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A trait-based analysis to assess the ability of cover plants to control weeds in Reunion

Christina M^{1,2}, Negrier A^{1,1}, Marnotte P^{1,2}, Viaud P^{1,2}, Mansuy A³, Auzoux S^{1,2}, Techer P^{2,4}, Hoarau E^{1,2}, Chabanne A^{2,5}

¹ CIRAD, UPR AIDA, F-97743 Saint-Denis, Réunion, France.

² AIDA, Univ Montpellier, CIRAD, Montpellier, France.

³ eRcane, F-97494 Sainte-Clotilde, Réunion, France

⁴ CIRAD, UPR AIDA, F-97455 Saint-Pierre, Réunion, France.

⁵ CIRAD, UPR AIDA, F-34398 Montpellier, France.

Abstract:

Cover plants have a high potential to manage weeds through competition for shared resources in tropical agrosystems. Assessing the abilities of a large number of different plant species to compete with weeds requires long-term experiments in different pedoclimatic environments. Our study was based on a set of 10 trials including 46 species of cover plants and performed from 2016 to 2018 in three sites in Reunion. Our aim was to identify and measure plant traits that optimize plant coverage and weed control by cover plants under tropical climate. We characterized two traits of interest (a soil coverage efficiency index and a coverage growth rate) using a hierarchical clustering analysis and compared them between plant area of origin, life cycle or growth habit. The ability for cover plant to cover efficiently and rapidly the soil increased with growth rate in height and leaf appearance rate while tends to decrease with thermal time for emergence. Accordingly, weed control efficiency (low weed coverage and dry mass) was strongly correlated and increasing with cover plant growth rate in coverage, height and biomass. The characterization of plant species using functional traits enabled to identify cover plants which could be used in tropical agrosystems as an alternative to herbicides. Assuming that the spatial and temporal combinations with the main crop will determine the performances of the system, we discussed a trait-based methodology to identify the cover plants adapted to sugarcane agrosystems in Reunion.

Keywords: cover crops; companion crops; green manures; plant traits; weeds; Reunion; sugarcane

1. Introduction

Weeds are a main biotic constraint to tropical agriculture (FAO, 2017). Weeds can induce a loss of yields in terms of quality and quantity, as well as increasing the crop production costs (Oerke, 2006; FAO, 2017). Not only, weeds are in competition with main crop for several resources, such as light, water or nutrients (Cordeau and Moreau, 2017), but they are alternative hosts for crop pests and pathogens (FAO, 2017). In most of tropical areas (except for Sudanese and Sahelian climates), weeds grow fast all year thanks to a favorable climate, which may strongly compete with main crop. Therefore, large amounts of chemical inputs, among which herbicides represent a large proportion of the active ingredients, are used (Oerke and Dehne, 2004).

In tropical agrosystems, the use of cover or companion plants to control weeds can be one of the solutions to help reduce herbicide inputs (e.g. Bhaskar et al., 2018; Ranaivoson et al., 2018; Mennan et al., 2000) before planting (Lu et al., 2000) or during crop growth as intercrop (Vandermeer, 1992). These plants are being increasingly used in innovative cropping systems to favour biological regulation and to deliver agro-ecosystem services such as weed, pest or erosion control (Snapp et al., 2005; Altieri et al., 2011; Koohafkan et al., 2012). Due to the large game of cover plant available, the choice of a plant to deliver these services is crucial because the spatial and temporal combinations with the main crop will determine the performances of the system (Malezieux et al., 2009).

The biological regulation mechanisms of weeds using cover plants are complex. They can be direct through competition for resources, allelopathy or a physical barrier to germination and emergence (Médiène et al., 2011; Teasdale et al., 2007), and indirect e.g. through seed predators or fungi responsible for damping-off (Cordeau and Moreau, 2017). In intensive tropical agrosystem, the hypothesis of competition especially for light is mainly put forward in biological regulation. The other resources are seldom limiting for plant growth (high fertilization rates, high rainfall or irrigation). The ability of a plant species to compete for light may result from the ability to access to light for the plant itself (e.g. overgrowth ability) or to reduce access to light by its neighbours (e.g. shading). Assessing the efficiency of the processes of light interception, light conversion, and carbon use may be challenging when studying a large range of cover plants.

Trait-based approaches, which originated in the field of comparative functional ecology, have a high potential to identify the most suitable plants and traits to control weeds (e.g. Damour et al., 2016, 2014). These approaches are based on the use of functional traits, i.e. morpho-physio-phenological features, which are measurable at the plant or group of plants level, and which have an impact on plant performances (Violle et al., 2007). Traits can be considered as an indicator of plant-driven processes and make it possible to compare wide ranges of cover crops. Although trait-based approaches have been extensively used in natural ecosystems, applications of these approaches to agrosystems are still currently increasing (Garnier and Navas, 2012; Tardy et al., 2015; Tixier et al., 2011; Damour et al., 2016, 2014).

In Reunion, weeds pressure is a main constraint for agriculture. Initiated in 2008 and 2018, the Ecophyto I and II programs aim to reduce the use of herbicides by 50% by 2025 in the French agricultural sector. In the island, sugarcane, the first agro-industrial sector, plays an

important economic, societal and environmental role covering more than 50% of agricultural land (Agreste, 2016). One of the main constraints of this crop is weeds: it's the first crop production in Reunion consuming herbicides (Antoir et al., 2016). Indeed, diseases and pests are mainly managed by varietal selection, except the larva of *Hoplochelus marginalis*, controlled by the fungi *Beauveria brongniartii* in biological control (Mouret et al., 2017). In this context, cover plants have a strong potential for the sugarcane sector.

The aim of this study was to investigate the trait-based characterization of a large range of cover plants in order to assess their ability to control weeds in tropical agrosystems, using the case study of Reunion. The objectives of this study were to identify among a wide variety of cover plant species, i) the species most suitable for tropical climatic conditions in terms of soil cover, ii) the species traits able to maximize soil cover and iii) to assess the ability of cover plants and traits to control weed growth.

To answer these questions, we combined a set of 10 field experiments conducted in Reunion from 2016 to 2018. Six of them were collection management experiments, to assess the cover plants performance in response to local climate (i.e. weeds were controlled manually). In the other four experiments, the ability of cover plants to control weed were assessed.

2. Materials and methods

2.1. Trials description

The trials described in this study were located in three experimental stations in Reunion from 2016 to 2018 between February and June (warm season and beginning of the cool season). The trials localization and description are detailed in Table 1. Two main types of trials were performed: the collection management trials and the weed control trials. In the collection trials, cover plants were grown without competition with weeds to assess their ability to grow in local climates. A manual weed control was performed after sowing and during the trial duration. Four collection trials were performed in La Mare (50 m asl), one in Bassin Plat (160 m asl) and one in Colimaçons (800 m asl). Each trial included pure cover plant plots of 12 or 16 m². Growth duration of cover plants ranged from 2.5 to 4 months depending on trials. In the weed control trials, no weed control was performed after sowing to assess the competition between cover plants and weeds. Four trials were performed in La Mare and Bassin Plat with plots from 20 to 100 m². Grow duration of cover plants was 2 months. In all weed control trials, each plot was associated with an adjacent control plot of natural weed flora. In all sites, daily average temperature (T_{MEAN}) were measured. Five of the trials were fertilized while the other five were not fertilized. The fertilizer applications are described in Table 1. All trials were irrigated (except for Colimaçons which present precipitation > 120 mm month⁻¹ during the growth period). Before sowing, a tillage has been carried out and herbicide was applied prior sowing. Seeds were sown manually following lines spaced by 40cm. Seeds density are indicated in Table S2. Sowing density for each species are described in Table S2 and were determined on the basis of bibliography, advice from suppliers and internal expertise.

Table 1. Cover crop collection and weed control trials. The cover crop species used in the different trials are listed in Table S1. For each trial, the site, latitude, longitude, altitude, soil type, year, average temperature (T_{MEAN}), number of species, plot area, sowing date, trial duration, fertilization regime are indicated.

Trial type	Site	Latitude	Longitude	Altitude	Soil type	Year	T_{MEAN}	Number of species (+ mixture)	Plot area (x repetition)	Sowing date (dd/mm)	Duration	Fertilization (kg ha ⁻¹)	Manual weed control	Trial ID	
Collection	La Mare	-20.9	55.53	50 m	Leptic cambisol	2016	23.0	33	16 m ² (x1)	30/03	3.5 months	NPK (36-82-60)	yes	1	
						2017	23.2	28		13/04	4 months	no		2	
						2018	22.7	26		27/04	4 months			3	
	Bassin Plat	-21.32	55.49	160 m	Cambisol andique	2016	24.0	19	16 m ² (x1)	04/03	2.5 months	NPK (36-77-48)		4	
	Colimaçon	-21.13	55.3	800 m	Brun andique	2016	20.5	18	16 m ² (x1)	16/03	2.5 months			5	
	La Mare	-20.9	55.53	50 m	Leptic cambisol	2018	25.7	16	12 m ² (x1)	20/02	3 months	no		no	6
22.0							12/04								
23.6							13/06								
Weed control	La Mare	-20.9	55.53	50 m	Leptic cambisol	2016	24.1	6 (+9)	36 m ² (x1)	04/04	2 months	NPK (30-80-60)	no		7
						2016	24.4	8	100 m ² (x1)	31/03					8
						2017	24.2	6 (+6)	20 m ² (x4)	13/04					9
	Bassin Plat	-21.32	55.49	160 m	Cambisol andique	2017	25.3	4 (+3)	24 m ² (x4)	03/03		no		10	

2.2. Cover plant species

A total of 46 cover plant species were tested in the different trials. The detail of cover plant species used in each experiment is presented in Table S1 and S2. These species included Asteraceae (n=2), Brassicaceae (n=3), Fabaceae (n=32), Poaceae (n=8) and Polygonaceae (n=1) plants. Among them, we have 21 temperate and 25 tropical species. The majority of species were annual (n=35) or perennial (n=8), and 1 biennial and 2 vivacious were characterized. The growth habit (creeping, erected or twining) are detailed in Table S1. Among weed control trials, 18 cover plant mixtures were also tested (Table 1), the list of mixture are detailed in Table S3 and included two species each time.

Table 2. Traits and variables measured in the trials and used in the study. The identification of each trials (Trial ID) where measurements were made was indicated. 0-1 indicated that the variable values ranged from 0 to 1.

	Index	Units	Description	Trial ID
Plant traits	COV _{EFF}	0-1	Coverage efficiency the growth period	All trial
	COV _{RATE}	% d ⁻¹	Growth rate in coverage per day between sowing and maximum coverage	All trial
	H _{RATE}	cm d ⁻¹	Growth rate in height per day since emergence	1,2,4,5,6,9,10
	Leaf _{RATE}	leaf d ⁻¹	Leaf appearance rate per day	1,2,4,5,6,9,10
	Emerg _{SDD}	°d	Thermal time for emergence since planting	1,2,4,5
	Flo _{SDD}	°d	Thermal time for flowering since planting	1,2,4,5
	ABV _{DM}	kgDM m ⁻²	Aboveground dry mass at the end of the trial	9,10
Weed control	WCE _{COV}	0-1	Weed control efficiency index based on weed coverage	7,8,9,10
	WCE _{DM}	0-1	Weed control efficiency index based on weed dry mass	9,10

2.3. Measurements

Cover crop traits and phenology were measured in the different trials (Table 2). Ground coverage by plants was measured in each plot weekly using a visual notation method described in Table S5 and used in previous studies (Mansuy et al., 2019; Mathieu & Marnotte, 2000; Marnotte et al., 1984). This method allows to assess the soil coverage of individual species in multi-species crop (e.g. cover plant and weeds). Between two dates of measurements, coverage (Cov, %) was linearly extrapolated each day. Then, we calculated an index of coverage efficiency (COV_{EFF}) over the growth based on the area under the curve of the daily dynamics of plant coverage:

$$COV_{EFF} = \frac{\sum_1^n Cov(i)}{n * 100\%}$$

Where Cov(i) was the plant coverage at day i and n the number of days of growth. The maximum coverage (COV_{MAX}, %) was defined at the maximum over growth. A growth rate in

coverage per day (COV_{RATE} , % d^{-1}) was calculated between sowing up to reaching the maximum coverage. Additionally, for each species, the height and number of leaves of 5 individuals per plot were measured weekly and averaged per date. From these measurements, a growth rate in height (H_{RATE} , cm d^{-1}) and a leaf appearance rate ($Leaf_{RATE}$, n d^{-1}) were calculated from emergence to flowering as the slope between plant height or leaf number and the number of day since planting. Considering phenology measurements, the thermal times for emergence ($Emerg_{SDD}$, °d) and flowering (Flo_{SDD} , °d) were calculated as the sum of daily T_{MEAN} from sowing to the state were 50% of plant emerged or flowered. Finally, to measure aboveground dry masses (ABV_{DM}) in weed control trials, all weeds and cover plants in three 50x50cm square in each plot were sampled and dried at 60°C over 2 days at the end of the experiment.

Additionally to cover plant traits, we assessed two weed control efficiency indices in terms of weed coverage (WCE_{COV}) and biomass (WCE_{DM}) in the weed control trials. Similarly to cover plants, a coverage efficiency index for weed over time (COV_{Weed}) was calculated in each plot of each trial. Then for each plot with cover plants, we assessed the WCE_{COV} as follows:

$$WCE_{COV} = 1 - \frac{Cov_{Weed,cp}}{\langle Cov_{Weed,pure} \rangle}$$

With $Cov_{Weed,cp}$ the weed coverage efficiency index in plot with cover plants and $\langle Cov_{Weed,pure} \rangle$ the average weed coverage efficiency index in control plots (pure weeds) among each trials. Similarly, the WCE_{DM} was calculated based on final weed dry mass (DM_{Weed}) in control and plot with cover crops:

$$WCE_{DM} = 1 - \frac{DM_{Weed,cp}}{\langle DM_{Weed,pure} \rangle}$$

With $DM_{Weed,cp}$ the aerial weed dry mass in plot with cover plants and $\langle DM_{Weed,pure} \rangle$ the average aerial weed dry mass in control plots among each trials. In case of mixture (Table S3), an average trait among cover plants was calculated as the mean of trait value per species weighted by the final coverage of each species. All experimental data are available online on CIRAD dataverse (<http://dx.doi.org/10.18167/DVN1/HA0V2G>).

2.4. Data analyses

First a principal component analysis (PCA) was performed on all plant traits in the collection trials to assess if plant behavior was different depending on temperature and fertilization regimes (R package FactoMineR and missMDA). As no effect of fertilization regime and temperature were identified (Fig. S1), we considered all trials as a pool in the following analyses. Secondly, a hierarchical clustering analysis was performed on the average COV_{EFF} and COV_{RATE} of cover plants in the collection management trials, to assess species ability to cover the soil and create clusters of similar behavior (R package FactoMineR). Comparison of mean between clusters of type of plants were tested using the non-parametric Dunn test (R package dunn.test). Finally, correlation between individual traits were assess with a Spearman correlation (ρ_{SPEAR} , R package Hmisc and corrplot). For visual purpose, polynomial smooth regressions were added in the figures using the loess R function. All data analyses were performed with R 3.4 (R Development Core Team, 2017).

3. Results:

3.1. Coverage dynamics in the collection trials

Based on a PCA performed on plant traits in the different trials, no effects of fertilisation regime or average temperature during growth were found (Fig. S1). To compare plant species, a hierarchical clustering on plant coverage efficiency (Cov_{EFF}) and the coverage rate (Cov_{RATE}) allowed to separate three clusters of cover plants (Fig. 1). They described a gradient of cover plant potential in terms of coverage. Average Cov_{EFF} were 0.18, 0.36 and 0.49 in the clusters 1, 2 and 3 respectively and average Cov_{RATE} were 0.56, 1.00 and 1.39 % d^{-1} in the clusters 1, 2 and 3, respectively (Table 3). The details of species composition of each cluster were given in Fig. 1.

Cov_{EFF} and Cov_{RATE} were similar among temperate and tropical species (Fig. 2a,b). Additionally, annual species showed a higher Cov_{RATE} than perennial species by 10% (Fig. 2d), while Cov_{EFF} was similarly whatever plant life cycle (Fig. 2c). Depending of species family, the Fabaceae showed lower Cov_{RATE} than Asteraceae by 30%, while no difference in Cov_{EFF} was found among species family (Fig. 2c,g). Considering the shape of plant, the twining species showed the highest Cov_{EFF} , in comparison to erected and creeping species (Fig. 2e). Cov_{RATE} was similar among growth habit (1.15 % d^{-1}) in average, except than twining plants showed a higher Cov_{RATE} than creeping plants by 30% (Fig. 2h).

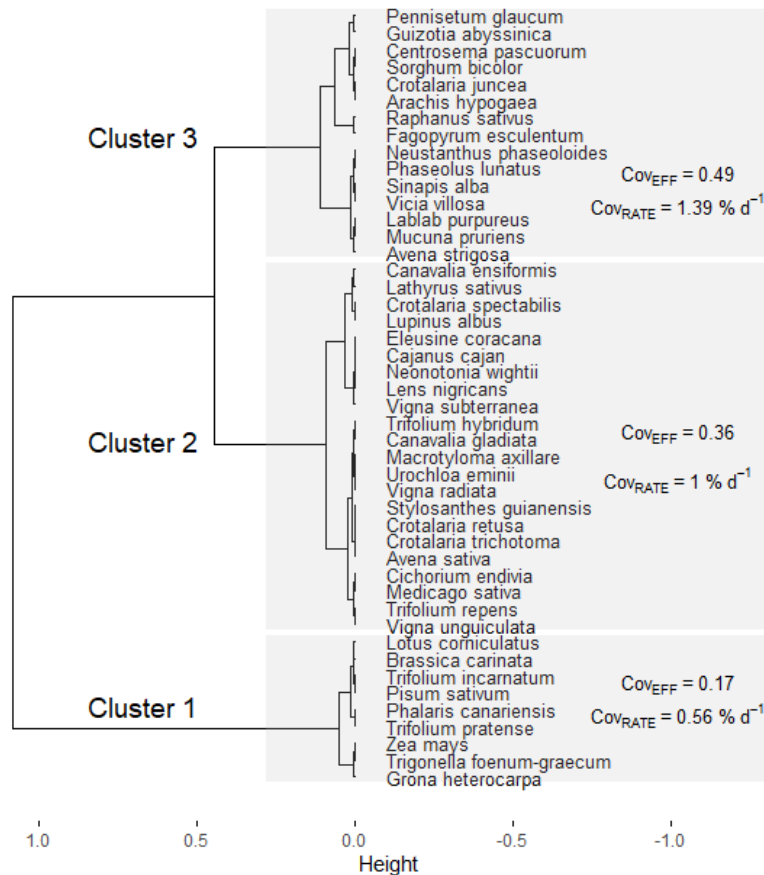


Fig. 1. Hierarchical clustering analysis on plant coverage efficiency (Cov_{EFF} , %) and coverage rate (Cov_{RATE} , % d^{-1}) per cover plant species used in the 6 collection trials described in Table 1. Three clusters were defined and the average Cov_{EFF} and Cov_{RATE} per cluster is indicated.

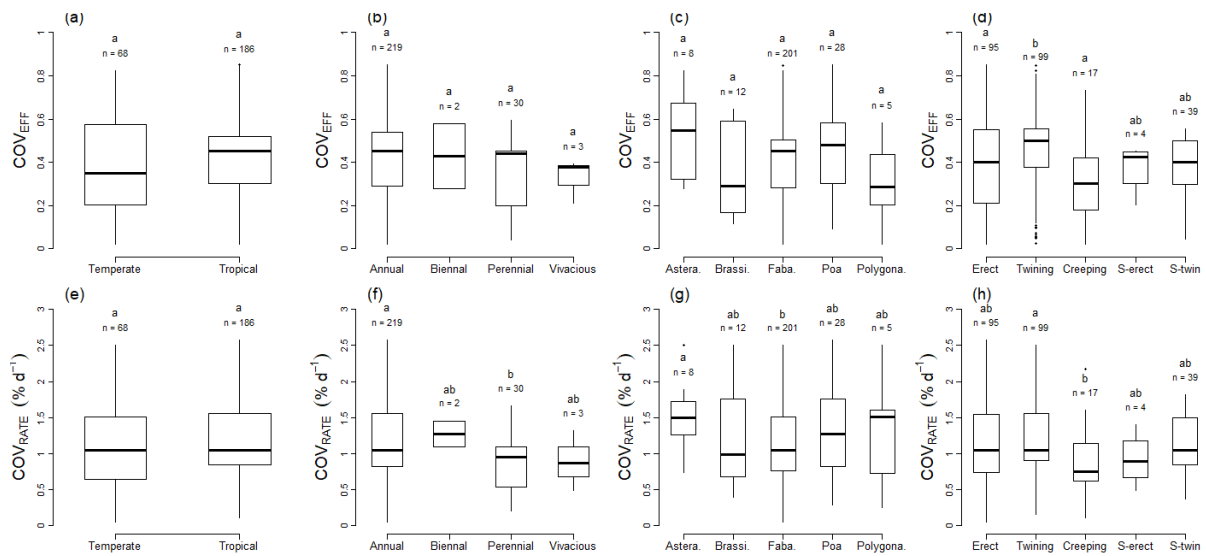


Fig. 2. Coverage efficiency (COV_{EFF}) and coverage rate (COV_{RATE}) of cover plant species used in the collection trials depending on area of origin (a,e), life cycle (b,f), species family (c,g) and growth habit (d,h). Plant families were abbreviated for Asteraceae (Astera.), Brassicaceae (Brassica.), Fabaceae (Faba.), Poaceae (Poa.) and Polygonaceae (Polygona.). Growth habits were abbreviated for erected (Erect), semi-erected (S-erect) and semi-twining (S-twin) plants. The differences between factors were tested using a Dunn test and indicated by letters a and b. The number of sample within each category is indicated by “n”.

3.2. Correlation between plant traits and coverage

At the cluster level, the two clusters with the highest coverage efficiency and coverage rate (clusters 2 and 3) also showed the highest growth rate in height with 0.78 cm d^{-1} in average (Table 3). $Leaf_{RATE}$ was higher by 18% in the cluster 3 than in the cluster 2. Considering thermal time for emergence and flowering, no difference among cluster were found. The average $Emerg_{SDD}$ and Flo_{SDD} were 170 and $1420 \text{ }^\circ\text{d}$, respectively.

At the species levels (Fig. 3), correlations were found between the two indices of coverage performance COV_{EFF} and COV_{RATE} ($\rho_{SPEAR}=0.73$; $p<0.001$). Additional correlations were found between coverage performance and other plant traits. On one hand, COV_{EFF} was positively correlated with H_{RATE} , $Leaf_{RATE}$ and Flo_{SDD} and negatively correlated with $Emerg_{SDD}$ (Fig. 3b,c). On the other hand, COV_{RATE} was positively correlated with H_{RATE} and negatively with $Emerg_{SDD}$ (Fig. 3d). In particular, COV_{EFF} reached its maximum values for H_{RATE} higher than 0.8 cm d^{-1} (Fig 3b). COV_{EFF} slightly increased with $Leaf_{RATE}$ and reached maximum values for $Leaf_{RATE}$ higher than 0.4 leaf d^{-1} (Fig 3c). Highest COV_{RATE} were also found for $Emerg_{SDD}$ lower than $150 \text{ }^\circ\text{d}$ (Fig. 3d). Moreover, additional significant correlations between plant traits were found (Fig. 3a). Flo_{SDD} was highly correlated with $Leaf_{RATE}$ ($\rho_{SPEAR} = 0.47$) and less with $Emerg_{SDD}$ ($\rho_{SPEAR} = 0.33$). $Leaf_{RATE}$ and H_{RATE} were also slightly correlated ($\rho_{SPEAR} = 0.26$)

Table 3. Coverage efficiency (Cov_{EFF}), growth rate in coverage (Cov_{RATE}), height (H_{RATE}), leaf appearance rate ($Leaf_{RATE}$), thermal time for flowering (Flo_{SDD}) and emergence ($Emerg_{SDD}$) depending of the species cluster obtained in Fig 1. The differences between clusters were tested using a Dunn test and indicated by letters a,b,c when p value < 0.025 . The number of sample within each group is indicated by “n”.

Species cluster	Cov_{EFF} (0-1)	Cov_{RATE} (% d^{-1})	H_{RATE} ($cm d^{-1}$)	$Leaf_{RATE}$ ($leaf d^{-1}$)	Flo_{SDD} ($^{\circ}d$)	$Emerg_{SDD}$ ($^{\circ}d$)
Cluster 1	0.18 \pm 0.13 a (n=14)	0.56 \pm 0.33 a (n=14)	0.29 \pm 0.21 a (n=7)	0.37 \pm 0.27 ab (n=7)	1163 \pm 14 a (n=2)	191 \pm 79 a (n=4)
Cluster 2	0.36 \pm 0.17 b (n=125)	1.00 \pm 0.45 b (n=125)	0.73 \pm 0.43 b (n=86)	0.33 \pm 0.34 a (n=85)	1497 \pm 433 a (n=71)	176 \pm 68 a (n=86)
Cluster 3	0.49 \pm 0.19 c (n=115)	1.39 \pm 0.57 c (n=115)	1.02 \pm 0.93 b (n=80)	0.39 \pm 0.33 b (n=80)	1353 \pm 393 a (n=63)	162 \pm 57 a (n=75)

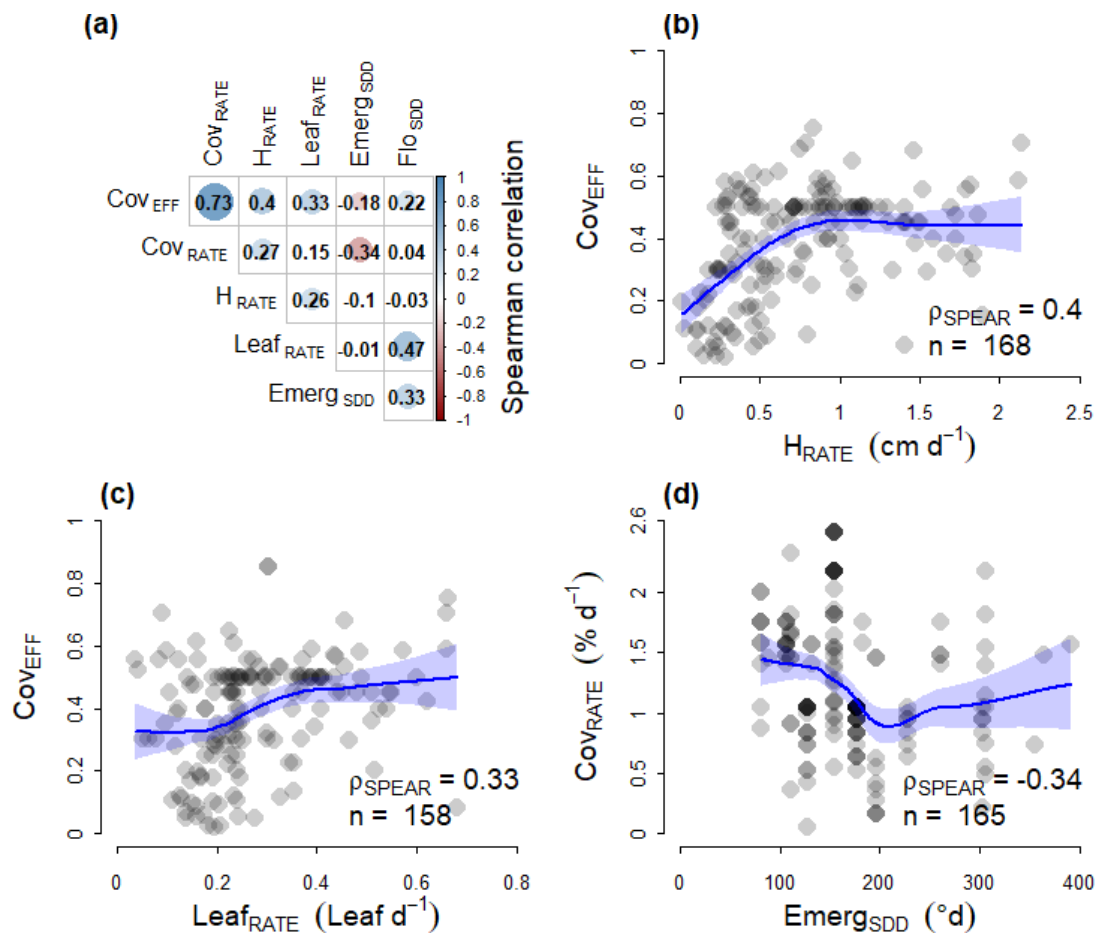


Fig 3. Spearman correlation (ρ_{SPEAR}) between cover plant traits in the collection trials (a). Significant positive and negative correlations were presented with blue and red circle, respectively. Relation between coverage efficiency (Cov_{EFF}) and height growth rate (H_{RATE}) and leaf appearance rate ($Leaf_{RATE}$) are detailed in (b) and (c). Relation between coverage rate (Cov_{RATE}) and thermal time for emergence ($Emerg_{SDD}$) is presented in (d). In each case, the number of sample is indicated (n) and a smooth regression were added using a polynomial smooth regression (blue line) with standard deviation (light blue).

3.3. Weed control and pure vs mixture cover plants

Weed control was assessed through the calculation of two weed control efficiency indices based on weed coverage (WCE_{COV}) and dry mass (WCE_{DM}). In average, cover plants in pure and mixture stands both successfully controlled weeds. Plots with cover plants showed lower weed coverage and weed dry mass by 69% and 74%, respectively (Fig 4b,c). Nevertheless, the variability of weed control was much lower in mixture ($sd = 17.7\%$ and 0.5 t ha^{-1}) than in pure stand ($sd = 29.4\%$ and 1.2 t ha^{-1} for coverage and dry mass, respectively). Only species of cluster 2 and 3 were tested in the weed control trials and both clusters showed a similar WCE_{COV} (0.5) over the experiment, even in mixture (Fig. 4d). However, average WCE_{DM} was higher by 119% in plots with cluster 3 species that in plots and with cluster 2 (Fig 4e). The mixture of cluster 2 and cluster 3 species showed an intermediate WCE_{DM} . The clustering analysis on average WCE_{COV} and WCE_{DM} (Fig. 4a) showed that the plant with highest weed control were mixture, *Avena sativa*, *Guizotia abyssinica* and *Pennisetum glaucum*. On the contrary, *Stylosanthes guianensis*, *Raphanus sativus* and *Crotalaria juncea* failed to control weed. Other species (Fig. 4a) presented intermediate weed control efficiency.

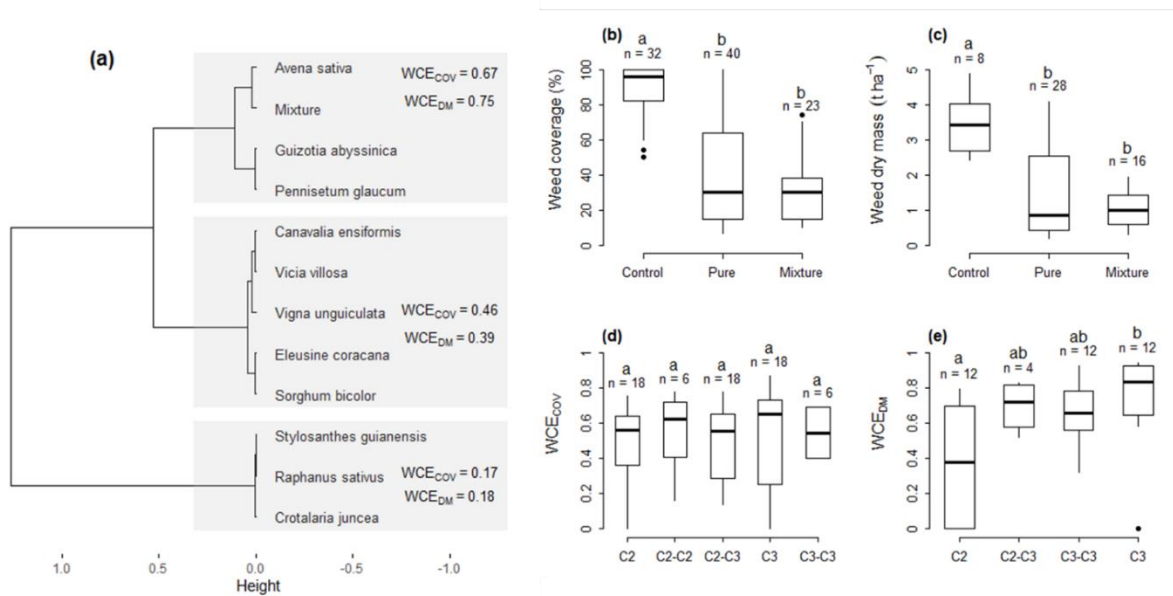


Fig. 4. Hierarchical clustering analysis on weed control efficiency in terms of weed coverage (WCE_{COV}) and dry mass (WCE_{DM}) per cover plant species or mixture used in the weed control trials (a). Change in WCE_{COV} and WCE_{DM} are presented depending on type of plot (control, pure or mixture of cover plants, b,c) and plant clusters defined in Fig1 (d,e). Mixture of plants from the same cluster are indicated by 'C2-C2' and 'C3-C3' while a mixture with plants from clusters 2 and 3 is indicated by 'C2-C3'. The difference between factors were tested using a Dunn test and indicated by letters a,b. The number of sample within each category is indicated by "n".

3.4. Weed control and plant traits

Among these species, the highest WCE_{COV} and WCE_{DM} were found for Asteraceae and Poaceae species ($WCE_{COV} = 0.69$ and $WCE_{DM} = 0.83$), while weed control remained low for Fabaceae species ($WCE_{COV} = 0.38$ and $WCE_{DM} = 0.17$, Fig. 5b,e). Twining (and to a lesser extent semi-twining) species showed a lower weed control than erected species (Fig. 5 c,d). WCE_{COV} and WCE_{DM} were lower by 35% and 65% for twining species compared to erected species. The area of origin (temperate or tropical) had no impact on WCE_{COV} and WCE_{DM} (Fig. 5a,d).

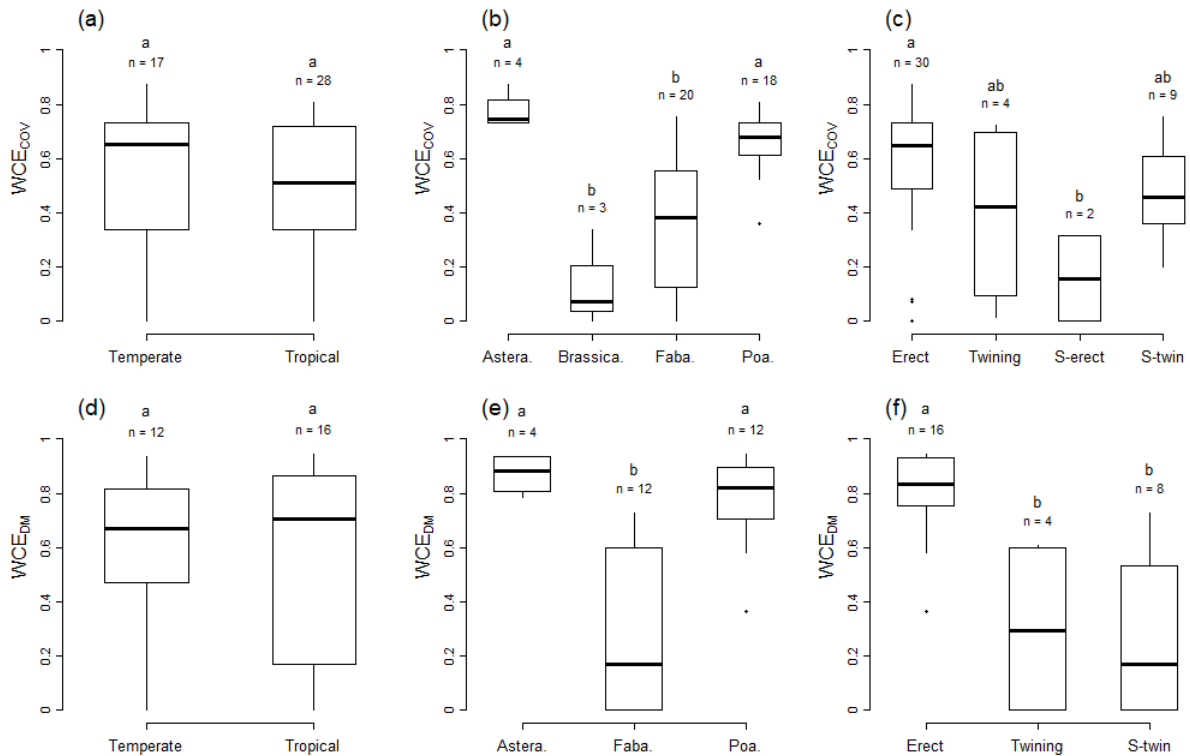


Fig. 5. Weed control efficiency based on weed coverage (WCE_{COV}) or dry mass (WCE_{DM}) depending on area of origin (a,d), species family (b,e) and growth habit (c,f). Only pure crop plots from the weed control trials are represented. Species family were abbreviated for Asteraceae (Astera.), Brassicaceae (Brassica.), Fabaceae (Faba.) and Poaceae (Poa.). Growth habits were abbreviated for erected (Erect), semi-erected (S-erect) and semi-twining (S-twin) plants. The difference between factors were tested using a dunn test and indicated by letters a and b. The number of sample within each category is indicated by “n”.

In terms of traits, WCE_{COV} and WCE_{DM} were positively correlated with coverage performance (COV_{EFF} and COV_{RATE}) but also with two plant traits (Fig. 6): H_{RATE} and plant dry mass (ABV_{DM}). In each correlation, WCE_{COV} reached its maximum values for $COV_{EFF} > 0.3$, $COV_{RATE} > 1 \text{ \% d}^{-1}$, $H_{RATE} > 1.8 \text{ cm d}^{-1}$ and $ABV_{DM} > 2 \text{ kg m}^{-2}$. WCE_{DM} had a similar response to plant traits. Correlation between weed coverage efficiency and leaf appearance rate was also tested but no significant correlations were found: spearman correlations were equal to -0.32 ($p=0.07$, $n=34$) and -0.17 ($p=0.37$, $n=34$) for WCE_{COV} and WCE_{DM} , respectively.

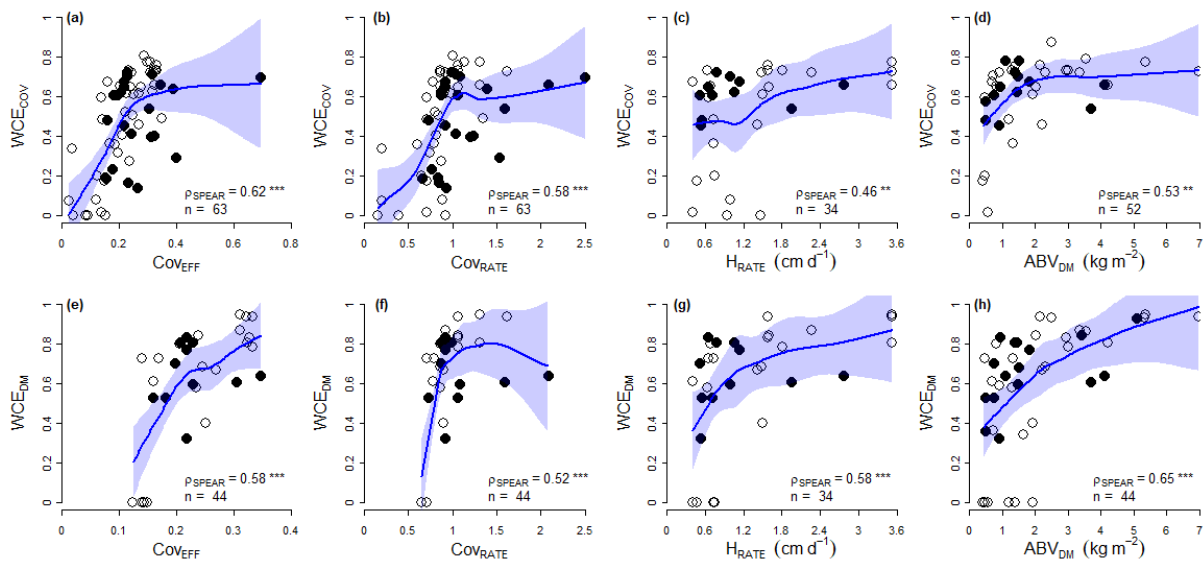


Fig. 6. Change in weed control efficiency based on weed coverage (WCE_{COV}) and dry mass (WCE_{DM}) depending on cover plant traits: coverage efficiency (COV_{EFF} , a,e), growth rate in coverage (COV_{RATE} , b,c), growth rate in height (H_{RATE} , e,g) and aerial dry mass (ABV_{DM} , d,h). The number of sample (n) and the spearman correlation coefficient (ρ_{SPEAR}) were indicated. Polynomial smooth regression between weed coverage and plant traits were added (blue line) with standard deviation (light blue). Pure and mixture cover plant were indicated by white and black points, respectively.

4. Discussions

4.1. Cover plant performance and weed control

The increasing interest of producers and researchers in cover plants might have been encouraged by the many positive aspects which are attributed to cover cropping. In particular, cover plants provide direct weed control during their establishment by competing with weeds for light, water, nutrients and space (Blanco-Cadi et al., 2015), as well as releasing allelochemical compounds into the environment (Gfeller et al., 2018). Additionally, cover plant residues retained on the soil surface can directly limit germination and growth of weeds in the following cash crop (Teasdale and Mirsky 2015; Mirsky et al. 2011; Ryan et al. 2011). Most importantly, they can help prevent the buildup of weed plant populations and therefore reduce future weed pressure.

In intensive tropical agrosystem, the hypothesis of competition especially for light is mainly put forward in weed regulation as the other resources are seldom limiting for plant growth (high fertilization rates, high rainfall or irrigation). As a sequence, we choose to focus in this study on the coverage growth rate (COVRATE) to identify species with early canopy closure and the coverage efficiency over time (COVEFF) to optimize ground cover over many months. Our results highlight how weed control by cover plant was improved with species with high coverage rate at the beginning of the growth and high coverage efficiency over time. Such observations confirm previous conclusion that species with early canopy closure generally show better weed suppression (Baraibar et al., 2018; Hayden et al., 2012). Additionally, in our study, cover plant with higher biomass also showed higher weed control, highlighting the role of competition for resources. High biomass production can increase the effect of competition (den Hollander et al., 2007; Tobin et al., 2012) and many studies highlighted this relation between cover plants biomass and weed control (e.g. Schappert et al, 2019; Bhaskar et al., 2018, Florence et al., 2019; Osipitan et al., 2019). Nevertheless, cover plant biomass is not always a good predictor of weed control (Baraibar et al., 2018; Kunz et al., 2016) which make some authors like Dorn et al. (2015) suggesting that rapid plant development after sowing is more important than the final biomass.

Some studies suggest that increased cover crop diversity results in greater weed suppression (Akemo et al. 2000; Brennan and Smith 2005; Lawson et al. 2015), while others are more nuanced (Baraibar et al., 2018; Schappert et al., 2019; Finnay et al., 2016; Smith et al., 2014). In our study, weed control efficiency was similar between pure and mixture cover plants species. Nevertheless, while mixtures were always efficient, the variability of weed control by pure cover plants was very large. In particular, stands of single cover plant species might not be able to buffer rapidly changing environmental conditions. Therefore, many studies have investigated the adaptability of mixtures (Hajjar et al., 2008; Tilman et al., 2001). In average, mixtures are not as effective as the best performing single sown cover plants in the literature. Nevertheless, species combinations increased resilience against weather conditions, an advantage to achieving efficient weed control over a long-term period.

In the objectives of identifying cover plant species adapted to new environment, assessing the efficiency of weed control may be challenging when studying a large range of cover plants and mixtures, particularly due to the variability of plant performance with soil and climate

variability. In addition, plant traits could be considered as indicators of plant-driven processes and make it possible to compare wide ranges of cover crops.

4.2. Plant traits and weed control

Trait-based approaches have a high potential to identify the most suitable plants and traits to control weeds (e.g. Damour et al., 2016, 2014). These approaches are based on the use of functional traits, i.e. morpho-physio-phenological features, which are measurable at the plant or group of plants level, and which have an impact on plant performances (Violle et al., 2007). Compared to the range of trait values measured in wild species worldwide in the TRY database (Kattge et al., 2011), measurements of cover plant traits are still limited (Garnier and Navas, 2012; Tardy et al., 2015; Tixier et al., 2011; Damour et al., 2016, 2014).

Plants which invest carbohydrates in a support structure to grow in height are erected plant species in our study. By re-using the terminology of Tardy et al. (2015), these species have a “shading” competition strategy, with no physical action on neighbours. Their ability to develop support structures in height allows them to be in the top layers of the canopy, and therefore to increase access to light and to shade neighbouring plants. On the contrary, plants which invest in leaf production with rapid growth can be either creeping or twining species. They have an “obstruction” competition strategy conferred by their ability to cover the soil and to avoid the germination and the emergence of weeds. When they are twining species, they also can smother weeds but also the main crop (Teasdale 1996).

While all species with high coverage and biomass succeeded in controlling weeds, our results highlight how the ‘shading’ strategy appeared more efficient than the ‘obstruction’ strategy in our tropical conditions. The positive correlation between height and plant coverage was also observed in previous studies in tropical conditions (Tardy et al., 2015). In temperate conditions, it was also observed that tall grasses (Poaceae) like cereals are highly weed suppressive due to their rapid growth rate (Brennan and Smith, 2005; Dorn et al., 2015; Finney et al., 2015; Hayden et al., 2012). Previous studies highlighted how Poaceae were often more efficient to control weeds than Fabaceae legume species (Ofori and Stern, 1987; Brainard et al., 2011; Baraibar et al., 2018), similarly to our results. The same observation was made for Asteraceae in this study.

4.3. Trait-based selection in Reunion

While the use of species with shading competition strategies could be very efficient to control weeds in crop rotations (Liebman and Dyck, 1993), their ability to be in the top layer in the canopy could have detrimental effects on main crop yield in crop mixtures. In that second case, it is necessary to find a trade-off between the ability of the cover plant to compete with weeds for light and their impact on main crop.

In Reunion, sugarcane plantations represent more than 50% of agricultural land (Agreste, 2016) and one of the main constraints of this crop is weeds management. As an alternative to herbicides, the use of cover plants is currently investigated in both rotation and intercropping (Christina et al., 2018; Mansuy et al., 2019). As a semi-perennial crop, sugarcane is planted every seven years in average. The use of erected species with high coverage and biomass, like

Pennisetum glaucum or *Guizotia abyssinica* are particularly adapted to the short periods (3-4 months) before replanting. Depending on sowing season, *Avena sativa* has also shown high weed control in this study.

Moreover, to reduce quantitatively the use of herbicide, sugarcane intercropping with cover plants is worthy investigating because rotation only occurs once seven years. Despite being considered a giant grass, sugarcane have a relatively slow growth rate the first three months after harvest, which make it sensitive to competition with weeds (Marion and Marnotte, 1992). To avoid competition, the choice should more focus on particular creeping or twining species which still showed high competition with weeds. In our study, *Vigna unguiculata* and *Canavalia ensiformis* have shown relatively high coverage and efficient weed control, despite having low growth rate in height. Such Fabaceae species have also the advantage to fix nitrogen from the atmosphere to deliver it to the main crop when it decomposes. Moreover, despite being semi-twining species, lianas were not observed in our climatic conditions for these two species.

The use of cover plants in rotation or intercropping with sugarcane is an increasing practices worldwide (Soares et al., 2017 in Brazil; Ali et al., 2018 and Teshome et al., 2015 in Africa; Paungfoo-Lonhienne et al., 2017 in Australia; Hemwong et al., 2009 in Asia). As cover plant performance will strongly vary with climatic conditions, the species selection performed in this study will only be valid in similar climatic areas. Nevertheless, the selection of traits that improve weed control should not depend on local climatic variability, highlighting the high potential of trait-based approaches to identify the most suitable plants and traits to control weeds.

5. Conclusion

Our study aimed to identify cover plant species and traits which optimize ground coverage and weed control in tropical agrosystems, based on a set of ten trials performed in Reunion Island. Little differences were found in terms of ground coverage depending on the life cycle, the species family. Nevertheless, the ability for cover plant to cover efficiently and rapidly the soil increased with growth rate in height or leaf appearance rate while tended to decrease with thermal time for emergence. While no difference of weed control were observed between pure and mixture of cover plants, weed control was more efficient with species or mixture with high growth rate in height or high aboveground biomass. Based on a trait-selection, we aimed to identify adapted to crop rotation or intercropping in the case of sugarcane plantations in Reunion, as an alternative to herbicides. While trait-based selection of cover plants appeared promising, weed traits will also influence plant-weed interactions. Consequently, future researches should focus on weed traits and their link with the harmfulness of natural flora.

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References

- Agreste, 2016. Réunion : enquête pratiques culturales canne – Le désherbage de la canne à sucre (No. 101). Daaf.
- Akemo, M.C., Regnier, E.E., Bennett, M.A., 2000. Weed Suppression in Spring-Sown Rye (*Secale cereale*): Pea (*Pisum sativum*) Cover Crop Mixes. *Weed Technology* 14, 545–549.
- Ali, M.A., Abd El-Lattie, E.A., Gad, A.A., Mekky, M.S., 2018. Study Impact of Integration Between Cover Crop and Weed Control Treatments on Weeds and Improved Sugarcane Productivity. *Assiut Journal of Agricultural Sciences* 49, 32–43. <https://doi.org/10.21608/ajas.2018.26821>
- Altieri, M.A., Lana, M.A., Bittencourt, H.V., Kieling, A.S., Comin, J.J., Lovato, P.E., 2011. Enhancing Crop Productivity via Weed Suppression in Organic No-Till Cropping Systems in Santa Catarina, Brazil. *Journal of Sustainable Agriculture* 35, 855–869. <https://doi.org/10.1080/10440046.2011.588998>
- Antoir, J., Goebel, F.R., Le Bellec, F., Esther, J.J., Maillary, L., Mansuy, A., Marion, D., Marnotte, P., Martin, J., Rossolin, G., Vincenot, D., 2016. Les bonnes pratiques de désherbage de la canne à sucre – Ile de La Réunion 2016. à sucre – Ile de La Réunion 2016. C.
- Baraibar, B., Hunter, M.C., Schipanski, M.E., Hamilton, A., Mortensen, D.A., 2018. Weed Suppression in Cover Crop Monocultures and Mixtures. *Weed Science* 66, 121–133. <https://doi.org/10.1017/wsc.2017.59>
- Bhaskar, V., Bellinder, R.R., DiTommaso, A., Walter, M.F., 2018. Living mulch performance in a tropical cotton system and impact on yield and weed control. *Agriculture (Switzerland)* 8, 1–17. <https://doi.org/10.3390/agriculture8020019>
- Blanco-Canqui, H., Shaver, T.M., Lindquist, J.L., Shapiro, C.A., Elmore, R.W., Francis, C.A., Hergert, G.W., 2015. Cover Crops and Ecosystem Services: Insights from Studies in Temperate Soils. *Agronomy Journal* 107, 2449–2474. <https://doi.org/10.2134/agronj15.0086>
- Brainard, D.C., Bellinder, R.R., Kumar, V., 2011. Grass–Legume Mixtures and Soil Fertility Affect Cover Crop Performance and Weed Seed Production. *Weed Technology* 25, 473–479. <https://doi.org/10.1614/WT-D-10-00134.1>
- Brennan, E.B., Smith, R.F., 2005. Winter Cover Crop Growth and Weed Suppression on the Central Coast of California. *Weed Research* 19, 1017–1024. <https://doi.org/10.1614/WT-04-246R1.1>
- Christina, M., Marnotte, P., Renaud, B., Marin, Y., Courtois, J., Virama, M., Chabanne, A., 2018. Crop cover selection to improve weed control in multi-species agrosystems in Reunion Island. Presented at the 18th European Weed Research Society Symposium: New approaches for smarter weed management, Agricultural Institute of Slovenia, Ljubljana, Slovenia.
- Cordeau, S., Moreau, D., 2017. Gestion des adventices au moyen des cultures intermédiaires multi-services: potentiels et limites. *Innovations Agronomiques* 62, 1–14.
- Damour, G., Dorel, M., Quoc, H.T., Meynard, C., Risède, J.M., 2014. A trait-based characterization of cover plants to assess their potential to provide a set of ecological services in banana cropping systems. *European Journal of Agronomy* 52, 218–228. <https://doi.org/10.1016/j.eja.2013.09.004>
- Damour, G., Guérin, C., Dorel, M., 2016. Leaf area development strategies of cover plants used in banana plantations identified from a set of plant traits. *European Journal of Agronomy* 74, 103–111. <https://doi.org/10.1016/j.eja.2015.12.007>

- den Hollander, N.G., Bastiaans, L., Kropff, M.J., 2007. Clover as a cover crop for weed suppression in an intercropping design: II. Competitive ability of several clover species. *European Journal of Agronomy* 26, 104–112. <https://doi.org/10.1016/j.eja.2006.08.005>
- Dorn, B., Jossi, W., Heijden, M.G.A. van der, 2015. Weed suppression by cover crops: comparative on-farm experiments under integrated and organic conservation tillage. *Weed Research* 55, 586–597. <https://doi.org/10.1111/wre.12175>
- FAO, 2017. Plant Production and Protection Division Integrated Weed Management [WWW Document]. <http://www.fao.org/agriculture/crops/thematic-sitemap/theme/spi/scpi-home/managing-ecosystems/integrated-weed-management/en/> (accessed 5.18.20).
- Finney, D.M., White, C.M., Kaye, J.P., 2016. Biomass Production and Carbon/Nitrogen Ratio Influence Ecosystem Services from Cover Crop Mixtures. *Agronomy Journal* 108, 39–52. <https://doi.org/10.2134/agronj15.0182>
- Florence, A.M., Higley, L.G., Drijber, R.A., Francis, C.A., Lindquist, J.L., 2019. Cover crop mixture diversity, biomass productivity, weed suppression, and stability. *PLoS ONE* 14, 1–18. <https://doi.org/10.1371/journal.pone.0206195>
- Garnier, E., Navas, M.-L., 2012. A trait-based approach to comparative functional plant ecology: concepts, methods and applications for agroecology. A review | SpringerLink. *Agronomy for Sustainable Development* 32, 365:399. <https://doi.org/10.1007/s13593-011-0036-y>
- Gfeller, A., Herrera, J.M., Tschuy, F., Wirth, J., 2018. Explanations for *Amaranthus retroflexus* growth suppression by cover crops. *Crop Protection* 104, 11–20. <https://doi.org/10.1016/j.cropro.2017.10.006>
- Hajjar, R., Jarvis, D.I., Gemmill-Herren, B., 2008. The utility of crop genetic diversity in maintaining ecosystem services. *Agriculture, Ecosystems & Environment* 123, 261–270. <https://doi.org/10.1016/j.agee.2007.08.003>
- Hayden, Z.D., Brainard, D.C., Henshaw, B., Ngouajio, M., 2012. Winter Annual Weed Suppression in Rye–Vetch Cover Crop Mixtures. *Weed Technology* 26, 818–825. <https://doi.org/10.1614/WT-D-12-00084.1>
- Hemwong, S., Toomsan, B., Cadisch, G., Limpinuntana, V., Vityakon, P., Patanothai, A., 2009. Sugarcane residue management and grain legume crop effects on N dynamics, N losses and growth of sugarcane. *Nutrient Cycling in Agroecosystems* 83, 135–151. <https://doi.org/10.1007/s10705-008-9209-8>
- Kattge, J., Bönsch, G., Díaz, S., Lavorel, S., Prentice, I.C., et al. 2019. TRY plant trait database – enhanced coverage and open access. *Global Change Biology* in press. <https://doi.org/10.1111/gcb.14904>
- Koohafkan, P., Altieri, M.A., Gimenez, E.H., 2012. Green Agriculture: foundations for biodiverse, resilient and productive agricultural systems. *International Journal of Agricultural Sustainability* 10, 61–75. <https://doi.org/10.1080/14735903.2011.610206>
- Kunz, C., Sturm, D.J., Varnholt, D., Walker, F., Gerhards, R., 2016. Allelopathic effects and weed suppressive ability of cover crops. *Plant, soil and environment* 62, 60–66.
- Lawson, A., Cogger, C., Bary, A., Fortuna, A.-M., 2015. Influence of Seeding Ratio, Planting Date, and Termination Date on Rye-Hairy Vetch Cover Crop Mixture Performance under Organic Management. *PLoS ONE* 10, e0129597. <https://doi.org/10.1371/journal.pone.0129597>
- Liebman, M., Dyck, E., 1993. Crop-Rotation and Intercropping Strategies for Weed Management. *Ecol. Appl.* 3, 92–122. <https://doi.org/10.2307/1941795>
- Lu, Y.-C., Watkins, K.B., Teasdale, J.R., Abdul-Baki, A.A., 2000. Cover crops in sustainable food production. *Food Reviews International* 16, 121–157. <https://doi.org/10.1081/FRI-100100285>
- Malézieux, E., Crozat, Y., Dupraz, C., Laurans, M., Makowski, D., Rapidel, B., Tourdonnet, S.D., Mal, E., Crozat, Y., Dupraz, C., Laurans, M., Makowski, D., 2009. Mixing plant species in cropping systems : concepts , tools and models . A review To cite this version : Review article Mixing plant species in cropping systems : concepts , tools and models . *Agronomy for Sustainable Development* 29, 43–62. <https://doi.org/10.1051/agro:2007057>
- Mansuy, A., Marmotte, P., Martin, J., Roux, E., Chouteau, R., Wilt, M., Soubadou, G., 2019. CanécoH : mise au point de leviers pour une Canne à sucre économe en Herbicide à La Réunion. *Innovations Agronomiques* 76, 103–119. <https://doi.org/10.15454/tskwve>
- Marion, D., Marnotte, P., 1991. Harmfulness of weed coverage on sugarcane. Presented at the 1. Rencontres Internationales en Langue Francaise sur la Canne a Sucre., Montpellier, France, 10-15 Jun.

- Marnotte, P., 1984. Influence des facteurs agroécologiques sur le développement des mauvaises herbes en climat tropical humide. Presented at the 7ème Coll. Int. Ecol. Biol. et Syst. des mauvaises herbes, COLUMA-EWRS, Paris, pp. 183–189.
- Mathieu, B., Marnotte, P., 2000. L'enherbement des sols à Muskuwaari au Nord-Cameroun. Presented at the Eleventh international conference on weed biology, AFPP, INRA, Dijon, France, pp. 151–158.
- Médiène, S., Valantin-Morison, M., Sarthou, J.-P., de Tourdonnet, S., Gosme, M., Bertrand, M., Roger-Estrade, J., Aubertot, J.-N., Rusch, A., Motisi, N., Pelosi, C., Doré, T., 2011. Agroecosystem management and biotic interactions: a review. *Agronomy Sust. Developm.* 31, 491–514. <https://doi.org/10.1007/s13593-011-0009-1>
- Mennan, H., Jabran, K., Zandstra, B.H., Pala, F., 2020. Non-Chemical Weed Management in Vegetables by Using Cover Crops: A Review. *Agronomy-Basel* 10, 257. <https://doi.org/10.3390/agronomy10020257>
- Mirsky, S.B., Curran, W.S., Mortensen, D.M., Ryany, M.R., Shumway, D.L., 2011. Timing of Cover-Crop Management Effects on Weed Suppression in No-Till Planted Soybean using a Roller-Crimper. *Weed Science* 59, 380–389. <https://doi.org/10.1614/WS-D-10-00101.1>
- Mouret, N., Martin, P., Roux, E., Goebel, F.-R., 2017. Multi-scale Evaluation of the Impacts of *Beauveria* sp. (Ascomycota: Hypocreales) Used to Control the White Grub *Hoplochelus marginalis* (Fairmaire) (Coleoptera: Scarabaeidae) on Sugarcane in Réunion. *Sugar Tech* 19, 592–598. <https://doi.org/10.1007/s12355-017-0526-6>
- Oerke, E.C., 2006. Crop losses to pests. *Journal of Agricultural Science* 144, 31–43. <https://doi.org/10.1017/S0021859605005708>
- Oerke, E.C., Dehne, H.W., 2004. Safeguarding production - losses in major crops and the role of crop protection. *Crop Prot.* 23, 275–285. <https://doi.org/10.1016/j.cropro.2003.10.001>
- Ofori, F., Stern, W.R., 1987. Cereal–Legume Intercropping Systems - ScienceDirect. *Advances in Agronomy* 41, 41–90.
- Osipitan, O.A., Dille, A., Assefa, Y., Radicetti, E., Ayeni, A., Knezevic, S.Z., 2019. Impact of Cover Crop Management on Level of Weed Suppression: A Meta-Analysis. *Crop Sci.* 59, 833–842. <https://doi.org/10.2135/cropsci2018.09.0589>
- Paungfoo-Lonhienne, C., Wang, W., Yeoh, Y.K., Halpin, N., 2017. Legume crop rotation suppressed nitrifying microbial community in a sugarcane cropping soil. *Sci Rep* 7, 16707. <https://doi.org/10.1038/s41598-017-17080-z>
- R Development Core Team, 2017. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Ranaivoson, L., Naudin, K., Ripoché, A., Rabeharisoa, L., Corbeels, M., 2018. Is mulching an efficient way to control weeds? Effects of type and amount of crop residue in rainfed rice based cropping systems in Madagascar. *Field Crops Research* 217, 20–31. <https://doi.org/10.1016/j.fcr.2017.11.027>
- Ryan, M.R., Curran, W.S., Grantham, A.M., Hunsberger, L.K., Mirsky, S.B., Mortensen, D.A., Nord, E.A., Wilson, D.O., 2011. Effects of Seeding Rate and Poultry Litter on Weed Suppression from a Rolled Cereal Rye Cover Crop. *Weed Science* 59, 438–444. <https://doi.org/10.1614/WS-D-10-00180.1>
- Schappert, A., Schumacher, M., Gerhards, R., 2019. Weed control ability of single sown cover crops compared to species mixtures. *Agronomy* 9. <https://doi.org/10.3390/agronomy9060294>
- Smith, R.G., Atwood, L.W., Warren, N.D., 2014. Increased Productivity of a Cover Crop Mixture Is Not Associated with Enhanced Agroecosystem Services. *PLOS ONE* 9, e97351. <https://doi.org/10.1371/journal.pone.0097351>
- Snapp, S.S., Swinton, S.M., Labarta, R., Mutch, D., Black, J.R., Leep, R., Nyiraneza, J., O'Neil, K., 2005. Evaluating cover crops for benefits, costs and performance within cropping system niches. *Agron. J.* 97, 322–332.
- Soares, M.B.B., Bianco, S., Finoto, E.L., Bolonhezi, D., Albuquerque, J. a. A., 2017. Phytosociological Study on the Weed Communities in Green Sugarcane Field Reform Using Conservation Tillage and Oilseed Crops in Succession. *Appl. Ecol. Environ. Res.* 15, 417–428. https://doi.org/10.15666/aer/1503_417428
- Tardy, F., Moreau, D., Dorel, M., Damour, G., 2015. Trait-based characterisation of cover plants' light competition strategies for weed control in banana cropping systems in the French West Indies. *European Journal of Agronomy* 71, 10–18. <https://doi.org/10.1016/j.eja.2015.08.002>

- Teasdale, J., Brandsater, L., Calegari, A., Skora Neto, F., 2007. Cover crops and weed management, in: *Non-Chemical Weed Management: Principles, Concepts and Technology*. CABI, Wallingford, pp. 49–64.
- Teasdale, J.R., Hatfield, J.L., Buhler, D.D., Stewart, B.A., 1996. Cover crops, smother plants, and weed management. *Advances in Soil Science*.
- Teasdale, J.R., Mirsky, S.B., 2015. Tillage and Planting Date Effects on Weed Dormancy, Emergence, and Early Growth in Organic Corn. *Weed Science* 63, 477–490. <https://doi.org/10.1614/WS-D-14-00112.1>
- Teshome, Z., Fantaye, A., Hagos, H., 2014. Effect of Nitrogen and Phosphorus on Yield Components, Yield and Sugarcane Juice Quality parameters of Soybean-Sugarcane Intercropping at Tendaho Sugar Factory. *Biochem Physiol* 4, 1000151. <https://doi.org/10.4172/2168-9652.1000151>
- Tilman, D., Reich, P.B., Knops, J., Wedin, D., Mielke, T., Lehman, C., 2001. Diversity and Productivity in a Long-Term Grassland Experiment. *Science* 294, 843–845. <https://doi.org/10.1126/science.1060391>
- Tixier, P., Lavigne, C., Alvarez, S., Gauquier, A., Blanchard, M., Ripoche, A., Achard, R., 2011. Model evaluation of cover crops, application to eleven species for banana cropping systems. *European Journal of Agronomy* 34, 53–61. <https://doi.org/10.1016/j.eja.2010.10.004>
- Tobin, M.F., Wright, A.J., Mangan, S.A., Schnitzer, S.A., 2012. Lianas have a greater competitive effect than trees of similar biomass on tropical canopy trees. *Ecosphere* 3, art20. <https://doi.org/10.1890/ES11-00322.1>
- Vandermeer, J.H., 1992. *The Ecology of Intercropping*. Cambridge University Press.
- Violle, C., Navas, M.-L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I., Garnier, E., 2007. Let the concept of trait be functional! *Oikos* 116, 882–892. <https://doi.org/10.1111/j.0030-1299.2007.15559.x>

Supplementary materials

Table S1. List of cover plant species used in the different trials. The family, life cycle (A=annual, P=perennial, Bi=biennial, V=vivacious), area of origin (Tr=tropical, Tm=temperate) and the growth habit (E=erected, Cr=creeping, Tw=Twining) of each species are described.

Family	Species	Cycle	Zone	Growth
Asteraceae	<i>Cichorium endivia</i> L.	Bi	Tm	E
	<i>Guizotia abyssinica</i> (L.f.) Cass.	A	Tm	E
Brassicaceae	<i>Brassica carinata</i> A.Braun	A	Tm	E
	<i>Raphanus sativus</i> L.	A	Tm	E
	<i>Sinapis alba</i> L.	A	Tm	E
Fabaceae	<i>Arachis hypogaea</i> L.	A	Tr	Cr
	<i>Cajanus cajan</i> (L.) Huth	P	Tr	E
	<i>Canavalia ensiformis</i> (L.) DC.	A	Tr	semi-Tw
	<i>Canavalia gladiata</i> (Jacq.) DC.	A	Tr	semi-Tw
	<i>Centrosema pascuorum</i> Mart. ex Benth.	A	Tr	Tw
	<i>Crotalaria juncea</i> L.	A	Tr	E
	<i>Crotalaria retusa</i> L.	A	Tr	E
	<i>Crotalaria spectabilis</i> Roth	A	Tr	E
	<i>Crotalaria trichotoma</i> Bojer	A	Tr	E
	<i>Grona heterocarpa</i> (L.) H. Ohashi & K. Ohashi	A	Tr	Cr
	<i>Lablab purpureus</i> (L.) Sweet	A	Tr	Tw
	<i>Lathyrus sativus</i> L.	A	Tm	Tw
	<i>Lens nigricans</i> (M.Bieb.) Webb & Berthel.	A	Tm	Tw
	<i>Lotus corniculatus</i> L.	A	Tm	Cr
	<i>Lupinus albus</i> L.	A	Tm	E
	<i>Macrotyloma axillare</i> (E.Mey.) Verdc.	P	Tr	Tw
	<i>Medicago sativa</i> L.	P	Tm	E
	<i>Mucuna pruriens</i> (L.) DC.	A	Tr	Tw
	<i>Neonotonia wightii</i> (Wight & Arn.) J.A.Lackey	P	Tr	Tw
	<i>Neustanthus phaseoloides</i> (Roxb.) Benth.	P	Tr	Tw
	<i>Phaseolus lunatus</i> L.	A	Tr	Tw
	<i>Pisum sativum</i> L.	A	Tm	Cr
	<i>Stylosanthes guianensis</i> (Aubl.) Sw.	P	Tr	semi-E
<i>Trifolium hybridum</i> L.	P	Tm	Cr	
<i>Trifolium incarnatum</i> L.	A	Tm	Cr	
<i>Trifolium pratense</i> L.	V	Tm	Cr	
<i>Trifolium repens</i> L.	V	Tm	Cr	
<i>Trigonella foenum-graecum</i> L.	A	Tm	E	
<i>Vicia villosa</i> Roth	A	Tm	Tw	
<i>Vigna radiata</i> (L.) R.Wilczek	A	Tr	Tw	
<i>Vigna subterranea</i> (L.) Verdc.	A	Tr	Cr	
<i>Vigna unguiculata</i> (L.) Walp.	A	Tr	semi-Tw	
Poaceae	<i>Avena sativa</i> L.	A	Tm	E
	<i>Avena strigosa</i> Schreb.	A	Tm	E
	<i>Eleusine coracana</i> (L.) Gaertn.	A	Tr	E
	<i>Pennisetum glaucum</i> (L.) R.Br.	A	Tr	E
	<i>Phalaris canariensis</i> L.	A	Tm	E
	<i>Sorghum bicolor</i> (L.) Moench	A	Tr	E
	<i>Urochloa eminii</i> (Mez) Davidse	P	Tr	semi-E
<i>Zea mays</i> L.	A	Tr	E	
Polygonaceae	<i>Fagopyrum esculentum</i> Moench	A	Tm	E

Crotalaria zanzibarica Benth. synonym of *Crotalaria trichotoma* Bojer

Desmodium heterocarpon (L.) DC. synonym of *Grona heterocarpa* (L.) H. Ohashi & K. Ohashi

Pueraria phaseoloides (Roxb.) Benth. synonym of *Neustanthus phaseoloides* (Roxb.) Benth.

Brachiaria decumbens Stapf synonym of *Urochloa eminii* (Mez) Davidse

Cenchrus americanus (L.) Morrone synonym of *Pennisetum glaucum* (L.) R.Br.

Table S2. Species composition of each trials and sowing density for pure crops. The trial ID description are detailed in Table 1.

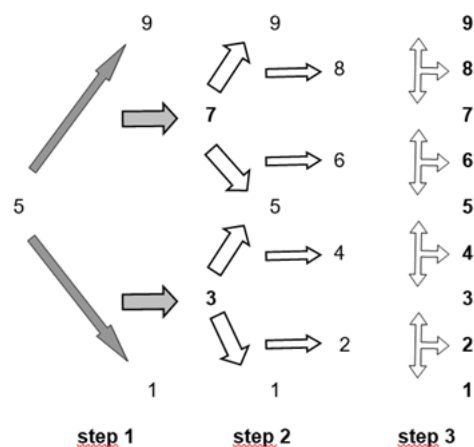
Species	Collection trial ID	Weed control trial ID	Sowing density (kg/ha)
<i>Cichorium endivia</i> L.	2,5		7
<i>Guizotia abyssinica</i> (L.f.) Cass.	1,2,3,6	9	10
<i>Brassica carinata</i> A.Braun	6		6
<i>Raphanus sativus</i> L.	1,2,3,4,5,6	10	10
<i>Sinapis alba</i> L.	3		10
<i>Arachis hypogaea</i> L.	1,2,3,		150
<i>Cajanus cajan</i> (L.) Huth	1,2,3,6		10
<i>Canavalia ensiformis</i> (L.) DC.	1,2,3,4,5,6	7,8,10	40
<i>Canavalia gladiata</i> (Jacq.) DC.	1,2,4		40
<i>Centrosema pascuorum</i> Mart. ex Benth.	1,4		15
<i>Crotalaria juncea</i> L.	1,2,3,4,5,6	7,8,9,10	40
<i>Crotalaria retusa</i> L.	1		25
<i>Crotalaria spectabilis</i> Roth	1,3,4,5,6		20
<i>Crotalaria trichotoma</i> Bojer	1,2,3,4,5		25
<i>Grona heterocarpa</i> (L.) H. Ohashi & K. Ohashi	1		20
<i>Lablab purpureus</i> (L.) Sweet	1,2,3,4,6		50
<i>Lathyrus sativus</i> L.	1,4,5		50
<i>Lens nigricans</i> (M.Bieb.) Webb & Berthel.	1		80
<i>Lotus corniculatus</i> L.	2		8
<i>Lupinus albus</i> L.	2		150
<i>Macrotyloma axillare</i> (E.Mey.) Verdc.	1,5		4
<i>Medicago sativa</i> L.	1,2,3,4,5		25
<i>Mucuna pruriens</i> (L.) DC.	1,2,3,4,5		35
<i>Neonotonia wightii</i> (Wight & Arn.) J.A.Lackey	1,2		25
<i>Neustanthus phaseoloides</i> (Roxb.) Benth.	1,2		20
<i>Phaseolus lunatus</i> L.	1,2,3,4,5		80
<i>Pisum sativum</i> L.	6		100
<i>Stylosanthes guianensis</i> (Aubl.) Sw.	1,2,4,5	7,8	8
<i>Trifolium hybridum</i> L.	3		15
<i>Trifolium incarnatum</i> L.	3		15
<i>Trifolium pratense</i> L.	3		8
<i>Trifolium repens</i> L.	3		10
<i>Trigonella foenum-graecum</i> L.	1,2,		35
<i>Vicia villosa</i> Roth	2,3,6	9	20
<i>Vigna radiata</i> (L.) R.Wilczek	1,2,3,4,5		10
<i>Vigna subterranea</i> (L.) Verdc.	1,2,3,5		90
<i>Vigna unguiculata</i> (L.) Walp.	1,2,3,4,5,6	9	15
<i>Avena sativa</i> L.	2,3,4,5,6	7,8,9	90
<i>Avena strigosa</i> Schreb.	2,3,6		40
<i>Eleusine coracana</i> (L.) Gaertn.	1	8	3
<i>Pennisetum glaucum</i> (L.) R.Br.	1,2,3,4,5,6	7,8,9,10	20
<i>Phalaris canariensis</i> L.	1		4
<i>Sorghum bicolor</i> (L.) Moench	1,2,4,5	7,8	11
<i>Urochloa eminii</i> (Mez) Davidse	1		8
<i>Zea mays</i> L.	3		15
<i>Fagopyrum esculentum</i> Moench	2,3,6		40

Table S3. Mixture of two species tested in the weed control trials. The trial ID description are detailed in Table 1. In case of mixture, sowing density was equal to half the density in pure crops.

Species mixture		Weed control trial ID
<i>Avena sativa</i>	<i>Canavalia ensiformis</i>	7
<i>Avena sativa</i>	<i>Crotalaria juncea</i>	7,9
<i>Avena sativa</i>	<i>Stylosanthes guianensis</i>	7
<i>Avena sativa</i>	<i>Vicia villosa</i>	9
<i>Avena sativa</i>	<i>Vigna unguiculata</i>	9
<i>Canavalia ensiformis</i>	<i>Pennisetum glaucum</i>	10,7
<i>Canavalia ensiformis</i>	<i>Raphanus sativus</i>	10
<i>Pennisetum glaucum</i>	<i>Crotalaria juncea</i>	7,9,10
<i>Pennisetum glaucum</i>	<i>Stylosanthes guianensis</i>	7
<i>Pennisetum glaucum</i>	<i>Vigna unguiculata</i>	9
<i>Guizotia abyssinica</i>	<i>Crotalaria juncea</i>	9
<i>Sorghum bicolor</i>	<i>Canavalia ensiformis</i>	7
<i>Sorghum bicolor</i>	<i>Crotalaria juncea</i>	7
<i>Sorghum bicolor</i>	<i>Stylosanthes guianensis</i>	7

Table S5. Visual notation methods to assess ground coverage by plants (weeds or cover plants).

Notation	Equivalence in percentage	coverage
1	1	Species present but rare
2	7	Less than one individual per m ²
3	15	At least one individual per m ²
4	30	30 % of coverage
5	50	50 % of coverage
6	70	70 % of coverage
7	85	High coverage
8	93	Very little apparent soil
9	100	Full coverage



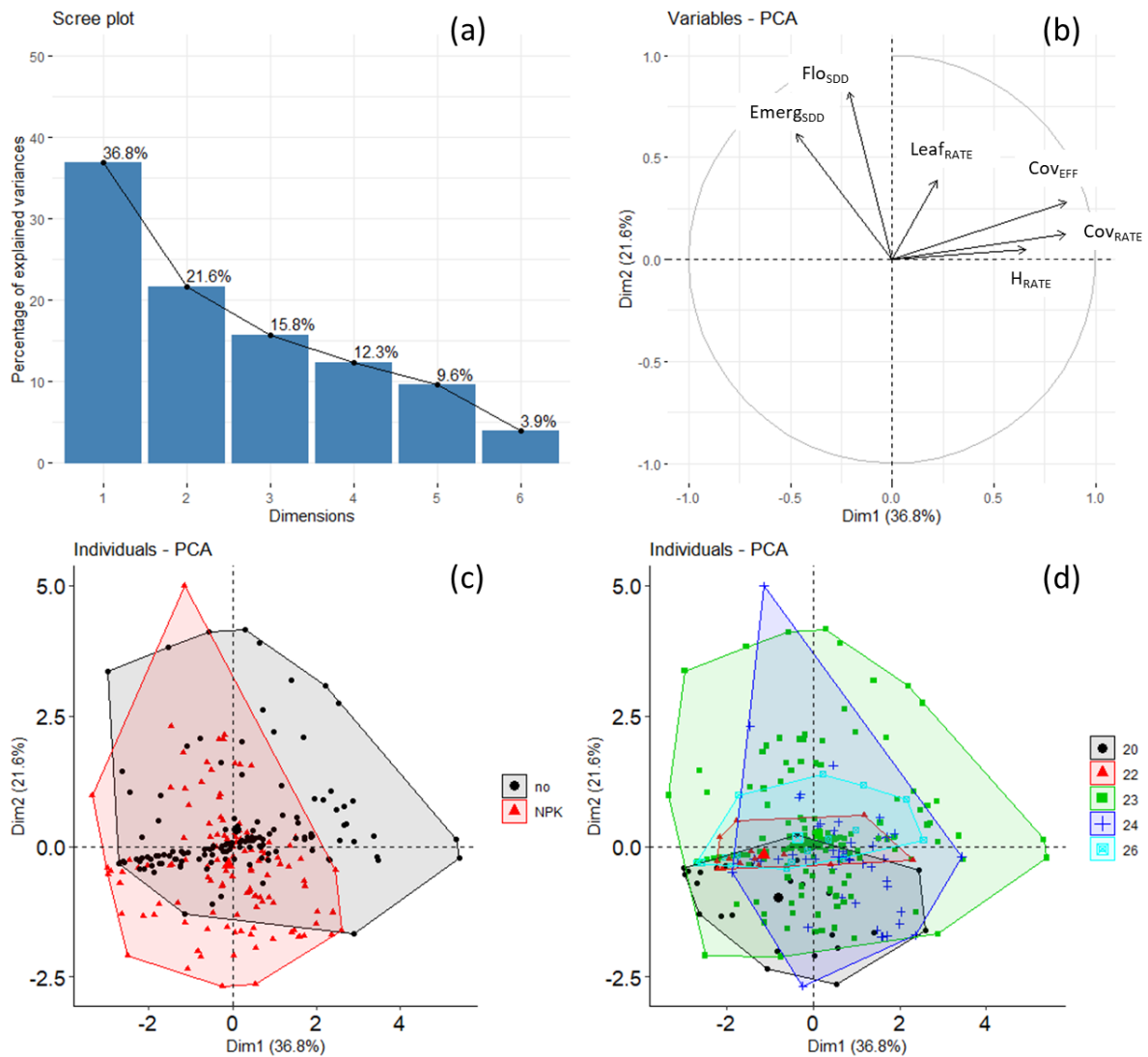


Figure S1. Principal component analysis (PCA) of the collection trials dataset. The percentage of explained variances of each dimensions are shown in (a). The correlation plot (b) shows the contribution of each variable to the two first principal components (Dim1, Dim2). Cover plant traits were clustered as a function of fertilization regime (no fertilization or NPK fertilization, c) or as a function of average temperature during the growth (d). Data point with a larger size in (c) and (d) correspond to the barycenter of each cluster. The quantitative variables considered in the PCA are described in Table 2.