#### **ORIGINAL PAPER**



# Pest thrips do not set field margins aside: preferred wildflowers sustain pest *Frankliniella* spp. (Thysanoptera: Thripidae) and their migration in commercial strawberry

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#### Abstract

Wildflowers in uncultivated field margin are important resources supporting both pest and non-pest thrips populations in agroecosystems. Environmental factors related to wildflowers have never been used as predictors to model pest thrips density in adjacent crops. Wild and cultivated flowers were sampled in strawberry field agroecosystem in Orléans Island, near Quebec City, Canada. Pest flower thrips *Frankliniella intonsa* and *F. tritici* had a wide wildflower host range, with preferences toward *Leucanthemum vulgare*, *Trifolium pratense*, *Sonchus asper*, and *Cichorium intybus*. Regression modeling revealed significant positive relationships between pest thrips density on specific wildflowers (*Vicia cracca, Sinapis arvensis, S. asper*, *C. intybus*, *L. vulgare*) and their density in strawberry flowers. Furthermore, thrips density within the crop decreased with distance from uncultivated field margin. Regarding crop management, knowing the associations between thrips pests and preferred wild flora as well as their spatial distribution in strawberry fields is an undeniable advantage.

**Keywords** Strawberry · Pest thrips · *Frankliniella intonsa* · *Frankliniella tritici* · Thysanoptera · Field margins · Wild host plants

## Introduction

Flowers host diverse insect species that use them as critical resources during their whole life cycle (Seimandi Corda 2018). While flower–insect interactions are well documented through pollination (Hahn and Brühl 2016), florivory and

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Department, Faculty of Agriculture and Food Sciences, Laval University, Quebec GOR 4J0, Canada flower resources use by phytophagous insect pests remain overlooked (McCall and Irwin 2006; Wardbaugh 2015).

Thrips (Thysanoptera) are closely associated with flowers, 25% of species being obligate flower feeders and breeding in angiosperm inflorescences (Atakan 2010; Mound 1997, 2005, 2009). Flower-inhabiting thrips are generally considered to be phytophagous opportunists, rarely limited to specific hostplant relationships. They can consume host plants leaves or flowers and exhibit invasive attributes such as high reproductive rate and vagility as adults (Mound and Tuelon 1995). Their aggregation behavior on flowers has been frequently reported (Bailey 1933; Katayama 2006; Northfield et al. 2008; Silva et al. 2018), including by Charles Darwin during his pollination experiments (Mound 2009). Such close associations reflect the essential role of inflorescences as ecological niche for thrips, providing both suitable microclimatic conditions and protection from predators, factors exerting substantial selection pressure on phytophagous insects (Strong et al. 1984). Data indicate that flower thrips larvae and adults perform better when feeding on floral rather than leaf tissues regarding larval survival, fecundity, longevity (Milne et al. 1996), and reproduction (Wäckers et al. 2007). In nature, flower-inhabiting thrips maximal densities yearly peak when flowering weed species are in bloom (Chellemi et al. 1994; Atakan and Uygur 2005; Silva et al. 2018). Besides, the presence of flowers is a significant driver of local colonization by thrips (Yudin et al. 1988; Nyasani et al. 2013).

Some flower-feeding thrips are major crop pests (Mound 2009), so their presence in agroecosystems should be considered in wildflowers naturally occurring in field's margins as well as in crop plants. In the early 1930s, wildflowers were already recognized as a major component of thrips outbreaks, supporting populations through winter (Bailey 1933). They are known as potential resources for pest thrips species, even in desert agroecosystems (Adler et al. 2014). Flowering hostplants in field margins both shelter pest thrips when crops are not available (Toapanta et al. 1996; Beaudoin and Kennedy 2012; Szostek and Schwartz 2015) and sustain their reproduction (Toapanta et al. 1996; Paini et al. 2008; Ripa et al. 2009). Thrips emergence over the season may occur in wild areas before they colonize crops (Pearsall and Myers 2000), moving close to ground level in spring but flying higher when temperature increases, and wild vegetation grows taller (Pearsall and Myers 2001). Historically, thrips immigration from surrounding wildflowers into crops has largely been neglected, as thrips population growth leading to economic losses was often assumed to be occurring within fields (Mound 1997). Identifying thrips' wildflower host plants is critical to understand their local resources use near crops yet disentangling thrips dynamics between wild and crop flowers is also essential for pest management. Silva et al. (2018) attributed Thrips tabaci (Lindeman) abundance in cotton fields to its abundance on surrounding wildflowers, based on seasonal abundance patterns and genetic relations between thrips collected on cotton and wild hosts. Pearsall and Myers (2001) found that nectarine orchard location relative to wild vegetation was the main factor determining colonization by Frankliniella occidentalis (Pergande), even over prevailing wind. Despite the acknowledged importance of wildflowers in thrips outbreaks, environmental factors directly related to flowering host plants in field margins (richness, abundance, pest thrips density on a given species) have not been used as predictors of thrips density within crops. Similarly, the spatial extent of wildflowers influence on thrips density within crops has rarely been assessed (Nicholls et al. 2001).

Flower-inhabiting thrips are major pests in berry crops (Rhodes and Liburd 2017; Rodriguez-Saona et al. 2010; Renkema et al. 2018), as larvae and adults damage both flowers and fruits (Mound 2009). This can reduce flowering and downgrade fruit appearance, resulting in economic losses (Steiner and Goodwin 2005; Koike et al. 2009). Thrips damage in strawberry production at higher latitudes is predicted to increase due to climate change and warmer conditions (Parikka and Tuovinen 2014). Thus, developing monitoring (Marullo et al. 2021) and efficient control strategies (Sampson and Kirk 2013,2016; Sampson et al. 2021) of thrips populations in strawberry are real issues. However, in Canada, thrips ecology has been overlooked since the observational study of Chiasson (1986) involving a survey of thrips–host plant relations covering the whole country.

Preliminary 2016-17 surveys (unpublished data) revealed that the exotic Frankliniella intonsa (Trybom) and the endemic Frankliniella tritici (Fitch) are dominant pest thrips species in strawberry agroecosystems of Orléans Island, Québec, Canada. As they were abundant on both strawberry flowers (95% of collected thrips) and surrounding wildflowers (43%) (Canovas et al. 2022), those Frankliniella spp. appeared as suitable models to set out the influence of wildflowers and wildflowers' use by pest thrips on their density in strawberry flowers. Besides, densities of both F. intonsa and F. tritici on strawberry flowers were correlated to their abundance in at least two common wildflower species in field margins of Orléans Island (Canovas et al. 2022). Therefore, the current study aims to 1) measure wildflowers use by Frankliniella spp. in uncultivated margins near strawberry crops and 2) model the effect environmental factors related to wildflowers on Frankliniella spp. density on strawberry flowers and its spatial distribution within fields. We hypothesize that wildflowers in uncultivated margins act as Frankliniella spp. sources, favoring strawberry field colonization by pest thrips. We predicted that biotic environmental factors such as floral species richness, floral abundance, and abundance of Frankliniella spp. on preferred wildflower hosts positively influence thrips density in strawberry flowers. We expected thrips density within fields to gradually decrease with growing distance to wildflowers naturally occurring in margins.

### **Materials and methods**

### Study sites and sampling periods

Sampling was conducted on Orléans Island, near Québec City, Québec, Canada, during the entire 2018 strawberry production season. Samples were collected once a week from mid-July until mid-September in four sites. Each site consisted of a 1-year-old Seascape cultivar open strawberry field (average 72 m long and 73 m wide) and the adjacent uncultivated field margin (average 3.7 m wide), naturally colonized by wildflowers. Sites were distributed among four farms applying conventional strawberry crop management with insecticide (©DELEGATE; active compound Spinetoram; pulverizations not synchronized between farms), which is the main control method for thrips in open fields (Reitz et al. 2020) including in strawberry production (Steiner et al. 2005). Partner producers carried out pesticide applications at

their discretion, based on the recommendations of their lead agronomists. Before any sampling event, each farm was systematically contacted to ensure that the deadline for returning to the field was respected following potential spraying of insecticides, fungicides, or herbicides. Monitored field margins were selected to standardize their width and vegetation cover and minimize the agricultural disturbances (access roads, material storage, irrigation network). No mowing was done before and during sampling near sampled areas.

The day-neutral Seascape cultivar (*Fragaria* × *ananassa* Duchesne) produces fruits from late spring until autumn, so our sampling season includes both the highest abundance period for flower thrips and the maximum strawberry fruit production. The sampling season was separated in three distinct periods, based upon crop production seasonality and *Frankliniella* spp. abundance in our system (Fig. 1):

- July (16 July–30 July 2018), early blooming and fruit harvest, moderate abundance of thrips in strawberry fields (mean  $3 \pm 0.8$  thrips/flower).
- August (06 August–20 August), intensive fruit harvest in strawberry fields and *Frankliniella* spp. abundance peak (mean 20±6 thrips/flower).
- September (28 August–17 September), reduced fruit harvest in strawberry fields and *Frankliniella* spp. abundance decrease (mean 4±1 thrips/flower).

Furthermore, each of these periods represents a distinct wildflower profile in uncultivated field margins (Table 1).

### Insect sampling and monitoring of floral resources

In each site, the field side was virtually subdivided crosswise into 10 m wide marked transects including both a strawberry field portion, and its adjacent uncultivated margin naturally colonized by wildflowers. For each sampling event (date) in each site, a single 10 m wide transect was randomly selected for sampling. The strawberry field portion of the selected transect was systematically sampled perpendicularly to the uncultivated margin, at intervals of 2, 7, 11, 15, and 19 m from the margin; those distances are corresponding to oddnumber strawberry rows of the field border. At each distance, four non-overlapping 1 m<sup>2</sup> quadrats of strawberry within the 10 m wide transect were randomly selected for sampling. In each quadrat, strawberry flowers in bloom were counted and a maximum of five flowers was collected. Similarly, in the same transect, the abutting margin was sampled for wildflowers in four 1 m<sup>2</sup> quadrats randomly selected within the same transect. The number of flower units in each quadrat was counted for each blooming wildflower species and a maximum of five flower units per species was collected. In the case of plants with compound inflorescences, such as Vetch (Vicia spp.) or Goldenrod (Solidago spp.), the entire raceme was collected and considered as one flower unit. During any sampling event in each site, the total vegetation area sampled in the randomly selected transect was 20  $m^2$  in the strawberry field portion, and 4  $m^2$  in the adjacent uncultivated field margin.

### **Thrips and flowers identification**

Thrips were extracted from flower units dissected in ethanol. In flower samples containing < 100 adult Thysanoptera, all individuals were identified to species. In those with > 100 or > 200 adult thrips, a fraction (respectively, 50% or 25%) of all individuals were randomly subsampled to be identified. For adult identification, thrips were slide-mounted in ethanol 45% and examined with an Olympus Bx41 compound microscope (Markham, Ontario, Canada). Adults were sexed and identified to species level using morphological keys from

Fig. 1 Mean *Frankliniella* spp. densities variation according to sampling date, periods, and sampling areas. Data presented are mean thrips/10 flowers  $\pm$  SE (n=4 sites) for a total sampling effort of 48 m<sup>2</sup> (July and August) or 64 m<sup>2</sup> (September) in uncultivated margins and 240 m<sup>2</sup> (July and August) or 320 m<sup>2</sup> (September) in strawberry fields



Sampling date

Wildflowers	Number	Thrips	
Scientific name		F. intonsa	F. tritici
Period 1 (July)			
Vicia cracca	52	<u>80</u>	28
Sinapis arvensis	86	32	25
Leucanthemum vulgare	32		48
Linaria vulgaris	31	17	1
Arctium minus	10	2	2
Cichorium inthybus	10	1	3
Convolvulus arvensis	4		3
Galeopsis tetrahit	36	3	
Ranunculus acris	2	2	
Solidago graminifolia	6		2
Achillea millefolium	10		1
Daucus carota	15		1
Persicaria maculosa	19	1	
Silene vulgaris	80		1
Period 2 (August)			
Vicia cracca	85	312	426
Cichorium inthybus	18	3	230
Sinapis arvensis	86	<u>97</u>	86
Sonchus asper	10		106
Oenothera biennis	5	16	32
Trifolium partense	3	6	41
Cirsium arvense	6	4	24
Linaria vulgaris	78	13	11
Persicaria maculosa	71	8	4
Solidago canadensis	13	2	5
Aster umbellatus	22	1	5
Matricaria inodora	8	3	2
Aster simplex	37	1	3
Solidago graminifolia	29	1	3
Sonchus oleraceus	5	1	2
Silene vulgaris	57		2
Erigeron annuus	6		1
Period 3 (September)			
Vicia cracca	87	256	<u>69</u>
Sinapis arvensis	90	<u>47</u>	<u>12</u>
Sonchus asper	5		20
Cichorium inthybus	17	5	14
Linaria vulgaris	110	12	2
Persicaria maculosa	79	7	2
Trifolium pratense	6	3	5
Aster simplex	159	0	8
Solidago canadensis	75		7
Taraxacum officinale	5	3	2
Trifolium hybridum	8	3	
Leucanthemum vulgare	5		2
Oenothera biennis	6	1	1
Symphiotrichum cordifolium	15		1

 Table 1
 Total number of Frankliniella spp. thrips on wildflower hosts according to periods

Table 1	(continued)
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Wildflowers	Number	Thrips	
Scientific name		F. intonsa	F. tritici
Aster umbellatus	12	1	
Erigeron annuus	10	1	
Tragopogon pratensis	10	1	
Silene vulgaris	48	1	
Solidago graminifolia	34		1

Data presented are total thrips number for a total cumulated sampling effort of ~1600 m<sup>2</sup> in margins. Underlined values indicate *F. intonsa* and *F. tritici* sufficient abundances to consider thrips–wildflower association as predictors in Mixed multiple regressions

Mound and Kibby (1998), Stannard (1968) and Hoddle et al. (2012). Specimens were also sent for identity validation to The Canadian National Collection of Insects, Arachnids, and Nematodes (CNC) of Agriculture and Agri-Food Canada. Immature thrips were not identified to species level considering taxonomic difficulties (Skarlinsky and Funderburk 2016). All flowering plants were identified to species level (Clemants and Gracie 2006; Data base from Ministère de l'Agriculture, des Pêcheries et de l'Alimentation and Ministère des Forêts, de la Faune et des Parcs 2019).

### **Statistical analysis**

Analyses were performed on R software (version 3.6.0; R Core Team 2022). Mixed multiple regressions were independently performed to assess the ability of 'Floral richness' (total number of flower species blooming), 'Floral abundance' (total flower units number per species blooming), and numbers of F. intonsa or F. tritici on selected wildflowers, to predict F. intonsa or F. tritici densities within strawberry flowers. Data from weekly sampling were pooled for each period and separately analyzed. Wildflower species used in models were the five to six main F. intonsa or F. tritici hosts, based on total thrips abundance for each period (Table 1). Only samples with a minimum of 10 thrips were included in models, considering that lower abundances likely reflected accidental visiting. Mixed multiple regressions were also performed to model the effect of 'Distance' from the uncultivated margin on thrips density in strawberry fields. An interaction term between 'Distance' and 'Thrips species' was added to detect any potentially different response from F. intonsa and F. tritici based on deviance analysis. Analyses were performed using the glmer.nb function from R lme4 package (Bates 2015), with significance threshold  $\alpha = 0.05$ . In all models, 'Sites' and 'Quadrats' were included as random effects. Overdispersion in thrips density was handled using Negative Binomial distribution. An offset term was added in all models to consider that systematic sampling of five flowers for each species in a quadrat was not always possible. Pseudo- $R^2$  was estimated on the fixed part of each model as a goodness-of-fit measure, corresponding to the squared correlation between predicted and observed values. Preliminary analyses were performed to ensure there was no violation of assumptions concerning residuals distribution and absence of collinearity among factors.

### Results

A total of 4 360 adult *Frankliniella* spp. were collected on 6 075 flower units including strawberry flowers. Nearly all phytophagous arthropods found in flowers were thrips and over 96% among all thrips in strawberry were *F. intonsa* or *F. tritici*. In wildflowers, they represented over 50% of the adult thrips collected. Among the 39 wildflower species sampled, 29 of them hosted at least one *F. intonsa* or *F. tritici* adult specimen and wildflowers not found to be used by them belonged to rarely sampled species (Table 1).

Generally, females of both *Frankliniella* spp. were more frequently collected than males (overall female:male sex ratio is 1:0.44). Generalist thrips predators were anecdotally found in flower samples, totaling 15 *Aeolothrips fasciatus* (Linnaeus) (Thysanoptera: Thripidae) and 50 *Orius* sp. (Hemiptera: Anthocoridae).

# Frankliniella species associations with wildflowers in margin

Thrips differently used wildflower resources depending on the period (Figs. 1, 2), as the availability of blooming wildflowers varied throughout the season both in terms of species composition and abundance (Supplementary material section). *Frankliniella intonsa* and *F.tritici* shared most of their wildflower host plant range, with, respectively, 22 and 24 wildflower host species (Table 1). Interestingly, *F. tritici* used *Leucanthemum vulgare* and *Sonchus asper* abundantly, despite the low availability of these wildflower species. (Table 1; Fig. 2).

Overall, the abundances of F. intonsa and F. tritici were not proportional to flower availability (Fig. 2). Some wildflower species with low relative abundance hosted high thrips densities, thus appearing as preferred hosts: Linaria vulgaris (Mill) in July, Trifolium pratense (Linnaeus) in August or Vicia cracca (Linnaeus) in September. Contrastingly, only four thrips were found on abundant Silene vulgaris ((Moench) Garcke) flowers, which represented 9% of available wildflowers. Vicia cracca and Sinapis arvensis (Linnaeus) flowers hosted both F. intonsa and F. tritici during all three sampling periods (Table 1; Fig. 2), suggesting thrips preference. Despite moderate availability, V. cracca, among others, supported the highest F. intonsa and F. tritici total densities: mean > 6 thrips/10 flower units, and hosted relatively high thrips larval densities: 6, 30, and 8 larvae/10 flowers, according to July, August, and September periods, respectively.

# Effect of thrips—wildflowers associations on thrips density within strawberry field

Thrips density in margins, particularly *F. intonsa* and *F. tritici* on specific wildflowers, positively correlated with their density within strawberry fields (Figs. 3, 4, 5; Tables 2, 3).



**Fig. 2** Mean *Frankliniella* spp. densities variation according to wild-flower species. Flowers relative abundance in percentage (black triangle) is presented on the right axis as a measure of flower availability for thrips. Only main wildflower species hosting more than 10 thrips

in each period are illustrated. Data presented are mean thrips/10 flowers  $\pm$  SE (n=4 sites) for a total sampling effort of 48 m<sup>2</sup> (July and August) or 64 m<sup>2</sup> (September) in 768 uncultivated margins



**Fig. 3** Factors related to wildflowers in field margins that significantly influenced *Frankliniella* spp. density within strawberry fields during July (16–30 July). Represented ranges in x axis correspond to observed values for a total 48 m<sup>2</sup> sampling effort in uncultivated mar-

gins. Data presented are predicted values  $\pm 95\%$  IC, separately calculated for each species (n=4 sites), dots corresponding to observed values. Statistics are shown in Tables 2 and 3



Fig. 4 Factors related to wildflowers in field margins that significantly influence *Frankliniella* spp. density within the field during August (6–20 August). Represented ranges in x axis correspond to observed values for a total 48 m<sup>2</sup> sampling effort in uncultivated mar-

gins. Data presented are predicted values  $\pm 95\%$  CI, separately calculated for each species (n=4 sites). Dots are observed values. Statistics are shown in Tables 2 and 3.

These thrips density effects varied with periods, with model respective pseudo- $R^2$  values of 0.38, 0.26, and 0.63 for *F. intonsa*; and 0.70, 0.63, and 0.81 for *F. tritici*, respectively, for July, August, and September periods. Flower abundance and flower richness variables were found to have mostly

insignificant effects on thrips density within the field, but a negative effect of floral richness for *F. intonsa* in July (Tables 2, 3). Considering *F. intonsa*, very few wildflower species supported enough individuals to be considered in modeling, and *S. arvensis* and *V. cracca* were selected as its



**Fig. 5** Factors related to wildflowers in field margins that significantly influence *Frankliniella* spp. density within the field during September (28 August–17 September). Represented ranges in x axis correspond to observed values for a total 64 m<sup>2</sup> sampling effort in

uncultivated margins. Data presented are predicted values  $\pm 95\%$  IC, separately calculated for each species (n=4 sites). Dots are observed values. Statistics are shown in Tables 2 and 3

 Table 2 Statistical modeling of Frankliniella intonsa density within strawberry field as predicted by 'Floral abundance' (total flower number regardless of species), 'Floral richness' (total species number), and its density (Frin) on most used wildflower species in field margins

Fixed effects	Estimate $(\pm SE)$	z	р
July			
Intercept	- 1.438 (0.469)	- 3.064	0.002*
Floral abundance	0.001 (0.001)	1.015	0.310
Floral richness	- 0.522 (0.087)	- 5.990	2.09e-09*
Frin on Sinapis arvensis	- 0.005 (0.025)	0.208	0.835
Frin on Vicia cracca	0.077 (0.011)	7.082	1.42e-12*
August			
Intercept	- 1.697 (0.391)	- 4.341	1.42e-05*
Floral abundance	- 0.001 (0.001)	- 1.200	0.230
Floral richness	0.004 (0.013)	- 0.306	0.759
Frin on Oenothera biennis	0.040 (0.035)	1.143	0.253
Frin on Sinapis arvensis	0.045 (0.017)	2.701	0.007*
Frin on Vicia cracca	0.033 (0.008)	3.995	6.47e-05*
September			
Intercept	- 2.876 (0.435)	- 6.617	3.68e-11*
Floral abundance	- 0.001 (0.001)	- 0.697	0.486
Floral richness	- 0.106 (0.115)	- 0.923	0.356
Frin on Sinapis arvensis	0.174 (0.036)	4.779	1.76e-06*
Frin on Vicia cracca	0.074 (0.008)	9.578	<2e-16*

Asterisks indicate significant value at  $\alpha = 0.05$  (n = 4 sites)

major hosts for all three periods. Frankliniella intonsa density on V. cracca in all periods, and on S. arvensis in August and September, had a strong positive correlation with its density in strawberry flowers (Fig. 3; Table 2). The abundance of F. intonsa on flowers of relatively rare Oenothera biennis in August had no effect. Regarding F. tritici, both S. arvensis and V. cracca also supported sufficient densities to be considered in models during all periods. Frankliniella tritici density on wildflowers correlated positively with its density in the field (Fig. 3, 4, 5; Table 3). Unlike F. intonsa, F. tritici was abundant on other wildflower hosts, which we also retained as predictors (Table 1). In July, L. vulgare sustained the highest F. tritici abundance (average 20 adults /10 flowers) and was then by far the best predictor among its wildflower hosts (Table 3). However, L. vulgare was unavailable in August and hosted very few F. tritici in September (Table 3). In July, *Cichorium intybus* (Linnaeus) hosted very few thrips (Table 1) but later, F. tritici density on this species correlated with F. tritici density in strawberry; this effect is highly significant in August (Table 3). Regarding S. asper, F. tritici density on preferred wildflowers within field margins in August and September had a strong effect on its density in strawberry (Table 3).

The overall average adult *Frankliniella* spp. density was about 10 times lower in strawberry flowers  $(1 \pm 1 / 10$  strawberry flowers) than in wildflowers  $(10 \pm 4 / 10$  wildflower flowers) (Fig. 1). A lesser but similar trend was also observed for unidentified thrips larvae:  $5 \pm 1$  larvae /

**Table 3** Statistical modeling of *Frankliniella tritici* density within strawberry field as predicted by 'Floral density' (total flower number regardless of species), 'Floral richness' (total species number), and F. tritici (Frtr) densities on most used wildflower species in field margins

Fixed effects	Estimate $(\pm SE)$	z	р
July			
Intercept	- 2.476 (0.389)	- 6.373	185e-10*
Floral abundance	0.001 (0.001)	1.661	0.097
Floral richness	- 0.187 (0.118)	- 1.585	0.113
Frtr on Leucanthemum vulgare	0.131 (0.022)	6.004	1.93e-09*
Frtr on Sinapis arvensis	0.074 (0.036)	2.037	0.0416*
Frtr on Vicia cracca	0.065 (0.048)	1.340	0.180
August			
Intercept	- 1.909 (0.213)	- 8.976	<2e-16*
Floral abundance	0.001 (0.001)	1.055	0.292
Floral richness	0.004 (0.015)	0.235	0.814
Frtr on Chicorium intybus	0.018 (0.005)	3.907	9.33e-05*
Frtr on Sinapis arvensis	0.008 (0.031)	0.251	0.801
Frtr on Sonchus asper	0.020 (0.006)	3.537	0.0004*
Frtr on Vicia cracca	0.020 (0.005)	4.357	1.32e-05*
September			
Intercept	- 2.496 (0.284)	- 8.802	<2e-16*
Floral abundance	- 0.001 (0.001)	- 1.136	0.256
Floral richness	0.053 (0.080)	0.656	0.512
Frtr on Chicorium intybus	0.084 (0.053)	1.583	0.144
Frtr on Sinapis arvensis	0.043 (0.135)	0.318	0.751
Frtr on Sonchus asper	0.081 (0.021)	3.854	0.0001*
Frtr on Vicia cracca	0.094 (0.017)	5.474	4.39e-08*

Asterisks indicate significant value at  $\alpha = 0.05$  (n = 4 sites)

10 strawberry flowers, versus  $12 \pm 2$  larvae /10 wildflower flowers. *Frankliniella tritici* adults were markedly dominant over *F. intonsa* adults in margins in mid-summer weeks (30 July—20 August) (Fig. 1), its density on wildflowers then being much higher than on strawberry flowers. Contrastingly, *F. intonsa* became dominant over *F. tritici* on wildflowers in early September (27th August-6th September), and from mid-August onward, its density was substantially higher on wildflowers than strawberry flowers for about five weeks (Fig. 1). *Frankliniella tritici* density in strawberry flowers appeared more stable in time and generally lower than that of *F. intonsa*, except briefly in late August (Fig. 1). From September onwards, both species densities in fields were similarly low, under 3 adults /10 strawberry flowers.

# Effect of distance from margins on thrips spatial distribution in strawberry fields

Thrips density in strawberry flowers generally decreased with distance of strawberry rows from the field margins (Fig. 6), with pseudo- $\mathbb{R}^2$  values of 0.19, 0.25, and 0.35, respectively, according to periods. This effect was highly significant in August and September (Table 4). Deviance analysis revealed no interaction between distance and thrips species explanatory variables in July (df = 1, $\chi^2 = 1.6978$ , P = 0.1926) and August (df = 1,  $\chi^2 = 0.0962$ , P = 0.7565) so interaction was removed from final models. In contrast, during September, this interaction was highly significant (df = 1,  $\chi^2$  = 20.582, P < 0.001). In July, thrips species was a significant predictor of thrips density in strawberry, but not distance (Table 4). Predicted density of F. intonsa in strawberry flowers was slightly higher than F. tritici density. In August, F. intonsa and F. tritici responded similarly to distance (Table 4), their



**Fig.6** Effect of 'Distance' from field margins in meters on *Frankliniella* spp. density distribution in strawberry agroecosystem according to periods. Distance 0 m represents the interface between margin

(-0.5 m) and field (1-20 m). Data presented are predicted values  $\pm 95\%$  CI (n=4 sites). Dots are observed values. Statistics are shown in Table 4

**Table 4** Statistical modeling of *Frankliniella* spp. density within strawberry field as predicted by 'Distance' in meters from uncultivated field margins and Thrips species

Fixed effects	Estimate $(\pm SE)$	z	р
July			
Intercept	- 1.587 (0.159)	- 9.955	<2e-16*
Distance	0.015 (0.011)	- 1.385	0.166
Thrips species	- 0.586 (0.154)	- 3.810	< 0.001*
August			
Intercept	- 0.807 (0.121)	- 6.666	2.63e- 11*
Distance	- 0.056 (0.009)	- 6.434	1.24e- 10*
Thrips species	- 0.105 (0.121)	- 0.874	0.382
September			
Intercept	- 1.981 (0.149)	- 13.308	<2e-16*
Distance	- 0.123 (0.020)	- 6.143	8.09e– 10*
Thrips species	- 0.110 (0.205)	- 0.538	0.591
Distance × Thrips species	0.104 (0.024)	4.264	2.00e- 10*

Asterisks indicate significant value at  $\alpha = 0.05$  (n = 4 sites)

predicted density decreasing by 5% per meter as distance from margin increased (Fig. 6). The model predicted that a great majority (85%) of adult thrips present in the field in August would be found between 0 and 15 m from the margins (11th strawberry row). In September, thrips density response to distance was highly significant again, but also varied significantly with thrips species (Fig. 6; Table 4). Adult F. intonsa density responded more strongly to distance than F. tritici. Predicted F. intonsa density decreased by 12% per meter away from the margin, with a predicted majority (85%) of F. intonsa being found between 0 and 12 m from margins (8th strawberry row). By comparison, there was only a 2% per meter decrease of density with distance for F. tritici, most of them were found between 0 and 15 m from margin (Fig. 6).

Generally, both *F. intonsa* and *F. tritici* in strawberry were clearly more abundant close to wildflower resources: 90% of adults and 98% of unidentified larvae were observed between 0 and 15 m within fields during the whole sampling program, while models predicted on average 85% of adults to be caught between 0 and 15 m (11th strawberry row) from uncultivated margins. This corroborates the trend observed during our previous extended sampling 50 m from the margin (preliminary 2016 survey, unpublished data).

#### Discussion

Our study illustrates specific *Frankliniella* spp. preferences among their large wildflower host range in strawberry agroecosystems and the role of specific wildflower species in their use of strawberry fields.

# Frankliniella species associations with wildflowers in margins

We recorded *F. intonsa* and *F. tritici* from more than twenty local wildflower species, which generally correspond to previous observations for *F. tritici* (Chellemi et al. 1994). To our knowledge, this is the first study of thrips–wildflower use in Québec since the work of Chiasson (1986). This author reported the presence of *F. tritici* on *S. arvensis* but *F. intonsa* was not recorded presumably because it had not yet established in Québec (Nakahara and Footitt 2007). Information about *F. intonsa* is scarce, regarding both its host range and its geographic origin, presumed to be western Asia (Hoddle et al. 2012). Conversely, *F. tritici* is native to eastern North America (Stannard 1968; Hoddle et al. 2012) and is abundantly observed in wildflowers (Chiasson 1986; Chellemi et al. 1994).

The observed tendency of F. intonsa and F. tritici to use wildflower resources beyond their availability illustrates their preference for specific species according to season, for example, L. vulgare or T. pratense (Fig. 2). Seasonal hostswitching in flower use is likely a response to flowering phenology and the generally ephemeral availability of wildflowers (Northfield et al. 2008). Several authors reported higher thrips densities on particular wildflower species within their host range (Chellemi et al. 1994; Northfield et al. 2008; Silva et al. 2018); however, thrips density was not quantitatively related to flower availability. Like our observations for F. intonsa and F. tritici, consistent flower preferences were reported for F. occidentalis (Pergande) in British Columbia, Canada (Pearsall 2000). In our system, strawberry flowers supported lower total numbers of F. intonsa and F. tritici than preferred wildflowers in margins. Density-independent flower selection behavior was also observed for F. occidentalis under field conditions (Pearsall 2000). Blooming traits often invoked to explain thrips preference include flower openness (Mound 2005), color (Funderburk et al. 2015), pollen nutritional value (Northfield et al. 2008), or scent (Pearsall 2000). Mound and Tuelon (1995) characterized flower-visiting thrips as opportunists; nevertheless, they proposed that under natural conditions, thrips could have adopted an intermediate feeding strategy between polyphagy and monophagy. Thus, thrips tend to have close relationships with some hosts for reproduction, while maintaining lower populations on others (Mound and Tuelon 1995). Our observations and those of Pearsall (2000) could illustrate such a host plant selection strategy.

Sinapis arvensis and V. cracca were consistent hosts for both F. intonsa and F. tritici throughout the three sampling periods (Fig. 2). Noticeably, other Vicia species were mentioned as poor hosts for Frankliniella species reproduction and development (Katayama 2006; Ripa et al. 2009).

# Effect of thrips—wildflowers associations on thrips density within strawberry field

As expected, density of *F. intonsa* and *F. tritici* on wildflowers in uncultivated margins could predict their density within strawberry fields in periods of high thrips abundance. Wildflowers are a key habitat for pest thrips in agroecosystems, some of them being known to frequently transit through the flowering field margins (Fernandes and Fernandes 2015). Therefore, blooming wildflowers can be considered the main source to be screened when monitoring the potential origins of *Frankliniella* species outbreaks, as suggested by Northfield et al. (2008).

Our models indicate that thrips density on major wildflower hosts is closely associated with both F. intonsa and F. tritici density in strawberry flowers (Tables 2, 3). This is a strong indicator of thrips dynamics between wildflowers and cultivated strawberry, complementary to other studies based on thrips sticky-cards trapping (Rodriguez-Saona et al. 2010) or genetic comparisons (Silva et al. 2018) in agroecosystems. Wildflowers such as mustard, vetch, chicory, or thistle are common in disturbed environments (Clemants and Gracie 2006). Previous studies already considered them as key hosts in crop colonization by F. occidentalis, T. tabaci, and other pest thrips species (Katayama 2006; Atakan 2010; Silva et al. 2018). In our study, S. arvensis and V. *cracca* bloomed through all three periods of sampling. They were jointly used by both F. intonsa and F. tritici, suggesting potential resource competition as hinted by the fact that thrips numbers on S. arvensis alternately predicted F. tritici densities in July and F. intonsa in August and September. Notably, F. intonsa and F. tritici are both reported to be involved in interspecific competition with F. occidentalis (Paini et al. 2008; Bhuyain and Lim 2019), but competitive interaction between F. intonsa and F. tritici has not been evaluated yet. On wildflowers species sustaining thrips numbers that significantly contributed to F. tritici density in strawberry flowers (i.e., L. vulgare, C. intybus and S. asper), we observed that F. tritici adults were highly aggregated. Population density should be one of the main stimuli driving thrips migration in agroecosystems (Fernandes and Fernandes 2015); thus, it is not surprising that thrips density on mostly used wildflowers (see, e.g., Fig. 2) was closely associated with thrips density increases in strawberry (Figs. 3, 4, 5). Both competition and population density pressures could be implicated in Frankliniella spp. emigration from hosts like V. cracca and S. arvensis, which needs further study. Despite their small size, thrips in flight may choose their landing area under favorable conditions (Kirk 1984) and use saltation for small-scale movements (Bournier 1983). In their studies, Pearsall (2000) and Pearsall and Myers (2001) attributed the net movement of F. occidentalis from wild areas toward nectarine orchards to the strong attractive effect of scented nectarine flowers. In strawberry, we speculate that the movement of F. intonsa and F. tritici from margins to the field could be partly due to attraction toward white strawberry flowers, as white color is known to be attractive to Frankliniella spp. (Funderburk et al. 2015 and references therein). White was the predominant color at landscape scale as the Seascape strawberry cultivar continuously produces flowers over an extended area, strawberry flowers thus being a non-negligible visual stimulus compared to isolated wildflowers in margins.

Floral richness and floral abundance explanatory variables generally had no effect on thrips density in strawberry fields, except in July, with *F. intonsa* density in fields being negatively affected by floral richness in margins. It is known that some *F. occidentalis* individuals continuously move from crops into nearby wild vegetation (Adler et al. 2014) and bi-directional thrips migration between fields and their margins has been reported by Fernandes and Fernandes (2015). In their study, immigration into margins was attributed to wildflower blooming periodically attracting thrips. Thus, in July, a negative effect of floral richness on *F. intonsa* density in strawberry might be linked to *F. intonsa* movement toward margins because of an attractive effect of wildflowers.

# Effect of distance from margins on thrips spatial distribution in strawberry fields

Distance from uncultivated margin negatively affected both F. intonsa and F. tritici density distribution within strawberry fields during much of the sampling program. According to our prediction, pest thrips density decreased in the fields as a function of distance from margins. In blueberries, Rodriguez-Saona et al. (2010) found a significant effect of distance from uncultivated margins on thrips sticky trap counts in blueberry fields and presumed that wild early flowering Vaccinium spp. could have been a thrips source. Contrastingly, wildflower corridors in organic grape production were found to decrease F. occidentalis density in their vicinity, by favoring crop colonization by natural enemies (Nicholls et al. 2001). Our results indicate that the activity of thrips natural enemies in strawberry fields of Orléans Island was negligible, as also observed in preliminary surveys in 2016-2017 (unpublished data). A possible explanation is the use of broad-spectrum insecticides in conventional strawberry crop management, which are particularly harmful to predatory thrips (Mautino et al. 2014) and anthocorid bugs (Funderburk et al. 2000). Nicholls et al. (2001) in grape found no apparent distance effect on F. occidentalis counts between field margins and field center. In their study, margin vegetation was a riparian forest, with available wildflowers species possibly being less diversified than F. occidentalis' common host range, typical of dryer disturbed areas. Therefore, forest margins could have been less suitable for thrips establishment, playing a negligible role as a thrips source. In contrast, we observed that F. intonsa and F. tritici may mainly breed in wildflowers and migrate into strawberry fields (Canovas et al. 2022). In our study, a vast majority (85%) of adult thrips present in strawberry would stay within 12-15 m from uncultivated margins, with density decrease from margins to fields' center. Fernandes and Fernandes (2015) reported such a thrips density gradient in tomato fields. Similarly, in nectarine orchards, F. occidentalis density decreased with distance from uncultivated areas (Pearsall and Myers 2001). The expression "edge effect" describes such a pattern of high thrips abundance in a cultivated area close to a thrips source: flying adult thrips leaving an old crop, or a patch of wildflowers, easily reach new cultivated hosts and mainly colonize the first ones encountered (Bournier 1983).

In July, distance from margin was not a significant predictor of *F. intonsa* and *F. tritici* density in strawberry (Table 4), so margins may not have been an immigration source of thrips in early summer. However, this is consistent with the putative movement of *F. intonsa* from strawberry flowers to wildflowers in July, based on the negative effect of floral richness on the density of this thrips species within field (Fig. 3). Despite wild floral vegetation being then less developed and less diversified than in August and September (Table 1), alimentation and / or reproduction of *Frankliniella* spp. on beneficial wildflower species may be necessary in early season for thrips populations establishment before thrips density increase in margins could significantly contribute to their migration in strawberry flowers.

Models based on distance from margins satisfyingly explained thrips density variations in strawberry flowers. A "moderate" fit was obtained for two of the three periods (mid- summer, early fall), which is substantial considering a disturbed agroecosystem context. However, despite being significant, distance and thrips species variables explained only 25% (August) to 35% (September) of overall variance, showing that *Frankliniella* spp. density distribution in strawberry fields was not determined solely by distance from wildflower resources. In spring, thrips populations in fields can originate from two main sources: immigration from outside crops, or from "resident" diapausing adults that survived winter (Rodriguez-Saona et al. 2010). Weekly emergence trapping in four sites in Orléans Island in May and June 2018 (Canovas et al. 2022) revealed that whereas many adults F. intonsa and F. tritici emerged from the field margins areas, only a few individuals were collected from adjacent strawberry. Thus, adults overwintering within the field negligibly contributed to springtime thrips populations built up in strawberry, which contrasts with F. occidentalis in partly sheltered outdoors strawberry in the United Kingdom (Sampson et al. 2021). Another aspect of thrips density patterns in crops is their markedly aggregated distribution (Cho et al. 2000 and references therein), also recorded for some Frankliniella species (Cho et al. 1995; Allan and Gillett-Kaufman 2018). In Swiss strawberry fields, Linder et al. (2006) reported high aggregation of a thrips complex including F. intonsa, with scattered groups of adults and larvae. Potential mechanisms to explain thrips aggregative behavior are chemical communication, local abiotic conditions (soil type, fertilization), wind and host flower numbers (Arévalo and Liburd 2007).

Our modeling primarily focused on the causal relationship between Frankliniella spp. densities on wildflowers and their densities on strawberry flowers, as previous work suggested that pest thrips' net movement in agroecosystems would be from uncultivated margins toward crops. This is based on trapping (Pearsall and Myers 2001; Rodriguez-Saona et al. 2010), joint observation of wild and crop host plants (Puche et al. 1995; Atakan and Uygur 2005; Silva et al. 2018) and genetic sequencing (Silva et al. 2018). However, we observed a negative effect of floral richness on F. intonsa density in strawberry in July, and a variable effect of distance on both Frankliniella spp. density within strawberry flowers according to period. Furthermore, F. intonsa density in strawberry flowers was higher in July and August than September and F. tritici density in strawberry was not distinctively higher at the population peak in August than in July or September, despite increasing floral abundance and richness over time in margins. These results hint to more complex migration dynamics than considering wildflowers as a permanent thrips source. Attraction of Frankliniella spp. toward wildflowers in early season may be beneficial for feeding and reproduction, potentially also acting as refuges against chemical sprayings (Beaudoin and Kennedy 2012; Cluever et al. 2016), or disturbance caused by harvesting in strawberry crops. Thus, the main thrips movement may then be from crops toward uncultivated margins, an "edge effect" being observed later in strawberry flowers when thrips densities on preferred wildflower species exceed a threshold, as illustrated by our models (Figs. 3, 4, 5). The use of thrips immunolabeling techniques would be an effective way to follow their movements in the environment for several weeks, as well as their use of specific host plants over time (Fernandes and Fernandes 2015).

As we monitored strawberry agroecosystems under conventional agricultural management, the influence of pesticide spraying cannot be totally excluded. However, we ensured that applications of insecticide, fungicide, or herbicide did not coincide with any of our samplings. As a delay of several days is necessary before producers can harvest or market the fruits after an application, the use of pesticides by producers tends to be reduced as much as possible. Considering that we monitored margins directly abutting the fields, we assume that interpretation of our results in terms of movement of thrips between wildflowers and strawberry flowers was carried out in closely similar conditions regarding pesticide sprays. To our knowledge, no study has specifically investigated the effect of chemical treatments on the dispersal of thrips between wild vegetation and crops, except Aliakbarpour and Salmah (2011) in tropical orchards, who concluded that the main effect of insecticide sprays is to promote the aggregation of adult thrips and larvae in protected microhabitats on the crop (mango panicles).

Local management of field margins was attempted on four sites in this study, based on weekly mowing or sowing attractive wildflowers. However, poor seedlings establishment, existence of wildflower seed banks, and mowing synchronization issues created unexpected interferences. We would recommend carrying out such uncultivated margins manipulations on an experimental farm rather than commercial fields, to standardize conditions and avoid pesticide use.

We used data from a single year to model thrips abundance, which limits the possibility for generalizing to other situations in time and space, despite replication of field sites and farms and weekly monitoring over a whole season. However, our 2018 observations regarding Frankliniella spp. are consistent with our unpublished data at lower thrips densities in 2016–2017. Thrips ecology under natural conditions is mediated by numerous biotic and abiotic interactions, difficult to measure in the field (Bournier 1983). Some parameters are already known to significantly influence the flight activity as well as the direction of thrips dispersal at the agricultural landscape scale, such as atmospheric conditions (Bournier 1983; Lewis 1991; Rodriguez-Saona et al. 2010) and crop age (Fernandes and Fernandes 2015). Future work is needed to jointly monitor more agroecosystems factors, and model multiannual thrips density variation, especially in the current context of climate change.

Considering crop management, knowing that close association of *F. intonsa* and *F. tritici* with specific wildflowers, especially *Vicia cracca, Sinapis arvensis* or *Sonchus asper*, forms a basis for future work aiming to reduce thrips damage in strawberry. For now, optimal flowering margins manipulation strategies to control thrips populations remain unclear. Native wildflower planting, as experimented in Northeastern USA strawberry fields (McCabe et al. 2017), would potentially decrease thrips population density pressure in margins. However, as *Frankliniella* species are anthophagous generalists, flower addition could also have undesirable positive donor effects on their density in crops (McCabe et al. 2017), possibly even attracting and sustaining more thrips in the system. On the other hand, wild vegetation suppression or sprayings with insecticides for thrips control in margins could lead to thrips dispersion and outbreaks in adjacent crops (Bailey 1933; Beaudoin and Kennedy 2012). Thus, further studies on thrips–wildflowers interactions are necessary to develop experimentally based margin management strategies for strawberry fields agroecosystems.

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#### Declarations

Conflict of interest The authors have no conflict of interest to declare.

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