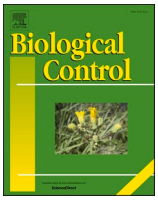
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Weekly pollen supply optimises the control of the tomato russet mite (*Aculops lycopersici*) by *Pronematus ubiquitus*

Dylan Maret [a], Lindsey Norgrove [a], Louis Sutter [b,*]

[a] School of Agricultural, Forest and Food Sciences HAFL, Bern University of Applied Sciences, Länggasse 85, 3052 Zollikofen, Switzerland
[b] Agroscope, Plant Production Systems, Route des Eterpys 18, 1964 Conthey, Switzerland

HIGHLIGHTS

- Population management of *Pronematus ubiquitus* was investigated through pollen feeding frequency.
- The more frequent pollen is provided, the better *P. ubiquitus* establishes on the crop.
- Providing pollen each week reduces almost completely damage on the stem.
- Number of *A. lycopersici* remained at low level, independently from the pollen frequency.
- Despite regular feeding, *P. ubiquitus* populations dramatically declined after reaching a peak.

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ABSTRACT

Biological control using natural predators offers a sustainable alternative to synthetic pesticides in agriculture. However, the successful use of biological control agents is often hindered by factors such as food availability and environmental conditions. This study investigated the role of the predatory mite *Pronematus ubiquitus* in the biological control of *Aculops lycopersici*, the tomato russet mite, in a controlled greenhouse environment. The effect of different pollen feeding frequencies on *P. ubiquitus* populations and its ability to suppress *A. lycopersici* infestation and damage were examined. Our results show that weekly pollen feeding maintained higher *P. ubiquitus* populations than feeding once every two or three weeks, by 60 % and 90 %, respectively. Consequently, it effectively limited *A. lycopersici* damage to tomato plants. However, a rapid decline in predator populations was observed after reaching peak levels, probably due to factors such as cannibalism and resource quality. While the treatment with weekly pollen supply resulted in minimal plant damage, lower pollen frequencies (once every two or three weeks) also provided some level of control. These findings highlight the importance of balancing predator population growth with sustainable food sources to optimize biological control strategies. This study contributes to the ongoing development of integrated pest management techniques in crop production systems, emphasizing the need for tailored approaches to predator food supply and population management.

1. Introduction

Biological control is considered a sustainable method to control various pests in agriculture (Hou et al., 2022; Pérez-Consuegra et al., 2018) and is a key component of integrated pest management. Thanks to such alternative control methods, it has been possible to reduce the use of pesticides and their negative impact on ecosystems and human health. However, the use of living organisms as natural enemies can present challenges (Hou et al., 2022; Maret et al., 2024). Their efficacy depends on environmental factors, such as climate and food availability, which can affect their life cycles. Consequently, the objective of protecting crops in an environmentally friendly way may be compromised, potentially leading growers to fall back on synthetic pesticides to secure yields. It is therefore essential to develop management strategies that optimise the performance of biological control agents (Koller et al. 2024). Alternative food sources, such as pollen, are essential for sustaining biological control agents, particularly in controlled environments where natural prey may not always be available. These food

* Corresponding author.
E-mail address: louis.sutter@agroscope.admin.ch (L. Sutter).

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sources provide a reliable and consistent supply of nutrition that supports the survival, reproduction, and population growth of predators. By offering supplemental food, it is possible to enhance the establishment of biological control agents and improve their long-term performance in pest suppression. This approach is vital for optimizing the effectiveness of integrated pest management strategies, as it helps maintain predator populations during periods when pest pressure may be low, ensuring continuous control of pest species over time.

Pronematus ubiquitus (McGregor), a predatory mite of the Iolinidae family, can suppress the tomato russet mite, *Aculops lycopersici* (Massee) (Acari: Eriophyidae) and tomato powdery mildew, *Oidium neolycopersici* L. Kiss (Maret et al., 2024; Pijnakker et al., 2022, 2021; Ueckermann et al., 2024). *Aculops lycopersici* poses a significant threat to tomato crops (Haque and Kawai, 2003; Royalty and Perring, 1998), feeding on all aerial parts, infestation and causing russeting of leaves, stems and fruits. Only a few curative chemical control options remain available, including abamectine, fenpyroximate and spirotetramat (https://www.psm.admin.ch). However, this list is likely to shrink due to policy trends and environmental and/or health concerns promoting the reduction of agrochemical use (EASAC, 2023; Van Leeuwen et al., 2010; Vervaet et al., 2021). Moreover, the emergence of resistance may further complicate control efforts (Vervaet et al., 2024). Therefore, developing alternative solutions, such as biological control using *P. ubiquitus,* is essential. Thanks to its varied diet (pollen, eriophyids and fungal spores), *P. ubiquitus* shows strong potential as a biological control agent (Pijnakker et al., 2023). Growers can pre-establish populations of this mite by supplying pollen (*Typha angustifolia* L.), thereby preventing the establishment of eriophyid pests and fungal diseases (Duarte et al., 2021). In Maret et al. (2024), pollen was supplied during the first weeks following predator release. This led to rapid population build-up and successful control of *A. lycopersici*. However, a sharp population decline occurred shortly after pollen feeding ceased, allowing *A. lycopersici* to re-establish and cause plant damage.

Our current hypothesis attributes this decline to food scarcity in the absence of prey, leading to population collapse. Cannibalism has also been suggested, as it has been documented in other iolinids (Knop and Hoy, 1983; Moerkens et al., 2023). Hence, a tailored pollen feeding strategy is required. In Moerkens et al. (2023), weekly pollen application at 500 g ha^{-1} enabled *P. ubiquitus* to successfully prevent *A. lycopersici* outbreaks. Here, we assessed the effect of different pollen supply frequencies (weekly, fortnightly, once every three weeks) on *P. ubiquitus* and *A. lycopersici* populations. We hypothesised that more frequent feeding would sustain higher *P. ubiquitus* populations and enhance their ability to prevent *A. lycopersici* outbreaks.

2. Material & methods

2.1. Study area and greenhouse

The replicated semi-field experiment was conducted from February to October 2023 in the facilities of Agroscope in Conthey (Valais, Switzerland). Fifteen walk-in cages (Diatex SAS, France) of 2.6 m^2 surface area and 2.5 m height with thrips-proof mesh (300 × 300 μm^2) were set up in a 90 m^2 glass greenhouse. The floor below the cages was covered with a white woven ground cloth (100 g/m^2). Temperature, relative humidity, and irrigation were managed using a remote-control system. No plant protection interventions were realised. The average temperature and relative humidity during the experiment were 26.4 °C ± 5.2 SD and 60.8 % ± 12.8 SD.

2.2. Biological material

Tomato seeds cv. San Marzano “Giulietta” (Wyss, Zuchwil, Switzerland) were sown on 23 February. Seedlings were transplanted after three weeks into 0.5 L pots, and later in 10 L pots. Tomato plants were placed in the trial greenhouse on 6 April, when they had four fully developed leaves. Tomato plants were assigned to the 15 insect-proof cages with three plants per walk-in cages. The experimental unit being the cage (N = 15) with three treatments and 5 replicates (n = 5) with all three plants per cage getting the same treatment. The main stem of each plant was trellised on a string attached to a wire above the cage and passed through an insect-proof hole in the ceiling of the latter. Secondary shoots were removed weekly, and plants were watered daily through drip irrigation. Before the experiment, *A. lycopersici* were reared in a separate greenhouse. *P. ubiquitus* was provided by Biobest Group N. V. (Westerlo, Belgium) in sawdust containing eggs, larvae and adults (100 individuals per gram).

2.3. Experimental setup and monitoring

The experiment followed a randomised block design with five blocks and one cage per treatment per block. The tested treatment was pollen frequency, tested at three levels: weekly (1/W), biweekly (1/2W), and every three weeks (1/3W). Pollen (0.1 g per plant per week) of *T. angustifolia* (Nutrimite™, Biobest Group N.V.) was provided with an electrical blower Nutrigun™ (Biobest Group N.V.). This pollen was chosen as we know from earlier research that *P. ubiquitus* can develop on it and as released individuals were fed with this pollen for their rearing (Duarte et al., 2021). Adults of *P. ubiquitus* were released on each plant on 6 April at a rate of 100 individuals per plant. During the first six weeks, all treatments received weekly pollen applications to support initial population growth of *P. ubiquitus*. From 17 May onwards, pollen was applied according to the treatment schedule: weekly (1/W), biweekly (1/2W), and every three weeks (1/3W). Each pollen application consisted of 0.1 g per plant. On 11 May, *A. lycopersici* was introduced by pinning infested stems from the rearing, containing approximatively 150 tomato russet mites, to each experimental plant at the height of the first leaf. Weekly monitoring and data collection started on 27 April and continued for 23 weeks, ending on 18 October. Pest and predatory mite populations were assessed by counting individuals on nine leaflets per cage (three per plant), randomly selected from the lower half of each plant. Crop damage was assessed by measuring the height (in cm) from the ground to the point where russeting symptoms transitioned to healthy stem tissue. The methodology was adapted from Maret et al. (2024) based on Mechant et al. (2015).

2.4. Statistical analysis

Statistical analyses were performed using R (version 4.5.0) with package *lme4* (Bates et al., 2015) for linear models. Three separate models were used to assess the effects of treatment on different dependent variables. The first model evaluated the number of *P. ubiquitus* with a log-transformed response to meet model assumptions. In this linear model, treatment and date were included as fixed effects, with an interaction term between date and treatment to account for potential variations over time. Cage was included as a random intercept to account for the repeated measurements within each cage. The second model assessed the effect of treatment on *A. lycopersici* counts, where a Poisson distribution was assumed. The same structure was used, with treatment and date included as fixed effects, and cage as a random intercept. No overdispersion was detected in the Poisson model. The third model examined damage, with treatment and date as fixed effects and cage as a random intercept. The response variable, damage, was square root-transformed to meet model assumptions of normality and homoscedasticity. A Gaussian error distribution was used for this model. Post-hoc pairwise comparisons between treatment levels were conducted for all three models using the emmeans package, with Bonferroni corrections applied to adjust for multiple comparisons. For all models, assumptions were checked according to the graphical validation procedures recommended by Zuur et al. (2009).

3. Results

3.1. Effect of pollen supply frequency on the predatory mite P. ubiquitus

Populations of *P. ubiquitus* increased rapidly during the first weeks of the experiment in all treatments (Fig. 1). On 14 June, mite numbers peaked in all treatments with 663 ± 41, 458 ± 81 and 509 ± 64 (mean ± SE) adult predatory mites per cage in 1/W, 1/2W and 1/3W, respectively. After this peak, *P. ubiquitus* populations began to decrease. A stabilisation phase occurred from mid-July, followed by a sharp decline starting in mid-August. Despite the initial population boost in 1/W populations, this treatment experienced the most pronounced decrease between 16 and 22 August. On the final sampling date, *P. ubiquitus* counts were 90.0 ± 23.9, 81.0 ± 7.4 and 70.0 ± 21.7 (mean ± SE) for 1/W, 1/2W and 1/3W, respectively. Throughout the season, the average number of *P. ubiquitus* in the treatment 1/W was 1.6 and 1.9 times higher than in 1/2W and 1/3W, respectively. The number of *P. ubiquitus* was significantly affected by both date and treatment, but there was no systematic linear change over time, as the interaction was not significant (Table 1 & Table 2). Multiple comparisons revealed differences between treatment 1/W and 1/2W ($P < 0.001$) and between 1/W and 1/3W ($P < 0.001$). The number of *P. ubiquitus* was significantly higher in 1/W than in the two other treatments. No statistical difference was found between 1/2W and 1/3W ($P = 0.26$).

3.2. Effect of pollen supply frequency on A. lycopersici

The populations of *A. lycopersici* remained low during the first half of the experiment (Fig. 2). At the beginning of August, populations began to rise in all treatments. The 1/2W treatment had the largest increase, reaching the highest infestation on 20 September, with 119.8 ± 56.0 (mean ± SE) mites. In the 1/W treatment, a peak was observed on 16 August with 39.6 ± 33.9 (mean ± SE) mites, while in the 1/3W treatment, the highest infestation occurred on 22 August with 53.4 ± 23.3 (mean ± SE) mites. On the last day of sampling, infestations in the 1/W, 1/2W, and 1/3W treatments were 97.4 ± 93.7, 76.5 ± 32, and 18.2 ± 8.8 (mean 139 ± SE) mites, respectively. No significant differences were found between the treatments according to the statistical test ($P = 0.062$) (Table 1). The significant Treatment x Date interaction shows that the effect changes over time, with no differences observed at the beginning (Table 1), but some differences emerging later; however, no significant treatment differences were found in the post-hoc comparisons.

Table 1
Results of mixed-effect models showing the effects of treatment, time (date) and their interaction on each response variable: *Pronematus ubiquitus* (PU), tomato russet mite *Aculops lycopersici* (TRM), and height of damage.

Response	Explanatory	F value	P	
PU [#]	Treatment	17.625	<0.001	*
	Date	127.945	<0.001	*
	Treatment*Date	2.891	0.056	
TRM [#]	Treatment	5.549	0.062	
	Date	4406.651	<0.001	*
	Treatment*Date	15.778	<0.001	*
Damage [cm]	Treatment	5.270	0.005	*
	Date	141.587	<0.001	*
	Treatment*Date	26.548	<0.001	*

Table 2
Estimate for the three evaluated foraging treatments 1/W 1/2W and 1/3W averaged over week from model output for the three measured parameters: Numbers of *P. ubiquitus,* Number of *A. lycopersici* and the crop damage on tomato stems.

Treatment	Estimate *P.ubiquitus*	Estimate *A.lycopersici*	Estimate Damage
1/W	224.269	2.242	0.084
1/2W	142.111	17.116	8.824
1/3W	119.705	4.932	7.627

3.3. Effect of pollen supply frequency on damage progress

The first appearance of damage occurred on 12 July in the 1/2W treatment, on 2 August in 1/3W, and on 9 August in 1/W (Fig. 3). On the last sampling day, the height of the damage on the stems was 54.9 ±

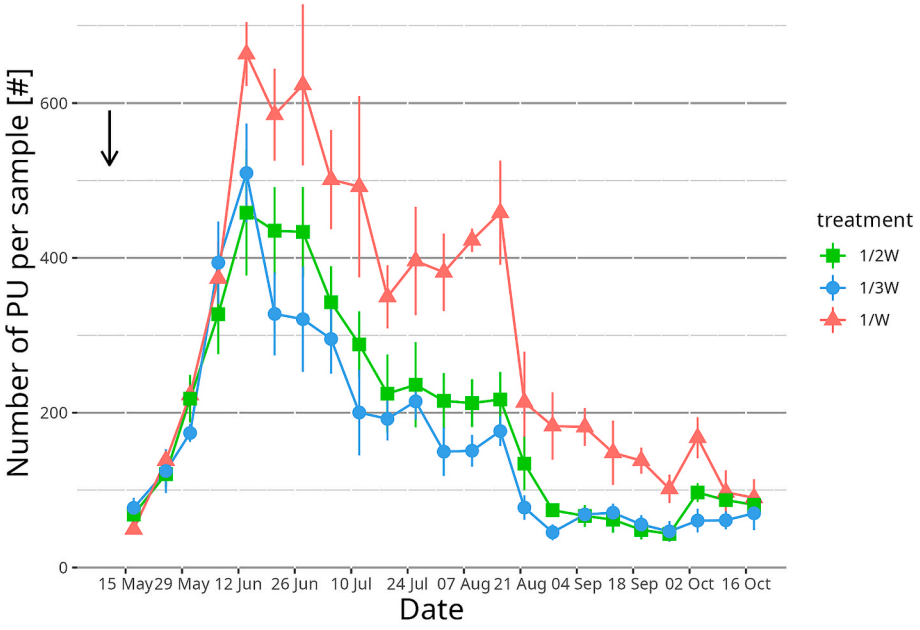


Fig. 1. Population dynamics of *Pronematus ubiquitus* (PU) under different pollen supply frequencies. Treatments: red = weekly (1/W), green = every two weeks (1/2W), blue = every three weeks (1/3W). Data represent the weekly number of predators on 9 leaflets (mean ± SE, n = 5). The black arrow indicates the time of *Aculops lycopersici* introduction.

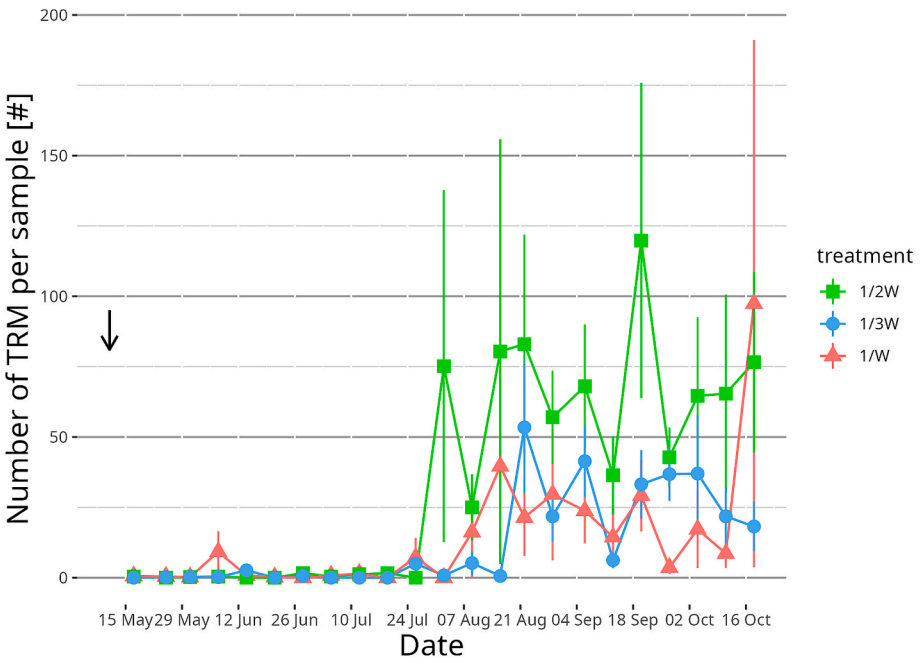


Fig. 2. Population dynamics of tomato russet mite *Aculops lycopersici* (TRM) under different pollen supply frequencies. Treatments: red = weekly (1/W), green = every two weeks (1/2W), blue = every three weeks (1/3W). Data represent the weekly number of tomato russet mites on 9 leaflets (mean ± SE, n = 5). The black arrow indicates the time of A. *lycopersici* introduction.

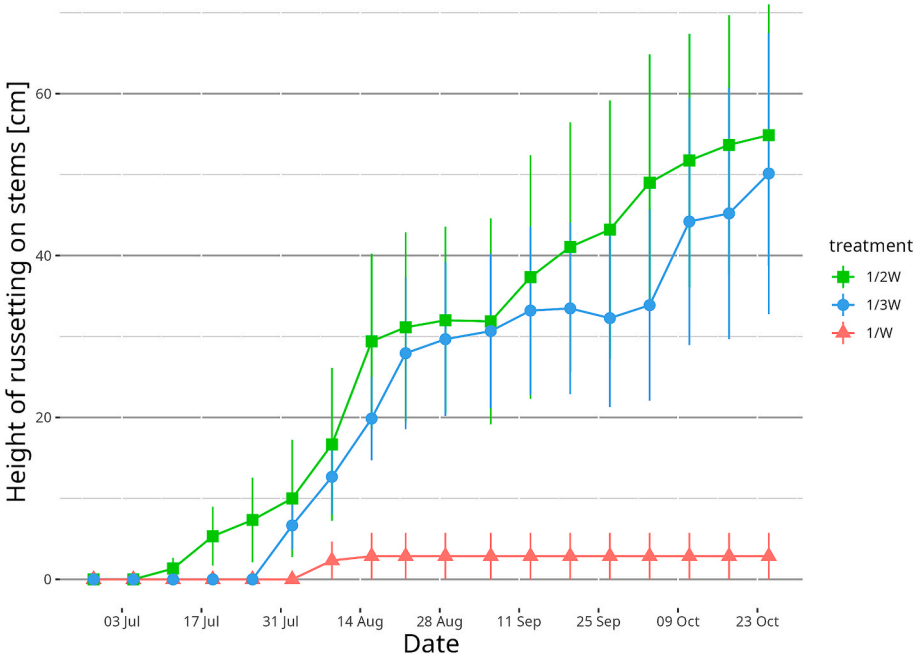


Fig. 3. Progression of *Aculops lycopersici* symptoms under different pollen supply frequencies. Treatments: red = weekly (1/W), green = every two weeks (1/2W), blue = every three weeks (1/3W). Height of russeting on plant stems was measured weekly (mean ± SE, n = 5). *Pronematus ubiquitus* was released on 6 April, and *A. lycopersici* on 11 May.

16.2 and 50.1 ± 17.37 (mean ± SE) cm in 1/2W and 1/3W, respectively. The highest damage in 1/W was 2.9 ± 2.9 (mean ± SE) cm on 16 August. Over the entire season, the average height of damage in the 1/2W and 1/3W treatments was 95 and 76 times greater, respectively, than in 1/W. The significant treatment x date interaction showed that differences emerged over time (Fig. 3, Table 1), with varying treatment effects as time progressed. Significant differences were observed between treatments (P = 0.005; Table 1). Differences occurred between 1/W and 1/2W (P = 0.012) and between 1/W and 1/3W (P = 0.016). The height of the damage limit was lower in treatment 1/W compared to the others. No statistical difference was found between 1/2W and 1/3W (*P* = 0.99).

4. Discussion

Our results show that it is possible to rapidly establish a strong population of *P. ubiquitus* during the growing season. However, in all treatments, populations peaked and then declined. According to Maret

et al. (2024), a minimum density of six *P. ubiquitus* per leaflet is sufficient for effective biological control. In that study, populations fell below this threshold, resulting in a rapid outbreak of *A. lycopersici*, with more than 600 individuals recorded at the final sampling. In the present experiment, *P. ubiquitus* densities generally remained above the threshold. Only three samples had fewer than six per leaflet, mostly due to a single faulty replicate in which the numbers of *A. lycopersici* also increased dramatically (Fig. 2). Consequently, most samples remained below 100 *A. lycopersici*. Moreover, the *P. ubiquitus* population stabilised in September, suggesting that maintaining the predator population at this minimal effective level may be feasible. However, the observed decline after a peak is not desirable. Given the tendency for cannibalism in the Iolinidae family at high densities (Knop and Hoy, 1983; Moerkens et al., 2023), it is hypothesized that aiming for excessively large populations may be counterproductive. In the treatment 1/W, the average number of *P. ubiquitus* per leaflet peaked at 73.6 individuals on 14 June. Hou et al. (2022) conducted an experiment with the predatory mite *Amblyseius herbicolus* (Chant) (Acari: Phytoseiidae) to evaluate how different alternative food sources influence cannibalism. They found highest fecundity with apple pollen, but also the highest cannibalism rate. Almond pollen produced the second-highest fecundity, with a cannibalism rate half of what was observed with apple pollen. The best result was obtained using the alternative prey mite *Oulenziella bakeri* (Hughes) (Acari: Winterschmidtiidae), which provided similar fecundity to almond pollen, but without any observed cannibalism. These results underscore the importance of food quality in regulating predator population dynamics. Duarte et al. (2021) reported that the most suitable alternative food for *P. ubiquitus* was cattail pollen, followed by the prey mite *Tarsonemus fusarii* (Cooreman) (Acari: Tarsonemidae). However, they did not evaluate the impact of alternative food type on the cannibalism rate. Thus, it remains unclear whether specific food sources could help prevent demographic decline of *P. ubiquitus*. A combination of pollen and alternative prey mite could offer a solution to reduce cannibalism and sustain predator population. Nonetheless, pollen feeding should be approached with caution, as pests such as thrips can also use pollen as a food source, potentially increasing damage, and needing complementary biocontrol interventions (Schneeberger et al., 2025). Providing both *T. fusarii* and pollen throughout the growing season could help prevent the decline in the predator population. In our experiment, *P. ubiquitus* reached very high levels in a short time. Rather than promoting such rapid population growth early in the season, we suggest reducing the amount of pollen provided initially to flatten the population peaks observed in Fig. 1. More research is needed to understand the ecology and behaviour of *P. ubiquitus* and potential combinations with other pest control interventions (Koller et al. 2023). Key parameters such as food type, climate niche, and intra- as well as interspecific interactions could be integrated into population modelling approaches (Grimm and Railsback, 2006; Kettle, 2015). Gathering such ecological data will be essential both to prevent undesirable behaviours, such as cannibalism, and to improve the implementation of biological control strategies in commercial crops. Moreover, *Homeopronematus anconai* (Baker) (Acari: Iolinidae) has shown similar results to *P. ubiquitus* in recent studies (Pijnakker et al., 2022; Vervaet et al., 2022). Differences in the ecological niche in these two related species may offer great advantages, if their behaviours can be successfully characterised. In such a case, a tailored biological control strategy could be implemented based on the specific growing conditions.

Our results showed no significant differences in *A. lycopersici* numbers between treatments. However, unexpectedly, the progression of damage differed significantly. Indeed, while damage increased steadily in the treatments 1/2W and 1/3W, almost no visible symptoms were observed in 1/W. Stem symptom progression was not directly correlated with the number of *A. lycopersici* sampled on the leaves. To date, no studies have been conducted on the spatial behaviour of *P. ubiquitus* within the crop, including their movement and predation locations. It might be possible that the leaves are more protected than the stem. Our experiment did not assess the impact of treatments on yield. Since only the stem showed visible damage, we hypothesise that the quality and quantity of the fruits may not have been affected. This assumption, however, requires further investigation. If the primary goal is to suppress *A. lycopersici* populations, providing pollen every three weeks may be sufficient and cost-effective. However, to effectively reduce damage progression, weekly pollen application is necessary. One strongly deviant cage in treatment 1/2W showed uncontrolled infestation for unknown reasons. This anomaly contributed to a higher pest number and more advanced damage in that treatment than in others, resulting in increased variability. Nonetheless, it is unlikely that this outlier significantly altered the overall conclusions regarding the population dynamics of *A. lycopersici*. Even if *P. ubiquitus* showed a great potential, it is unrealistic to expect flawless efficacy. However, the initial infestation of *A. lycopersici* was extremely high. Indeed, 100–200 pest mites per plant is a considerable infestation. A greenhouse experiment under grower conditions is recommended to improve our understanding of the predator and pest populations dynamics.

5. Conclusion

P. ubiquitus confirmed its potential as an effective biological control agent in the preventive control of *Aculops lycopersici*. However, adjustments to the feeding regime are necessary to maintain sufficient predation pressure on the pest mite. Our experiment showed that more frequent pollen applications provided better protection to tomato plants against russeting damage. Nevertheless, further improvements are needed to sustain a stable population of *P. ubiquitus* throughout the season. It may be more effective to maintain a lower but persistent predator population in the long term. Optimal parameters still need to be identified for such an approach to develop a tailored and robust biological control strategy.

CRediT authorship contribution statement

Dylan Maret: Writing – review & editing, Writing – original draft, Visualization, Methodology, Formal analysis, Data curation, Conceptualization. **Lindsey Norgrove:** Writing – review & editing, Writing – original draft, Supervision, Investigation, Conceptualization. **Louis Sutter:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Resources, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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