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RESEARCH ARTICLE

Cover crops combined with soil tillage impact the spontaneous species density, richness and diversity in banana cover cropping systems

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Abstract

Soil tillage and cover crops impact spontaneous vegetation in agrosystems. Soil tillage destroys seedlings and can affect the soil seedbank. Cover crops compete with naturally occurring spontaneous species. Our aim was to gain insight into how soil tillage (here, the false seedbed technique) and cover crops impact the spontaneous vegetation in fallows preceding banana crops. In a fallowed field in Guadeloupe (French West Indies), two factors were combined in a split-plot design: the soil tillage modality before cover crop sowing (with or without the false seedbed technique) and the cover crop species (*Crotalaria spectabilis*, *Pueraria phaseoloïdes*, a 50/50 mix of *Brachiaria decumbens* + *Brachiaria ruziziensis*, a spontaneous vegetation control). On a monthly basis, in three permanent quadrats per sub-plot, all spontaneous species were identified and their numbers counted, while calculating the species richness and Shannon's diversity index. The spontaneous vegetation dynamics contrasted depending on the treatment. From 7 months post-sowing the species density, richness and Shannon index were significantly lower in treatments with *B. decumbens* + *B. ruziziensis* and *P. phaseoloïdes*, while in treatments with *C. spectabilis*, the species density and richness were significantly higher with than without the false seedbed technique. These effects were probably related to differences in the competitive ability of the cover crop used and, to a lesser extent, to the false seedbed effects on the soil seedbank. This is the first study to show that under a tropical climate, sown cover crop species combined with different soil tillage modalities have substantial impacts on the species density, richness and diversity of the spontaneous plant community over a 1-year period. These results could help farmers in their weed control strategies by providing them with a deeper understanding of the effects of practices on the spontaneous plant community.

Keywords *Brachiaria decumbens* · *Brachiaria ruziziensis* · *Crotalaria spectabilis* · Species diversity · False seedbed technique · *Pueraria phaseoloïdes* · Species richness · Weed

1 Introduction

In agrosystems, spontaneous species may compete for resources with crops and decrease yields. Chemical management has long been the main control strategy, but the detrimental effects on the environment have prompted exploration of alternative strategies. Apart from herbicide applications, several non-chemical control methods have been used for a relatively long time (Petit et al. 2011).

Among them, soil tillage is one of the main methods used to control spontaneous vegetation. The effects of this approach on the spontaneous species depend on the tools used, the soil tillage depth and the spontaneous species composition (Cordeau et al. 2017; Senarathne and Sangakkara 2009). Tillage is known to affect the seed depth distribution and abundance in soils (e.g. Colbach et al. 2000), while also destroying the growing vegetation and upsetting seed production, consequently affecting the viable soil seedbank. However, tillage can also churn old seeds up to the surface and promote the germination of seed cohorts near the surface (e.g. Colbach et al. 2014). The well-known false seedbed technique aims to deplete the spontaneous species seedbank (seeds and rhizomes) in the topsoil (Ringselle et al. 2019).

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Successive false seedbed operations promote seed germination and destroy seedlings, hence often decreasing the seedbank in the topsoil (Lamour and Lotz 2007; Ringselle et al. 2019). This technique is efficient for controlling of annual species (Lamour and Lotz 2007). It can also be used to control perennial species that reproduce via underground storage and proliferation organs by fragmenting and thus weakening them (Ringselle et al. 2019).

The use of cover crops is another method for controlling the development and composition of the spontaneous species community. There is considerable evidence on the short- and long-term effects of the sown crops and soil tillage on the spontaneous vegetation (Gunton et al. 2011). Cover crops also provide other beneficial services such as erosion mitigation and soil nitrogen enhancement via atmospheric fixation (Lu et al. 2000; Bàrberi and Mazzoncini 2001; Snapp et al. 2005; Damour et al. 2015). Cover crops can affect the development and growth of spontaneous species through competition for above- and below-ground resources or by providing a physical barrier to seed germination and seedling emergence (Teasdale et al. 2007; Médiène et al. 2011). The race for height and soil cover between weeds and cover crops that happens during the first weeks following plant emergence determines which plants will prevail over the others throughout the rest of their cycles (e.g. den Hollander et al. 2007). However, cover crop control of the spontaneous vegetation is often incomplete, leading to the development of mixed communities of the sown cover crop and some spontaneous species (Damour et al. 2018).

The combined use of cover crops with other methods with different mechanisms of action could enhance the control of spontaneous species. For example, tillage followed by sowing cover crops appears to be a promising solution. Some studies have shown that soil tillage is more effective than growing cover crops with regard to weed control under temperate climatic conditions (Bàrberi and Mazzoncini 2001). Indeed, under these conditions, when tillage is used to control spontaneous species, seasonal effects characterised by substantial temperature and humidity changes markedly decrease seed germination and plant growth due to the low temperatures and humidity (Cordeau et al. 2017; Fried et al. 2019). In the tropics, however, seasonal effects are negligible on temperature, light and humidity variations, which are less pronounced. To our knowledge, no studies have been conducted to test the impact of soil tillage followed by cover crop sowing in tropical conditions.

In banana cropping systems, cover crops can be used during fallows or banana crop cycles to provide services such as enhanced soil fertility or pest control (Damour et al. 2015). In these systems, managing the spontaneous vegetation during the fallow period will reduce the presence of these plants and thus their impact on subsequent banana crop cycles, while decreasing herbicide treatments, which are commonly used and problematic in banana cropping systems (Risède et al. 2010). Some studies have focused on describing the potential effects of cover crops on the growth of spontaneous species in banana cropping systems based on their morphological and physiological features (e.g. Tardy et al. 2015). Yet to our knowledge, no studies have assessed the impact of combined management practices on the development of the spontaneous plant community, despite the fact that the findings could help farmers tailor their management practices according to their objectives (Snapp et al. 2005).

The main objective of this study was to gain insight into how soil tillage (here, the false seedbed technique) and cover crops impact spontaneous plant communities in fallows preceding banana cropping. We thus monitored spontaneous vegetation growth over 12 months in a fallowed field where a cover crop species (three species tested) was combined with one soil tillage modality (two modalities tested) and calculated the density of the spontaneous plant community, its species richness, diversity and composition.

2 Material and methods

2.1 Experimental site and design

The experiment was carried out in a banana plantation in Capesterre-Belle-Eau in Guadeloupe, French West Indies (16° 04′ 39.1″ N; 61° 36′ 17.3″ W; 285 m a.s.l.), from June 2018 to June 2019. This is the standard duration of a fallow in banana cropping systems in the French West Indies. The chosen field was representative of the agro-climatic conditions and of the crop management techniques of the banana production area in Guadeloupe. Over this 1-year study period, the cumulated precipitation was 4489 mm (annual 10-year mean of 4500 mm), with a mean daily temperature of 24.2 °C (range 21.5–27.5 °C) and a mean solar radiation of 422.30 MJ/m^2/month. The soil was an andosol (FAO 2014). A 0.9-ha field that had been under fallow since October 2017 was selected for the experiment. The plant community was visually observed to be homogeneously distributed within the field. A split-plot design with five blocks was adopted. The field was divided into ten strips of four sub-plots each. Two factors were applied: the soil tillage modality (applied in strips, two modalities, one strip per modality and per block) (see Fig. 1 and SM1) and the sown cover crop species (applied on a sub-plot in strips, four modalities, sown at the same date in all sub-plots). The blocks were separated by 1-m-wide alleys, and each sub-plot was 196 m^2. In the whole field, the vegetation was cut with a rotary slasher 7 weeks before the cover crops were sown to facilitate soil tillage. In five strips (one per block), the soil was ploughed to 40 cm depth with a

Fig. 1 The two soil tillage modalities tested in a banana field under fallow in Guadeloupe (French West Indies). The false seedbed technique (modality M2: "with false seedbed") was applied with a seedbed cultivator (equipment on the left side), and coarse tillage not followed by the false seedbed technique (modality M1: "without false seedbed") was applied with a rotary spading machine (equipment on the right side). Photograph by Diane Rakotomanga

spading machine the day before sowing to destroy and bury the current vegetation and improve the soil seedbed for the future crop (modality M1: "without false seedbed") (SM1). In the five other strips (one per block), the soil was tilled four times at different depths and with different tools (modality M2: "with false seedbed") (SM1). Seven weeks before the cover crop was sown, the soil was ploughed to 40 cm depth with a spading machine. Then, the superficial soil layer was fragmented three times to 5 cm depth to eliminate seedlings that had emerged and deplete the soil seedbank (false seedbed technique): (i) 5.5 weeks before sowing with a seedbed cultivator, (ii) 4 weeks before sowing with a power harrow and (iii) the day before sowing with a seedbed cultivator. In late June 2018, three tropical cover crop species were sown, each on a sub-plot per strip: a 50–50 mixture of *Brachiaria decumbens* (Stapf, 1919) and *Brachiaria ruziziensis* (Germ. & C.M.Evrard, 1953) (modality B), *Crotalaria spectabilis* (Roth, 1821) (modality C) and *Pueraria phaseoloïdes* (Roxb.) Benth. (modality P). The main species characteristics, sowing densities and sowing depths are presented in Table 1. In each strip, a fourth sub-plot was not sown and was used as a spontaneous vegetation control (modality T). M1T was the control without false seedbed, and M2T was the control with false seedbed. The eight treatments were named according to the abbreviations of the two factors. Note that caterpillar attacks on *C. spectabilis* leaves were observed between the 4th and the 5th months post-sowing without being quantified, and this may have affected plant survival.

2.2 Measurements

In each sub-plot, three 25 cm × 25 cm permanent quadrats were installed far from the borders and marked with construction tape on stakes. Each month from July 2018 to June 2019 (dates t1 to t12, with t3 and t6 missing values due to bad weather, thus preventing us from obtaining measurements), the spontaneous species growing in the quadrats were identified and the number of individuals of each species was counted. The number of cover crop individuals was also counted. For each quadrat, at each date, the density of each species (d_i for species i) was calculated as the number of individuals of that species per m^2. The total densities of all species and of spontaneous species (d_{tot} and d_{spont}, respectively) were calculated as the sum of the densities of all species and spontaneous species, respectively. The relative density of each species (p_i for species i) was calculated as $p_i = d_i \,/\, d_{\mathrm{tot}}$. The species richness of the spontaneous plant community (S) was calculated as the number of spontaneous species counted in the quadrat. Shannon's diversity index for the spontaneous plant community (H') was calculated as follows:

$$H' = -\sum_{i=1}^{S} p_i \log_2 p_i,$$

with i being the spontaneous species i

The frequency of occurrence of each species (F_i for species i) per treatment was also calculated as the number of quadrats of the treatment where a species occurred divided by the total number of sampled quadrats of the treatment (Fried et al. 2020).

Table 1 Main cover crop characteristics, sowing densities and depth used in the experiment

Code of the modality	Abbreviation	Full name	Family	Cycle	Growth habit	Sowing density (kg/ha)	Sowing depth (cm)
B	BD	*Brachiaria decumbens* (Stapf.1919)	Poaceae	Perennial	Semi-erect	10	3
	BR	*Brachiaria ruziziensis* (Germ. & C.M.Evrard. 1953)	Poaceae	Perennial	Semi-erect	10	3
C	CS	*Crotalaria spectabilis* (Roth. 1821)	Fabaceae	Annual (6 months)	Erect	30	3
P	PPh	*Pueraria phaseoloïdes* (Roxb.) Benth.	Fabaceae	Perennial	Twining	30	3

Modality B is a 50–50 mixture of two species

2.3 Data analysis

All statistical analyses were performed with R software (version 3.5.3) (R Core Team 2018). The effects of cover crop species and soil tillage modalities on d_{spont}, species richness and Shannon's diversity index were tested at each date with a nested ANOVA with the cover crop species factor nested in the soil tillage modality factor. Tukey post hoc tests were used to assess differences between the treatment means. The effects of the monitoring date on d_{spont}, species richness and Shannon's diversity index were tested, for each treatment, with a one-way ANOVA, followed by a Tukey post hoc test. Beforehand, the effects of blocks and sub-plots were tested with ANOVA (results not presented). They were not significant and thus not included in subsequent models. The relative difference between the densities of spontaneous species observed in a treatment and the one observed in the control treatment M1T ($\text{RelD}iff_{d_{spont}}$) was calculated as

$$\text{RelDiff}_{d_{\text{spont}}} = 100 \cdot \left[d_{\text{spont}}(\text{trt}_i) - d_{\text{spont}}(\text{M1T})\right] / d_{\text{spont}}(\text{M1T})$$

with trt_i in {M1B, M2B, M1P, M2P, M1C, M2C}.

The relative difference between the species richness observed in a treatment and the one observed in the control treatment M1T (RelDiff_S) was calculated similarly. Lastly, a principal component analysis (PCA) was performed on the densities of the 13 spontaneous species whose maximal frequency of occurrence was over 80% (combined dates and treatments). For each species, the contribution of variables to the first two axes was also assessed. Differences in the PCA axis 1 and 2 scores among treatments were tested by one-way ANOVA, followed by a Tukey HSD post hoc test.

3 Results

3.1 Dynamics of the density, species richness and diversity of the spontaneous plant community over 12 months

The spontaneous species community dynamics were contrasted over the 1-year monitoring period, depending on the treatment (Table 2). The first 2 months post-sowing the spontaneous plant densities in all treatments decreased significantly. Thereafter, the density of spontaneous species (d_{spont}) of communities without false seedbed associated with *C. spectabilis* (M1C) and the control (M1T) varied slightly but not significantly. The d_{spont} of communities with false seedbed associated with *C. spectabilis* (M2C) and the control (M2T) increased until 7 months post-sowing and then stabilised. Conversely, the d_{spont} of spontaneous species associated with *P. phaseoloïdes* (P) and the *Brachiaria* mixture (B) decreased significantly until 4 months post-sowing and then stabilised. The species richness (*S*) and Shannon's diversity index (*H′*) presented the same variation pattern as d_{spont} (Table 2).

3.2 Effects of treatments on the density, species richness and diversity of the spontaneous species community

The sown cover crop species, soil tillage modality and their interaction affected the species density, richness and diversity (Shannon's diversity index) (Fig. 2, SM2). For these three variables, differences between treatments appeared 2 months post-sowing. At this date, the interaction between the sown cover crop species and the soil tillage modality was significant. From 4 months post-sowing the interaction remained significant and the sown cover crop species was always highly significant thereafter.

From 2 months post-sowing the densities of spontaneous species (d_{spont}) associated with *P. phaseoloïdes* (P) and the *Brachiaria* mixture (B) were lower than those in the control M1T (about 80% and 75%, respectively, 12 months post-sowing). On the contrary, the densities of spontaneous species (d_{spont}) with false seedbed associated with *C. spectabilis* (M2C) and the control (M2T) were higher than those in the control M1T (about 50 and 40%, respectively, 12 months post-sowing) (Fig. 2A). From 5 months post-sowing the relative difference in d_{spont} with the control M1T ($\text{RelD}iff_{d_{spont}}$) for treatments associated with *P. phaseoloïdes* (P) and the *Brachiaria* mixture (B) was significantly lower than that observed in the other treatments. From 7 months post sowing, $\text{RelD}iff_{d_{spont}}$ was significantly lower for spontaneous

Table 2 Mean densities (d_{spont}), species richness (*S*) and Shannon's diversity index (*H*′) of the spontaneous species communities in each treatment and at each measurement date (t*i*), followed by the corresponding standard deviation

	t1	t2	t4	t5	t7	t8	t9	t10	t11	t12
d_{spont}										
M1B	259.7 ± 123.1 c	173.6 ± 100.2 b	57.7 ± 34.4 a	45.6 ± 27.5 a	45.1 ± 34.8 a	41.1 ± 25.4 a	33.9 ± 22.6 a	41.3 ± 39.2 a	37.1 ± 35.2 a	28.3 ± 26.6 a
M1C	304.5 ± 84.0 b	173.6 ± 91.2 a	96.8 ± 45.2 a	141.9 ± 90.2 a	181.3 ± 99.0 a	185.9 ± 57.2 a	185.6 ± 80.2 a	159.5 ± 68.0 a	165.6 ± 92.7 a	166.1 ± 99.2 a
M1P	235.4 ± 70.0 d	155.0 ± 113.3 c	107.1 ± 67.0 bc	50.2 ± 32.1 ab	52.3 ± 37.9 ab	49.2 ± 23.7 ab	40.0 ± 24.8 a	38.8 ± 26.8 a	22.2 ± 20.6 a	10.5 ± 7.8 a
M1T	313.3 ± 75.1 c	177.4 ± 78.5 ab	165.6 ± 55.3 ab	150.7 ± 46.8 a	231.7 ± 66.8 b	177.5 ± 43.2 ab	180.5 ± 69.5 ab	192.0 ± 58.7 ab	194.9 ± 45.8 ab	206.4 ± 78.7 ab
M2B	228.5 ± 76.7 c	123.7 ± 68.5 b	125.6 ± 104.5 b	43.2 ± 32.3 a	45.6 ± 36.3 a	41.1 ± 29.7 a	33.6 ± 22.1 a	26.4 ± 19.1 a	22.9 ± 24.3 a	16.3 ± 16.1 a
M2C	241.3 ± 73.5 b	106.1 ± 37.5 a	221.1 ± 94.9 ab	217.9 ± 133.9 ab	302.1 ± 132.6 b	276.5 ± 67.6 b	309.9 ± 102.7 b	272.5 ± 81.1 b	294.7 ± 105.6 b	279.2 ± 120.3 b
M2P	266.4 ± 68.5 c	109.3 ± 63.8 b	101.1 ± 71.8 b	43.7 ± 32.6 a	38.4 ± 30.8 a	36.8 ± 22.8 a	30.7 ± 13.2 a	23.5 ± 13.5 a	20.8 ± 18.0 a	16.0 ± 13.4 a
M2T	269.3 ± 90.1 b	137.1 ± 59.1 a	219.5 ± 55.0 ab	196.0 ± 102.8 ab	244.3 ± 112.3 b	230.4 ± 69.5 ab	232.5 ± 64.8 ab	242.1 ± 79.5 b	236.5 ± 78.5 b	222.7 ± 106.2 ab
S										
M1B	5.6 ± 1.8 b	5.9 ± 1.6 b	3.4 ± 2.3 a	2.1 ± 1.3 a	1.9 ± 0.9 a	2.3 ± 1.2 a	2.1 ± 0.9 a	2.1 ± 1.1 a	2.3 ± 1.7 a	2. ± 1.2 a
M1C	6.1 ± 1.3 ad	5.3 ± 1.9 ac	4.0 ± 1.6 ab	3.5 ± 1.1 a	6.1 ± 2.7 ad	6.6 ± 2.6 bcd	7.1 ± 3.1 cd	6.5 ± 2.6 bcd	6.7 ± 3.4 bcd	8.6 ± 3.5 d
M1P	5.5 ± 1.2 b	5.0 ± 1.9 b	4.1 ± 2.7 b	1.6 ± 0.8 a	1.9 ± 1.4 a	2.1 ± 1.3 a	1.9 ± 1.1 a	2.0 ± 1.4 a	1.8 ± 1.5 a	1.4 ± 0.8 a
M1T	6.0 ± 1.3 bc	4.4 ± 1.7 ab	4.7 ± 1.6 ab	3.5 ± 1.1 a	6.5 ± 1.9 bc	5.6 ± 1.6 ac	6.6 ± 2.8 bc	6.1 ± 2.0 bcd	7.5 ± 2.4 c	10.1 ± 2.7 d
M2B	6.4 ± 1.1 c	5.4 ± 1.1 bc	4.4 ± 2.4 b	2.6 ± 1.3 a	2.7 ± 1.5 a	2.4 ± 1.1 a	2.4 ± 1.0 a	2.0 ± 1.0 a	1.6 ± 0.9 a	1.9 ± 1.3 a
M2C	6.1 ± 0.8 a	6.3 ± 1.7 a	7.1 ± 1.8 ab	6.5 ± 2.5 a	8.3 ± 2.3 abc	8.7 ± 2.9 ad	10.3 ± 2.0 cd	9.4 ± 2.0 bd	9.8 ± 2.6 bd	11.3 ± 3.3 d
M2P	5.7 ± 0.8 c	5.4 ± 1.4 c	3.9 ± 1.7 b	2.1 ± 1.7 a	2.1 ± 1.6 a	1.7 ± 0.9 a	1.9 ± 0.7 a	1.8 ± 0.8 a	1.5 ± 0.7 a	1.2 ± 0.7 a
M2T	5.8 ± 0.8 a	6.1 ± 1.3 ab	7.0 ± 1.6 ac	6.1 ± 1.9 ab	8.6 ± 1.7 cd	8.1 ± 1.5 bcd	9.1 ± 1.9 cd	8.4 ± 1.7 cd	9.1 ± 3.0 cd	9.3 ± 2.8 d
H′										
M1B	1.8 ± 1.8 b	1.9 ± 1.6 b	1.3 ± 2.3 ab	0.7 ± 1.3 a	0.6 ± 0.9 a	0.8 ± 1.2 a	0.8 ± 0.9 a	0.7 ± 1.1 a	0.8 ± 1.7 a	0.7 ± 1.2 a
M1C	1.8 ± 1.3 ac	1.6 ± 1.9 ab	1.5 ± 1.6 ab	1.3 ± 1.1 a	1.9 ± 2.7 ac	2.2 ± 2.6 c	2.2 ± 3.1 c	2.1 ± 2.6 bc	2.1 ± 3.4 bc	2.4 ± 3.5 c
M1P	1.9 ± 1.2 c	1.6 ± 1.9 c	1.3 ± 2.7 bc	0.4 ± 0.8 a	0.5 ± 1.4 a	0.7 ± 1.3 ab	0.6 ± 1.1 ab	0.6 ± 1.4 ab	0.6 ± 1.5 ab	0.3 ± 0.8 a
M1T	1.9 ± 1.3 bd	1.5 ± 1.7 ab	1.6 ± 1.6 bc	1.1 ± 1.1 a	2.0 ± 1.9 cd	1.9 ± 1.6 bd	2.1 ± 2.8 cd	2.0 ± 2.0 bd	2.2 ± 2.4 de	2.7 ± 2.7 e
M2B	1.9 ± 1.1 c	1.8 ± 1.1 c	1.7 ± 2.4 bc	1.0 ± 1.3 ab	1.0 ± 1.5 ab	0.9 ± 1.1 ab	1.0 ± 1.0 ab	0.7 ± 1.0 a	0.5 ± 0.9 a	0.7 ± 1.3 a
M2C	1.9 ± 0.8 a	2.2 ± 1.7 ab	2.4 ± 1.8 ac	2.1 ± 2.5 ab	2.4 ± 2.3 bc	2.4 ± 2.9 bc	2.7 ± 2.0 c	2.7 ± 2.0 c	2.7 ± 2.6 c	2.8 ± 3.3 c
M2P	1.7 ± 0.8 b	2.0 ± 1.4 b	1.5 ± 1.7 b	0.6 ± 1.7 a	0.7 ± 1.6 a	0.5 ± 0.9 a	0.7 ± 0.7 a	0.6 ± 0.8 a	0.5 ± 0.7 a	0.3 ± 0.7 a
M2T	1.7 ± 0.8 a	2.1 ± 1.3 ac	2.4 ± 1.6 bcd	2.0 ± 1.9 ab	2.5 ± 1.7 cd	2.4 ± 1.5 bcd	2.7 ± 1.9 d	2.5 ± 1.7 cd	2.5 ± 3.0 cd	2.5 ± 2.8 cd

Different letters indicate a significant difference between dates for one treatment (Tukey HSD test with $\alpha = 0.05$); all tests were highly significant ($p < 0.001$). M1B: without false seedbed + *Brachiaria* mixture; M1C: without false seedbed + *Crotalaria spectabilis*; M1P: without false seedbed + *Pueraria phaseoloïdes*; M1T: without false seedbed + spontaneous vegetation; M2B: with false seedbed + *Brachiaria* mixture; M2C: with false seedbed + *Crotalaria spectabilis*; M2P: with false seedbed + *Pueraria phaseoloïdes*; M2T: with false seedbed + spontaneous vegetation

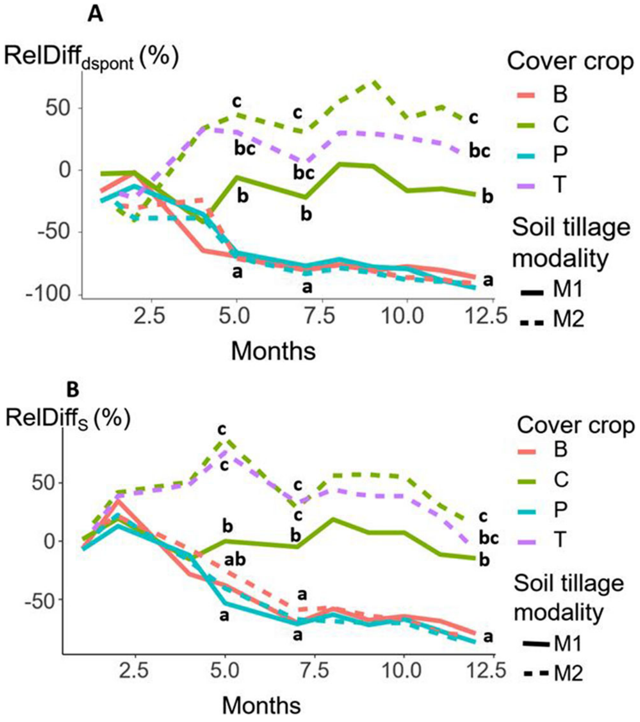


Fig. 2 Relative difference between the densities of spontaneous species observed in a treatment and the one observed in the control treatment M1T ($RelDiff_{d_{spont}}$) (**A**) and relative difference between the species richness observed in a treatment and that observed in the control treatment M1T ($RelDiff_S$) (**B**) in the eight treatments over 12 months for the 120 quadrats (8 × 15). Different letters indicate a significant difference between treatments (Tukey HSD test with $\alpha = 0.05$). M1B: without false seedbed + *Brachiaria* mixture; M1C: without false seedbed + *Crotalaria spectabilis*; M1P: without false seedbed + *Pueraria phaseoloïdes*; M1T: without false seedbed + spontaneous vegetation; M2B: with false seedbed + *Brachiaria* mixture; M2C: with false seedbed + *Crotalaria spectabilis*; M2P: with false seedbed + *Pueraria phaseoloïdes*; M2T: with false seedbed + spontaneous vegetation

species associated with *C. spectabilis* (C) without false seedbed (M1C) than with false seedbed (M2C). d_{spont} in M2C stayed far higher than that in the control M1T (30 to 50%), while d_{spont} in M1C stayed slightly lower than that in the control M1T.

The species richness (S) of spontaneous species generally showed the same trends as d_{spont}, except that differences in S between M2C and M2T compared to the other treatments where more pronounced.

Shannon's diversity index (H') was significantly lower for treatments with *Brachiaria* sp. (B) and *P. phaseoloïdes* (P) than that for the treatments with *C. spectabilis* (C) and the control (T) 7 months and 12 months post-sowing (SM2).

3.3 Community composition 12 months post-sowing

The cover crop species and soil tillage modality affected the composition of the monitored communities after 12 months (Figs. 3 and 4). All of the identified spontaneous species, along with their name abbreviations, are presented in the Supplementary Material (SM3).

The first two PCA axes constructed on the densities of the 13 most frequent spontaneous species explained 41.6% of the total variance. *Bidens alba* (BA), *Ludwigia octovalvis* (LO) and *Fimbristylis dichotoma* (FD) contributed the most to axis 1 (5.64%, 12.75% and 11.65%, respectively). *Mikania micrantha* (MM), *Lindernia crustacea* (LC), *Kyllinga erecta* (KE) and *Filicophyta* sp. (F) contributed the most to axis 2 (20.25%, 16.15%, 15.52% and 15.30%, respectively). *Fimbristylis dichotoma* (FD) and *Peperomia pellucida* (PPe) densities appeared to be closely correlated according to their positions on the ACP (Fig. 3A, close arrows). The same results were obtained for *Digitaria ciliaris* (DCi), *Mecardonia procumbens* (MP) and *Ludwigia octovalvis* (LO) on the one hand, and *Filicophyta* sp. (F) and *Kyllinga erecta* (KE) on the other.

Two groups of treatments were clearly distinguished on the PCA: treatments with *Brachiaria* sp. (B) and *P. phaseoloïdes* (P) on the left side and treatments with *C. spectabilis* (C) and the control (T) on the right. These two groups were significantly different on both axes (Tukey test performed on the axis 1 and 2 coordinates, Fig. 3C and D, $p < 0.05$). Moreover, M2C did not overlap with M1C and M1T on both axes (Fig. 3D).

No species were specifically present in one treatment, but two spontaneous species succeeded in becoming established in every treatment, i.e. *Bidens alba* (BA) and *Mikania micrantha* (MM) (Fig. 4). Communities associated with *P. phaseoloïdes* (P) included only a few species (see species richness results). Only the two ubiquitous species *Bidens alba* (BA) and *Mikania micrantha* (MM) were found in M1P, while *Digitaria ciliaris* (DCi) was also found in M2P. Spontaneous plant communities in treatments associated with *Brachiaria* sp. (B) were slightly richer, with *Bidens alba* (BA), *Mikania micrantha* (MM), *Digitaria ciliaris* (DCi), *Fimbristylis dichotoma* (FD) and *Ludwigia octovalvis* (LO) in M1B and the same species as well as *Hedyotis lancifolia* (HL) and *Mecardonia procumbens* (MP) in M2B. Several spontaneous species were only present in treatments with *C. spectabilis* (C) and the control (T).

4 Discussion

The results of our study were obtained over a 1-year period on a single site. However, considering that during this year there were no extreme climatic events, that rainfall was similar to the 10-year annual mean and that the chosen field and its management were representative of banana crop fields in Guadeloupe, we consider that our results would be transposable to other years and fields with similar characteristics.

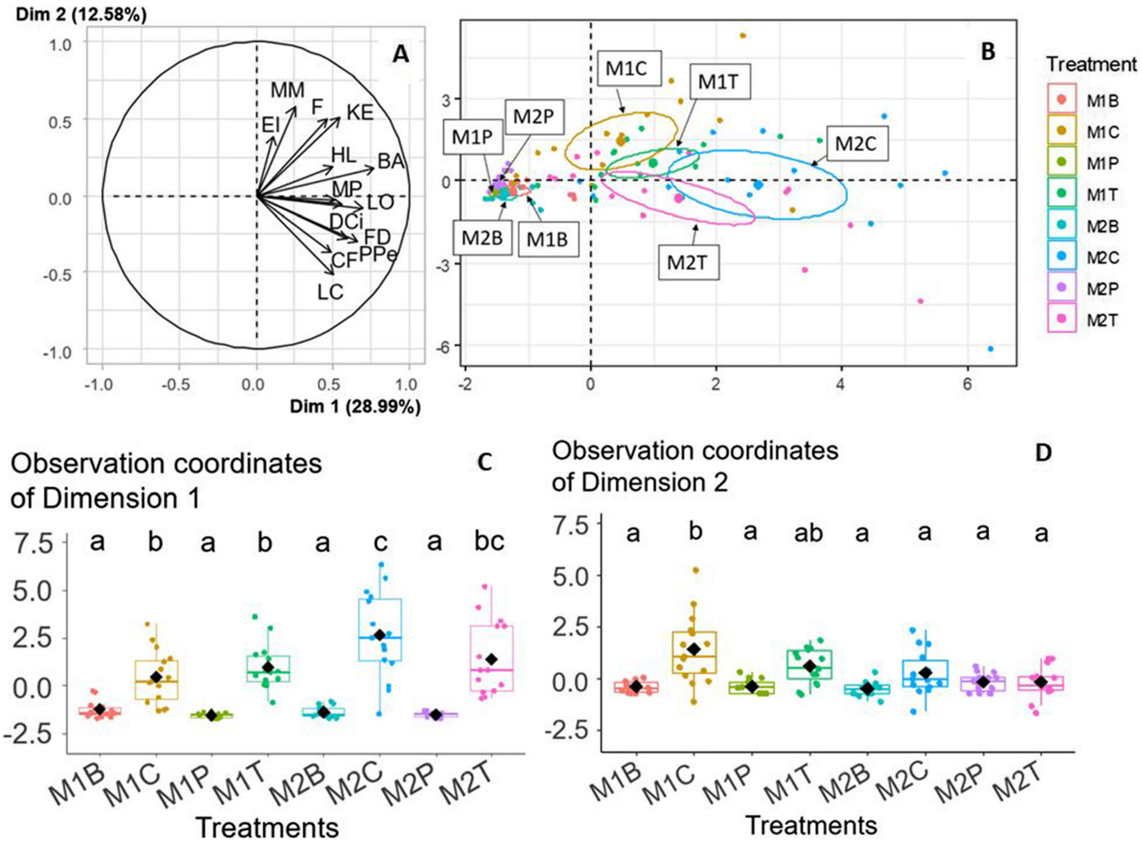


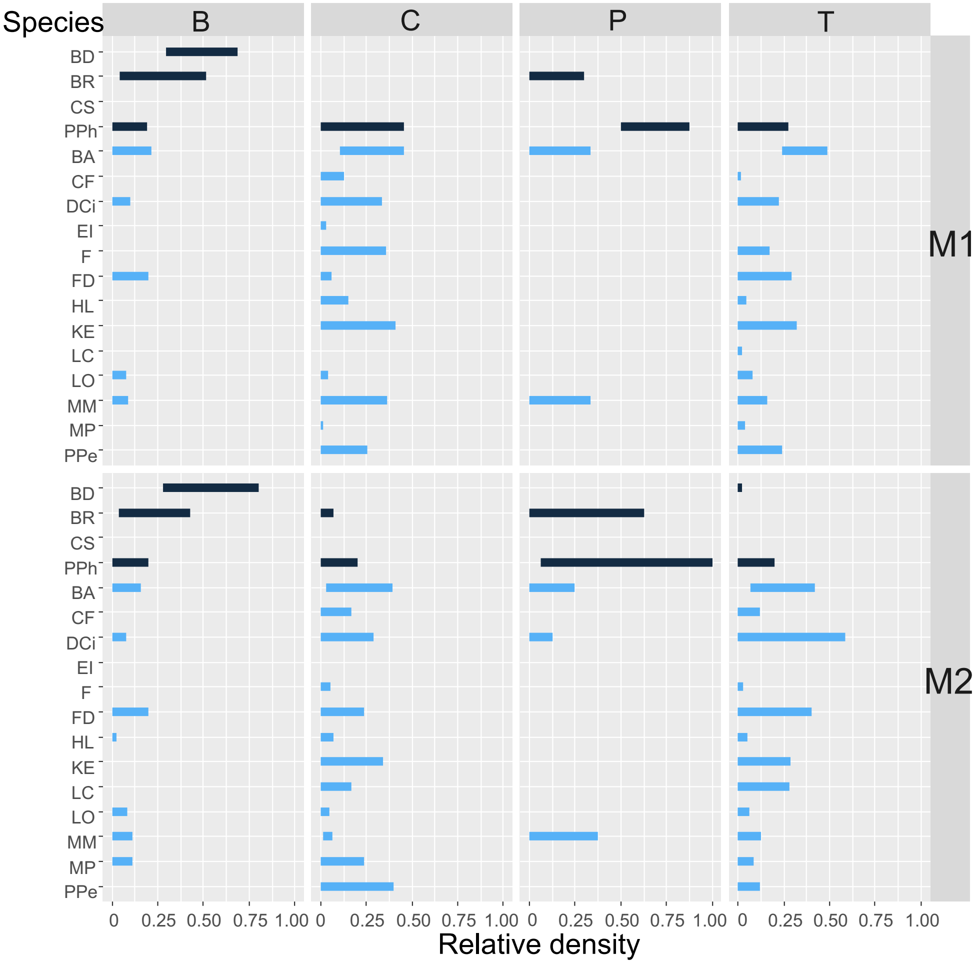
Fig. 3 Principal component analysis (PCA) performed on densities of the 13 most frequent spontaneous species of the communities monitored at 12 months post-sowing: **A** correlation circle between variables on the first two axes; **B** observations in the first two axes with representation of the treatments (ellipses and colours); Observation coordinates in dimension 1 (**C**) and dimension 2 (**D**). EI: *Eleusine indica*; MM: *Mikania micrantha*; F: *Filicophyta* sp.; KE: *Kyllinga erecta*; HL: Hedyotis lancifolia; BA: *Bidens alba*; MP: *Mecardonia procumbens*; LO: *Ludwigia octovalvis*; DCi: *Digitaria ciliaris*; PPe: *Peperomia pellucida*; FD: *Fimbristylis dichotoma*; CF: *Cardamine flexuosa*; LC: *Lindernia crustacea*; M1B: without false seedbed + *Brachiaria* mixture; M1C: without false seedbed + *Crotalaria spectabilis*; M1P: without false seedbed + *Pueraria phaseoloïdes*; M1T: without false seedbed + spontaneous vegetation; M2B: with false seedbed + *Brachiaria* mixture; M2C: with false seedbed + *Crotalaria spectabilis*; M2P: with false seedbed + *Pueraria phaseoloïdes*; M2T: with false seedbed + spontaneous vegetation

4.1 The cover crop affects the density, richness and diversity of the spontaneous vegetation

In this study, we showed that the spontaneous plant communities had contrasted dynamics over 1 year, depending on the sown cover crop species. However, the first 2 months post-sowing, the spontaneous plant densities in all treatments decreased markedly. This could possibly be explained by a high level of insect predation on the seedlings just after emergence (Petit et al. 2011), or even mollusc predation, which we observed during the study. After these 2 months, a marked difference was observed between communities associated with *P. phaseoloïdes* (P) and *Brachiaria* sp. (B) on the one hand, and communities associated with *C. spectabilis* (C) and the control (T) on the other, i.e. the species richness and diversity decreased with time in communities associated with *P. phaseoloïdes* (P) and *Brachiaria* sp. (B), whereas these metrics increased with time in communities associated with *C. spectabilis* (C) and the control (T). These results suggest differences in the abilities of these cover crop species to compete for resources (mainly light) or to develop a physical barrier to seed germination and seedling emergence, i.e. the two main processes by which cover crops can limit the growth of neighbouring species (Teasdale et al. 2007; Médiène et al. 2011).

Indeed, *Pueraria phaseoloïdes* (PPh) is a perennial twining liana with large leaves that climb on other species and stifle them by occupying the space and reducing their access to light. This species appears to be a particularly strong competitor, according to the very low species richness and density of the spontaneous plant community we observed. Tardy et al. (2015) showed that *Pueraria phaseoloïdes* invests carbohydrates in support and light acquisition structures (stems and leaves, respectively), while rapidly producing substantial biomass. These growth characteristics could be associated with efficient light interception and acquisition to the detriment of the neighbouring plants. In our experiment, the only species that succeeded to grow with *Pueraria phaseoloïdes* were (i) the liana *Mikania micrantha* (MM), which has the same growth habit as *Pueraria phaseoloïdes*

Fig. 4 Relative densities of the 13 most frequent spontaneous species and of the cover crop species at 12 months post-sowing. Data correspond to the densities measured on the quadrats of each treatment. BD: *Brachiaria decumbens*; BR: *Brachiaria ruziziensis*; CS: *Crotalaria spectabilis*; PPh: *Pueraria phaseoloïdes*; EI: *Eleusine indica*; MM: *Mikania micrantha*; F: *Filicophyta*; KE: *Kyllinga erecta*; HL: *Hedyotis lancifolia*; BA: *Bidens alba*; MP: *Mecardonia procumbens*; LO: *Ludwigia octovalvis*; DCi: *Digitaria ciliaris*; PPe: *Peperomia pellucida*; FD: *Fimbristylis dichotoma*; CF: *Cardamine flexuosa*; LC: *Lindernia crustacea*; B: modality with *Brachiaria* mixture; C: modality with *Crotalaria spectabilis*; P: modality with *Pueraria phaseoloïdes*; T: modality with control; M1: without false seedbed; M2: with false seedbed; in dark blue: the four cover crops; in pale blue: the 13 most common spontaneous species of the study



and seems to grow more quickly, and (ii) and the erect species *Bidens alba* (BA), whose rapid growth may allow it to rise above the *Pueraria phaseoloïdes* cover, thereby avoiding being stifled by this species.

Brachiaria decumbens (BD) and *Brachiaria ruziziensis* (BR) are perennial semi-erect species with a high growth rate and biomass that is invested in expanding the leaf area (Damour et al. 2016; Tardy et al. 2015). They tend to maximise light interception with light acquisition organs (Tardy et al. 2015). They also densely cover the soil by tillering and emitting stolons, which consequently prevent seed germination and emergence. Indeed, under *Brachiaria decumbens* and *Brachiaria ruziziensis* cover, we observed high humidity and low incident light, which could have prevented seed germination and growth. It likely also prevented small spontaneous species from colonising the area, which was the case for *Cardamine flexuosa* (CF) and *Mecardonia procumbens* (MP) (Fig. 4) and could explain the low species richness and diversity observed in these communities. However, other species succeeded in growing within *Brachiaria decumbens* and *Brachiaria ruziziensis* cover. The liana *Mikania micrantha* (MM) had likely grown by twinning on the supporting *Brachiaria decumbens* and *Brachiaria ruziziensis* plants. The erect species *Bidens alba* (BA) likely succeeded in growing because of its tall habit, which enabled it to pierce through the *Brachiaria* cover.

Crotalaria spectabilis (CS) is an annual erect plant with a low crown width (Tardy et al. 2015). This low crown width was probably responsible for poor soil shading and poor space and light competition. This poor competitive ability, in addition to the caterpillar attack that occurred between the 4th and the 5th months post-sowing which probably contributed to the decrease in the *C. spectabilis* population, may explain the marked development of spontaneous species in these treatments. Moreover, *Crotalaria spectabilis* is an annual species with a 6-month cycle. This may explain why communities in treatments associated with *C. spectabilis* (C) thereafter tended to have the same dynamics as communities in the control treatment (T) without cover crops.

4.2 Soil tillage affects spontaneous plant communities depending on the cover crop sown

Our results showed that the soil tillage operations affected the spontaneous species density and the species richness of the spontaneous plant community only when the *Crotalaria spectabilis* cover crop had been sown. These results could probably be explained by an effect of soil tillage on the seedbank, which may germinate and grow if the cover crop competition intensity is moderate.

Without false seedbed (modality M1), the soil was ploughed with a spading machine at 40 cm depth 1 day before sowing. Therefore, mixed spontaneous species seeds were likely present within the 0–40-cm soil layer, i.e. a depth at which they would be unable to germinate because of their small size. When the false seedbed technique was used (M2), the 5-cm upper soil layer was fragmented three times before sowing at 5 cm depth with a seedbed cultivator and a power harrow. These supplementary soil operations took place after seedling emergence so as to destroy them and prevent further growth, as well as to deplete the spontaneous species soil seedbank (seeds and rhizomes) (Ringselle et al. 2019). Our results showed that spontaneous species densities either did not differ between the two soil tillage modalities (treatments associated with *P. phaseoloïdes* (P) and *Brachiaria* sp. (B) and the control (T)), or they were higher with the false seedbed technique than without (treatments associated with *C. spectabilis* (C)). This suggests that the spontaneous species soil seedbank was not depleted sufficiently and that seed germination was favoured. Indeed, seed germination could have been favoured in treatments with false seedbed (M2) via improvement in the ground-seed contact (Senarathne and Sangakkara 2009) and consequently also in seed moistening. Otherwise, seed germination and seedling emergence could have been promoted with false seedbed because seeds were placed in a more fragmented superficial soil layer with better access to light and oxygen. Moreover, the false seedbed technique may have failed to destroy rhizomes present in the superficial layers (Lamour and Lotz 2007; Ringselle et al. 2019). Conversely, the successive soil operations may have resulted in these rhizomes being chopped into small pieces and disseminated across the sub-plots. We observed more rhizome species like *Fimbristylis dichotoma* (FD) and *Digitaria ciliaris* (DCi) with false seedbed (M2) than without false seedbed (M1) (Fig. 4). Consequently, we concluded that successive passages of the power harrow and seedbed cultivator were probably responsible for the higher density and richness of spontaneous species we observed with the false seedbed modality (M2) because the soil seedbank depletion by repeated destruction of emerging seedlings did not offset the favourable effects on seed germination and weed dissemination by rhizome fragmentation.

Finally, this is the first study to show that, under a tropical climate, sown cover crop species combined with different soil tillage modalities have strong impacts on the species density, richness and diversity of the spontaneous plant community over a 1-year period.

4.3 Taxonomic diversity vs functional diversity

In this experimental study, we tested three cover crop species and revealed their contrasted effects. However, a broad range of cover crop species may be used in agrosystems and testing all of them is not possible. Above we discussed that the plant growth habit (erect, semi-erect, liana) and some cover crop morphological characteristics reported in the literature could be a useful basis for discussing the competitive ability of species and the effects of cover crops on the spontaneous plant community composition and density. A trait-based approach, as described in Duarte et al. (1995) and Garnier et al. (2018), could be used to describe species (cover crops and spontaneous species) according to traits related to competition relationships, to gain in genericity and save research time. Among these traits, the flowering dates of the cover crops and spontaneous species (Storkey 2006), their heights (Storkey 2006) (proxy of light availability for neighbours) and biomass (Bàrberi and Mazzoncini 2001; Senarathne and Sangakkara 2009) (proxy of competition intensity) would warrant measurement, in addition to the growth habit.

The analysis of such traits could also help measure the functional diversity of the communities and not only their species diversity. Functional diversity would have the advantage of shedding light on the mechanisms by which cover crops affect the spontaneous plant community (Díaz et al. 2007; Petchey and Gaston 2006). The species diversity we observed in some treatments (e.g. treatments associated with *C. spectabilis* (C) with high diversity or slightly higher richness, although not significant, in treatments associated with *Brachiaria* sp. (B) compared to treatments associated with *P. phaseoloïdes* (P)) may have hidden functional redundancy, e.g. a similar response of some spontaneous species to a treatment.

4.4 Management strategies to control spontaneous species

We showed that two management strategies (the use of cover crops and soil tillage) could partially control spontaneous species and that combining them could, in some conditions, improve this control. Other strategies like regular vegetation cutting with a rotary slasher could be combined to further enhance control.

Some of the spontaneous species observed in this study seemed be very hard to control. In tropical areas, lianas represent a major functional type, which could be responsible for serious economic problems in crop production (Wyka et al. 2013). This is the case with regard to *Mikania micrantha* (MM), a liana that can twine on banana plants and slow down its growth, particularly young banana plants. This liana did not respond well to the management practices we tested in this study. Other alternatives would be required to control them, such as manual detouring of each banana plant, which is a long and fastidious task.

Beyond the efficiency of these strategies, the targeted level of control of spontaneous species should be defined, depending on the farmer's objectives and on the nuisance these species generate. Maintaining some diversity in the field could improve the delivery of ecosystem services and the system resilience (Jackson et al. 2010; Gaba et al. 2014). For example, maintaining a certain level of spontaneous species in a diversified community may provide shelter for auxiliary fauna to help control pests or food for pollinator insects (Gaba et al. 2014). In our study, *Bidens alba* (BA) was present in all treatments—this species produces flowers year-round and may be a substantial pollination service.

5 Conclusion

Here, we showed for the first time that, under a tropical climate, sown cover crop species combined with different soil tillage modalities had substantial impacts on the species density, richness and diversity of the spontaneous plant community over 1 year, during the fallow period in banana cropping systems. This impact differed according to the cover crop and the soil tillage modality, probably related to differences in the competitive ability of the cover crop used and, to a lesser extent, to soil tillage effects on the soil seedbank. A functional approach could be used in further studies to gain further insight into the mechanisms by which plants compete and become established in the field. Ultimately, it could help farmers in their weed control strategies by boosting their understanding of the associated mechanisms.

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Data availability The datasets generated during and/or analysed during the current study are only available from the corresponding author on reasonable request.

Code availability Not applicable

Declarations

Ethics approval and consent to participate Not applicable

Consent for publication Not applicable

Conflict of interest The authors declare no competing interests.

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