ORIGINAL CONTRIBUTION

Spatiotemporal population dynamics of the banana rind thrips, *Elixothrips brevisetis* (Bagnall) (Thysanoptera: Thripidae)

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Abstract

The understanding of how environmental factors and agricultural practices affect population dynamics of insect pests is necessary for pest management. Here, we provide insight into the ecology of the banana rind thrips *Elixothrips brevisetis* (Bagnall) (Thysanoptera: Thripidae) by collecting and analysing a spatiotemporal database of population estimates in Martinique (West French Indies). We assessed the influence of climatic variables (which were rainfall and temperature) and biotic variables (which were banana and three weed species) on the adult thrips abundance for different components of the banana plant (sucker, mother plant and bunch) and evaluated the effect of thrips abundance and standard bunch covers on damages. The abundance of thrips on the sucker, the mother plant, and the bunch was significantly related to the abundance on neighbouring banana plants, and spatial autocorrelation indicated that *E. brevisetis* dispersed for only short distances. The number of thrips on the mother plant and on the bunch was positively related to the number of thrips on the sucker, suggesting that the thrips may disperse from the sucker to the mother plant and then to the bunch. The abundance of thrips on the sucker increased with sucker height and was positively correlated with the mean daily rainfall during the 17 days before sampling; the length of that period might correspond with the time required for an individual to complete its life cycle. Covered bunches had 98% fewer thrips than non-covered bunches, and the damage caused by thrips was linearly related to the number of thrips present between the 2nd and 4th week after flowering. Finally, we found that the presence of *Alocasia cucullata*, *Dieffenbachia seguine* and *Peperomia pellucida* is significantly related with a decrease in thrips abundance on banana plants, suggesting the use of these weeds as potential trap plants.

Introduction

The banana rind thrips *Elixothrips brevisetis* (Bagnall) (Thysanoptera: Thripidae) is a phytophagous species that causes rusty marks in banana fruit peels. In feeding on banana fruit peels, *E. brevisetis* empties the cells of the peel, causing the cells to become silvered and then brown. When the feeding is substantial, the resulting aesthetic damage prevents the fruits from being marketed (Rey 2002). These damages are similar to those caused by the banana silver rust thrips *Hercinothrips femoralis* (Reuter), which has been replaced by *E. brevisetis* in Martinique (Rey 2002).

Bananas are rhizomatous herbaceous plants whose terminal bud produces the inflorescence. Each banana plant can be regarded as being an individual

composed of the mother plant, sucker and bunch. Each individual successively produces a series of stems from a lateral shoot, and each stem produces a single bunch. The sequence can be repeated for multiple generations, which means that the crop can be considered semi-perennial. The main developmental stages of banana plants include growth of mother plant, suckers appearance (and selection of only one sucker by the farmer), flowering and harvest. Banana plants emit new leaves until the flowering stage is reached and are cut at harvest. Banana crops are a collection of individual plants derived from vegetative propagules which developed at their own rhythm and do not follow a synchronous cycle (Lassoudière 2007).

Management of *E. brevisetis* includes the use of insecticides and both standard and insecticide-impregnated bunch covers (Pinese 1987; Henriques et al. 1997; Rey 2002). Rey (2002) has shown that the use of standard bunch covers (i.e. covers without insecticide), if deployed when the last hand has opened, prevents the thrips from reaching the bunch and damaging the fruits.

To our knowledge, only one study has focused on *E. brevisetis* (Rey 2002) and the life cycle of *E. brevisetis* remains unknown. The host range of *E. brevisetis* and the effects of abiotic factors, including rainfall and temperature, on *E. brevisetis* are also poorly described. Apart from banana plants, *E. brevisetis* has been observed on *Chiococca alba* (Rubiaceae) and *Lantana camara* (Verbenaceae) in the Galapagos Islands (Hoddle and Mound 2011). These results confirm that *E. brevisetis* is at least oligophagous, but its host range remains to be studied. No male has been observed in this species (Muruvunda 1986; Rey 2002) and females are likely to reproduce by parthenogenesis. Here, we assessed (i) the influence of abiotic variables (rainfall and temperature) and biotic variables (banana and other host plants) on the spatiotemporal dynamics of an *E. brevisetis* adult population; (ii) how adult thrips abundance differs among different components of the banana plant (sucker, mother plant and bunch); and (iii) the effect of thrips abundance and standard bunch covers on damage.

Materials and Methods

Study site

The study was conducted at the Fijo banana plantation, Sainte-Marie, Martinique, French West Indies (14°47′20.9″9N, 61°02′09.5″W). The banana crop was in its third cycle when the data were collected (Cavendish Grande Naine cultivar). The climate at the study site is humid tropical with a mean (±SE) annual temperature of $25.8 \pm 0.7°C$ and a mean monthly rainfall of 265.7 ± 70.4 mm. The altitude of the site is 254 m a.s.l. We randomly selected 30 banana plants in an inner area that was 23.7 m × 12.8 m.

Population dynamics and environmental data

Beginning on 15 October 2012 (when mother plants had a selected sucker) and ending on 3 April 2013 (when all bunches were harvested), we examined the 30 selected banana plants once a week. At each observation time, we counted the *E. brevisetis* individuals on three parts of each plant: sucker leaves, mother plant leaves and fruits. The thrips were enumerated by direct, visual observation because this method has been proven to be effective (Delattre and Torregrossa 1975; Reisig et al. 2011). At each observation time, we also collected information on the height of the sucker, the phenological status (pre-flowering or flowering) of the mother plant and the presence of weeds in a 1-m radius around each banana plant. Temperature and rainfall data were obtained from the Météo France database (Pérou station, Sainte-Marie, Martinique, France).

Damage as affected by standard covers on fruits and by thrips abundance

Standard covers (i.e. covers without insecticide) were obtained from SAPACI COSTA RICA S.A (San Rafael de Escazu, San Jose, Costa Rica). The covers were made with plastic and had pores that permitted gas exchange but were too small for thrips passage. When the last hand had opened, 19 bunches were covered and 11 bunches were left uncovered; each of the 30 bunches was on a separate banana plant. At harvest (which varied among the banana plants; harvest began on 27 February 2013 and ended on 3 April 2013), we counted the number of thrips marks on each fruit of the last hand of 11 covered and 11 uncovered bunches.

Statistical analysis

We considered each banana plant to be an individual composed of the mother plant, sucker and bunches. We defined the *neighbourhood* of a target individual as being the list of other individuals, called *neighbours*, which are in a given radius from the target individual. For determining how thrips numbers were associated among neighbours, we summed the number of thrips

observed on the sucker and on the mother plant of each individual. To test the hypothesis that thrips numbers were positively correlated among neighbours, we used Geary's *C* index (Geary 1954). For each observation date and for neighbourhood distances ranging from 2 to 10 m, we calculated the Geary's *C* index for the cumulative number of thrips on individuals (i.e. on the sucker and the mother plant of each individual). We calculated Geary's *C* with the ade4 R-package (Thioulouse et al. 1997). Values close to 0 indicated a positive correlation among neighbours (spatial autocorrelation), and values close to 1 indicated no correlation among neighbours.

We used quasi-generalized linear models with a Poisson error (qGLMs) to analyse the relationship between the number of thrips on a sucker and the following variables (if not specified, the variables are continuous): the height of the sucker; the number of thrips on the mother plant; the number of thrips in the neighbourhood; the absence/presence (categorical variable) of three weed species [*Alocasia cucullata* (Aracae), *Dieffenbachia seguine* (Aracae), *Peperomia pellucida* (Piperacae)]; temperature and rainfall. To test the influence of the latter variables, we first compared the AIC values of models, which differed in their assessment of the temperature and rainfall means: we calculated the means for periods beginning at different times before sampling (from 0 to 28 days) and for periods of different length (from 1 to 28 days). We then selected the temperature and rainfall means for which AIC values were the lowest and used means determined in this manner in the complete models to test their significance. We used qGLMs to analyse the relationship between the number of thrips on the mother plant and the following variables: the number of thrips on the sucker; the phenological status (non-flowering or flowering; categorical variable) of the mother plant; and the number of thrips in the neighbourhood. We used qGLMs to analyse the relationship between the number of thrips on the bunch and the following variables: the number of thrips on the mother plant; the presence/absence of a bunch cover (categorical variable); and the number of thrips in the neighbourhood. The qGLMs were selected by following a backward-stepwise process: we compared the complete model to nested submodels using F-tests; we then removed non-significant fixed effects from the complete model and continued the backward-stepwise process until a model was found in which all effects were significant (Zuur et al. 2009).

We used generalized linear mixed models (GLMMs) with a Gaussian error to analyse the relationship between damage, the location of fruits in the bunch (inner or outer face; categorical variable) and the number of thrips on the fruits. To test the influence of the latter variable on damage, we first compared the AIC values of models, which differed in their estimates of the cumulative number of thrips on the fruits: we calculated the sums for periods beginning at 0–8 weeks after flowering and for periods that were 1–8 weeks long. To consider the correlation between damage on fruits of the same bunch, we used the banana plant as an individual-level random effect. The GLMMs were selected as follows: we first examined the need to include the random effects using likelihood ratio tests (LRTs) (Bolker et al. 2009). Based on the LRTs, we then removed non-significant fixed-effect parameters in a backward-stepwise process.

All statistical analyses were performed with R 2.15.0 (R Development Core Team 2014) and with an alpha level of 0.05. All qGLMs and GLMMs were computed and estimated using the 'lme4' package (Bates et al. 2012).

Results

Population dynamics

We observed no larva on the banana individuals along the sample period. We thus used the adult abundances as a surrogate of *E. brevisetis* population. The abundance of *E. brevisetis* on mother plants increased until the 10th week of monitoring and then decreased (fig. 1). Similarly, the abundance of *E. brevisetis* on suckers increased until the 12th week of monitoring and then decreased (fig. 1). Thrips were
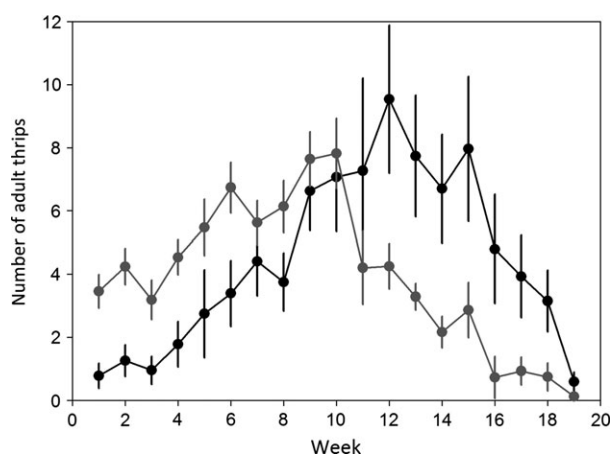
Fig. 1 Population dynamics of *Elixothrips brevisetis* on suckers (black line) and mother plants (grey line) in a banana plantation in French West Indies. Values are means of the 30 replicate banana plants, and error bars represent the 95% confidence intervals.

more abundant on fruits in bunches without covers than with covers (fig. 2); for both covered and non-covered bunches, abundance peaked on the 14th week of monitoring (fig. 2).
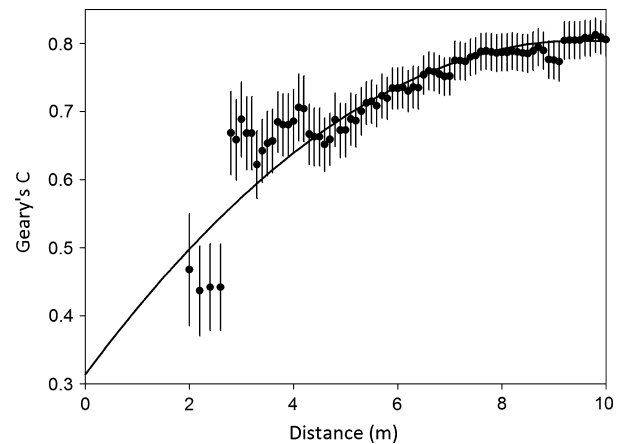
Spatial autocorrelation

We found a positive spatial autocorrelation in the numbers of thrips (the sum of the numbers of thrips on the sucker and on mother plant) among neighbours at distances up to almost 8 m; in GLMs, we used the values of the cumulative number of thrips on neighbour individuals that we obtained for a distance of neighbourhood of 5 m, distance at which each individual had at least one neighbour (fig. 3). The assessment of spatiotemporal dynamics of thrips numbers revealed the existence of foci from which the thrips dispersed for only short distances, resulting in a patchy, aggregated distribution of thrips among the banana plants (fig. 4).

Thrips population dynamics on the sucker

With respect to rainfall, the lowest AIC value for thrips abundance was found when mean daily rainfall data were derived from a 17-day period beginning 17 days before sampling (fig. 5a). With respect to temperature, the lowest AIC value for thrips abundance was found when mean daily temperature data were derived from a 5-day period beginning 23 days before sampling (fig. 5b). After incorporating these means for daily rainfall and daily temperature into the complete model, we proceeded with the backward
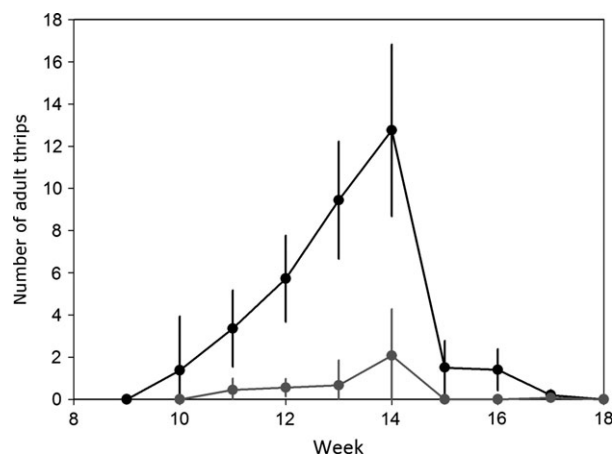
Fig. 3 Geary's *C* index for relationships between thrips numbers per individual banana plant (cumulated number of thrips on the mother plant and the sucker) and numbers per neighbouring banana plants as a function of distance to neighbours ($r^2 = 0.853$).

model selection. The number of thrips a sucker was significantly associated with the height of the sucker ($F_{1,1060} = 533.3$; $P < 0.001$), the number of thrips in the neighbourhood ($F_{1,1060} = 31.3$; $P < 0.001$), rainfall ($F_{1,1060} = 19.7$; $P < 0.001$), the presence of the weed *A. cucullata* ($F_{1,1060} = 52.4$; $P < 0.001$), the presence of the weed *D. seguine* ($F_{1,1060} = 14.6$; $P < 0.001$) and the presence of the weed *P. pellucida* ($F_{1,1060} = 10.2$; $P = 0.0014$). The number of thrips on a sucker was significantly affected by the quadratic terms of sucker height ($F_{1,1060} = 203.0$; $P < 0.001$). The number of thrips on a sucker was not significantly related to the mean daily temperature ($F_{1,1060} = 1.4406$; $P = 0.23$), and the latter term was removed from the final model. The number of thrips on a sucker was not significantly related to the number of thrips on the mother plant ($F_{1,1060} = 3.5$; $P = 0.06$), and the latter term was removed from the final model.

The number of thrips on a sucker first increased linearly with the height of the sucker and then decreased (table 1). The number of thrips on a sucker increased linearly with the number of thrips in the neighbourhood and the mean rainfall during the 17-day period before an observation event (table 1). The presence of *A. cucullata*, *D. seguine* and *P. pellucida* decreased the number of thrips on a sucker (table 1).

Thrips population dynamics on the mother plant

The number of thrips on the mother plant was significantly associated with the number of thrips on the sucker ($F_{1,1067} = 36.4$; $P < 0.001$), flowering

Fig. 2 Population dynamics of *Elixothrips brevisetis* on non-covered bunches (black line) and covered bunches (grey line) in a banana plantation in French West Indies. Values are means of 11 replicate bunches, and error bars represent the 95% confidence intervals.
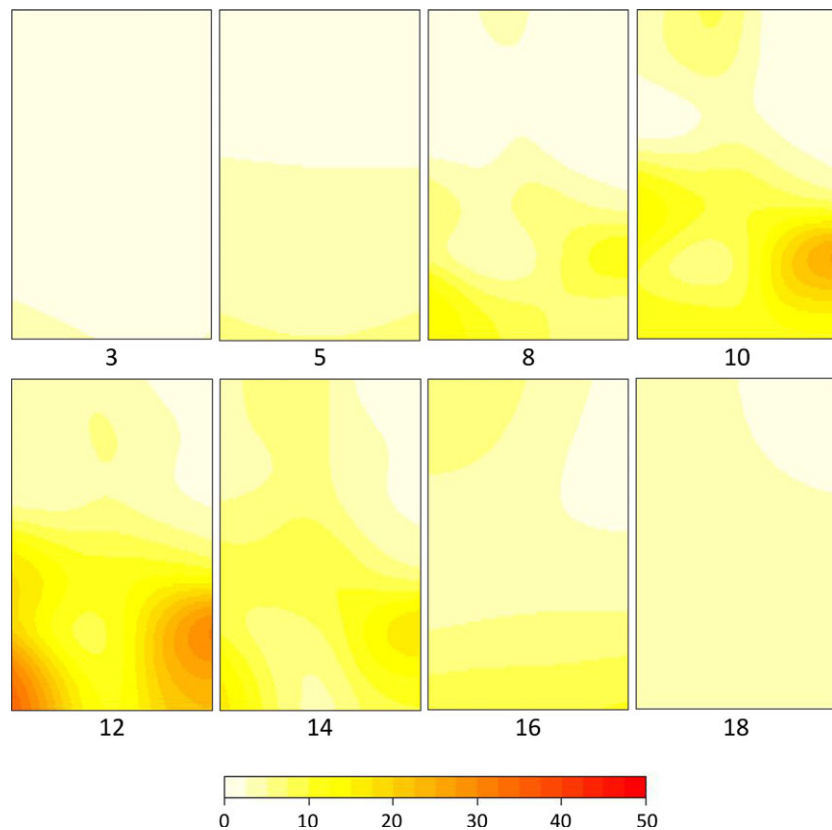
Fig. 4 Spatiotemporal population dynamics of *Elixothrips brevisetis* on banana suckers. Each panel represents the study site, which was a 23.7-m × 12.8-m area containing 30 banana plants in a banana plantation in French West Indies. Panels correspond to eight observation dates (from week 3 to week 18) as indicated. The colour scale indicates the number of observed adult thrips. Note that thrips abundance increased from week 3 to 10, peaked on week 12 and then declined.
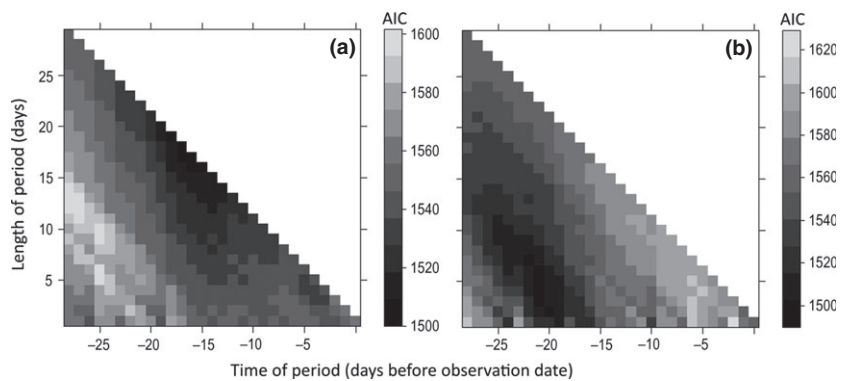
Fig. 5 AIC values of qGLMs explaining the abundance of thrips on suckers based on (a) daily rainfall means and (b) daily temperature means for periods that differed in their starting date with respect to when observations were made (the *X*-axis) and how long they lasted (the *Y*-axis).

($F_{1,1067} = 171.6$; P < 0.001) and the number of thrips in the neighbourhood ($F_{1,1067} = 86.9$; P < 0.001). The number of thrips on the mother plant increased linearly with the number of thrips on the sucker and the number of thrips in the neighbourhood (table 1). The number of thrips on the mother plant was lower before flowering than during flowering (table 1).

Thrips population dynamics on the bunch

The number of thrips on the bunch was significantly related to the number of thrips on the sucker ($F_{1,245} = 6.2$; P = 0.013), the covering of bunches ($F_{1,245} = 191.1$; P < 0.001) and the number of thrips in the neighbourhood ($F_{1,245} = 9.2$; P = 0.0026). The number of thrips on the bunch increased linearly with the number of thrips on the sucker and the number of thrips in the neighbourhood (table 1). Thrips were less abundant on covered bunches than on non-covered bunches (table 1).

Damages

We measured feeding marks on 292 fruits of the last hand of 22 bunches (11 covered and 11 uncovered). There were 0.98 ± 3.04 (mean ± SE)

Table 1 Relationships between dependent variables and thrips numbers on suckers, mother plants and bunches as indicated by quasi-generalized linear models

| Plant component and dependent variable	Estimate	SE	d.f.	F	P-value
Sucker					
Height[1]	0.05579	0.003225	7, 1060	533.296	<0.001
Neighbourhood[2]	0.01451	0.002584	7, 1060	31.342	<0.001
Mean daily rainfall	0.01851	0.004916	7, 1060	19.745	<0.001
Mean daily temperature	0.0337	0.02894	9, 1060	1.4406	0.2303053
Number of thrips on mother plant	0.008679	0.004706	8, 1060	3.5285	0.0605984
Alocasia cucullata	−0.3915	0.05545	7, 1060	52.360	<0.001
Dieffenbachia seguine	−0.185	0.0504	7, 1060	14.594	<0.001
Peperomia pellucida	−0.1879	0.05888	7, 1060	10.221	0.0014296
Height[3]	0.00008	0.0000069	7, 1060	202.990	<0.001
Mother plant					
Number of thrips on sucker	0.02616	0.004295	3, 1067	36.459	<0.001
Neighbourhood	0.03008	0.003166	3, 1067	171.591	<0.001
Flowering	−0.9237	0.079640	3, 1067	86.867	<0.001
Bunch					
Number of thrips on sucker	0.03698	0.01627	3, 245	6.2132	0.01335
Neighbourhood	0.02502	0.00910	3, 245	9.2328	0.002638
Bunch covers	−3.9912	0.56075	3, 245	191.078	<0.001

[1]Height of the sucker.
[2]Number of thrips on neighbouring plants.
[3]Quadratic term of the height of the sucker.

and 20.42 ± 19.45 marks per covered and non-covered bunch, respectively. Regarding the relationship between thrips abundance and damage, the cumulative number of thrips observed between the 2nd and 4th week after flowering provided the lowest AIC value (fig. 6a) and lowest P-value (fig. 6b). When those data for cumulative thrips abundance were used, the level of damage was significantly correlated with thrips abundance (LRT: P = 0.001, χ^2 = 10.78, d.f. = 1). The location of fruits in the bunch (inner or outer face) did not significantly affect the damage (LRT: P = 0.37, χ^2 = 0.82, d.f. = 1). The number of marks increased linearly with the cumulative number of thrips on the bunch observed between the 2nd and 4th week after flowering (value of the estimate of the GLMM: 0.137 ± 0.035).
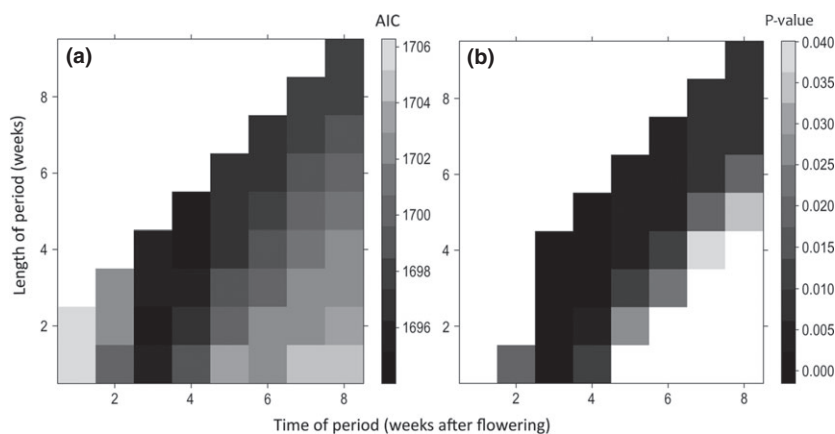
Fig. 6 (a) AIC values of generalized linear mixed models (GLMMs) explaining fruit damage caused by *Elixothrips brevisetis* based on different values for the sum of the number of thrips on bunches. The sums were based on time periods that differed in their starting date with respect to flowering (the *X*-axis) and how long they lasted (the *Y*-axis). (b) P-values of likelihood ratio tests (LRTs) between GLMMs with and without the sum of the number of thrips on bunches as affected by the timing and length of the observational period (n.s. indicates non-significant differences).

Discussion

We found that the abundance of thrips on suckers was first positively correlated with the height of the sucker, suggesting that the population dynamics of *E. brevisetis* may be resource dependent as has been shown for the thrips *Anaphothrips obscurus* (Reisig et al. 2011). An alternative hypothesis is that the number of thrips on the banana plant is dependent on the number of young leaves. Previous studies on other thrips species have shown an influence of young leaves on thrips abundance (Ananthakrishnan and Raman 1989; Nasruddin and Mound 2012) or on oviposition preference (de Kogel et al. 1997). Recently, authors have suggested that young leaves could be of better quality than old leaves and, consequently, could increase thrips fecundity (Nasruddin and Mound 2012). In plants of the *Senecio* genus, it has been evidenced that young leaves were more photosynthetically active, produced and contained more primary metabolites than older leaves (Leiss et al. 2009), making the young leaves more attractive to herbivores. Our results on thrips abundance on the mother plants are consistent with these previous studies. Indeed, we found that the number of thrips on mother plants decreased at flowering, which is the stage during which banana plants no longer produce new leaves. However, thrips abundance also decreased on suckers during the flowering stage even though suckers continue to produce new leaves during that time. We suggest that the presence of adult thrips on suckers is mostly influenced by the height of the sucker and the dispersal ability of *E. brevisetis*. The absence of larvae on banana plants suggests that observed *E. brevisetis* thrips may choose to pupate in soil like the western flower thrips *Frankliniella occidentalis* (Steiner et al. 2011; Holmes et al. 2012) or in crevices of surrounding weeds rather on banana plants. *Elixothrips brevisetis* adults move through small flights and seem unable to fly on long distances, as supported by our results on spatial aggregation. It is then likely that the emerging adult thrips move to the nearest source of food or the nearest shelter, which may be young suckers or weeds rather than high banana plants. This assumption is consistent with the lower abundances of *E. brevisetis* observed on suckers when the weeds *A. cucullata*, *D. seguine* or *P. pellucida* were nearby.

At the beginning of our study, the number of thrips was higher on the mother plants than on the suckers. This difference may be explained by the leaf type: young suckers have narrower leaves than older suckers or mother plants (Lassoudière 2007), and the leaves might differ in quality and/or attractiveness for thrips.

The decrease in thrips abundance on the mother plant after flowering suggests that the presence of fruits does not increase the attractiveness of banana plants. Moreover, we found that the numbers of thrips on mother plants and bunches both depend on the abundance of thrips on the suckers, but that the abundance on suckers does not depend on the abundance on mother plants. These results, along with the spatial autocorrelation data, indicate that *E. brevisetis* disperses only short distances on banana plants. We hypothesize that adult thrips move from the soil to suckers and from suckers to mother plants and then to bunches. As discussed later, however, this path may be altered by the presence of certain weed species.

According to our results, the daily mean temperature did not influence the population dynamics of *E. brevisetis*, perhaps because the range of daily mean temperatures was narrow. The abundance of thrips on suckers, and then on other components of the banana individuals, was positively correlated with the mean daily rainfall in the 17-day period before observation dates. In a recent study (Nasruddin and Mound 2012), Nasruddin and Mound found a positive relationship between the abundance of the thrips *Crotonothrips polyalthiae* and the rainfall 6–8 weeks before sampling. These authors suggested that the rainfall indirectly influenced the abundance of thrips by providing new leaves 2–4 weeks after the rainfall peak. *Crotonothrips polyalthiae* completes its life cycle in a gall and is therefore probably less sensitive than *E. brevisetis* to the environment. We suspect that the development of *E. brevisetis* is highly dependent on rainfall because rain, through the increase of relative humidity, may increase adult fecundity and/or larval and pupal survival. We hypothesize that the *E. brevisetis* developmental cycle, from oviposition to adult, might be around 17 days long. The life cycle of the banana silver rust thrips, *H. femoralis*, which has been replaced by *E. brevisetis* in Martinique (Rey 2002), requires 19 days at 27°C (Laughlin 1971). Elsewhere, previous studies have shown that the choice of pupation site of *F. occidentalis* depends on the relative humidity (Steiner et al. 2011; Holmes et al. 2012). When the relative humidity is too low (almost 80%), *F. occidentalis* dropping behaviour is enhanced and up to 99% of the larvae choose to pupate in the soil (Steiner et al. 2011; Holmes et al. 2012). Such a behavioural strategy in *E. brevisetis* would support the hypothesis enunciated above that the emerging adult thrips move to the nearest source of food or the nearest

shelter, explaining the decrease of thrips abundance on high suckers we observed at the end of the sampling period. The abundance of *E. brevisetis* was negatively correlated with the presence of the weeds *A. cucullata*, *D. seguine* or *P. pellucida* in the neighbourhood, and we observed *E. brevisetis* on these weeds. The results suggest that these plants are attractive to *E. brevisetis* and probably act as host plants which could be used as trap plants for *E. brevisetis* management. Moreover, wild plants may host natural enemies of phytophagous thrips (Bosco et al. 2008; Nammour et al. 2008).

Elixothrips brevisetis was much less abundant on covered than on non-covered banana bunches. In addition, the damage caused by *E. brevisetis* was positively correlated with its numbers between the 2nd and 4th week after flowering. These results agree with those of Rey (2002).

In conclusion, our results highlight the importance of suckers in the population dynamics of *E. brevisetis* and thus in the damage caused by this pest. Because suckers play a central role in the movement of this pest to the mother plant and to the bunch, *E. brevisetis* control should be focused on suckers. The use of *A. cucullata*, *D. seguine* or *P. pellucida* as trap plants should also be evaluated. Recently, the alteration of the trophic network in banana plantation by the addition of a cover plant has been demonstrated through a metabarcoding approach (Mollot et al. 2014). Experiments should be carried out to define the place of *E. brevisetis* in such a trophic network and the effect of the adding of the potential trap plants. Such studies could provide useful knowledge for the management of this pest. Finally, we found that the bunch covers should be installed before the 2nd week after the beginning of flowering to prevent damage to fruit.

Acknowledgements

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