

Banker plants promote functional biodiversity and decrease populations of the cabbage whitefly *Aleyrodes proletella*

Sebastian Laurenz  | Rainer Meyhöfer 

Leibniz Universität Hannover, Institute of Horticultural Production Systems, Section Phytomedicine, Hannover, Germany

Correspondence and present address

Sebastian Laurenz, Georg-August-Universität Göttingen, Department of Crop Sciences, Agricultural Entomology, Grisebachstraße 6, 37077 Göttingen, Germany.

Email: sebastian.laurenz@uni-goettingen.de

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Abstract

In this study, potential banker plant systems against the cabbage whitefly *Aleyrodes proletella* Linnaeus (Hemiptera: Aleyrodidae) were developed under controlled conditions. The two most promising banker plant systems, that is, the parasitoid *Encarsia tricolor* Förster (Hymenoptera: Aphelinidae) either with *Aleyrodes loniceriae* Walker on European columbine (columbine system) or with *Trialeurodes vaporariorum* Westwood (Hemiptera: Aleyrodidae) on Hokkaido squash (pumpkin system), were further evaluated in the field. Although the pumpkin system produced three times more parasitoids than the columbine system, both banker plants led to an 1.5-fold increase in *A. proletella* parasitism rates. However, only the pumpkin system increased the abundance of syrphid larvae on cabbage by 61.5% and reduced *A. proletella* populations on average by 4.4%–25.8% depending on the respective assessment date. In conclusion, the pumpkin system revealed to be a promising (supplementary) control measure against *A. proletella*. Options for further improvement and standardization of the pumpkin system as well as a potential implementation in cabbage production are discussed.

KEYWORDS

Aleyrodidae, alternative hosts/prey, biological control, *Encarsia tricolor*, habitat manipulation, natural enemies

1 | INTRODUCTION

Since the 1990s, the cabbage whitefly *Aleyrodes proletella* Linnaeus (Hemiptera: Aleyrodidae) has regained increased importance; it has spread worldwide and has become a major pest on several *Brassica* crops in Europe (De Barro & Carver, 1997; Evans, 2007b; Loomans et al., 2002; Nebreda & Nombela, 2005; Trdan et al., 2003).

Especially organic cabbage producers lack efficient control measures against *A. proletella*. Although conventional control with chemical insecticides has proven high efficacies against *A. proletella* under controlled and field conditions, there is an increasing demand

for insecticide-free and ecologically sustainable pest management (Kovářiková et al., 2017; Richter & Hirthe, 2014). Alternatives to conventional insecticides are therefore desperately needed. Besides cropping of resistant cabbage plants (Hondelmann et al., 2020), cultural control measures like fine crop cover netting can lead to a remarkable reduction of *A. proletella* populations (Saucke et al., 2011). However, this effect often disappears later in the growing season; crop cover nets are labour intensive, may facilitate aphid pests and hinder colonization by natural enemies (Ludwig & Meyhöfer, 2016). Biological control strategies exploiting natural enemies pose another non-chemical alternative to reduce *A. proletella* populations on cabbage crops.

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Arthropodan natural enemies of *A. proletella* comprise hymenopteran parasitoids, syrphid larvae, spiders, coccinellids, predatory bugs, lacewing larvae, predatory flies and predatory gall midges (Butler, 1936; Evans, 2007b; Gumovsky, 2005; Laurenz et al., 2019; Mound & Halsey, 1978; Noyes, 2020; Pütz et al., 2000; Springate, 2017; Springate & Arnold, 2011; Stein, 1958; van Rijn et al., 2008). The only specialists on whiteflies are the parasitoid species and the coccinellid *Clitostethus arcuatus* Rossi (Coleoptera: Coccinellidae). While the majority of these whitefly specialists is only found in low numbers, *Encarsia tricolor* Förster (Hymenoptera: Aphelinidae) is often the dominating parasitoid and supposed to be the most important natural enemy of *A. proletella* (Laurenz et al., 2019; Stein, 1958). However, *E. tricolor* may appear too late in the season or in insufficient numbers to suppress *A. proletella* populations significantly (Laurenz et al., 2017; Springate, 2016).

Well-timed release of *E. tricolor* may serve a solution. Although mass release by hand is promising under semi-field conditions on caged cabbage plants, results under field conditions are variable (Saucke et al., 2011; Springate, 2016). A release of natural enemies on banker plants can be more effective than hand-release (Kidane et al., 2018; Pickett et al., 2004). Banker plants are a biological control method for an early and continuous release of natural enemy populations in a crop. A banker plant system consists of a plant species deliberately infested with herbivores which serve as alternative hosts/prey for natural enemies of the target pest. Alternative hosts/prey as well as shelter and reproduction habitats are permanently provided even in absence of the pest.

Banker plant systems are well adopted in greenhouse crops against aphids, whiteflies and other pests (Huang et al., 2011). However, studies reporting the use of banker plants against whitefly pests in field crops are limited (Goolsby & Ciomperlik, 1999; Kidane et al., 2018; Pickett et al., 2004). Goolsby and Ciomperlik (1999) successfully released estimated numbers of 4,156–68,946 *Eretmocerus hayati* (Hymenoptera: Aphelinidae) parasitoids per acre on cantaloupe banker plants preinfested with the silverleaf whitefly *Bemisia argentifolii* (Hemiptera: Aleyrodidae). In another study, parasitism rates of the sweet potato whitefly *Bemisia tabaci* could be increased by the release of *Eretmocerus* spp. on cantaloupe banker plants, but whitefly densities were not affected (Pickett et al., 2004). Kidane et al. (2018) evaluated two banker plant systems, *Encarsia sophia* on melon and *Er. hayati* on castor bean (both with *B. tabaci* as host), in a semi-field study. Next to higher parasitism rates, either system also decreased *B. tabaci* infestations on tomato as target crop.

The host range of *E. tricolor* comprise at least 18 whitefly species worldwide. Among these whiteflies, the honeysuckle whitefly *Aleyrodes lonicerae* Walker and the greenhouse whitefly *Trialeurodes vaporariorum* Westwood (both Hemiptera: Aleyrodidae) are the only whiteflies that are distributed to Central Europe, possess herbaceous host plants and are not known to cause damage to *Brassica* crops (Else & Farnham, 1994; Evans, 2007a; Mound & Halsey, 1978; Noyes, 2020). Therefore, both whitefly species are considerable alternative hosts for *E. tricolor* as natural enemy in a banker plant system against *A. proletella*.

The aim of this study is to develop and evaluate different banker plant systems with *E. tricolor* as natural enemy against *A. proletella* under controlled conditions and in the field.

2 | MATERIAL AND METHODS

2.1 | Insects and plants

All insects used in this study derived from rearings established at the Section Phytomedicine, Institute of Horticultural Production Systems, Leibniz Universität Hannover, Germany. The whiteflies, that is, *A. lonicerae*, *A. proletella* and *T. vaporariorum*, were reared on *Aegopodium podagraria* (ground elder), *Brassica oleracea* var. *gemmifera* (Brussels sprouts) and *Cucurbita maxima* 'Uchiki Kuri' (Hokkaido squash), respectively. Recently emerged females (wings translucent and not yet fully expanded) and males were collected from the respective rearing to be used in the experiment. *Aleyrodes proletella* on Brussels sprouts was used as rearing system for *E. tricolor*. Mated *E. tricolor* females for experiments were produced as follows: leaves with parasitized whitefly puparia (dark) were placed in a plastic box with a translucent, perforated lid and incubated at room temperature for 48 hr. About 20 emerged females and five males were then transferred to a snap-cap vial (height: 80 mm, diameter: 30 mm) with a perforated lid and honey droplets as food source. They were kept together for another 4 days. The 5–6 days old females were then expected to be mated and were used for experiments. Ground elder was propagated from rhizomes, all other experimental plants from seeds. Plants were grown in pots (diameter: 120 mm) under greenhouse conditions before being used for experiments when three to six true leaves were fully expanded.

2.2 | Whitefly performance

Reproduction and development of the alternative whitefly hosts were evaluated on selected host plants and Brussels sprouts as control treatment. Selected host plants were *Aquilegia vulgaris* (European columbine), *Campanula persicifolia* (peach-leaved bellflower), *Elsholtzia ciliate* (Vietnamese balm), *Fragaria vesca* (wild strawberry), *Geum urbanum* (wood avens), *Hypericum perforatum* (St John's wort), *Lysimachia vulgaris* (garden loosestrife), *Melissa officinalis* (lemon balm), *Origanum vulgare* (oregano) and *A. podagraria* (ground elder) for *A. lonicerae*, and *C. maxima* 'Uchiki Kuri' (Hokkaido squash) for *T. vaporariorum* (Bährmann, 2002; Huldén, 1986; Mound & Halsey, 1978). These herbaceous plants are compatible with the environmental conditions on Central European farmland and are neither known as economically relevant pest weeds nor as host plants for *A. proletella* (Ellenberg, 1979; Mound & Halsey, 1978; Weber & Gut, 2005). The performance of *A. proletella* was evaluated on the seven most suitable host plants for *A. lonicerae* and *T. vaporariorum* and on Brussels sprouts as control treatment. Therefore, a recently emerged whitefly female and three conspecific males were

transferred to a leaf cage (Ø 140 mm), which was fixed to the first fully expanded true leaf of a plant (Rechner et al., 2017). The leaf cage was built of a Petri dish with a gauze lid; a small opening (sealed with cotton wool) on one side for the leaf petiole enables to insert an entire living leaf or a leaflet. A construction of three wooden sticks glued to a Petri dish lid held the cage stable in the appropriate position and a clip on each wooden stick enabled to adjust the height of the cage. The males were removed after 14 days. Female mortality was evaluated every 2–3 days to compare its longevity on the different plant species. In an interval of 14 days, females were shortly immobilized with carbon dioxide and gently transferred to another plant of the same age. Deposited eggs (sum of hatched and not hatched eggs) were counted and further observed to determine egg-adult development times and nymphal mortality. Six replicates were conducted of each treatment. Experiments were performed under controlled conditions at 16 hr day (light, $25 \pm 1^\circ\text{C}$, $61 \pm 5\%$ r. h.) and 8 hr night (dark, $18 \pm 1^\circ\text{C}$, $67 \pm 5\%$ r. h.).

2.3 | Parasitoid performance

The performance of *E. tricolor* was investigated on the following four whitefly-plant combinations: *A. lonicerae* on the two most suitable host plants based on the whitefly's performance, *T. vaporariorum* on Hokkaido squash and *A. prolella* on Brussels sprouts (control). Therefore, 30 adult whiteflies were caged to the underside of the youngest fully expanded leaf for 48 hr. The offspring developed into the second and third nymphal stage before being gently reduced to 25 individuals per leaf with the help of a dissection needle. A 5–6 days old mated *E. tricolor* female was then caged to the whitefly nymphs and allowed to deposit eggs for 24 hr. Parasitoid offspring that turned into pupae (dark whitefly nymph) were individually transferred to gel capsules and further observed until adult emergence. The numbers of pupal and adult offspring as well as developmental times were evaluated daily. To investigate parasitoid fitness, the head widths of emerged *E. tricolor* adults as well as length and width of the respective whitefly nymphs' exuviae were determined under the microscope (van Lenteren et al., 1976; Williams, 1995). The areal host size was calculated from the exuviae length and width by expecting an ellipse host shape applying the following formula: areal host size = π (length/2) (width/2). Each treatment was replicated 14–21 times and all *E. tricolor* females within one treatment derived from different leaves. Experimental conditions were the same as described before.

2.4 | Field evaluation

Two banker plant systems were evaluated under field conditions, that is, European columbine with *A. lonicerae* and *E. tricolor* (columbine system), and Hokkaido squash with *T. vaporariorum* and *E. tricolor* (pumpkin system). An experimental plot consisted of two areas of Brussels sprouts plants (each 4 m × 2.4 m, 0.6 m between

rows, 0.5 m between plants). The area between the Brussels sprouts (2.4 m × 2 m) was planted with the columbine system (0.25 m between rows and plants), the pumpkin system (0.75 m between rows and plants) or covered with mulch foil to prevent vegetation (control treatment). Plots were arranged in a randomized block design with six replicates and 14–17 m distance between plots. The space between the plots was covered with grass, which was kept short by regular mowing.

The banker plant species were grown separately under two gauze tents in the greenhouse. When one to three true leaves were fully expanded, European columbine and Hokkaido squash plants were evenly infested with 3,000 females of the respective alternative host (nine and 83 females per plant, respectively; Goolsby & Ciomperlik, 1999; Pickett et al., 2004). After 14 days, 375 *E. tricolor* females were evenly released European columbine and Hokkaido squash plants (one and 10 females per plant, respectively). Banker plants were left under the gauze tents for another 11 days and then removed from the greenhouse for cold hardening for five days before being planted to the experimental plots.

Eight Brussels sprouts plants (in each of the two Brussels sprouts areas in a plot two plants in 1.5 m and two plants in 4 m distance to the banker plants), four European columbine plant and the central 2 m² of the pumpkin system were assessed per plot in a 14-day interval. Same plants were taken for assessments throughout the experiment. Non-parasitized and parasitized whitefly puparia were counted per plant to calculate parasitism rates. Further determined parameters were the numbers of adult *E. tricolor*, whitefly predators and herbivores other than whiteflies.

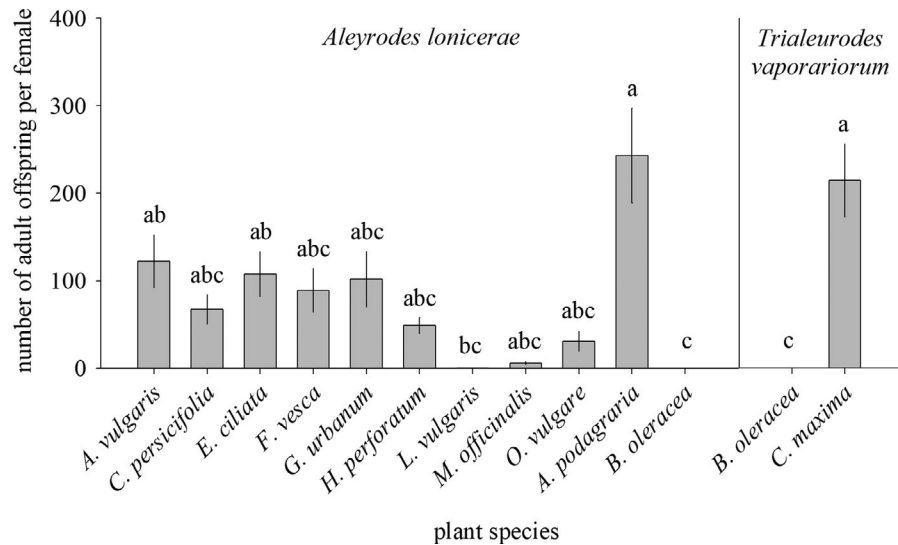
2.5 | Statistics

Data were statistically analysed with R version 3.5.1 (R Core Team, 2019). The packages 'FSA' (Fisheries Stock Analysis) and 'car' provided data and plots, respectively, for descriptive statistics (Fox & Weisberg, 2011; Ogle et al., 2019).

Under controlled conditions, the whitefly performance (longevity, fecundity, developmental success) on selected plant species was evaluated by applying Kruskal–Wallis rank sum tests with Dunn's post hoc and Holm-adjusted *p*-values (R package 'PMCMRplus'; Pohlert, 2018). Egg-adult development times of the parasitoid *E. tricolor* were analysed with a linear model (lm) followed by an analysis of variance (ANOVA function) and multiple comparisons of means after Tukey, if applicable (package 'multcomp'; Hothorn et al., 2008). The nonparametric Kruskal–Wallis test with Dunn's post hoc and Holm-adjusted *p*-values was applied to analyse the head width of *E. tricolor* offspring, as well as the number of pupal and adult offspring and the size of the whitefly host. The relationship between the head width of *E. tricolor* and the host size was analysed by Spearman's rank correlation after assessment of linearity (scatter plot) and bivariate normal distribution ('MVN' package; Korkmaz et al., 2014).

For the field experiment, data collected on the 28.09.2015 were excluded from statistical analysis due to mistakes in data collection.

FIGURE 1 Lifetime fecundity (mean \pm SE) of alternative hosts (*Aleyrodes loniceræ*, *Trialeurodes vaporariorum*) on selected host plants and Brussels sprouts (*Brassica oleracea* var. *gemmifera*) as control. Different letters indicate significant differences between treatments ($p \leq .05$; Kruskal–Wallis test followed by Dunn–Holm post hoc test)



The numbers of parasitized whitefly puparia on banker plants were summed per plot before determining differences between the two banker plant systems with a two-sided Wilcoxon rank sum test ('PMCMRplus' package; Pohlert, 2018). Generalized linear mixed-effects models (glmer) fit by maximum likelihood were applied to compare the banker plant systems with each other and with the control treatment in terms of parasitism rates as well as numbers of herbivores, *E. tricolor* adults and predators on cabbage plants (response variables; package 'lme4'; Bates et al., 2015). Count data were fitted with negative binomial models (glmer.nb) and a log link function to account for overdispersion in count data (Hilbe, 2011). Dispersion parameters were determined with package 'blmeco' (Korner-Nievergelt et al., 2015). A binomial distribution with a logit link function was used in case of parasitism rates. Explanatory variables were the treatment (pumpkin system, columbine system and control), assessment date, distance to the banker plants (1.5 and 4 m), position to the banker plants (upwind and downwind) and block (one to six). An identification number (plot ID) was assigned to each of the 18 plots. Plot ID was taken as random effect to account for temporal non-independence of repeatedly collected data from the same plots. Models were evaluated based on the Akaike information criterion (AIC). The model with the lowest AIC value (highest accuracy) was chosen for each response variable to compute an analysis of deviance table (ANOVA function). Multiple comparisons of means were conducted with Tukey post hoc to determine differences between treatments (package 'multcomp'; Hothorn et al., 2008). Due to low numbers of adult *E. tricolor*, unparasitized/parasitized herbivores others than *A. proletella* and predators on cabbage plants, individual arthropod counts on the eight cabbage plants per plot were summed for each plot and assessment date before computing the data. Therefore, the explanatory variables distance and position to banker plants needed to be removed from models with these response variables. Partial Spearman's rank correlations were computed between the numbers of parasitized whiteflies on banker plants and the *A. proletella* parasitism rate on cabbage plants 14d later while controlling for assessment date and blocks (package 'ppcor'; Kim, 2015).

3 | RESULTS

3.1 | Performance of alternative hosts

The longevity of the alternative hosts on the evaluated host plants ranged between 71 ± 10 days (mean \pm SE) for *A. loniceræ* on *A. podagraria* and 34 ± 5 days for *T. vaporariorum* on Hokkaido squash. Longevities on the hosts plants did not differ to each other (all $p > .05$), but to the ones on Brussel sprouts ($\chi^2(12, N = 76) = 41.62, p < .001$). *Aleyrodes loniceræ* died earlier on Brussels sprouts (on average after 10 ± 4 days) than on *A. podagraria*, *H. perforatum* (68 ± 5 days) and *E. ciliate* (64 ± 4 days; $p = .007, p = .006$ and $p = .012$, respectively). A difference between the longevity of *T. vaporariorum* on Brussels sprouts (7 ± 1 days) and on Hokkaido squash was not determined ($p > .05$).

In terms of total and daily deposited eggs per female, there was no difference of the evaluated host plants to each other (all $p > .05$) but to Brussels sprouts ($\chi^2(11, N = 72) = 40.27, p < .001$ and $\chi^2(11, N = 72) = 37.32, p < .001$, respectively). *Aleyrodes loniceræ* deposited on average between 1 ± 1 egg per female on Brussels sprouts and 329 ± 62 eggs per female on *A. podagraria* during its lifetime ($p < .001$). The host plants *A. podagraria* (4.7 ± 0.7 eggs per day) and *A. vulgaris* (3.9 ± 0.7 eggs per day) received more eggs per *A. loniceræ* female per day than Brussels sprouts (0.1 ± 0.1 eggs per day; $p < .001$ and $p = .007$, respectively). Egg numbers and developmental rate could not be determined for *T. vaporariorum* due to the small size and high number of deposited eggs.

The developmental success of *A. loniceræ* from egg to adult differed between plants ($\chi^2(11, N = 60) = 42.34, p < .001$). It was most successful on *A. vulgaris* ($76 \pm 3\%$), *A. podagraria* ($71 \pm 5\%$) and *G. urbanum* ($69 \pm 6\%$). No or hardly any development to the adult stage was observed on Brussels sprouts (0%), *L. vulgaris* ($3 \pm 3\%$) and *M. officinalis* ($4 \pm 0.2\%$). *Aleyrodes loniceræ* developed better on *A. vulgaris*, *A. podagraria* and *G. urbanum* than on *L. vulgaris* ($p = .012, p = .020$ and $p = .039$, respectively). Additionally, development was

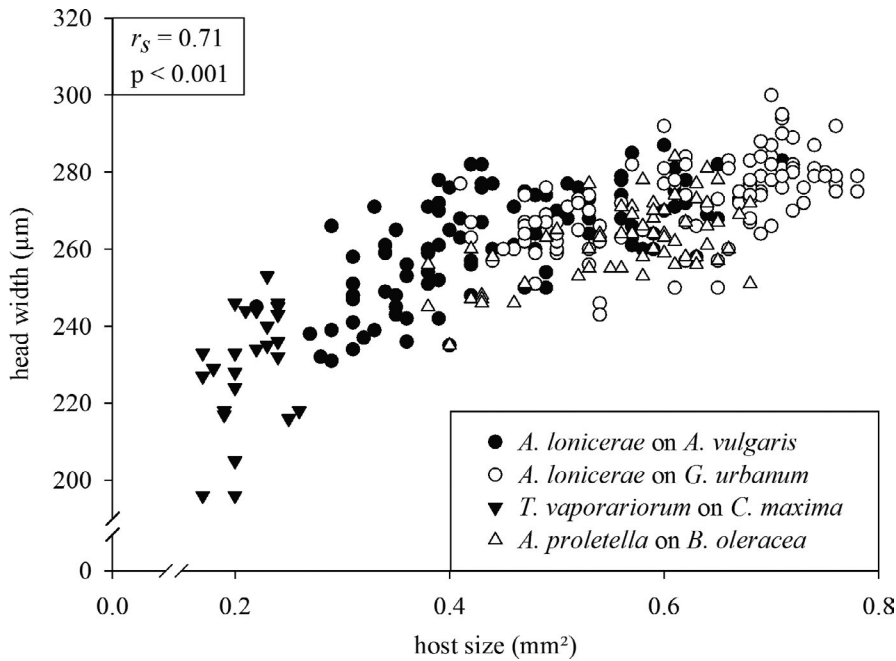


FIGURE 2 Correlation between the head widths of *Encarsia tricolor* females and the size of their whitefly host nymphs (Spearman's rang correlation pooled data of all evaluated whitefly/plant combinations, $\alpha = 0.05$)

more successful on *A. vulgaris* and *A. podagraria* compared to *M. officinalis* ($p = .029$ and $p = .046$, respectively).

Total lifetime fecundity in terms of adult offspring per *A. loniceræ* female differed between plants (χ^2 (12, $N = 76$) = 58.81, $p < .001$; Figure 1). Most adult offspring were produced by *A. loniceræ* on *A. podagraria* (243 ± 54 adults/female) followed by *A. vulgaris* (123 ± 30 adults/female), *E. ciliata* (108 ± 26 adults/female) and *G. urbanum* (102 ± 32 adults/female). On average, 215 ± 42 offspring per *T. vaporariorum* female reached adulthood on Hokkaido squash. Both whitefly species could not complete their development on Brussels sprouts.

3.2 | Performance of the cabbage whitefly

Longevity of *A. prolella* differed between plant species (χ^2 (7, $N = 48$) = 15.02, $p = .036$). *Aleyrodes prolella* survived most days on Brussels sprouts (control; 46 ± 12 days), but it died earlier on Hokkaido squash ($p = .046$). No differences were detected between the seven potential banker plant species selected based on the alternative host performances (all $p > .05$); longevity on these plants ranged between 9 ± 2 days on Hokkaido squash and 45 ± 13 days on *C. persicifolia*.

The average number of deposited eggs per female during its lifetime (between 7 ± 5 eggs on *E. ciliata* and 108 ± 43 eggs on *C. persicifolia*) and per day (between 0.3 ± 0.1 eggs on *E. ciliata* and 2.6 ± 1.1 eggs on *A. podagraria*) differed among plant species (χ^2 (7, $N = 48$) = 18.13, $p = .011$ and χ^2 (7, $N = 48$) = 17.55, $p = .014$, respectively). More total and daily eggs per female were led on Brussels sprouts (128 ± 45 /female and 2.3 ± 0.5 daily eggs) compared to Hokkaido squash (*T. vaporariorum* host plant), where no oviposition was observed ($p = .022$ and $p = .024$, respectively). However, oviposition on the six *A. loniceræ* host plants was not different to each other and neither to Brussels sprouts (all $p > .05$).

Aleyrodes prolella showed variable developmental success on evaluated plants (χ^2 (6, $N = 31$) = 18.13, $p = .011$). It developed better on Brussels sprouts ($70 \pm 9\%$) and *A. vulgaris* ($62 \pm 6\%$) than on *G. urbanum* ($2 \pm 1\%$; $p = .002$ and $p = .033$, respectively). The average number of adult offspring produced by *A. prolella* either differed among plant species (χ^2 (7, $N = 48$) = 18.06, $p = .012$). It ranged between no adults/female on Hokkaido squash and 98 ± 37 adults/female on Brussels sprouts ($p = .012$). No more differences were observed (all $p > .05$).

3.3 | Parasitoid performance

The host/plant combinations *A. loniceræ/A. vulgaris* (AL/AV), *A. loniceræ/G. urbanum* (AL/GU) and *T. vaporariorum/C. maxima* 'Uchiki Kuri' (TV/CM) were evaluated as most promising for a banker plant system based on the whiteflies' performances. Therefore, *E. tricolor* performance was investigated on these combinations and on *A. prolella/B. oleracea* (AP/BO) as control.

The number of pupae and adult offspring per *E. tricolor* female differed among host/plant combinations (χ^2 (3, $N = 69$) = 7.99, $p = .046$ and χ^2 (3, $N = 69$) = 16.70, $p < .001$, respectively). The most productive host/plant combination was AL/AV with 7.8 ± 1.1 pupae and 7.4 ± 1.1 adult offspring per *E. tricolor*. Less than half as many pupae (3.8 ± 0.6) and adults (3.3 ± 0.6) developed on AP/BO ($p > .05$ and $p = .048$, respectively). Furthermore, AL/AV as well as AL/GU (5.4 ± 1.2) produced more adult offspring than TV/CM (1.6 ± 0.4 ; $p < .001$ and $p = .048$, respectively). No other differences in terms of the number of pupae and adult offspring per *E. tricolor* female were observed (all $p > .05$). In addition, the host/plant combination affected the egg-adult development of *E. tricolor* ($F_{3,49} = 12.61$, $p < .001$). It took longer on TV/CM (21.9 ± 0.3 days) compared to AL/GU (20.2 ± 0.3 days), AL/AV (19.7 ± 0.3 days) and AP/BO (19.6 ± 0.2 days; all $p < .001$).

The size of *E. tricolor* females differed depending on the host/plant combination they developed on (χ^2 (3, $N = 69$) = 34.60, $p < .001$). *Encarsia tricolor* that emerged from AL/GU ($275 \pm 2 \mu\text{m}$ head width) were larger than the ones from AL/AV ($262 \pm 2 \mu\text{m}$), AP/BO ($261 \pm 2 \mu\text{m}$) and TV/CM ($229 \pm 5 \mu\text{m}$) based on the head width ($p = .009$, $p = .004$ and $p < .001$, respectively). In addition, adult females that developed on TV/CM possessed a smaller head width than females from AL/AV and AP/BO ($p = .014$ and $p = .009$, respectively). The size of whitefly hosts also differed among host/plant combinations (χ^2 (3, $N = 69$) = 41.48, $p < .001$). Hosts from TV/CM ($0.20 \pm 0.01 \text{ mm}^2$) were 124%–217% smaller than hosts from AL/AV ($0.44 \pm 0.03 \text{ mm}^2$), AP/BO ($0.55 \pm 0.02 \text{ mm}^2$) and AL/GU ($0.62 \pm 0.02 \text{ mm}^2$; $p = .040$, $p < .001$, $p < .001$, respectively). Additionally, hosts from AL/GU were larger than ones from AL/AV ($p < .001$). Hosts from AP/BO did not differ in size from hosts on AL/AV and AL/GU (both $p > .05$). Parasitoid head widths correlated positively with the size of the hosts they emerged from ($r_s = .71$, $p < .001$; Figure 2).

3.4 | Field evaluation

The sum of parasitized puparia over the entire growing season was three times higher on the pumpkin system ($1,626 \pm 266$ individuals m^{-2}) compared to the columbine system (546 ± 134 individuals m^{-2} ; $U = 0$, $p = .002$). A higher parasitoid production by the pumpkin system was determined on the 3rd, 17th (peak) and 31st August 2015 ($p = .030$, $p = .002$ and $p = .002$, respectively). There was no difference on the other assessment dates ($p > .05$). The number of parasitized whitefly puparia on pumpkin and European columbine correlated positively with the parasitism rate of *A. prolella* on cabbage 14 days later ($r_s = .82$, $p < .001$ and $r_s = .51$, $p < .001$, respectively; Figure 3).

The banker plants affected *A. prolella* parasitism rates on cabbage (χ^2 (2, $N = 700$) = 41.92, $p < .001$). The pumpkin system ($22.7 \pm 1.2\%$) as well as the columbine system ($22.5 \pm 1.2\%$) increased the average whitefly parasitism rate on cabbage plants compared to the control without banker plants ($14.9 \pm 0.9\%$; both $p < .001$; Figure 4). Parasitism rates were 1.4-fold to 2.8-fold (pumpkin system) and 1.3-fold to 4.3-fold (columbine system) higher than the control depending on the assessment date. The direction and distance of the cabbage plants to the banker plants did not affect these differences between the treatments (both $p > .05$). However, pumpkin as banker plant led to higher whitefly parasitism rates on cabbage in 1.5 m distance ($24.4 \pm 1.8\%$) than in 4 m distance ($21.0 \pm 1.7\%$; $p = .001$) and on the downwind side ($26.1 \pm 1.9\%$) compared to the upwind side ($19.3 \pm 1.5\%$; $p < .001$). No differences in terms of whitefly parasitism rate neither between the two distances nor between the two directions were determined in European columbine or control treatment (all $p > .05$).

Furthermore, banker plants influenced the abundance of adult *E. tricolor* on cabbage plants (χ^2 (2, $N = 90$) = 27.56, $p < .01$). The columbine system (6.4 ± 1.5 adults per plant) and the pumpkin system (6.2 ± 1.3 adults per plant) increased the numbers of *E. tricolor* on cabbage by 50.3% and by 46.8%, respectively, compared to the control (4.3 ± 1.2 adults per plant; both $p < .001$). The two banker plant systems did not differ from each other ($p > .05$).

Syrphids were either affected by banker plants (χ^2 (2, $N = 126$) = 9.89, $p < .01$). There was an increase in syrphid larvae abundance on cabbage plants by 61.5% in the pumpkin system (0.44 ± 0.08 larvae per plant) compared to the control (0.27 ± 0.05 larvae per plant; $p = .006$). The number of syrphid larvae on cabbage next to the columbine system (0.32 ± 0.05 larvae per plant) did neither differ from the control nor from the pumpkin system (both $p > .05$). Banker plants had no effect

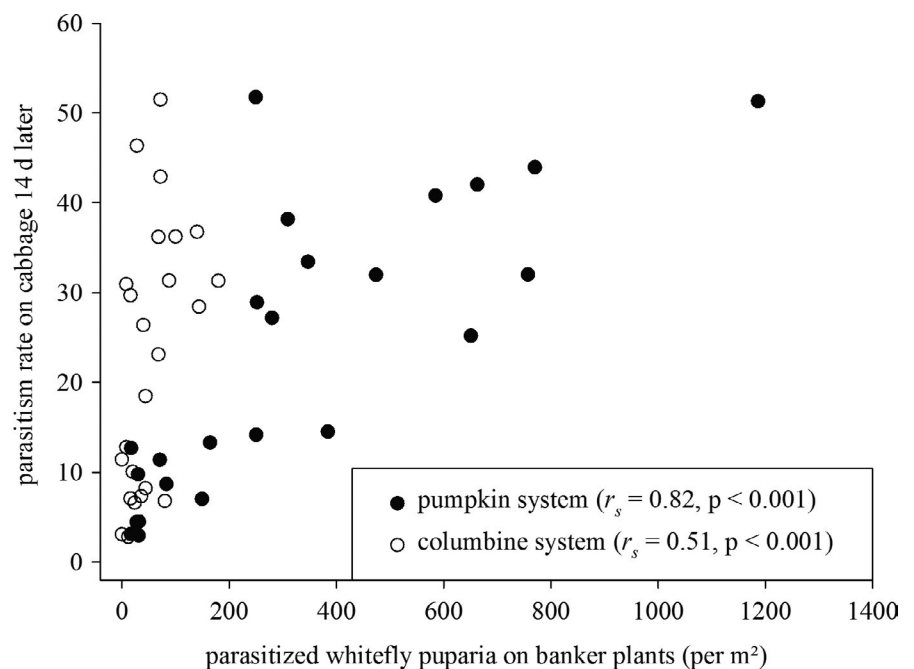


FIGURE 3 The number of parasitized whitefly puparia on banker plants in relation to the parasitism rate of *Aleyrodes prolella* on cabbage 14 days later (partial Spearman's rang correlation with time and block as controlling variables, $\alpha = 0.05$)

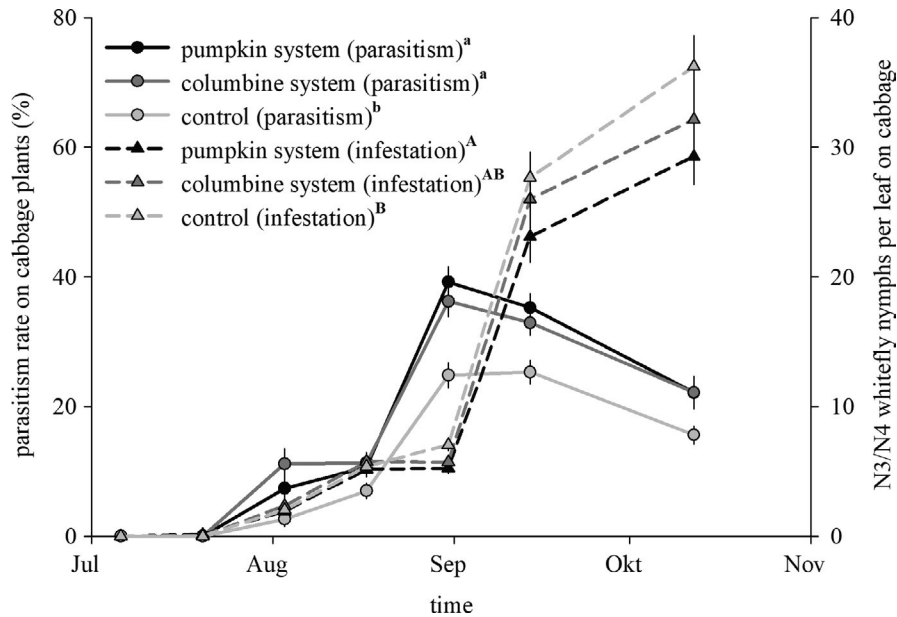


FIGURE 4 Parasitism rate of *Aleyrodes proletella* and number of *A. proletella* nymphs (N3/N4) on cabbage plants (mean \pm SE) with (columbine system, pumpkin system) and without banker plants (control). Different superscript letters indicate significant differences between treatments in terms of parasitism rate (lower-case letters) and whitefly infestation (upper-case letters; $p \leq .05$; glmer, binomial and negative binomial distribution, respectively)

on aphid infestation (χ^2 (2, $N = 126$) = 2.64, $p > .05$) and spiders (χ^2 (2, $N = 126$) = 4.46, $p > .05$) on cabbage plants. Data on other predators (i.e. ladybeetles, predatory bugs, lacewing larvae, predatory flies, gall midge larvae and predatory thrips) and parasitized aphids on cabbage could not be analysed statistically due to insufficient numbers.

Finally, *A. proletella* infestations differed between treatments (χ^2 (2, $N = 1,008$) = 9.99, $p < .01$). The pumpkin system (on average 9.26 ± 0.74 puparia per leaf) decreased *A. proletella* numbers by 4.4%–25.8% depending on assessment date (on average 17.3%) compared to the control (on average 11.19 ± 0.87 puparia per leaf; $p = .005$; Figure 4). There were no other differences between treatments, distances or directions in terms of whitefly infestation (all $p > .05$). Harvested pumpkins from the pumpkin system yielded on average 321 ± 12 dt/ha.

4 | DISCUSSION

This study evaluated the pumpkin system as the most promising annual banker plant system against *A. proletella* under field conditions. It produced more parasitoids than other banker plants, facilitated populations of parasitoids and syrphid larvae on cabbage, increased *A. proletella* parasitism rates and finally decreased infestation by *A. proletella*.

The marketability of pumpkin is another economic advantage over the other evaluated banker plant systems. Pumpkin plants were able to tolerate the deliberate infestation with *T. vaporariorum*. The yield of the pumpkin system in this study (321 ± 12 dt/ha) was comparable with the yield reported in literature for uninfested plants of the same Hokkaido squash variety 'Uchiki Kuri', which ranges between 300 and 325 dt/ha (Hirthe & Heinze, 2007). Same was the case for cantaloupe melon production by cantaloupe banker plants preinfested with *B. argentifolii* and *Er. hayati* (Goolsby

& Ciomperlik, 1999). Exploiting pumpkin as banker plants may therefore lead to multiple economic and ecological benefits for producers and environment.

Wind and distance affected *A. proletella* parasitism rates only with the pumpkin system, but not with the other treatments. A reason may be that the pumpkin plants were taller and therefore more wind exposed than the European columbine plants. Thus, *E. tricolor* adults on the pumpkin leaves were more likely to be wind spread since small flying insects like whitefly parasitoids mainly show a wind-borne dispersal (Kristensen et al., 2013; Ludwig et al., 2018; 2019). This suggests an installation of the pumpkin system upwind from the cabbage crop to achieve maximum parasitism rates of *A. proletella*. However, this study does not reveal the distance limit of the pumpkin system, because the parasitism rates were still enhanced at the maximum investigated distance of 4 m from the banker plants. More research is needed to determine the most effective distance between strips of banker plants as well as the optimal strip size (ratio banker plants: cabbage crop). Future studies also need to investigate the optimal ratio between uninfested and preinfested pumpkin plants taking into account pest control services on the one hand and production costs for banker plants on the other hand.

A commercial production of pumpkin banker plants needs to ensure high-quality and standardized products. There are several options to optimize the production process. For instance, increasing the initial parasitism on planted banker plants certainly will further enhance parasitism rates of *A. proletella* especially at the beginning of the growing season (Figure 3). An increased parasitism on banker plants may also lead to the production of more males, which are necessary for a long-term maintenance of a stable and effective *E. tricolor* population. Another option is the use of larger whitefly hosts like *A. proletella* or *A. loniceriae* in the rearing of *E. tricolor*. Larger hosts will lead to larger and fitter *E. tricolor* females that deposit their eggs on the banker plants during production (Figure 2; Hora et al., 1995; Luo & Liu, 2011; Williams, 1995). This

may increase the quantity and quality of *E. tricolor* on the planted pumpkin banker plants which will lead to higher parasitism rates of *A. proletella* on cabbage (Figure 3).

Another natural enemy as alternative or in addition to *E. tricolor* in the banker plant system could also improve the impact on *A. proletella* populations. For instance, a combined use of *E. tricolor* and whitefly predators like *C. arcuatus* or syrphid larvae in a banker plant system may lead to additive or synergistic effects (Schultz et al., 2009). Furthermore, the whitefly parasitoid *E. inaron* may be a potentially better alternative to *E. tricolor*. *Encarsia inaron* used to be highly abundant in at least certain parts of Europe up to the 1950s (Butler, 1938; Stein, 1958), but has almost disappeared as parasitoid of *A. proletella* since that time (Gumovsky, 2005; Laurenz et al., 2019; Springate, 2017). The displacement of *E. inaron* may have facilitated the outbreaks of this whitefly pest in recent decades (Williams, 1996), because *E. inaron* may perform better on primary hosts (159 eggs per female on *Siphoninus phillyreae*) than *E. tricolor* (85 eggs per female on *A. proletella*; Gould et al., 1995; Williams, 1995). However, comparative studies on the performance of the two *Encarsia* species on *A. proletella* and alternative hosts like *T. vaporariorum* are needed for further conclusions.

Encarsia tricolor suffered a high pupal mortality with late instars of *T. vaporariorum* as hosts, but not with the other host species at the same developmental stage. Same was reported for *E. inaron* when parasitizing preferred fourth instars of *B. tabaci* and *Trialeurodes abutiloneus* (Brady & White, 2012). Reasons may be the relatively fast development to the adult stage or the small size of *Trialeurodes* and *Bemisia* nymphs, which may result in insufficient time and limited nutritional resources for *E. tricolor* to complete its development.

The quantity of alternative hosts/prey seemed to be more important for the success of a banker plant system than the quality. *Aleyrodes lonicerae* was a qualitatively better host for *E. tricolor* than *T. vaporariorum* in terms of reproduction, development and fitness of offspring (see 3.3 Parasitoid performance). However, the latter developed much higher population sizes than *A. lonicerae* under field conditions. This high availability of alternative hosts/prey on the pumpkin system led not only to a higher parasitoid production and increased parasitism rates of *A. proletella*, but also to an increase in syrphid larvae on the cabbage plants and finally to decreased *A. proletella* populations. These contradicting results between laboratory and field also underline the importance of and the need for more solid field studies.

The impact of general predators like syrphid larvae on *A. proletella* populations may often be underestimated. In this study, both banker plant systems evaluated in the field increased parasitism rates of *A. proletella* to a similar extent (Figure 4). However, only the pumpkin system led to higher numbers of syrphid larvae on the cabbage plants as well as a decrease in *A. proletella* infestation. This suggests that predation by syrphid larvae can have a significant impact on the population size of *A. proletella*. Therefore, more research is desired to develop and implement respective measures like flower

strips, potentially as a combined strategy with banker plants, to further promote syrphids (Laurenz & Meyhöfer, 2016).

Perennial banker plants are another option to permanently increase the local abundance of natural enemies in order to promote biological control services. Therefore, perennial host plants of non-pest whitefly species could be installed in field margins as shelter, overwintering and reproduction habitat for alternative host/prey and natural enemies in the agricultural landscape (Gurr et al., 2017). Potential candidates are some of the here investigated herbaceous host plants of *A. lonicerae* (e.g. *A. podagraria*, *G. urbanum*, *A. vulgaris*, *F. vesca*) or even woody plants like *Lonicera* spp. for *A. lonicerae*, *Fraxinus* spp. for *S. phillyreae* or *Viburnum* spp. for *Aleurotuba jelinekii* (Evans, 2007b; Mound & Halsey, 1978; Pickett & Wall, 2003). More research is needed to identify suitable perennial banker plants and to permanently increase the functional biodiversity in agricultural landscapes in order to counteract biodiversity loss and suppress mass outbreaks of pest populations.

Conclusively, the pumpkin system promoted the functional biodiversity and reduced *A. proletella* populations. Future research should for instance investigate the optimal size, distance and ratio between banker plants and cabbage, and a combined strategy of banker plants with other control measures like crop cover netting or flower strips in large scale farm trials. Furthermore, research gaps were identified concerning further improvements, standardization of commercial production and feasibility of the banker plant system. Generally more field studies are needed to confirm the results under different conditions (e.g. climate, *A. proletella* infestation levels).

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CONFLICT OF INTEREST

The authors declare that they have no conflict of interest and confirm that there are no disputes over the ownership of the data presented and all contributions have been attributed appropriately.

AUTHOR CONTRIBUTION

Sebastian Laurenz conducted experiments, analysed data statistically and wrote the manuscript. Rainer Meyhöfer secured funding. Both authors conceived research as well as read and approved the manuscript.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in LUH-Projekt Seafire at <https://doi.org/10.25835/0017692> (Laurenz & Meyhöfer, 2020).

ORCID

Sebastian Laurenz  <https://orcid.org/0000-0003-2540-2877>

Rainer Meyhöfer  <https://orcid.org/0000-0001-5624-001X>

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