Bulletin of Entomological Research (2012) **102**, 583–588 doi:10.1017/S0007485312000089

Effect of environment and fallow period on *Cosmopolites sordidus* population dynamics at the landscape scale

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Abstract

Understanding how the population dynamics of insect pests are affected by environmental factors and agricultural practices is important for pest management. To investigate how the abundance of the banana weevil, *Cosmopolites sordidus* (Coleoptera: Curculionidae), is related to environmental factors and the length of the fallow period in Martinique, we developed an extensive data set (18,130 observations of weevil abundance obtained with pheromone traps plus associated environmental data) and analysed it with generalized mixed-effects models.

At the island scale, *C. sordidus* abundance was positively related to mean temperature and negatively related to mean rainfall but was not related to soil type. The number of insects trapped was highest during the driest months of the year. Abundance of *C. sordidus* decreased as the duration of the preceding fallow period increased.

The latter finding is inconsistent with the view that fallow-generated decomposing banana tissue is an important resource for larvae that leads to an increase in the pest population. The results are consistent with the view that fallows, in association with pheromone traps, are effective for the control of the banana weevil.

Keywords: banana weevil, fallow period, generalized mixed-effects models, pheromone trapping, population dynamics

(Accepted 31 January 2012; First published online 12 March 2012)

Introduction

Understanding how the population dynamics of insect pests are linked to environmental factors and agricultural practices remains an important research area in pest management (Barberi *et al*., 2010; Rusch *et al*., 2012). Determining the influence of environmental factors on insect populations in the field is a difficult task because the data are often highly variable. In the case of insect pests of crops, the task is even more difficult because agricultural practices introduce additional variation that must be disentangled from the variation caused by environment. Environmental factors, such as temperature and rainfall, are known to have a huge influence on pest distribution and population dynamics (Huffaker & Gutierrez, 1999). In addition, the distribution of insects at the landscape scale may result from dispersal by humans and may, therefore, reflect the invasion history of the insects (Tscharntke *et al*., 2002).

One way to study the influence of environmental factors on populations in the field is to use an extensive data set that includes, in addition to data on insect abundance, wide ranges in soil type, temperature, rainfall and other environmental factors over a relatively small area. Such a data set should

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enable researchers to identify correlations despite the high variability of data. The island of Martinique (area = 1128 km^2) is especially suitable for this kind of study because the abiotic environment of Martinique, like that of other volcanic tropical islands, changes greatly in a relatively small area. Because rainfall is linked to topographic relief, annual rainfall on Martinique can range from 1000 mm at sea level to >6000 mm at higher elevations. Given this great range of climate and also a great range in the nature and age of the source rocks, soil on Martinique is also quite variable (Colmet-Daage *et al*., 1965).

The banana weevil, *Cosmopolites sordidus* (Coleoptera: Curculionidae) (Germar, 1825), is the most serious insect pest of banana and plantain in the West Indies and other areas (Gold *et al*., 2001). *Cosmopolites sordidus* is a narrowly oligophagous pest, attacking wild and cultivated clones in *Musa* (banana, plantain and abaca) and the related genus *Ensete* (Gold *et al*., 2001). Banana fields can be infested with *C. sordidus* through the planting of infested material (resulting in random distributions), through spread from a heavily infested neighbouring field (resulting in linear distributions) or through adults that have survived the last planting (resulting in patchy distributions) (Vinatier *et al*., 2010). Adult weevils usually disperse by walking on the soil during the night (Vinatier *et al*., 2009, 2010). After eggs have been laid on the banana corm, larvae hatch and bore galleries inside the corm for feeding (Koppenhofer, 1993). Although *C. sordidus* is found under different climatic conditions, the effects of abiotic factors and season on *C. sordidus* population dynamics are still unclear (Gold *et al*., 2001). As is the case for most insects, increasing temperatures support faster *C. sordidus* life cycles, and the upper elevation threshold for *C. sordidus* (1600–2000 m) is likely to be temperature related (Gold *et al*., 2001).

Control of *C. sordidus* is mainly based on pheromone mass trapping (Tinzaara *et al*., 2005; Rhino *et al*., 2010). Yellow pitfall traps containing the Sordidin aggregation pheromone, which is emitted by *C. sordidus* males (Beauhaire *et al*., 1995), are buried in the soil. *Cosmopolites sordidus* populations are also likely to be affected by fallow periods, which are increasingly used to control plant-parasitic nematodes (Duyck *et al*., 2009). The effects of fallow periods on *C. sordidus* population dynamics, however, are poorly known and controversial. On the one hand, fallow could increase problems with *C. sordidus* control because the destruction of the host plant may cause significant dispersion of adults. Similarly, the decomposing banana pseudostems that remain during fallow may represent a high quantity of resource for larvae and may lead to an increase in *C. sordidus* numbers. On the other hand, the combination of fallow and mass trapping could drastically reduce pest numbers before banana planting (Rhino *et al*., 2010).

To study the influence of environmental factors and fallow periods on the abundance of the banana weevil, *C. sordidus*, we first built an extensive data set based on the trapping (18,130 observations) of the weevil. Using this data set and generalized mixed-effects models, we then studied the influence of temperature, rainfall, soil type, plantation duration and fallow duration on *C. sordidus* population dynamics.

Materials and methods

Collection of field data

Cosmopolites sordidus was surveyed during three years (from January 2006 to January 2009) in 12 commercial banana plantations (600 ha total area) in Martinique (French West Indies, 14°N, 61°W). The abundance of *C. sordidus* was assessed using pitfall traps (APEX, France, Martinique) with the Sordidin aggregation pheromone (Cosmolure®, ChemTica Internacional, S.A., San José, Costa Rica) that were randomly in a total of 128 plots at the mean density of one trap per ha (with a total of 600 traps). The pheromone was changed every four weeks (Beauhaire *et al*., 1995). The *C. sordidus* in each trap (18,130 observations in total) were counted once per month. Although the effectiveness of pheromone traps can be influenced by numerous factors, including temperature, wind speed and relative humidity that may modify the diffusion of the pheromone in the air, we considered that uncertainty about trap effectiveness was reduced by the high number of observations.

Mean annual temperature and cumulative annual rainfall in the different locations on Martinique were provided for a 30-year period by Météo-France Martinique, Service Climatique (fig. 1). Soil types (young soils on pumice, andosols, nitisols, ferralsols, vertisols and fluvisols) were determined using a soil type map (Colmet-Daage *et al*., 1965).

Statistical analysis

Generalized linear mixed-effects models (GLMM (Bolker *et al*., 2009)) with a Poisson error were used to examine the relationship between *C. sordidus* abundance and mean annual temperature, mean annual rainfall, soil type, month of trapping, duration (months) since planting, duration of fallow period and interactions. In this type of model, the linear predictor contains random effects in addition to fixed effects. The inclusion of random effects allowed us to account for the effect of variables that create variance but that are not important to be tested. We treated ‘plot’ as a random effect to account for pseudo-replication and because we assumed that plots contained unobserved heterogeneity that we could not model. Overdispersion was taken into account by using ‘sample number’ as an individual-level random variable. The GLMMs were fitted by the Laplace approximation using the *glmer* function in ‘lme4’ (Bates *et al*., 2011) in the statistical programme R 2.12.1 (R Development Core Team, 2010). We started from the most complex model (including all interactions and quadratic terms for continuous variables) and kept eliminating higher-order terms as long as they remained insignificant. The significance of each term was assessed by comparing models with and without that term. ΔAIC (difference in Akaike information criterion) assesses the difference between each model and the best model. A null model with no environmental variables was included for comparative purposes.

Results

The total number of samples was 18,130. The mean (± SE) number of *C. sordidus* captured per month from all traps was 24.34 (± 9.30). The largest number of individuals collected per sample was 600, and 3254 samples had zero *C. sordidus* (1st quartile = 2, median = 11, and 3rd quartile = 30 individuals collected).

The GLMMs indicated significant effects of mean annual temperature, mean annual rainfall, month of trapping, duration since planting and duration of fallow period on *C. sordidus* abundance (table 1). Soil type had no significant effect on abundance ($P > 0.05$) and was removed from the

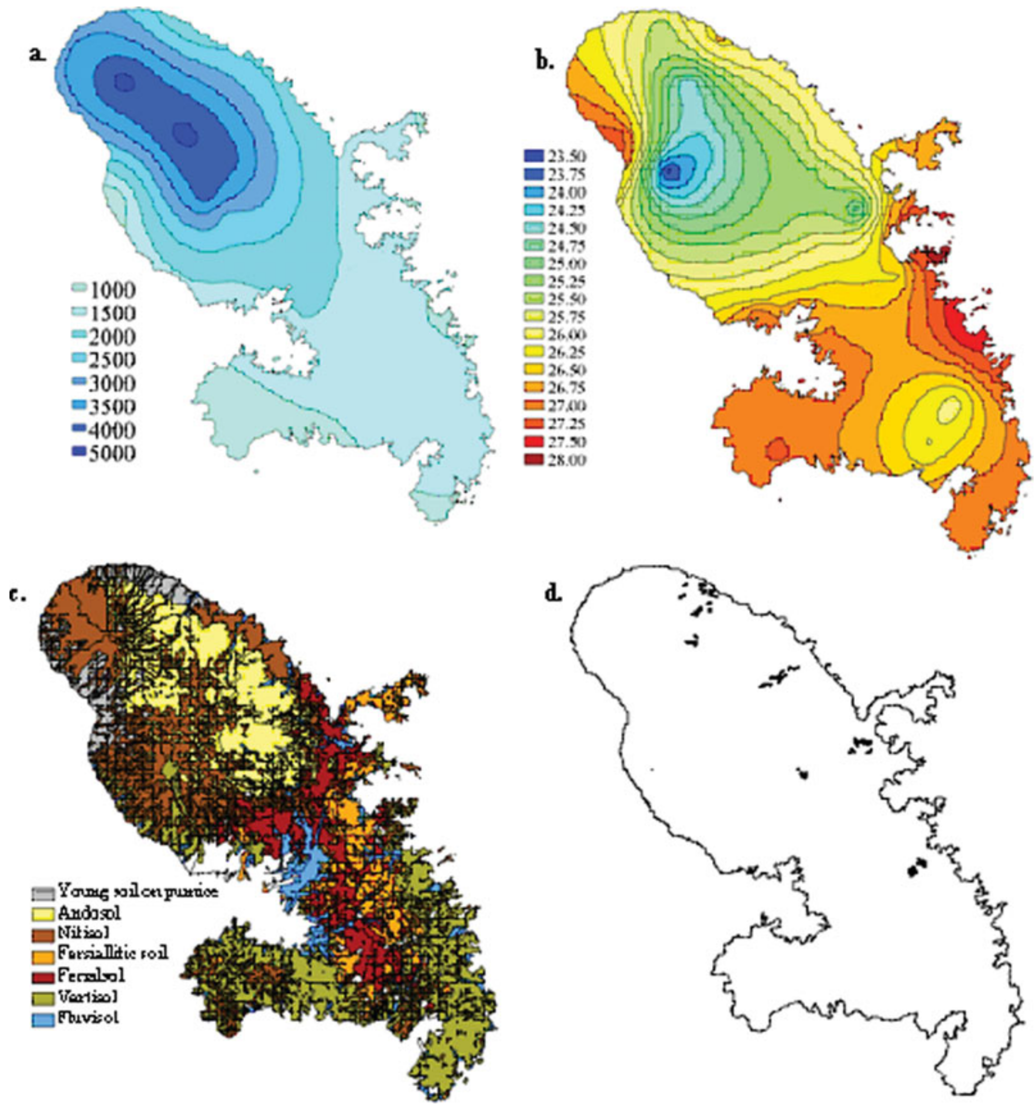

Fig. 1. Rainfall, temperature, soil types and sampling locations on Martinique. (a) Mean annual rainfall (mm) from 1971 to 2000; (b) mean annual temperature (°C) from 2007 to 2008; (c) distribution of soil types (Colmet-Daage & Lagache, 1965); (d) distribution of traps.

model. Quadratic terms of duration since planting and duration of fallow period had significant effects on *C. sordidus* abundance, while this was not the case for annual temperature and rainfall. Mean abundance of *C. sordidus* increased greatly as mean annual temperature increased and decreased as mean annual rainfall increased (fig. 2).

Mean abundance of *C. sordidus* increased during the first 36 months after planting and then decreased (fig. 3). Abundance of *C. sordidus* decreased drastically during the first 12 months of fallow and then tended to plateau for the next 18 months of fallow (fig. 3). The effect of the fallow period declined with increasing duration of banana cultivation and was negligible after 80 months of cultivation. The peak in *C. sordidus* abundance that occurred after 12 months of cultivation was largest if the cultivation was not preceded by fallow and decreased with increasing duration of the preceding fallow. The abundance of *C. sordidus* was larger from March to June (fig. 4), corresponding to the driest months in Martinique.

Discussion

Effect of length of fallow and banana cultivation on C. sordidus *abundance*

Our study shows that fallow decreases the abundance of *C. sordidus* at the scale of Martinique. The abundance of *C. sordidus* in the banana crop following the fallow period decreases as the fallow period increases up to 12 months but does not decrease further with longer fallow periods. These findings are important because destruction of the resource may cause significant dispersion of adults (Vinatier *et al.*, 2010, 2011) and because of concerns that the banana residues that decompose during fallow may be a favourable resource for larvae. This study shows, however, that 12 months of fallows, which is usually recommended for nematode control (Duyck *et al.*, 2009), can be useful for banana weevil control. Although banana plants are absent during the fallow period, many other plants are usually present; and these support communities of

Table 1. Analyses of the abundance of *Cosmopolites sordidus* by generalised mixed-effect models with Poisson error (18, 130 samples). Abundance was determined with pheromone traps, and the values indicate the number captured per trap per month. All models include two random effects: 'sample' and 'plot'. A null model with no environmental variables is included for comparison. The significance of each effect was tested by removing the variable from one of the two complete models. ΔAIC (difference in Akaike information criterion) assesses the difference between each model and the best model.

Model	df	AIC	ΔAIC	Log-likelihood	P value
t, r, m, d, f, d^2, f^2	20	64821	0	−32391	
$-d^2$	19	64954	133	−32458	<0.00001
$-f^2$	19	64873	52	−32417	<0.00001
t, r, m, d, f	18	65005	184	−32485	
−t	17	65030	209	−32498	<0.00001
−r	17	65011	190	−32488	<0.00001
−m	7	65679	858	−32833	<0.00001
−d	17	65012	191	−32489	0.003
−f	17	65030	209	−32498	<0.00001
Null	2	65754	933	−32874	

t, mean annual temperature; r, mean annual rainfall; m, month of trapping; d, duration since planting; f, duration of fallow period

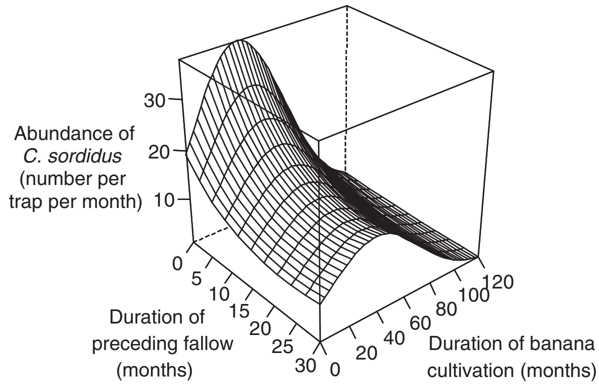

Fig. 3. Abundance of *Cosmopolites sordidus* as a function of duration of banana cultivation and of duration of preceding fallow. Abundance was determined with pheromone traps, and the values indicate the number captured per trap per month. Because there was no interaction between climate (rainfall and temperature) and plantation age and duration of fallow, data are presented for temperature = 25.75°C and rainfall = 2100 mm. For other temperatures and rainfall levels, the absolute values may differ but the effect of plantation age and duration of preceding fallow will be the same.

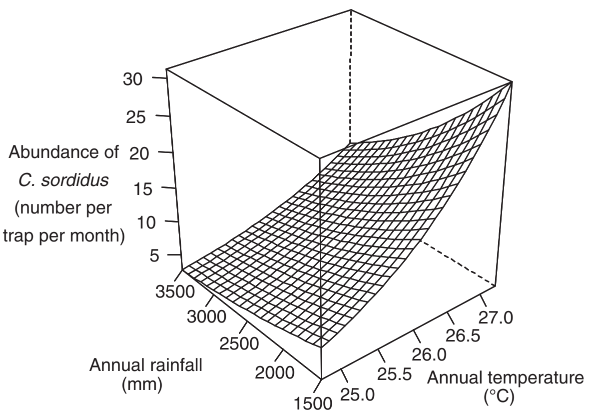

Fig. 2. Influence of temperature (t, °C) and rainfall (r, mm) on the abundance of *Cosmopolites sordidus*. Abundance was determined with pheromone traps, and the values indicate the number captured per trap per month. Because there was no interaction between climate (rainfall and temperature) and plantation age (duration of banana cultivation) and duration of fallow, the effect of climate is presented using data for plantation age = 3 months and duration of fallow = 3 months. For other plantation ages and durations of fallow, the absolute values may differ but the effect of temperature and rainfall will be the same.

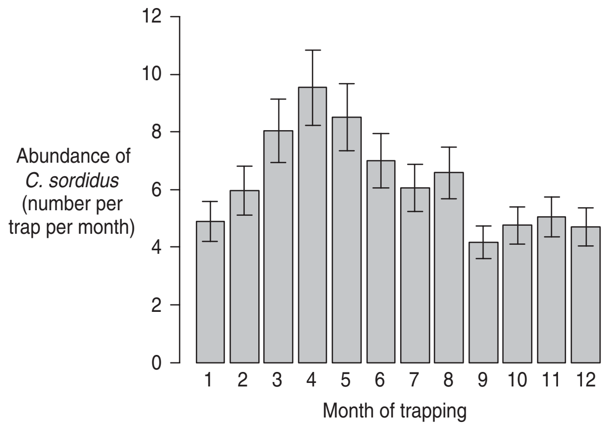

Fig. 4. Influence of the month of trapping (1 = January through 12 = December) on the abundance (mean ± SE) of *Cosmopolites sordidus*. Abundance was determined with pheromone traps, and the values indicate the number captured per trap per month. Because there was no interaction between month of trapping and other factors, data are presented for temperature = 25.75°C, rainfall = 2100 mm, plantation age = 3 months and duration of fallow = 3 months.

soil organisms, including potential predators of *C. sordidus* like ants (Abera-Kalibata *et al.*, 2007; Duyck *et al.*, 2011). In addition to contributing to pest control, fallows improve soil fertility (Ayuke *et al.*, 2011).

Regardless of fallow duration in the current study, *C. sordidus* abundance decreased when banana was cultivated for more than 36 months. This decrease can be explained by two mechanisms. First, the pheromone traps could have progressively reduced the numbers of *C. sordidus*, i.e. the pest may have been controlled by mass trapping (Gold *et al.*, 2001; Tinzaara *et al.*, 2005). Second, *Beauveria bassiana* (Gold *et al.*, 2001) and other entomopathogenic fungi, as well as generalist predators (Duyck *et al.*, 2011), could have increased and contributed to *C. sordidus* control.

In choosing the duration of the fallow period, farmers attempt to optimize the trade-off between the gain from reducing pest numbers and the loss from extending the non-productive period. The current results indicate that fallows should last about 12 months. The current results also indicate that mass trapping should focus on the critical period that extends between 40 and 80 months after planting.

Effect of temperature, rainfall, and soil type on C. sordidus *abundance*

Our analysis indicates that temperature and rainfall greatly affect the abundance of *C. sordidus*. Temperature almost always affects the distribution and the population dynamics of insects because it greatly affects insect metabolism (Birch, 1948). The effect of temperature on *C. sordidus* populations has already been mentioned with respect to altitude (Gold *et al.*, 2001). Lescot (1988) surveyed 45 sites in Cameroon and found a negative correlation between weevil damage and elevation; damage was greatest at altitudes below 1000 m, was very low between 1500 and 1600 m, and was absent (as was the weevil) at altitudes greater than 1600 m. Lescot (1988) also indicated that elevation thresholds were similar in Burundi, Rwanda and Colombia. The upper elevation threshold for the banana weevil is likely to be temperature related. Cuillé (1950), Mesquita & Alves (1983) and Lescot (1988) suggested that the minimal thermal threshold for adult activity was 15–18°C, while the optimal temperature has been estimated to be 25°C (Cuillé, 1950). In a controlled study, Traore *et al.* (1993, 1996) found that the minimal thermal threshold was 12°C for eggs and 10°C for larvae and that the highest rates of hatching and larval development occurred between 25°C and 30°C. These data suggest that extended periods with low night temperatures at higher elevations may severely limit larval development and/or adult survival. In Cameroon, for example, night temperatures fall below 12°C at 1300 m (Lescot, 1988).

The effect of rainfall and, more generally, humidity on insects is variable and is often species specific (Juliano *et al.*, 2002; Duyck *et al.*, 2006). Even within the species *C. sordidus*, the effect of humidity is controversial. While adult banana weevils are susceptible to desiccation (Cuillé, 1950; Roth & Willis, 1963), researchers have reported a positive effect, a negative effect or no effect of humidity on the number of weevils trapped (Gold *et al.*, 2001). Our study shows a negative effect of annual rainfall on *C. sordidus* abundance at the scale of Martinique. This is consistent with reports that numbers of weevils trapped were greatest during the driest period in Uganda (Gold *et al.*, 2001, 2002).

Cosmopolites sordidus abundance was unrelated to soil type in the current study, and to our knowledge, no effect of soil type on *C. sordidus* has been reported in other studies. Although no direct effect of soil type on the insect was anticipated, soil type could affect the adults by affecting soil moisture and by affecting entomopathogenic nematodes and fungi (Gold *et al.*, 2001, 2002).

Influence of season on C. sordidus *abundance*

We showed that the abundance of *C. sordidus*, as indicated by the number of adults trapped, was highest from February to August, and especially from March to May, which is the dry season. This can be explained by higher numbers of *C. sordidus* during the driest season or by an increase in trap efficiency during the driest season, or both. In Africa, most researchers have reported the highest trapping rates during the rainy season, but some researchers in South America and the Caribbean have reported highest trapping rates during the dry season (Gold *et al.*, 2001). We can hypothesize that, given the soil and climate of Martinique, the negative effect of humidity indicated in figs 2 and 4 may be the result of two complementary mechanisms. First, high soil moisture potentially results in an increased number of suitable 'resting sites' for adults (for example, the adults could remain under wet residues), which would reduce the proportion of *C. sordidus* that move, as demonstrated in another study on weevil dispersal (Vinatier *et al.*, 2011). Second, rain and high humidity could reduce the evaporation and diffusion of the pheromone in the air, and there is usually less wind during wet season; these wet-season factors could reduce perception of pheromone and result in reduced movement. Why numbers of *C. sordidus* trapped were highest in the dry season in this and other studies in the Caribbean and South America but were highest in the wet season in Africa is unclear but might reflect differences in the nature of the dry seasons and wet seasons in the two areas. We note, however, that the trends observed in African studies were not strong and were not based on extensive data sets.

Conclusion

Although several studies have shown that fallow reduces nematode numbers in banana plantations (Okolle *et al.*, 2009), only one has reported the effect of this cultural practice on the banana weevil; Price (1994) reported that fallow reduced the damage caused by the banana weevil. According to Rhino *et al.* (2010), the prevention of the build-up of *C. sordidus* populations in banana fields requires that mass trapping be associated with a high level of field sanitation. Our results are consistent with the view that fallows, in association with pheromone traps, are effective for the control of the banana weevil. By using a data set covering a wide range of soil and climate conditions in Martinique, we disentangled the effects of soil and climate conditions on the efficiency of fallow (combined with mass trapping) for *C. sordidus* control. From an applied perspective, these results suggest that trapping should be conducted during two periods when the largest numbers of *C. sordidus* are trapped; these periods are (i) between the 40th and 80th month after planting and (ii) during the dry season. In addition, fallows should last at least 12 months. Finally, future research should explicitly investigate the effect of spatial distribution of traps within and between plots on the efficiency of mass trapping.

Acknowledgements

This work was supported by CIRAD. The authors are grateful to Kevin Pinte and Marine Dumas (Cemagref) for their help with the Geographic Information System. We thank Pierre René and Patrick Legares (APEX) for monitoring *C. sordidus* in the field. We also thank David Dural and Karine Vincent (BANAMART) and farmers for providing field data.

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