laboratory experiment (control, no biocontrol agent/control with biocontrol agents/one-banker plant system/two-banker plant system). We used four glass greenhouses located in the Noah

Organic Farm (100 × 14 m, height 4.2 m). Each greenhouse was composed of ten independent chambers (12 × 12 m) isolated with plastic membranes preventing arthropod movement between chambers. In each chamber, we transplanted 56 tomato plants in seven rows with eight plants per row (Fig. 2). We transplanted two *R. communis* plants in each of four random points among the nine blue points shown in Fig. 2 in each chamber. In the two-banker plant system chambers, we also added two *G. max* plants in each of four other randomly selected points. In the control chambers, no banker plant nor associated alternative prey/host was provided. Two days after transplantation, 14 tomato plants randomly selected in each chamber were infested with *B. tabaci* adults and the *R. communis* banker plants were infested with *T. ricini* adults, following the same method as in the laboratory experiment. After three days—whitefly nymphs had emerged by then—another 14 randomly selected tomato plants were infested with 30 3rd–4th *M. persicae* aphid nymphs per plant, and *G. max* plants were infested with 250 *M. japonica* aphid nymphs each. After two more days, 20 parasitoid female adults were released on each of the eight *R. communis* plants, and five ladybird 4th instar larvae were released on each of the eight *G. max* plants per cage if the banker plants were present, or in four of the nine blue points randomly selected if the banker plants were absent. In the control—no natural enemy treatment, no biocontrol agents were released. Each treatment was replicated in ten chambers, randomly selected across the four greenhouses. The insect densities in greenhouses were chosen based on authors’ preliminary surveys, and populations of alternative hosts/prey on banker plants were large enough throughout the 14-week duration of the experiment to efficiently sustain natural enemies.

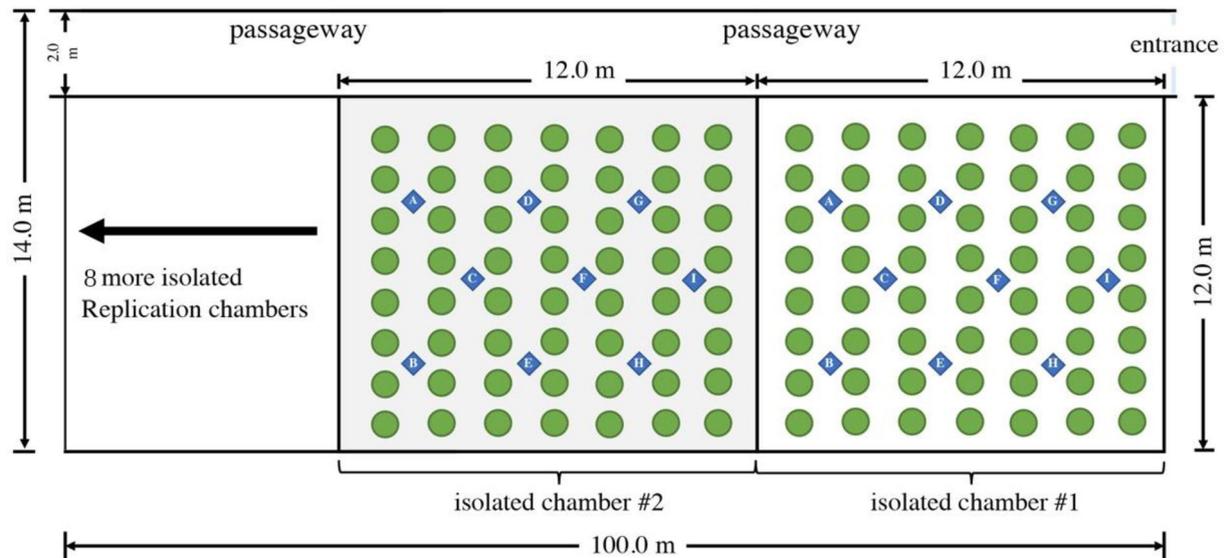


Fig. 2 Description of the greenhouse experiment. Green dots: position of tomato plants and blue dots: position of infested banker plants in one greenhouse chamber. In each chamber, only four positions were used for each banker plant system

We monitored population dynamics of the two targeted pest species (*B. tabaci* and *M. persicae*) and of the two introduced biocontrol agents (*E. formosa* and *P. japonica*), starting one week after biocontrol agent releases and every Monday from June 1st to September 28th, 2020. At each sampling date, we randomly selected eight plants per chamber and inspected all plant parts, and counted all insect individuals (except eggs). We calculated the total number of insects of each species per eight plants by summing numbers counted in each of the eight plants, so as to obtain one value per greenhouse chamber and per week. The environmental conditions inside greenhouses followed seasonal trends (June: 26.9 ± 0.4 °C, $32.2 \pm 1.9\%$ RH; July: 26.3 ± 0.4 °C, $41.6 \pm 1.6\%$ RH; August: 26.2 ± 0.4 °C, $36.5 \pm 1.9\%$ RH; September: 21.4 ± 0.5 °C, $24.8 \pm 1.5\%$ RH).

Statistical analyses

All statistical analyses were performed with R Core Team (2020) version 3.6.3. We analysed the impact of the treatment (control—no natural enemy/control—with natural enemies/one-banker plant system/two-banker plant system) on the number of insects per six plants in the laboratory experiment independently for each insect pest (*B. tabaci* vs. *M. persicae*) and natural enemy (*E. formosa* vs. *P. japonica*) species, because of large differences in densities and population dynamics (see Results). We used Generalized Linear Models (GLMMs) with a negative binomial distribution recommended for count data with overdispersion (function ‘glmer.nb’, library ‘lme4’; Bates et al. 2015). Treatment was

used as a fixed effect, while cage and week were used as random effects to account for repeated measures through time, and patterns of insect population dynamics, respectively. Treatment significance was tested with an ANOVA based on a χ^2 test. Model validity was verified a posteriori (functions ‘simulateResiduals’ and testDispersion’, library ‘DHARMA’; Hartig 2020). To assess whether means across treatments were significantly different, we performed a post hoc comparison of means by computing estimated marginal means (function ‘emmeans’, library ‘emmeans’; Lenth 2021). Statistical tests used for the greenhouse experiment were identical to those described for the laboratory experiment.

Table 2 Impact of the treatment (control—no natural enemy/control—with natural enemies/one-banker plant system/two-banker plant system) on the abundances of the two pest species *B. tabaci* and *M. persicae* and of their respective biocontrol agents *E. formosa* and *P. japonica* in the laboratory and the greenhouse experiments

	χ^2	d.f	P
Laboratory experiment			
<i>B. tabaci</i>	143	3	<0.001***
<i>M. persicae</i>	120	3	<0.001***
<i>E. formosa</i>	69.7	2	<0.001***
<i>P. japonica</i>	84.6	2	<0.001***
Greenhouse experiment			
<i>B. tabaci</i>	194	3	<0.001***
<i>M. persicae</i>	118	3	<0.001***
<i>E. formosa</i>	71.0	2	<0.001***
<i>P. japonica</i>	66.1	2	<0.001***

*** $P < 0.001$

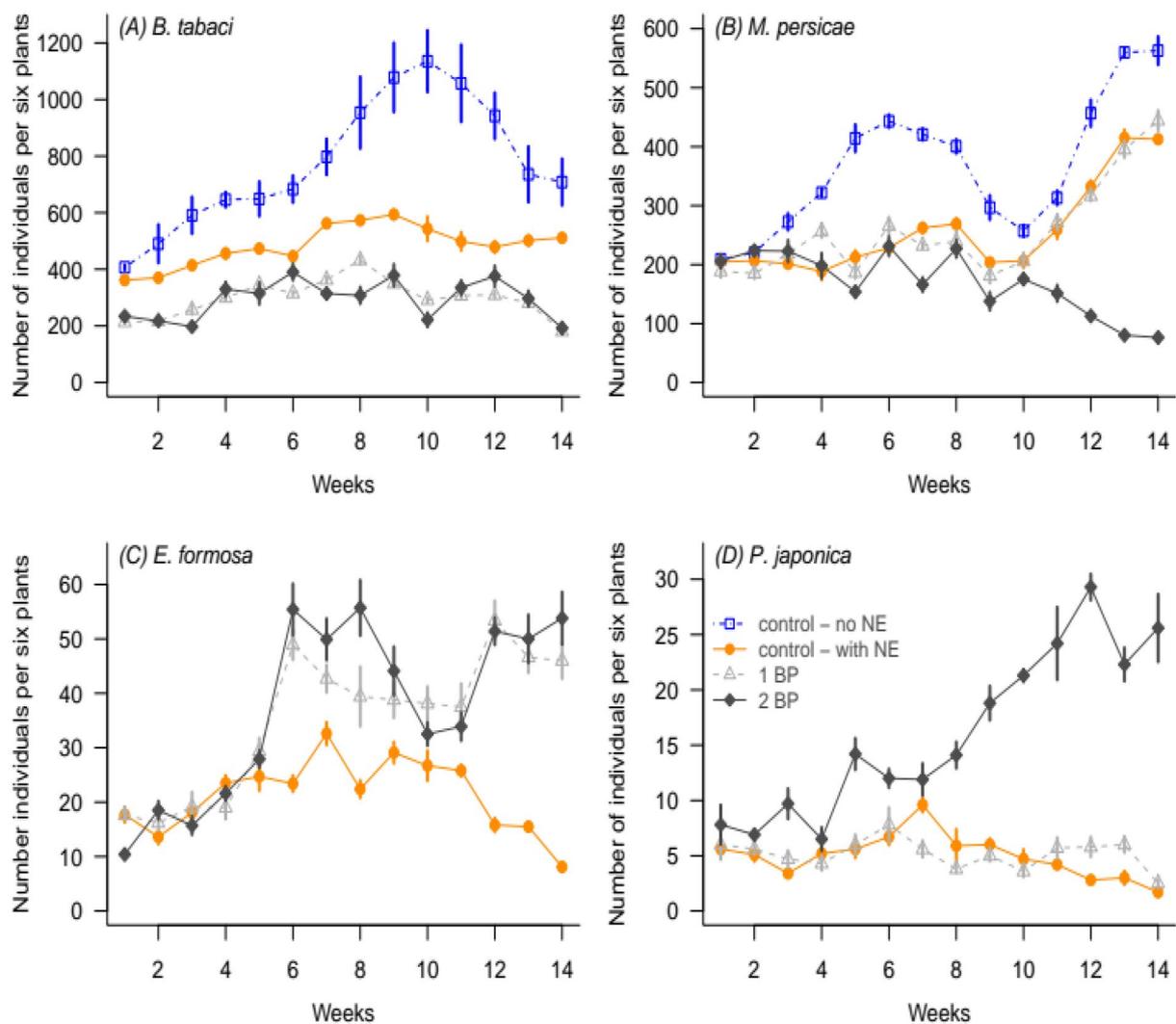


Fig. 3 Insect population dynamics in laboratory cages in the one-banker plant systems (dashed, light grey), two-banker plant systems (solid, dark grey), or without banker plants and with natural enemies (solid, orange) or without natural enemies (dashed, blue). Mean \pm SE per week of individuals per six tomato plants (adults and juveniles)

of pests: (A) *B. tabaci*, (B) *M. persicae*; and of natural enemies: (C) *E. formosa*, (D) *P. japonica* ($N=10$ cages per treatment). NE: natural enemy; 1 BP: one-banker plant system; 2 BP: two-banker plant system

Results

Laboratory experiment

The presence of natural enemies and of banker plants significantly affected the abundances of all four species (Table 2, Fig. 3). The presence of natural enemies prevented the early pest outbreaks of *B. tabaci* (populations 1.6 times lower in average: mean \pm SE of individuals per six plants: control—no natural enemy 777 ± 29 , control—with natural enemies 485 ± 7 ; Table 3, Fig. 3a) and of *M. persicae* (populations 1.4 times lower in average: control—no natural enemy 368 ± 10 , control—with natural enemies 257 ± 7 ; Table 3, Fig. 3b) in Weeks 2–8.

Adding one banker plant type (*R. communis*—*T. ricini*) caused a further significant reduction in *B. tabaci* numbers (297 ± 6 , 0.6 times lower) compared with the control—with natural enemies systems, but this was not true for *M. persicae* (256 ± 7). Finally, adding a second banker plant type (*G. max*—*M. japonica*) caused a further significant reduction in *M. persicae* numbers (169 ± 5 , 1.5 times lower) compared with the control—with natural enemies systems or the one-banker plant systems, and thanks to the suppression of the second aphid population outbreak in Weeks 10–14. Conversely in *B. tabaci*, no second outbreak was observed, and numbers were not different between the two-banker plant systems (293 ± 9) and the one-banker plant systems.

Table 3 Comparisons of means between treatments in the number of individuals per six plants for each insect species in the laboratory experiment (emmeans: contrast estimates \pm SE and associated *P*-value)

	Estimate \pm SE	<i>P</i>
<i>B. tabaci</i>		
1BP–2BP	0.0109 \pm 0.0320	0.99
1BP–Control (no NE)	–0.950 \pm 0.032	<0.001***
1BP–Control (with NE)	–0.501 \pm 0.032	<0.001***
2BP–Control (no NE)	–0.961 \pm 0.032	<0.001***
2BP–Control (with NE)	–0.512 \pm 0.032	<0.001***
Control (no NE)–Control (with NE)	0.450 \pm 0.032	<0.001***
<i>M. persicae</i>		
1BP–2BP	0.361 \pm 0.037	<0.001***
1BP–Control (no NE)	–0.361 \pm 0.037	<0.001***
1BP–Control (with NE)	–0.00732 \pm 0.037	0.99
2BP–Control (no NE)	–0.722 \pm 0.037	<0.001***
2BP–Control (with NE)	–0.369 \pm 0.037	<0.001***
Control (no NE)–Control (with NE)	0.353 \pm 0.037	<0.001***
<i>E. Formosa</i>		
1BP–2BP	–0.0373 \pm 0.042	0.64
1BP–Control (with NE)	0.457 \pm 0.044	<0.001***
2BP–Control (with NE)	0.494 \pm 0.044	<0.001***
<i>P. japonica</i>		
1BP–2BP	–1.11 \pm 0.06	<0.001***
1BP–Control (with NE)	0.0385 \pm 0.0712	0.85
2BP–Control (with NE)	1.15 \pm 0.06	<0.001***

****P* < 0.001

Populations of *E. formosa* were enhanced by the presence of the *R. communis*–*T. ricini* banker plant systems with a 1.2 increase in numbers of *E. formosa* individuals per six plants at Week 5 (mean \pm SE: 35 \pm 1; Fig. 3c) compared with the control—with natural enemies systems (21 \pm 1; Table 3, Fig. 3c). However, adding a second banker plant type had no significant effect on *E. formosa* numbers compared (37 \pm 2) with one banker plant type only. Finally, *P. japonica* numbers per six plants were not significantly different in presence (5.2 \pm 0.2) or in absence of one banker plant type (5.0 \pm 0.2), but they were 3.2 times higher in the two-banker plant systems (16 \pm 1; Fig. 3d, Table 3).

Greenhouse experiment

Similar to the laboratory experiment, the presence of banker plant systems in the greenhouse experiment significantly impacted the population densities of all four species (Fig. 4; Table 2). The presence of natural enemies prevented the first pest outbreak in Weeks 2–8, with *B. tabaci* numbers per eight plants 1.6 times lower in the control—with natural enemies systems (mean \pm SE of individuals per eight plants: 672 \pm 11) compared with the control—no natural

enemy systems (1,068 \pm 22; Fig. 4a, Table 4), and *M. persicae* numbers 1.3 times lower in the control—with natural enemies systems (182 \pm 6) compared with the control—no natural enemy systems (250 \pm 6; Fig. 4b, Table 4). Also, adding one banker plant system (*R. communis*–*T. ricini*) caused a further significant reduction in *B. tabaci* numbers (428 \pm 6, 1.6 times lower) compared with the control—with natural enemies systems, but this was not true in *M. persicae* (180 \pm 6). Finally, adding a second banker plant system (*G. max*–*M. japonica*) resulted in a further decrease in *M. persicae* numbers (105 \pm 3, 1.7 times lower) compared with the control—with natural enemies systems, again thanks to the suppression of the second aphid population outbreak in Weeks 10–14. Conversely and consistent with the laboratory experiment, there was no second population outbreak in *B. tabaci* populations, and their numbers in the two-banker plant systems (406 \pm 7) were not different than in the one-banker plant systems.

Consistent with the laboratory experiment, *E. formosa* populations were enhanced by the presence of the *R. communis*–*T. ricini* banker plant system with populations increasing from Week 3 and 2.1 times higher in average in the one-banker plant systems (mean \pm SE of individuals per eight plants: 145 \pm 7) compared with the control—with natural enemies systems (67 \pm 3; Fig. 4c, Table 4). However, their numbers were not different in the two-banker plant systems (142 \pm 6) compared with the one-banker plant systems. Finally, *P. japonica* numbers per eight plants were not different between the one-banker plant systems (41 \pm 2) and the control—with natural enemies systems (42 \pm 2), but they were significantly increased and 2.2 times higher in the two-banker plant systems (92 \pm 4) compared with the one-banker plant systems, thanks to a continuous increase in population densities from Week 3 to 13 (Fig. 4d, Table 4).

Discussion

The use of banker plants has been proposed as a sustainable and economically viable solution to enhance the populations of natural enemies by supporting alternative arthropod prey or host populations (Huang et al. 2011). They could help decrease the cost of biocontrol agent releases and increase pest control effectiveness (Naranjo et al. 2015; Stiling and Simberloff 2000). Yet, with the increased complexity in biocontrol application systems, the use of single banker plant systems may not be efficient to support multiple released biocontrol agent species. In the present study, we tested the potential for a combination of two banker plant systems to promote the simultaneous control of two major tomato pests by two biocontrol agents, in a laboratory and a greenhouse experiment. We showed that combined banker plant systems increased the control of both the main tomato pest

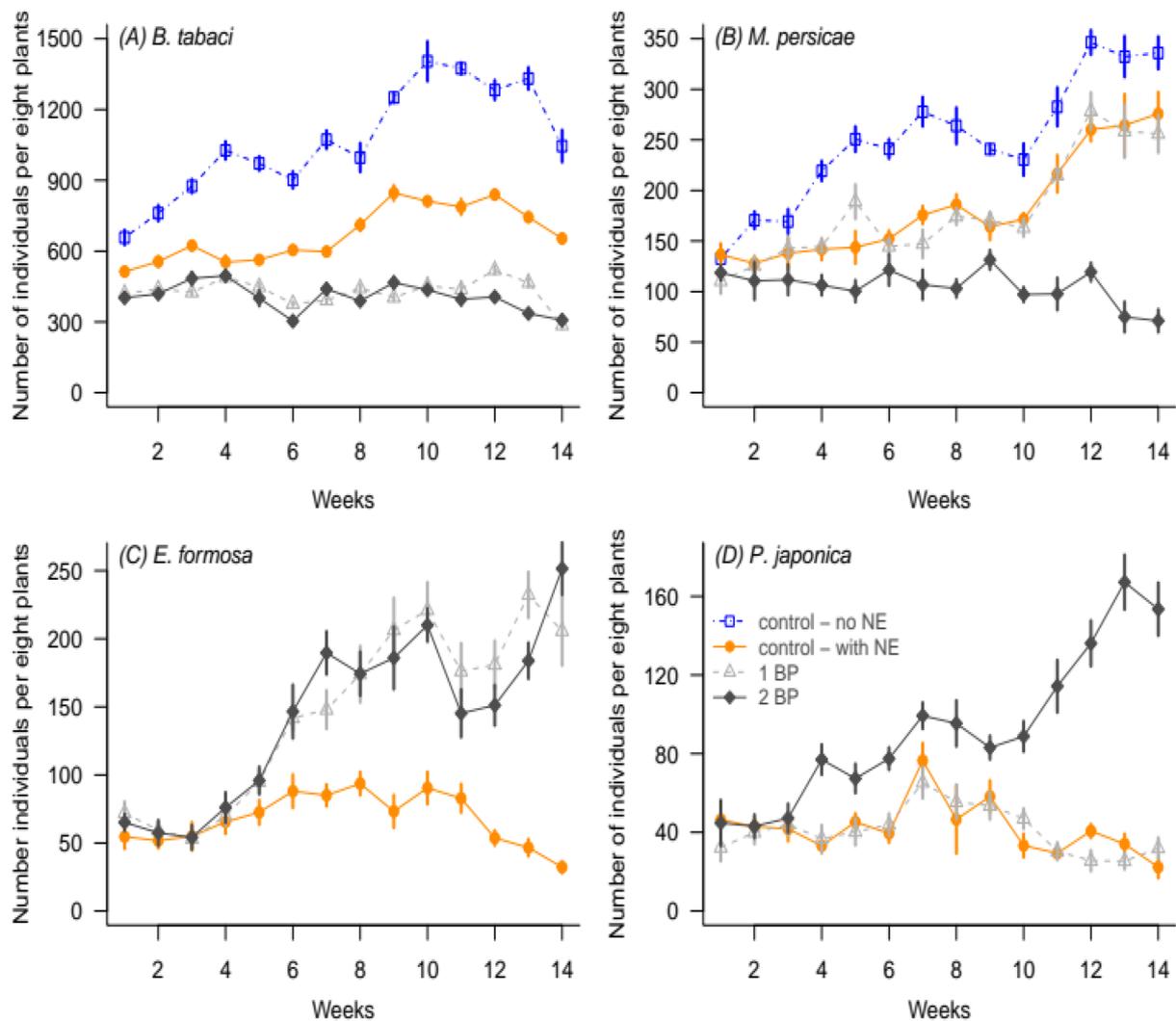


Fig. 4 Insect population dynamics in greenhouse chambers in the one-banker plant systems (dashed, light grey), two-banker plant systems (solid, dark grey), or without banker plants and with natural enemies (solid, orange) or without natural enemies (dashed, blue). Mean \pm SE per week of number of individuals per eight tomato plants

(adults and juveniles) of pests: **(A)** *B. tabaci*, **(B)** *M. persicae*; and of natural enemies: **(C)** *E. formosa*, **(D)** *P. japonica* ($N=10$ chambers per treatment). NE: natural enemy; 1 BP: one-banker plant system; 2 BP: two-banker plant system

B. tabaci by *E. formosa* and the secondary pest *M. persicae* by *P. japonica* in both laboratory and greenhouse settings. Notably, adding the *R. communis*—*T. ricini* banker plant system allowed the suppression of the early population outbreak in *B. tabaci*, while adding the *G. max*—*M. japonica* system allowed the suppression of the early and late population outbreaks in *M. persicae*.

As expected, we found that the *R. communis*—*T. ricini* banker plant system promoted the populations of *E. formosa* resulting in an increased control of *B. tabaci* populations, while only the use of the *G. max*—*M. japonica* system promoted *P. japonica* populations and resulted in an increased control of the secondary pest *M. persicae*. This proves the efficacy of the chosen banker plant

systems to promote these target biocontrol agent species, but also their strong specificity to the target biocontrol agents. This is because *E. formosa* is specialized on whiteflies, and hence cannot use aphids as alternative hosts (Tao et al. 2018). Similarly, the predatory ladybird *P. japonica*, although polyphagous (Yang et al. 2014), primarily feeds on aphids and has a reduced fitness when fed on *B. tabaci* (Liu et al. 2008). This would explain that the *R. communis*—*T. ricini* system did not enhance *P. japonica* populations, resulting in poor control of *M. persicae*. Indeed the densities of *P. japonica* populations were too low to prevent the late population outbreak of *M. persicae*, suppressed in the two-banker plant systems only, in which *P. japonica* populations reached twice as high densities.

Table 4 Comparisons of means between treatments in the number of individuals per eight plants for each insect species in the greenhouse experiment (emmeans: contrast estimates \pm SE and associated *P*-value)

	Estimate \pm SE	<i>P</i>
<i>B. tabaci</i>		
1BP–2BP	0.0530 \pm 0.0211	0.058
1BP–Control (no NE)	–0.902 \pm 0.021	<0.001 ***
1BP–Control (with NE)	–0.444 \pm 0.021	<0.001 ***
2BP–Control (no NE)	–0.955 \pm 0.021	<0.001 ***
2BP–Control (with NE)	–0.497 \pm 0.021	<0.001 ***
Control (no NE)–Control (with NE)	0.459 \pm 0.021	<0.001 ***
<i>M. persicae</i>		
1BP–2BP	0.489 \pm 0.040	<0.001 ***
1BP–Control (no NE)	–0.331 \pm 0.039	<0.001 ***
1BP–Control (with NE)	–0.0162 \pm 0.0393	0.98
2BP–Control (no NE)	–0.820 \pm 0.040	<0.001 ***
2BP–Control (with NE)	–0.506 \pm 0.040	<0.001 ***
Control (no NE)–Control (with NE)	0.314 \pm 0.039	<0.001 ***
<i>E. Formosa</i>		
1BP–2BP	0.0273 \pm 0.054	0.90
1BP–Control (with NE)	0.660 \pm 0.056	<0.001 ***
2BP–Control (with NE)	0.636 \pm 0.056	<0.001 ***
<i>P. japonica</i>		
1BP–2BP	–0.813 \pm 0.067	<0.001 ***
1BP–Control (with NE)	–0.0299 \pm 0.0671	0.90
2BP–Control (with NE)	0.783 \pm 0.067	<0.001 ***

****P* < 0.001

The limited overlap between natural enemies supported by distinct banker plant systems could be beneficial to avoid the disruption of pest control. Such disruption could occur if natural enemies compete for the same pest resource—the main pest—and this could notably cause population outbreaks of secondary pest species (Bhattacharyya and Sinha 2009) through intraguild predation (Liang et al. 2021) or through apparent competition in multi-pest systems (Jaworski et al. 2015).

Both in the laboratory and greenhouse experiments, we observed a niche partitioning between the main tomato pest *B. tabaci* and the secondary tomato pest *M. persicae* in absence of natural enemies. Aphid populations rose rapidly in Weeks 2–6 and then decreased in Weeks 7–10 under high summer temperatures, while *B. tabaci* populations rose slower to peak in Week 10. However, once *B. tabaci* populations decreased in late summer, aphid populations broke out again. Such dynamics are common in tomato cropping systems, and highlight the need for long-term sustainable pest control solutions that target both main and secondary pests (Lu et al. 2004; Ap et al. 2019). In the banker plant systems, the alternative host *T. ricini*

and prey *M. japonica* did not occupy the niche left empty by the control of *B. tabaci* and *M. persicae* populations as they preferred their primary host plants *R. communis* and *G. max*, respectively. Therefore, they did not damage tomato crops, showing their suitability as banker plant systems for pest control in commercial greenhouse crops.

In the present study, we deliberately released *E. formosa* at higher densities than *P. japonica*, and proportionally to the densities of their respective target pests *B. tabaci* and *M. persicae*. These pest densities simulated real conditions commonly found in commercial greenhouse cropping systems, and in response multi-species releases of biocontrol agents are often asymmetric (Liu et al. 2013; Ma et al. 2018). The specialist natural enemy is released at higher densities to control the main pest species, while the generalist natural enemy is released at lower density to provide the suppression of the populations of secondary pest species throughout the cropping season (Garey and Ruffié 1987; Fonseca et al. 2020).

One key aspect in the commercial development of banker plant systems is to adjust the balance between the densities of the target and alternative hosts/prey (Frank 2010). Since they are targeted by a shared natural enemy, the target and alternative host/prey are under apparent competition in cropping systems enriched with banker plants (van Veen et al. 2006; Jaworski et al. 2015). Hence, adding too many banker plant units may cause natural enemies to reduce pressure on target pests, resulting in poor control (Orrock et al. 2010). Conversely, adding too few banker plant units may be insufficient to enhance natural enemy populations resulting in too low densities and poor establishment of their populations and therefore a poor pest control in the long term. Future research in banker plant applications should focus on developing flexible systems to accurately adjust the density of alternative prey/hosts and improve the sustainable control of arthropod complex by using multi-species biocontrol agent releases. Finally, it could be useful to investigate the potential for dual functions of banker plants, such as supporting populations of alternative prey/hosts and providing alternative floral resources (Wäckers and van Rijn 2012). This would allow the design of IPM strategies supporting populations of specialist and generalist biocontrol agent species in multi-species systems and providing pest control over the short-term and the long-term.

In conclusion, our study showed that the combined use of multiple banker plant systems targeting distinct biocontrol agents significantly increased the control of both main and secondary target pest populations. Banker plants were necessary to avoid pest outbreaks and to provide long-term pest control via the establishment of natural enemy populations at high densities.

Author contributions

SW, ND, CCJ, YL and XG designed the study; CX and JW performed the experiments; CX, HDJ and CCJ analysed the data; YL, CX, CCJ, LSZ and SW wrote the manuscript. All authors read and approved the manuscript for submission.

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Declarations

Conflict of interest Authors declare they have no competing interests.

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