


ARTICLE

“Strawberry fields forever”: flower-inhabiting thrips (Thysanoptera: Thripidae) communities and their spatial interactions in strawberry agroecosystems in Québec, Canada, with first mention of pest *Frankliniella intonsa* (Trybom)

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Abstract

Thrips (Thysanoptera: Thripidae) communities in agroecosystems are poorly known, particularly in Québec, Canada, where thrips can cause damage in strawberry crops. The phenology of anthophagous thrips and their use of cultivated and wildflower resources were monitored in strawberry agroecosystems, encompassing strawberry (Rosaceae) fields and adjacent uncultivated margins, on Orléans Island, Québec, Canada. A community comprised of 11 thrips species was described, dominated during the whole season by pest species *Frankliniella tritici* and *F. intonsa*, which is a first mention in Eastern Canada. Surprisingly, the major strawberry pest *F. occidentalis* was absent in our samples. Thrips species richness and abundance on wildflowers varied, with few flowering plant species supporting a majority of the community. Sampling sites and local wildflower presence influenced the thrips species assemblage observed on strawberry crops. Such a high thrips diversity was unexpected in this agroecosystem. The identified associations between pest thrips and wildflower species will be useful to develop better control programmes in strawberry crops.

Résumé

Les communautés de thrips dans les agroécosystèmes sont méconnues, notamment au Québec où les thrips peuvent causer des dégâts en fraisières. La phénologie de la communauté de thrips anthophages, ainsi que son utilisation des ressources florales cultivées et sauvages, ont été suivies dans l'agroécosystème des fraisières, englobant les champs de fraises (Rosaceae) et leurs bordures non cultivées, à l'île d'Orléans, Québec, Canada. La communauté comprenait onze espèces de thrips, et était dominée durant toute la saison par les espèces de ravageurs *Frankliniella tritici* et *F. intonsa*, cette dernière étant mentionnée pour première mention dans l'Est du Canada. Étonnamment, le ravageur notoire de la fraise *F. occidentalis* était totalement absent de nos échantillons. La richesse spécifique des thrips et leur abondance sur les fleurs sauvages variaient, peu d'espèces de plantes à fleurs soutenant la majorité de la communauté. Les sites d'échantillonnage et la présence locale de fleurs sauvages influençaient significativement l'assemblage d'espèces de thrips observé dans la culture de fraises. Une telle diversité d'espèces de thrips dans l'agroécosystème était inattendue. De plus, les associations identifiées entre les thrips ravageurs et les espèces de fleurs sauvages qu'ils fréquentent seront des indices précieux pour le développement de programmes de lutte en fraisières.

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Introduction

Thrips (Thysanoptera: Thripidae) are best known as phytophagous pests threatening various agroecosystems worldwide (Mound 2005; Silva *et al.* 2018; Rodriguez-Saona *et al.* 2019) including in North America. However, besides being pest species, thrips are a highly diversified insect order (Mound 2009). Climate change is expected to enhance major pest thrips fitness (Reitz *et al.* 2020) and globally expand thrips species geographical distribution by modifying their local faunal habitats (Park *et al.* 2014; He *et al.* 2017).

Thrips occur in almost all terrestrial ecosystems and are usually associated with both dead (fungus decomposers) and living vegetation (phytophagans and predators; Mound 2018). About one-quarter of thrips species depend upon flowering plants for feeding and reproduction (Mound 2009). In agroecosystems, flower-feeding species often use both cultivated and uncultivated vegetation, creating small-scale migratory dynamics that favour crop colonisation by pest thrips from adjacent wild host plants (Mound and Tuelon 1995; Silva *et al.* 2018). Wildflower vegetation in crop field margins can therefore be an important source of pest thrips in agricultural landscapes (Pearsall and Myers 2001; Northfield *et al.* 2008), and monitoring thrips distribution and plant use in peripheral habitats could be critical to prevent pest thrips outbreaks. However, identification delay or lack of local taxonomic updates are frequent issues complicating pest thrips management (Reitz *et al.* 2011; Sabahi *et al.* 2017; Wu *et al.* 2018). Most studies on thrips have primarily focused on economic losses and control of common pest species in crops (Moreira *et al.* 2014; Renkema *et al.* 2018), which represent only approximately 1% of all thrips species (Morse and Hoddle 2006). Consequently, thrips local community composition beyond crop pests, mainly associated with wild host plants near crops, remains neglected. Thrips communities in agroecosystems require more attention because their local diversity quickly evolves through changes in land use and crop production practices (Mound 2018). Flowers are appropriate sampling units to describe thrips fauna in agroecosystems because they allow thrips screening in both the crops and the surrounding wild vegetation (Northfield *et al.* 2008).

Thrips are pests in small fruit and berry crops and are frequently reported to attack raspberries (Rosaceae) (Leach and Isaacs 2018) and blackberries (Moraceae) (Rhodes and Liburd 2017), as well as strawberries (Rosaceae), which are particularly susceptible (Mound 2009). With specialised sucking mouthparts, thrips larvae and adults pierce plant cells to suck their contents (Bournier 1983). Thrips feeding and oviposition on strawberries create characteristic net-like russet discolouration called bronzing (Koike *et al.* 2009). Thrips pollen feeding and oviposition on strawberry flowers cause less injury, although high populations damage stamens and limit pollen maturation (Steiner and Goodwin 2005). Strawberry bronzing due to thrips is widely reported in the United States of America (Dara *et al.* 2018; Renkema *et al.* 2018), Europe (Linder *et al.* 2006; Sampson and Kirk 2013), the Middle East (Coll *et al.* 2007), and Australia (Steiner and Goodwin 2005). Main pest thrips issues in strawberry involve the invasive *Frankliniella occidentalis* (Pergande) (Coll *et al.* 2007; Sampson and Kirk 2016), whereas *F. tritici* (Fitch) seems to be dominant in eastern North America (Matos and Obrycki 2004; Northfield *et al.* 2008), possibly migrating yearly into Canada from southern locations via prevailing winds (Lewis 1991). Thrips damage is predicted to increase due to the higher temperatures and atmospheric CO₂ concentration that accompany climate change (Reitz *et al.* 2020), including at high latitudes (Parikka and Tuovinen 2014). Thrips are key pests in Canada's strawberry-producing provinces (Tellier 2021; Ontario Ministry of Agriculture, Food and Rural Affairs 2022). Thrips species diversity remains overlooked in Canada (Footitt and Maw 2019) and has not been evaluated in Québec since the extensive work of Chiasson (1986), who described thrips–host plant relationships in Canada based on widely collected thrips across the country and maintained her own collections in Ontario and Québec.

In the present study, we investigated the abundance and diversity of thrips in strawberry agroecosystems (*i.e.*, field and adjacent uncultivated margins) on Orléans Island, near Quebec

City, a region known for strawberry production. Based on preliminary work in 2016 and 2017 (C. Cloutier, unpublished data), sampling covered the entire strawberry production season in 2018 in both cultivated and wild areas, with emphasis on potential relations between these environments. After describing the flower thrips community and its phenology in the strawberry agroecosystem, we tested whether wildflower resources and their associated thrips affected the pest thrips assemblage in the strawberry fields. We expected that, despite the presence of various thrips species associated with wildflowers, *F. occidentalis* and *F. tritici* would likely predominate. In addition, we presumed that those thrips species may not overwinter on Orléans Island because of the region's cold winters and thus may recolonise local strawberry fields annually, arriving after the spring thaw and early springtime period. Finally, we assumed that local wildflower resources and the densities of the main pest thrips species on frequently used wildflower species would influence pest thrips densities that we would observe in strawberry flowers due to their net movement from wild hosts towards crops.

Materials and methods

Study sites and seasonal partitioning of sampling

Weekly sampling of day-neutral strawberries on raised beds covered with plastic mulch was conducted on Orléans Island, near Quebec City, Québec, Canada during the 2018 strawberry production season. Initially, our study also covered the 2016 and 2017 seasons (June–October), but data were not included in the final analyses due to very low thrips abundance (C. Cloutier, unpublished data). Samples were collected weekly from mid-May until mid-October 2018 at 13 sites. Each site consisted of a day-neutral strawberry field (approximately 83 m long × 80 m wide) that was planted with “Seascape” cultivar and one of its uncultivated field margins (an approximately 3-m-wide field border) that was naturally colonised by wildflowers. Sites were distributed among four farms that applied conventional strawberry crop management, which includes the use of pesticides, the main control method for thrips generally (Reitz *et al.* 2020) and in strawberry (Steiner and Goodwin 2005). Sampled uncultivated margins were selected so as to standardise the width as well as the degree of vegetation cover while minimising the influence of access roads and the nearby proximity of crops other than strawberries.

The day-neutral Seascape cultivar (*Fragaria* × *ananassa* Duchesne) continuously produces fruits from early summer until autumn. Typically, strawberry fields are exploited during a two-year rotation cycle, two-year-old plants being destroyed due to disease susceptibility after early summer production. The thrips sampling season was divided into three periods based on the seasonality of crop production and thrips abundance in 2018. The first period, referred to as May–June (18 May–03 July), corresponded to harvest in two-year-old fields in early season. The second period, or July–September (10 July–17 September), corresponded to harvest in one-year-old fields, with sampling starting as soon as the first flowers appeared in all sampled sites; this was the main fruit-production and high thrips-abundance season. In the third period, or October (24 September–16 October), fruit harvest in one-year-old crops was reduced, and thrips abundance declined. During this period, fields were sheltered at night with polyethylene covers until permanent sheltering for winter. Each of the three periods also presented a distinct wildflower profile in the uncultivated field margins. Four sites were sampled in May–June, six sites were sampled in July–September, and three sites were sampled in October because of logistical constraints.

Early season thrips emergence

Emergence traps were randomly installed in the strawberry fields and their uncultivated margins. Each trap consisted of an inverted opaque plastic box (31 cm × 28 cm × 14 cm) with a

150-mL collecting vial filled with water and a drop of liquid soap. Traps were set up on 8 May and checked weekly during May and June 2018, with four traps deployed in the strawberry field and four traps in the adjacent uncultivated margin at each site (total sampling effort of 12.5 m²/site in each environment). Trapped specimens were collected once each week. After each sampling event, traps were randomly moved 2 m away from their earlier position to increase trapping probability.

Thrips captures on flowers and fruit damage monitoring

Sampling events for thrips in strawberry flowers and wildflowers from May to October occurred at weekly intervals. In each site, the strawberry field–uncultivated margin interface was subdivided lengthwise into 10-m-wide strips that extended into both environments for concurrent sampling. During a sampling event at each site, one strip was randomly selected among the eight available for sampling. The field was sampled with 1-m² quadrats at intervals of 2, 7, 11, 15, and 19 m from the field–margin interface, each corresponding to strawberry rows (0.76 m wide, spaced by 0.61 m). In each field quadrat, strawberry flowers were counted, and a maximum of five flowers were collected in one vial. Ripe and unripe strawberry fruits were also counted, and one unripe fruit was collected. In line with the field transect, uncultivated field margins were similarly sampled in four 1-m² quadrats that were randomly selected within the 10-m-wide strip. In each quadrat, flowers were counted for each wildflower species, and a maximum of five flowers per species was collected. In the case of plants with compound inflorescences, such as vetch (*Vicia* sp.) (Fabaceae) or goldenrod (*Solidago* spp.) (Asteraceae), the entire raceme was collected and considered as one flower unit. The total vegetation area sampled at each site during a sampling event amounted to 20 m² in the strawberry field and 4 m² in the field margin. Samples were stored at 4 °C until dissection under a stereomicroscope (Zeiss, Oberkochen, Germany) to detect thrips. Adult and larval thrips were counted and stored in 45% ethanol to prevent muscle stiffening. Strawberry fruits were observed under a stereomicroscope to identify bronzing that could be attributable to thrips, and scoring of bronzing was ranked for severity from 1 (low) to 5 (high), based on the proportion of the fruit that was affected by bronzing.

Thrips and flower identification

In flower, fruit, or trap samples containing fewer than 100 adult thrips, all individuals were identified to species. In those samples with more than 100 or 200 adult thrips, a fraction (50% or 25%, respectively) of all individuals were randomly subsampled, slide-mounted in 45% ethanol, and examined with an Olympus B × 41 compound microscope (Markham, Ontario, Canada). Adults were sexed and identified using morphological keys by Mound and Kibby (1998), Stannard (1968), and Hoddle *et al.* (2012). Specimens were sent for identity validation to Agriculture and Agri-Food Canada's Canadian National Collection of Insects, Arachnids and Nematodes (Ottawa, Ontario, Canada), and voucher specimens were deposited at the Laboratoire d'expertise et de diagnostic en phytoprotection (Québec Ministry of Agriculture, Fisheries and Food; Québec, Canada; <https://www.mapaq.gouv.qc.ca/fr/Productions/Protectiondescultures>). Because we were mainly interested in Terebrantia thrips diversity, Tubulifera were identified only to genus. Immature thrips were not identified to species due to taxonomic difficulties, even for dominant species identified in our system (Skarlinsky and Funderburk 2016). All flowering plants were identified to species (Clemants and Gracie 2006; Ministère de l'Agriculture, des Pêcheries et de l'Alimentation and Ministère des Forêts, de la Faune et des Parcs 2019).

Statistical analyses

Analyses were performed using R software, version 3.6.1 (<https://cran.utstat.utoronto.ca/bin/windows/base/old/3.6.1>). Redundancy analyses were used to assess how variations of thrips

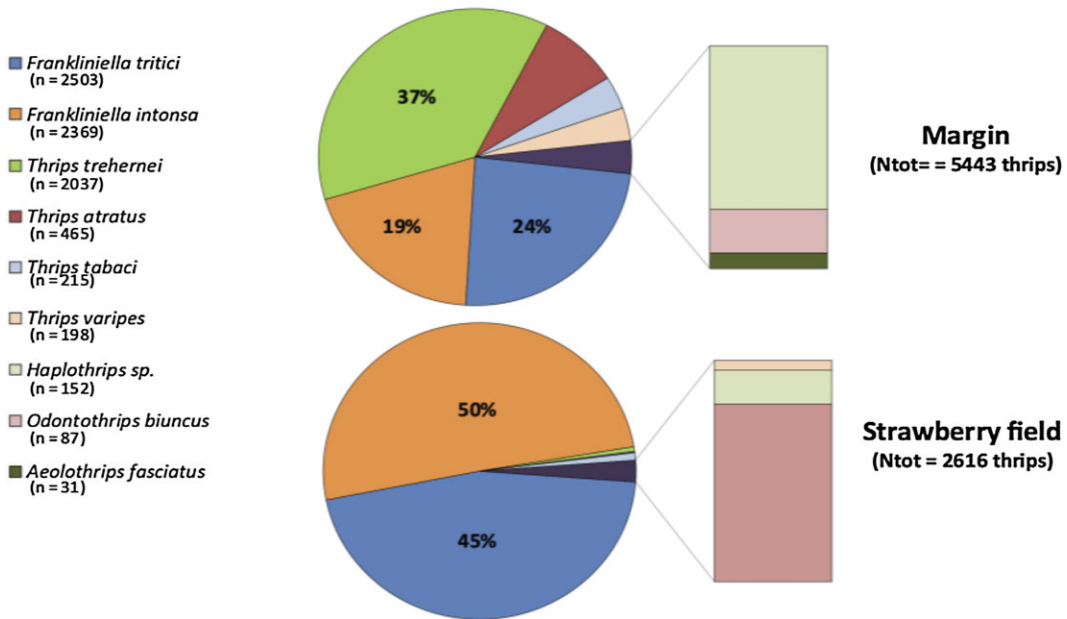


Figure 1. Thrips species relative abundance (%) during the entire sampling season and by sampling environment. Total adult thrips per sampling environment (Ntot) and per thrips species in both environments (n) are shown in brackets. In the legend, thrips species are in descending order of relative abundance, detailed on the right for *Haplothrips sp.*, *O. biuncus* and *A. fasciatus*. *Aeolothrips crassus* and *Chirothrips manicatus* were two additional species anecdotally observed in margins.

diversity and abundance in strawberry (*i.e.*, the response variables) might be related to their abundance and diversity on wildflowers in field margins (*i.e.*, the explanatory variables). Redundancy analysis is particularly suitable for statistical testing at the community level (Legendre and Legendre 2012; Borcard *et al.* 2018). Because we expected that regional, local, and seasonal factors (*e.g.*, phenology and wildflower community composition) might be important, site and wildflower species variables were initially considered as explanatory variables.

Analyses were performed using the “rda” function from the vegan package (Oksanen *et al.* 2019). Considering that wildflower diversity and abundance vary greatly in time and space, thereby preventing systematic sampling of five flowers per species, analyses were performed on mean thrips densities per flower unit. As data contained a high proportion of collected samples with no (0) thrips (71%), the Hellinger transformation was applied to response variables (Borcard *et al.* 2018). Inflating collinearity among the explanatory variables (thrips–wildflower associations ($n = 20$)) was avoided by using the function “vif.cca”. Important explanatory variables were then forward selected with the “ordistep” function based on the Akaike information criterion, using the 5% threshold for inclusion (Blanchet *et al.* 2008). The predictive value of the final model was evaluated using the “Rsquare Adj” function. The proportion of variance explained by each explanatory variable included in the final model was examined using “varpart” function.

Results

From the 44 species of flowering plants sampled, including strawberry, about 10 000 flowers were collected and more than 12 000 thrips specimens were extracted, of which 73% were adults. A total of 11 thrips species were identified from the margins and fields (Fig. 1). Only one species belonged to the Tubulifera suborder: this was an undetermined *Haplothrips sp.* Most species were phytophagous thrips of the Thripidae family, with the exception of two predatory *Aeolothrips sp.* (*Aeolothripidae*). Sampled only on strawberry flowers and fruits, immature thrips were first- or

Table 1. Emerged adult thrips captures in the May–June period. Data presented are total adult thrips numbers ($n = 4$ sites) for a total sampling effort of 12.5 m² in both uncultivated margins and strawberry field.

Species	Total		Total	
	Sex	Margin	Field	Margin + field
<i>Haplothrips</i> sp.	na	86	0	86
<i>Thrips trehernei</i>	♀	35	3	38
	♂	4	0	4
<i>Frankliniella tritici</i>	♀	25	7	32
	♂	1	0	1
<i>Frankliniella intonsa</i>	♀	20	4	24
<i>Chirothrips manicatus</i>	♀	17	0	17
<i>Thrips atratus</i>	♀	8	1	9
<i>Odontothrips biuncus</i>	♀	7	0	7
	♂	1	0	1
<i>Thrips varipes</i>	♀	3	0	3
<i>Thrips tabaci</i>	♀	2	0	2
	♂	1	0	1
Total		210	15	225

second-instar larvae, with very few pro-pupae and pupae recognisable to their wingtips (Bournier 1983), observed only four times in the strawberry flowers.

Orius spp. (Hemiptera: Anthocoridae), a genus that includes common thrips predators occurring in crop fields in North America (Kelton 1963), were rarely found in flowers. Nineteen were caught in wildflowers, and 37 were captured in strawberry flowers. Among other thrips natural enemies, Chrysopidae (Neuroptera) and Coccinellidae (Coleoptera) were occasionally observed in the wild and cultivated vegetation, but no specimens were found in the strawberry fruit or flower samples.

Thrips emergence in early season

Close to 92% of adult thrips emergence in the spring (May–June period) occurred in the uncultivated field margins. Nine species emerged from margins, and four from the fields (Table 1; Fig. 2). The first captures in emergence traps occurred on 15 May (Supplementary material, Table S1) when daily mean air temperature approached 10 °C. *Thrips trehernei* (Priesner), *F. tritici*, *F. intonsa* (Trybom), and *T. atratus* (Haliday) were the first species to emerge in the margins (Supplementary material, Table S1). During May–June, the above four species emerged in margins but rarely in the field. The undetermined *Haplothrips* sp. was the most numerous species to emerge, first in early June, with peak emergence in late June (Supplementary material, Table S1). Overall, five species emerged in numbers exceeding 10 individuals, 97% of which were females, with rare males of *T. trehernei*, *F. tritici*, *Odontothrips biuncus* (John), and *T. tabaci* also emerging (Table 1). Notably *F. tritici* and *F. intonsa* were among the few thrips to emerge from the strawberry fields (Supplementary material, Table S1).



Figure 2. Total captured thrips adults from two sampling environments during May–June (18 May–3 July). Data are mean number of thrips per trap (\pm standard error; $n = 4$ sites) for a total sampling effort of 12.5 m² in both uncultivated margin and strawberry field.

Flower–thrips community composition and phenology in strawberry and wildflowers

Diversity and abundance of thrips in flowers varied according to sampling environment (margins *versus* strawberry fields) and period (Fig. 3). In strawberry flowers, thrips diversity was largely dominated by *F. intonsa* and *F. tritici*, representing more than 95% of all adult thrips collected throughout the season (Fig. 3). Other species collected on strawberry were *T. tabaci* (2%) and *T. atratus* (1%), with even fewer *Haplothrips* sp., *T. trehernei*, *T. varipes*, and *O. biuncus* collected (Supplementary material, Tables S2, S3, and S4).

On flowers of two-year-old strawberry plants in the May–June period, *F. intonsa* and *F. tritici* reached their maximum densities around 3 July, particularly *F. intonsa* (Fig. 4). During the July–September period, on flowers of 1-year-old strawberry plants, densities of *F. intonsa* (especially females) peaked twice, around mid-August and again in early September. In contrast, *F. tritici* had a single peak around 20 August (Fig. 4). Density of thrips larvae on strawberry flowers started to rise in mid-July and peaked around mid-August (Fig. 4); no thrips were observed in early September.

Comparatively, in wildflowers, *Frankliniella* spp. densities per flower unit were low to moderate until August. *Frankliniella tritici* densities peaked sharply in uncultivated margins, also around 20 August, the only time when its densities exceeded those of *F. intonsa*. Both species were found at low densities in strawberry fields and margins until sampling ended in mid-October.

Bronzing attributable to thrips feeding was rarely observed. Only 27 adult thrips were caught on unripe fruits, which were mostly female *F. intonsa* ($n = 16$) and *F. tritici* ($n = 6$), with single mentions of *T. tabaci* (both sexes), *T. atratus*, and *Aeolothrips fasciatus* (Linnaeus) (one female each). No immature thrips were found on strawberry fruits during the May–June and October periods, but 37 larvae were detected under sepals in July–Sept, mostly in mid-July.

On wildflowers, the three dominant species were *F. tritici* (31% of total abundance) *F. intonsa* (29%), and *T. trehernei* (25%; Fig. 1; Supplementary material, Tables S2, S3, and S4), which

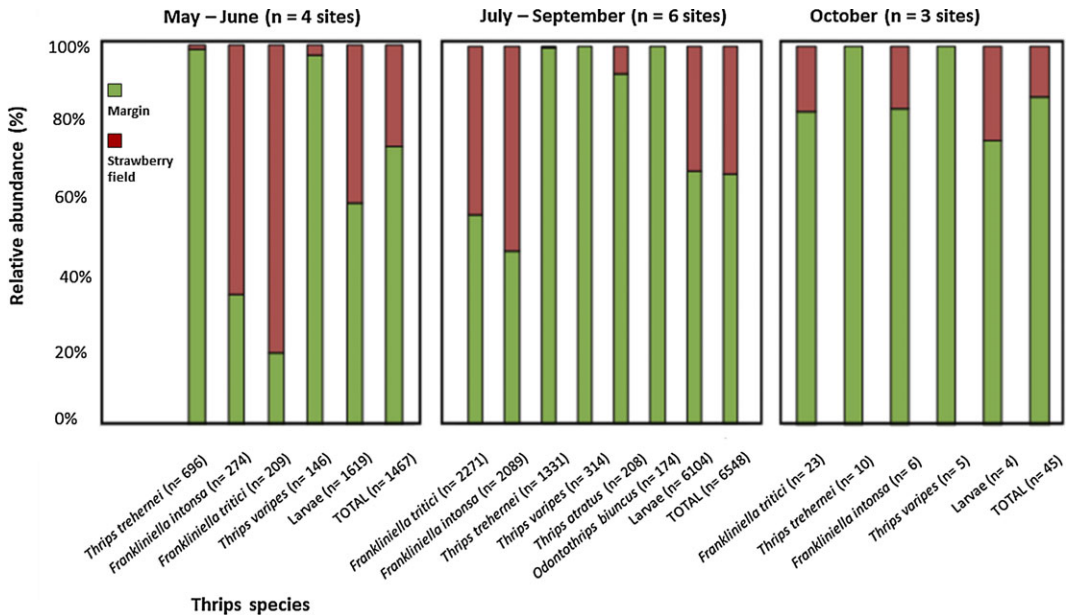


Figure 3. Thrips species relative abundance (%) in margins and strawberry fields, by sampling period. Numbers of thrips per species (n) as well as total of all identified adults, including unrepresented species (TOTAL), are indicated. Only species with more than 100 collected adults are represented, except in the October period where all individuals are represented. Number of sites varied with periods, but sampling effort in each site at each sampling event was fixed at 4 m² in margin and 20 m² in strawberry field.

together accounted for approximately 85% of all adult thrips collected on wildflowers. Other major species were *T. atratus* (Haliday), *T. tabaci*, and *T. varipes* (Hood) (Fig. 1). Sex ratio was generally skewed in favour of females, except for *F. tritici* and *T. trehernei*, which had nearly 1:1 male:female ratios.

Females of *Haplothrips* sp. and *Odontothrips biuncus* were rarely collected in high numbers on wildflowers (> 50), they represented only 3% and 4% of total abundance, respectively. Another minor thrips species collected in uncultivated margins was *A. fasciatus*. Anecdotally, single records of female *Aeolothrips crassus* (Hood) and *Chirothrips manicatus* (Haliday) were observed, respectively, in the July–September period on *Vicia cracca*, and in the May–June period on *Taraxacum officinale* (Weber ex F.H. Wiggers).

Target species *F. intonsa* and *F. tritici* were collected on 18 May on *Tussilago farfara* (Asteraceae) and *Taraxacum officinale* flowers and shortly after on strawberry flowers (21 May). By the end of May–June, 10 species had been collected on strawberry flowers, among which three numbered fewer than 10 individuals (Supplementary material, Table S2). In July–September, when sampling switched to one-year-old strawberry, total species richness was also 10, including nine species that were previously found in May–June in two-year-old fields (Supplementary material, Table S3). However, total thrips abundance was more than four times higher than in May–June. In October, total species richness decreased to five, few thrips being caught other than *F. intonsa* (n = 6), *F. tritici* (n = 23), and *T. trehernei* (n = 10; Supplementary material, Table S4), especially on strawberry flowers (6 of 45 captured specimens). The last captures of *F. intonsa* and *F. tritici* on strawberry flowers occurred 2 October and again two weeks later in margins on *Sinapis arvensis* (Linnaeus) (Brassicaceae), where females of these thrips species coexisted until 9 October.

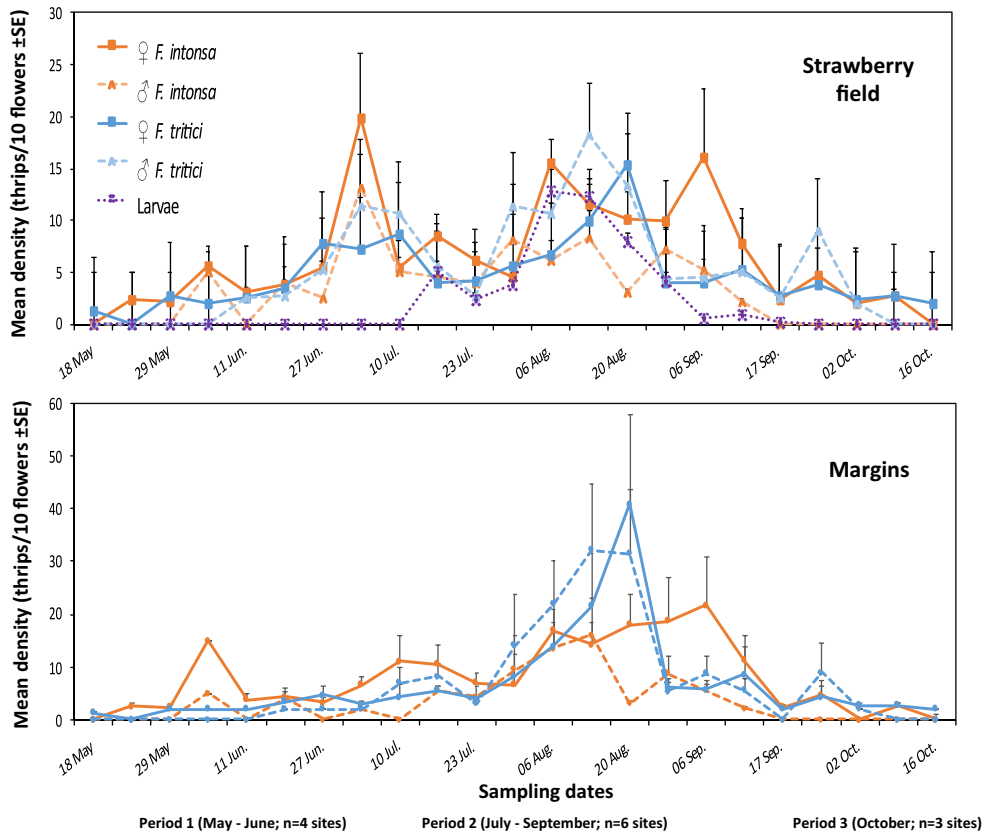


Figure 4. Mean density of *Frankliniella intonsa* and *F. tritici* by sex, and of unidentified thrips larvae, by sampling date. Density of larvae, which we could reasonably assume mostly derived from *Frankliniella* reproduction, shown only for strawberry flowers. Data presented are mean thrips/10 flowers \pm standard error. Number of sites varied with periods, but sampling effort in a site for each date was fixed at of 4 m² in margin and 20 m² in a strawberry field.

Use of wild floral resources in margins by pest and nonpest thrips species

Adult and larval thrips densities per floral unit of each host plant species varied during the season (Fig. 4), as observed in 2017 in preliminary surveys (C. Cloutier, unpublished data). Several thrips species were mostly or exclusively associated with wildflowers, e.g., *T. trehernei*, *Haplothrips* sp., and *O. biuncus*, whereas others, in particular *Frankliniella* species, occurred on both wild and strawberry flowers (Figs. 2 and 3). Flower species diversity gradually increased during the sampling season, with the most abundant wildflower hosts (e.g., *Vicia cracca*) blooming in late summer, from August onwards (Fig. 5). Some wildflowers appeared as key hosts for specific thrips species, and particular thrips–wildflower associations prevailed. The main uncultivated thrips host plant overall was *Vicia cracca* Linnaeus, which sustained approximately 34% of the total adult thrips sampled in margins and hosted 10 of the 11 thrips species present, particularly *T. trehernei*, *F. tritici*, *F. intonsa*, and *O. biuncus* (Fig. 6; Supplementary material, Fig. 1). Together with *V. cracca*, flowers of *Sinapis arvensis*, *Sonchus asper* (Linnaeus), *Cichorium intybus* (Linnaeus) (Asteraceae), *Taraxacum officinale*, and *Oenothera biennis* (Linnaeus) (Onagraceae) supported approximately 80% of all adult thrips. Notably, *F. intonsa*, *F. tritici*, *T. trehernei*, and *T. varipes* shared much of their large wildflower host range, which was most clear in July–September (Fig. 6B). Wildflower species also varied in their contribution to thrips immature development, the wildflower hosts mostly used by larvae in May–June and July–September being *Vicia cracca* and *Leucanthemum vulgare* (Lamarck) (Supplementary material, Tables 2 and 3; Fig. 4).

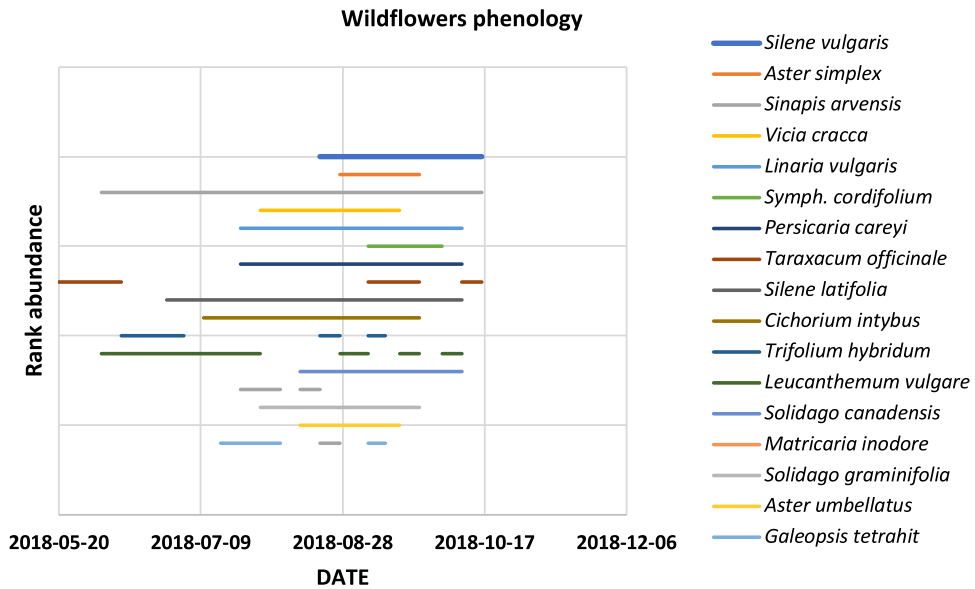


Figure 5. Flowering phenology of the most common uncultivated wildflowers bordering strawberry fields in 2018 on Orléans Island. Wildflower species shown ($N = 17$) in descending order of seasonal abundance represent approximately 90% of all flowers examined for thrips presence.

Relationships between thrips in strawberry and margins

Possible causal relationships between thrips in field margins and strawberry crops were revealed by redundancy analysis using the observed thrips–wildflower associations in margins ($n = 20$) that we considered as potential explanatory variables (Supplementary material, Tables 2, 3, and 4) of the abundance of main thrips species in strawberry. Colinearity between the 20 explanatory variables was deemed minor, as revealed by $vif.cca$ (colinearity index < 10). The two explanatory variables retained in the redundancy analysis model (ordistep; 5% significance threshold) were the density of *F. intonsa* on *S. arvensis* and the density of *F. tritici* on *Vicia cracca* (Fabaceae) (Table 2; Fig. 7).

The final redundancy analysis model was highly significant ($F_{4,96} = 3.702$; $P = 0.007$), with an adjusted R-square value of 0.072 and both redundancy analysis axe 1 ($P = 0.040$) and axe 2 ($P = 0.038$) being significant (above the 5% level). The marginal effects of explanatory variables “Frin_wild mustard” ($P = 0.0108$) and “Frtr_tufted vetch” ($P = 0.0370$) were both significant (Table 2).

Figure 7 shows the redundancy analysis model fitted to the data for the whole season. Note that angles between variables (eigenvectors) of thrips densities in strawberry fields and on their major host plants in the field margins reflect their correlations. Centroids for each month (blue dots) reflect how well, as the season advanced, densities of *F. intonsa* and *F. tritici* in strawberry crops correlated with their densities in the field margins on main host plants, according to the model.

Discussion

Thrips community composition and phenology

We found 11 thrips species in the strawberry agroecosystems of Orléans Island. Most of the species are already known from flora of North America (Chiasson 1986), with *F. intonsa* being newly reported for eastern Canada (Nakahara and Footitt 2007). Surprisingly, the strawberry pest *F. occidentalis* was absent. Thrips richness and abundance on wildflowers varied, with a few

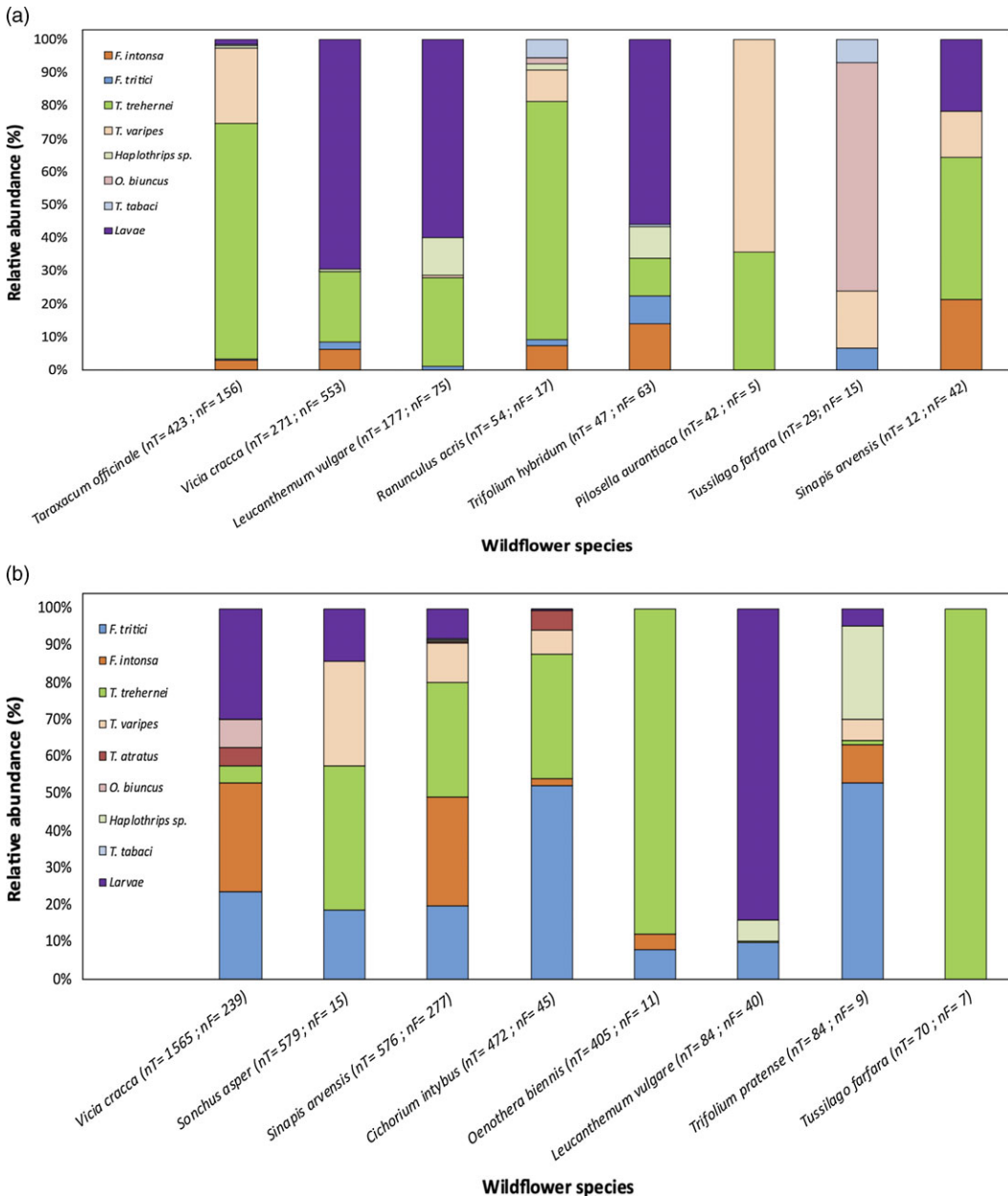


Figure 6. Relative abundance of main thrips species on major wildflower species in margins: **A**, during May–June (18 May–27 June) on wildflowers hosting more than 10 adult thrips and for thrips species with more than 10 individuals; **B**, during July–September (10 July–17 September) for wildflowers hosting more than 70 adult thrips, for thrips with more than 50 individuals. Numbers of thrips (nT) and flower units (nF) in brackets, excluding thrips larvae, not identified to species. In legend for each period thrips species listed in descending order of relative abundance.

flowering plants supporting the majority of the community. Our results found local wildflowers and sampling sites influenced thrips abundance on strawberry.

In the uncultivated field margins, the thrips community was more diversified than in the strawberry crops but was dominated by three species. First, *T. trehernei* predominated, being found on 25 wildflowers. Widespread in North America, this species probably originated from

Table 2. Analysis of variance table for explanatory variables considered in redundancy analysis model of thrips abundance in strawberry, and thrips abundance on wildflowers in field margins (with *site* as a random factor). Variables are ranked in order of importance based on permutational selection.

Explanatory variable	<i>df</i>	Variance	<i>F</i>	<i>P</i>
<i>Frankliniella intonsa</i> on wild mustard	1	0.012022	4.400	0.0108
<i>Frankliniella tritici</i> on tufted vetch	1	0.008236	3.045	0.0370
Residuals	96	0.262302		

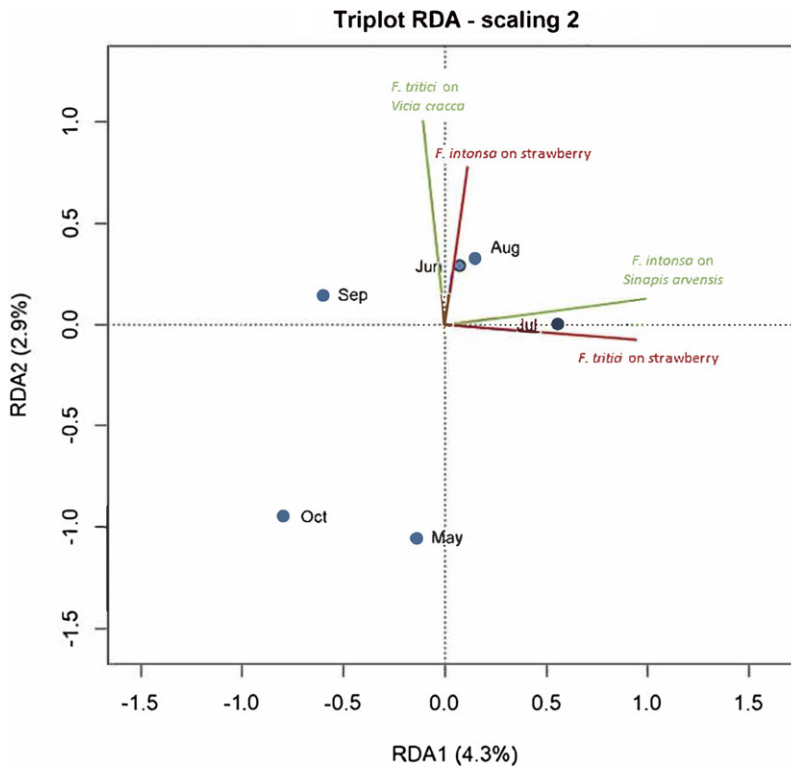


Figure 7. Redundancy analysis (RDA) correlation Triplot on density of thrips *Frankliniella intonsa* and *F. tritici* in strawberry fields over the season, as explained by their density on wildflowers in field margins. Red lines represent thrips density in strawberry, and green lines represent thrips density on wildflower hosts retained as significant explanatory variables. Blue dots are the fit to the redundancy analysis model of data for each month.

Europe and was previously reported from Québec (Nakahara 1994) as a polyphage on *Taraxacum* spp. (Asteraceae), *Sonchus* spp. (Asteraceae), and *Oenothera* spp. (Onagraceae) (Chiasson 1986; Nakahara 1994). Second in importance, *F. tritici* was found on 29 wildflowers. As a native species (Stannard 1968; Hoddle *et al.* 2012), *F. tritici* was known in flowers from disturbed habitats such as *Sonchus* spp., *Trifolium* spp. (Fabaceae), or *Aster* spp. (Asteraceae) (Chiasson 1986; Chellemi *et al.* 1994). The third main species in the field margins, *F. intonsa*, was previously reported from British Columbia, Canada on *Prunella vulgaris* (Lamiaceae) (Chiasson 1986). It has been found in Washington State, United States of America, from various flowers, weeds, and other plants since 1972 (Nakahara and Footitt 2007). Presumably from Asia, it spread to Europe where it occurs on *Sinapis* (Brassicaceae), *Trifolium*, or *Ranunculus*

(Ranunculaceae) flowers (Atakan and Uygur 2005; Hoddle *et al.* 2012). In the present study, it was found on 26 wildflowers.

Numerous other, less abundant thrips were found in the field margins. *Thrips varipes* was present in all periods. It is widely distributed in the United States of America (Chiasson 1986; Nakahara 1994) on flowers of Ranunculaceae (Stannard 1968). We found it on 12 wildflowers, mainly on *Sonchus asper*. *Odontothrips biuncus* was found almost exclusively on *V. cracca*, in agreement with its known association to Fabaceae (Mound and Kibby 1998). Few *T. atratus* were observed despite being a widespread polyphagous thrips in the Northern Hemisphere on Compositae (Asteraceae) flowers. It was already known in Canada and United States of America (Chiasson 1986; Nakahara 1994). *Haplothrips* sp. was mainly found on *Leucanthemum vulgare* (Asteraceae). Several *Haplothrips* spp. were known from Québec as pollen feeders on Compositae (Chiasson 1986; Mound and Kibby 1998). Few *T. tabaci* and *A. fasciatus* were observed, both previously known from Québec flora (Chiasson 1986). *Thrips tabaci* is cosmopolitan, being found on field or greenhouse crops and wild vegetation (Reitz *et al.* 2011). *Aeolothrips fasciatus* is a facultative predator and pollen feeder (Mound and Kibby 1998). A single female *A. crassus*, a rare species in United States of America (Stannard 1968), was found. Likewise, a single female of *Chirothrips manicatus* was found, a species that is widespread in temperate areas and associated with Poaceae, probably disseminated *via* the seed trade (Hoddle *et al.* 2012). *Frankliniella intonsa* and *F. tritici* predominated in strawberry fields. *Frankliniella intonsa* was previously reported to damage strawberry in Europe (Buxton and Easterbrook 1988; Linder *et al.* 2006; van Kruistum and den Belder 2016) and in Japan (Fujiwara 2022). In Denmark, it is the major pest species in sheltered strawberry, ahead of *T. tabaci* (Nielsen *et al.* 2021). In Asia, *F. intonsa* is a crop pest that also exploits wild vegetation (Wang *et al.* 2019). A few *T. tabaci* and *T. atratus* occurred on strawberry in the present study. *Thrips tabaci* is common in Italy (Gremo *et al.* 1997), England (Buxton and Easterbrook 1988), the Netherlands (van Kruistum and den Belder 2016), Denmark (Nielsen *et al.* 2021), Brazil (Pinent *et al.* 2011), and Australia (Steiner and Goodwin 2005).

Frankliniella intonsa and *F. tritici* may overwinter on Orléans Island: they were found at the beginning of the strawberry production season and until October. Our results approximate what was observed for *F. occidentalis* in orchards in British Columbia, Canada. Springtime emergence of females occurred in wild areas, followed by migration towards orchards (Pearsall and Myers 2000). In Florida, *F. tritici* overwinters as active, reproducing adults (Chellemi *et al.* 1994; Northfield *et al.* 2008). Winter activity can be excluded on Orléans Island in natural habitats, where winter temperatures fall well below freezing for many months. In western Canada, thrips may overwinter in soil as mated females (Pearsall and Myers 2000). Local overwintering in soil on Orléans Island would be consistent with the early arrival of *Frankliniella* spp. males from mid-June. In Europe, *Frankliniella* thrips could survive natural winter conditions (Trdan *et al.* 2003), including in strawberry (Sampson *et al.* 2021). Abundance of *F. intonsa* and *F. tritici* in strawberry flowers from mid-May and their predominance thereafter suggest that the unidentified larvae captured in strawberry fields in July and August in the present study were likely current season offspring.

When sampling switched to one-year-old strawberry in July, high densities of both *Frankliniella* spp. were observed, suggesting their capacity to colonise new fields (Rodriguez-Saona *et al.* 2010) or an attraction towards younger crops (Bournier 1983; Fernandes and Fernandes 2015), although long-distance migration cannot be excluded.

Voltnism is unclear for *F. intonsa* in our data, with at least two density peaks. However, one generation of *F. tritici* most likely occurred. Thrips larval density was negligible until mid-July and peaked once, in August. However, sampling resolution and potential thrips movement between fields (Fernandes and Fernandes 2015) prevent confirmation of the actual generation timing. Only one *F. occidentalis* generation has been reported on nectarine in British Columbia (Pearsall and Myers 2000). Appearance of males of both *Frankliniella* species in the present study relatively

early suggests sexual reproduction until September. Males of these species seem to be rare in autumn in Québec, which is unlike *F. occidentalis* in British Columbia (Pearsall and Myers 2000).

Well-known *F. occidentalis* (Pergande) was absent from our samples, despite its cosmopolitan distribution (Kirk and Terry 2003) and known association with strawberry (Sampson and Kirk 2016). Strawberry and other suitable hosts in field margins at Orléans Island (clovers, dandelions, goldenrods) would likely sustain it locally (Chellemi *et al.* 1994; Northfield *et al.* 2008). Low *F. occidentalis* densities in the eastern United States of America have been attributed to competitive exclusion by *F. tritici* at larval stages (Paini *et al.* 2008). Both interference and exploitation competition were found between *F. intonsa* and *F. occidentalis*, favouring *F. intonsa* (Bhuyain and Lim 2019). To our knowledge, strawberry agroecosystems on Orléans Island represent the first environment where coexisting *F. intonsa* and *F. tritici* are reported. The interactions between these two species and the potential cumulative impacts on *F. occidentalis* should be further studied because co-occurrence of two competitively superior *Frankliniella* spp. could negatively affect *F. occidentalis* under field conditions, resulting in “asymmetrical occurrence,” as Bhuyain and Lim (2019) suggest. Future investigations could target *F. occidentalis* in protected crops on Orléans Island, such as strawberries, raspberries, and blueberries grown under tunnels, which are potential habitats for winter survival in semiprotected contexts, as Sampson *et al.* (2021) described.

Influence of wild floral resources on strawberry thrips

Variations in thrips richness and density were observed between wild and strawberry flowers and between wildflowers in field margins. Distinction between a diversified thrips community in uncultivated field margins and one dominated by two species in strawberry crops illustrates the influence of local floral diversity over strawberry thrips community composition. This appears to be similar to the thrips community in tomato agroecosystems (Chellemi *et al.* 1994). In the thrips–tomato system, a small portion of wildflowers within the field margins sustained the thrips community.

Thrips abundance on uncultivated vegetation is widely considered a positive determinant of thrips abundance in adjacent crops (Mound and Tuelon 1995; Pearsall and Myers 2001; Silva *et al.* 2018). We intuitively expected *F. intonsa* and *F. tritici* density on major wildflower hosts to correlate with their density in strawberry (Northfield *et al.* 2008; Silva *et al.* 2018). Our redundancy analyses results indicate possible causal effects between densities of *F. intonsa* and *F. tritici* in field margins and their densities on strawberry flowers (Table 2). The abundance of *F. intonsa* in strawberry in July was partly explained by its abundance in July on *Sinapis arvensis* in margins (Fig. 6). Similarly, the abundance of *F. tritici* in strawberry in June, August, and September correlated with its abundance on *V. cracca* in field margins. This supports our prediction of a relation between thrips abundance in margins and in strawberry, even though the predictive power of the redundancy analysis model was modest (7.2%) – probably due to the multiple ecological factors at work – over a long seasonal gradient (Borcard *et al.* 2018).

Conclusion

Observations in strawberry agroecosystems on Orléans Island revealed a community of 11 flower-inhabiting thrips. This community mostly encompasses species already recorded from North American flora and is dominated by the endemic *F. tritici* and the exotic *F. intonsa*. This newly mentioned species for eastern Canada appears as a major thrips pest in day-neutral strawberry. Data suggest that both *F. intonsa* and *F. tritici* can overwinter under natural conditions in the agroecosystems of Orléans Island. Females emerged early in the season, mostly from uncultivated areas, established quickly in strawberry crops, and were present until late in the season. Thrips species richness was higher in uncultivated margins than in strawberry fields, but

only six wildflower species (of the 44 present) sustained high thrips densities. Field site affected thrips density, which may be linked to farming practices and local wildflower profiles. Additional investigations are warranted to determine the mechanisms shaping the thrips community assemblage in strawberry crops. Our results contrast with the vision of a strawberry production system dominated by *F. tritici* in eastern North America (Matos and Obrycki 2004). New information regarding thrips species in strawberry, their abundance in wild vegetation, and their overwintering potential should help pest decision making in strawberry (Coll *et al.* 2007). The first record of *F. intonsa* in Québec raises awareness about thrips as emerging pests in cold temperate latitudes. Identification of *F. tritici* and *F. intonsa* as the major pests could lead to more efficient pest control in strawberry (Lim and Mainali 2009).

Supplementary material. The supplementary material for this article can be found at <https://doi.org/10.4039/tce.2023.15>.

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Competing interests. The authors declare they have no competing interests involving authors of this paper.

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