

A trait-based analysis to assess the ability of cover crops to control weeds in a tropical island

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▶ To cite this version:

Mathias Christina, Adrien Négrier, Pascal Marnotte, Pauline Viaud, Alizé Mansuy, et al.. A trait-based analysis to assess the ability of cover crops to control weeds in a tropical island. 2020. hal-02612563v2

HAL Id: hal-02612563 https://hal.science/hal-02612563v2

Preprint submitted on 7 Sep 2020 (v2), last revised 27 May 2021 (v4)

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A trait-based analysis to assess the ability of cover plants to 1 control weeds in a tropical island 2 3 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}, 4 Hoarau $E^{1,2}$, Chabanne $A^{2,5}$ 5 6 ¹ CIRAD, UPR AIDA, F-97743 Saint-Denis, Réunion, France. 7 ² AIDA, Univ Montpellier, CIRAD, Montpellier, France. 8 ³ eRcane, F-97494 Sainte-Clotilde, Réunion, France 9 ⁴ CIRAD, UPR AIDA, F-97455 Saint-Pierre, Réunion, France.

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15 Highlights:

16	•	46 cover plants species performance were assessed in Reunion Island over three years
17	•	Plant height and leaf appearance rate were traits optimizing ground coverage
18	•	Weed control was similar between pure and mixture of cover plants
19	•	Weed control was more efficient with species or mixture with high coverage, biomass
20		and growth rate in height.
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32 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; weeds; Reunion; sugarcane

61 **1. Introduction**

Weeds are a main biotic constraint to tropical agriculture (FAO, 2017). Weeds can induce a 62 loss of yields in terms of quality and quantity, as well as increasing the crop production costs 63 (Oerke, 2006; FAO, 2017). Not only, weeds are in competition with main crop for several 64 65 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 66 and Sahelian climates), weeds grow fast all year thanks to a favorable climate, which may 67 strongly compete with main crop. Therefore, large amounts of chemical inputs, among which 68 69 herbicides represent a large proportion of the active ingredients, are used (Oerke and Dehne, 70 2004).

71 In tropical agrosystems, the use of cover or companion plants to control weeds can be one of 72 the solutions to help reduce herbicide inputs (e.g. Bhaskar et al., 2018; Mennan et al., 2000; Ranaivoson et al., 2018) before planting (Lu et al., 2000) or during crop growth as intercrop 73 74 (Vandermeer, 1992). These plants are being increasingly used in innovative cropping systems 75 to favour biological regulation and to deliver agro-ecosystem services such as weed, pest or 76 erosion control (Altieri et al., 2011; Koohafkan et al., 2012; Snapp et al., 2005). Due to the large 77 game of cover plant available, the choice of a plant to deliver these services is crucial because 78 the spatial and temporal combinations with the main crop will determine the performances of 79 the system (Malezieux et al., 2009).

The biological regulation mechanisms of weeds using cover plants are complex. They can be 80 direct through competition for resources, allelopathy or a physical barrier to germination and 81 emergence (Médiène et al., 2011; Teasdale et al., 2007), and indirect e.g. through seed predators 82 or fungi responsible for damping-off (Cordeau and Moreau, 2017). In intensive tropical 83 agrosystem, the hypothesis of competition especially for light is mainly put forward in 84 biological regulation. The other resources are seldom limiting for plant growth (high 85 fertilization rates, high rainfall or irrigation). The ability of a plant species to compete for light 86 87 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 88 89 of light interception, light conversion, and carbon use may be challenging when studying a large 90 range of cover plants.

91 Trait-based approaches, which originated in the field of comparative functional ecology, have92 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-physiophenological 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 (Damour et al., 2016, 2014;
Garnier and Navas, 2012; Tardy et al., 2015; Tixier et al., 2011).

In Reunion, weeds pressure is a main constraint for agriculture. Initiated in 2008 and 2018, the 100 Ecophyto I and II programs aim to reduce the use of herbicides by 50% by 2025 in the French 101 agricultural sector. In the island, sugarcane, the first agro-industrial sector, plays an important 102 economic, societal and environmental role covering more than 50% of agricultural land 103 104 (Agreste, 2016). One of the main constraints of this crop is weeds: it's the first crop production 105 in Reunion consuming herbicides (Antoir et al., 2016). Indeed, diseases and pests are mainly 106 managed by varietal selection, except the larva of Hoplochelus marginalis, controlled by the 107 fungi Beauveria brongniartii in biological control (Mouret et al., 2017). In this context, cover plants have a strong potential for the sugarcane sector. 108

109 The aim of this study was to investigate the trait-based characterization of a large range of cover 110 plants in order to assess their ability to control weeds in tropical agrosystems, using the case 111 study of Reunion. The objectives of this study were to identify among a wide variety of cover 112 plant species, i) the species most suitable for tropical climatic conditions in terms of soil cover, 113 ii) the species traits able to maximize soil cover and iii) to assess the ability of cover plants and 114 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.

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2. Materials and methods

125 **2.1. Trials description**

126 The trials described in this study were located in three experimental stations in Reunion from 127 2016 to 2018 between February and June (warm season and beginning of the cool season). The 128 trials localization and description are detailed in Table 1. Two main types of trials were 129 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 130 climates. A manual weed control was performed after sowing and during the trial duration. Four 131 collection trials were performed in La Mare (50 m asl), one in Bassin Plat (160 m asl) and one 132 in Colimaçons (800 m asl). Each trial included pure cover plant plots of 12 or 16 m². Growth 133 134 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 135 plants and weeds. Four trials were performed in La Mare and Bassin Plat with plots from 20 to 136 100 m². Grow duration of cover plants was 2 months. In all weed control trials, each plot was 137 associated with an adjacent control plot of natural weed flora. Dominant weed flora presented 138 in these sites are described in Table S4. In all sites, daily average temperature (T_{MEAN}) were 139 measured. Five of the trials were fertilized while the other five were not fertilized. The fertilizer 140 applications are described in Table 1. All trials were irrigated (except for Colimaçons which 141 present precipitation > 120 mm month⁻¹ during the growth period). Before sowing, a tillage has 142 been carried out and herbicide was applied prior sowing. Seeds were sown manually following 143 144 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 145 146 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	TMEAN	Number of species (+ mixture)	Plot area (x repetition)	Sowing date (dd/mm)	Duration	Fertilization (kg ha ⁻¹)	Manual weed control	Trial ID
					Leptic	2016	23.0	33		30/03	3.5 months	NPK (36-82- 60)		1
	La Mare	-20.9	55.53	50 m	cambisol	2017	23.2	28	16 m² (x1)	13/04	4 months	20		2
						2018	22.7	26		27/04	4 months	no		3
Collection	Bassin Plat	-21.32	55.49	160 m	Cambisol andique	2016	24.0	19	16 m² (x1)	04/03	2.5 months	NPK (36-77-	yes	4
Coll	Colimaçon	-21.13	55.3	800 m	Brun andique	2016	20.5	18	16 m² (x1)	16/03	2.5 months	48)	~ ·	5
					T		25.7			20/02	_			
	La Mare	-20.9	55.53	50 m	Leptic cambisol	2018	22.0	16	12 m² (x1)	12/04	3 months	no		6
					• uniteriser		23.6			13/06				
lc	ure				T	2016	24.1	6 (+9)	36 m² (x1)	04/04	_	NPK (30-80-		7
ontro	l Mare	-20.9	55.53	50 m	Leptic cambisol	2016	24.4	8	100 m² (x1)	31/03		60)		8
sd cc	La				cumonsor	2017	24.2	6 (+6)	20 m² (x4)	13/04	2 months		no	9
Weed control	Bassin Plat	-21.32	55.49	160 m	Cambisol andique	2017	25.3	4 (+3)	24 m² (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

159 ranged from 0 to 1.

	Index	Units	Description	Trial ID
raits	COVEFF	0-1	Coverage efficiency over the growth period	All trial
	COVRATE	% d ⁻¹	Growth rate in coverage per day between sowing and maximum coverage	All trial
	HRATE	cm d ⁻¹	Growth rate in height per day since emergence	1,2,4,5,6,9,10
Plant traits	Leaf _{RATE}	leaf d ⁻¹	Leaf appearance rate per day	1,2,4,5,6,9,10
с.	Emerg _{SDD}	°d	Thermal time for emergence since planting	1,2,4,5
	Flosdd	°d	Thermal time for flowering since planting	1,2,4,5
	ABVDM	kgDM m ⁻²	Aboveground dry mass at the end of the trial	9,10
ed trol	WCEcov	0-1	Weed control efficiency index based on weed coverage	7,8,910
Weed control	WCEDM	0-1	Weed control efficiency index based on weed dry mass	9,10

166 **2.3. Measurements**

Cover crop traits and phenology were measured in the different trials (Table 2). Ground 167 168 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; 169 170 Marnotte et al., 1984). This method allows to assess the soil coverage of individual species in 171 multi-species crop (e.g. cover plant and weeds). Between two dates of measurements, coverage 172 (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 173 plant coverage: 174

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$$Cov_{EFF} = \frac{\sum_{i=1}^{n} Cov(i)}{n * 100\%}$$

176 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 177 coverage per day (Cov_{RATE}, % d⁻¹) was calculated between sowing up to reaching the maximum 178 coverage. Additionally, for each species, the height and number of leaves of 5 individuals per 179 180 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 181 emergence to flowering as the slope between plant height or leaf number and the number of day 182 183 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 184 sowing to the state were 50% of plant emerged or flowered. Finally, to measure aboveground 185 dry masses (ABV_{DM}) in weed control trials, all weeds and cover plants in three 50x50cm square 186 in each plot were sampled and dried at 60°C over 2 days at the end of the experiment. 187

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:

$$WCE_{COV} = 1 - \frac{Cov_{Weed,cp}}{< Cov_{Weed,pure} >}$$

With Cov_{weed,cp} the weed coverage efficiency index in plot with cover plants and <Cov_{weed,pure}>
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:

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$$WCE_{DM} = 1 - \frac{DM_{Weed,cp}}{< DM_{Weed,pure} >}$$

198 With $DM_{Weed,cp}$ the aerial weed dry mass in plot with cover plants and $\langle DM_{Weed,pure} \rangle$ the 199 average aerial weed dry mass in control plots among each trials. In case of mixture (Table S3), 200 an average trait among cover plants was calculated as the mean of trait value per species 201 weighted by the final coverage of each species. All experimental data are available online on 202 CIRAD dataverse (http://dx.doi.org/10.18167/DVN1/HA0V2G).

203 **2.4. Data analyses**

First a principal component analysis (PCA) was performed on all plant traits in the collection 204 trials to assess if plant behavior was different depending on temperature and fertilization 205 regimes (R package FactoMineR and missMDA). As no effect of fertilization regime and 206 temperature were identified (Fig. S1), we considered all trials as a pool in the following 207 analyses. Secondly, a hierarchical clustering analysis was performed on the average Cov_{EFF} and 208 209 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 210 211 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 212 213 correlation (p_{SPEAR}, R package Hmisc and corrplot). For visual purpose, polynomial smooth 214 regressions were added in the figures using the loess R function. All data analyses were 215 performed with R 3.4 (R Development Core Team, 2017).

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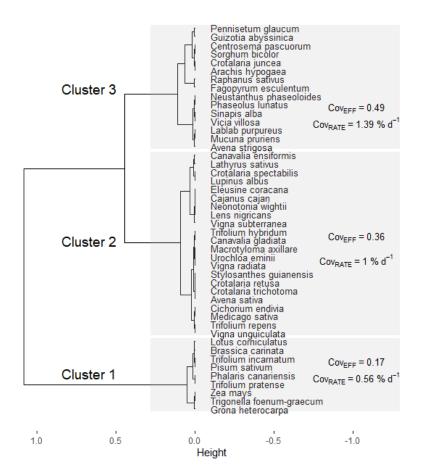
217 **3. Results:**

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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). 228 229 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, 230 231 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 232 233 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 234 higher Cov_{RATE} than creeping plants by 30% (Fig. 2h). 235



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Fig. 1. Hierarchical clustering analysis on plant coverage efficiency (Cov_{EFF} , %) and coverage rate

238 (Cov_{RATE}, % d⁻¹) per cover plant species used in the 6 collection trials described in Table 1. Three clusters

239 were defined and the average Cov_{EFF} and Cov_{RATE} per cluster is indicated.

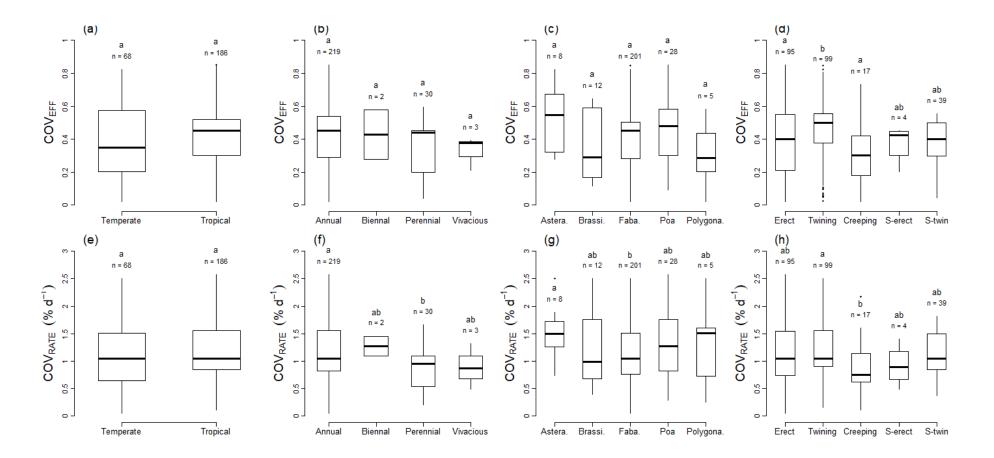


Fig. 2. Coverage efficiency (COV_{EFF}) and coverage rate (COV_{RATE}) of cover plant species used in the collection trials depending on area of origin (a,e), life cycle (b,f), species family (c,g) and growth habit (d,h). Plant families were abbreviated for Asteraceae (Astera.), Brassicaceae (Brassica.), 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

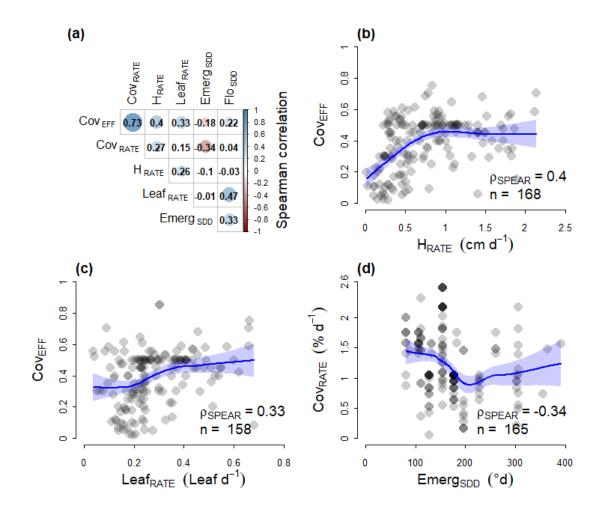
At the cluster level, the two clusters with the highest coverage efficiency and coverage rate (clusters 2 and 3) also showed the highest growth rate in height with 0.78 cm d⁻¹ in average (Table 3). Leaf_{RATE} was higher by 18% in the cluster 3 than in the cluster 2. Considering thermal time for emergence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

At the species levels (Fig. 3), correlations were found between the two indices of coverage 245 performance Cov_{EFF} and Cov_{RATE} (p_{SPEAR}=0.73; p<0.001). Additional correlations were found 246 247 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. 248 3b,c). On the other hand, Cov_{RATE} was positively correlated with H_{RATE} and negatively with 249 Emerg_{SDD} (Fig. 3d). In particular, Cov_{EFF} reached its maximum values for H_{RATE} higher than 250 0.8 cm d⁻¹ (Fig 3b). Cov_{EFF} slightly increased with Leaf_{RATE} and reached maximum values for 251 Leaf_{RATE} higher than 0.4 leaf d⁻¹ (Fig 3c). Highest Cov_{RATE} were also found for Emerg_{SDD} lower 252 than 150 °d (Fig. 3d). Moreover, additional significant correlations between plant traits were 253 254 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 ($\rho_{SPEAR} = 0.26$) 255

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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 ermegence ($Emerg_{SDD}$) 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	Cov _{eff}	Cov _{RATE}	H _{RATE}	Leaf _{RATE}	Flo _{sdd}	Emerg _{sdd}
cluster	(0-1)	(% d ⁻¹)	(cm d ⁻¹)	(leaf d ⁻¹)	(°d)	(°d)
Cluster 1	0.18 ±0.13	0.56 ±0.33	0.29 ±0.21	0.37 ±0.27	1163 ±14	191 ±79
	a (n=14)	a (n=14)	a (n=7)	ab (n=7)	a (n=2)	a (n=4)
Cluster 2	0.36 ±0.17	1.00 ±0.45	0.73 ±0.43	0.33 ±0.34	1497 ±433	176 ±68
	b (n=125)	b (n=125)	b (n=86)	a (n=85)	a (n=71)	a (n=86)
Cluster 3	0.49 ±0.19	1.39 ±0.57	1.02 ±0.93	0.39 ±0.33	1353 ±393	162 ±57
	c (n=115)	c (n=115)	b (n=80)	b (n=80)	a (n=63)	a (n=75)



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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).

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3.3. Weed control and pure vs mixture cover plants

Weed control was assessed through the calculation of two weed control efficiency indices based 277 on weed coverage (WCE_{COV}) and dry mass (WCE_{DM}). In average, cover plants in pure and 278 mixture stands both successfully controlled weeds. Plots with cover plants showed lower weed 279 coverage and weed dry mass by 69% and 74%, respectively (Fig 4b,c). Nevertheless, the 280 variability of weed control was much lower in mixture (sd = 17.7 % and 0.5 t ha⁻¹) than in pure 281 stand (sd = 29.4% and 1.2 t ha⁻¹ for coverage and dry mass, respectively). Only species of cluster 282 2 and 3 were tested in the weed control trials and both clusters showed a similar WCE_{COV} (0.5)283 over the experiment, even in mixture (Fig. 4d). However, average WCE_{DM} was higher by 119% 284 in plots with cluster 3 species that in plots and with cluster 2 (Fig 4e). The mixture of cluster 2 285 and cluster 3 species showed an intermediate WCE_{DM}. The clustering analysis on average 286 WCE_{COV} and WCE_{DM} (Fig. 4a) showed that the plant with highest weed control were mixture, 287 Avena sativa, Guizotia abyssinica and Pennisetum glaucum. On the contrary, Stylosanthes 288 guianensis, Raphanus sativus and Crotalaria juncea failed to control weed. Other species (Fig. 289 4a) presented intermediate weed control efficiency. 290

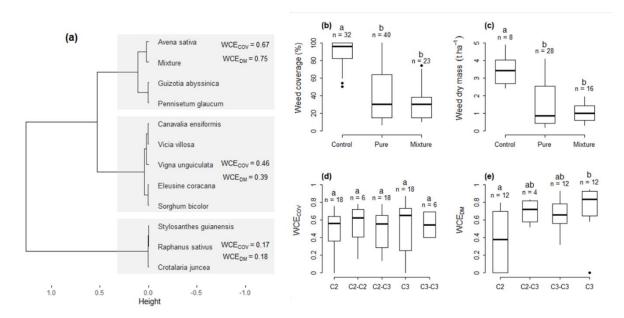


Fig. 4. Hierarchical clustering analysis on weed control efficiency in terms of weed coverage (WCE_{cov}) and dry mass (WCE_{DM}) per cover plant species or mixture used in the weed control trials (a). Change in WCE_{cov} and WCE_{DM} are presented depending on type of plot (control, pure or mixture 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 semitwining) 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).

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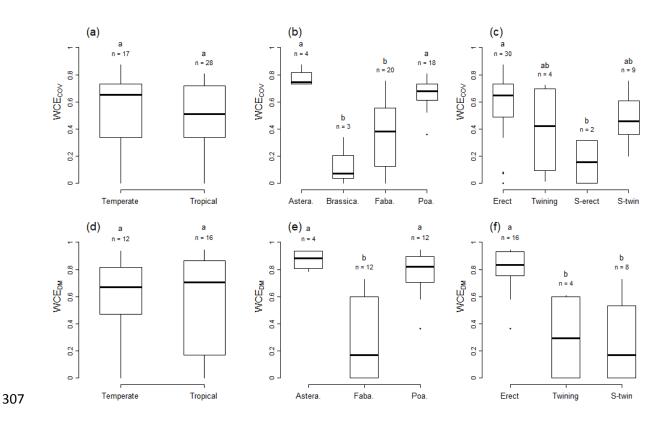


Fig. 5. Weed control efficiency based on weed coverage (WCE_{COV}) or dry mass (WCE_{DM}) depending on area of orgin (a,d), species family (b,e) and growth habit (c,f). Only pure crop plots from the weed control trials are represented. Species family were abbreviated for Asteraceae (Astera.), Brassicaceae (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 % d⁻¹, H_{RATE} > 1.8 cm d⁻¹ and ABV_{DM} > 2 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.

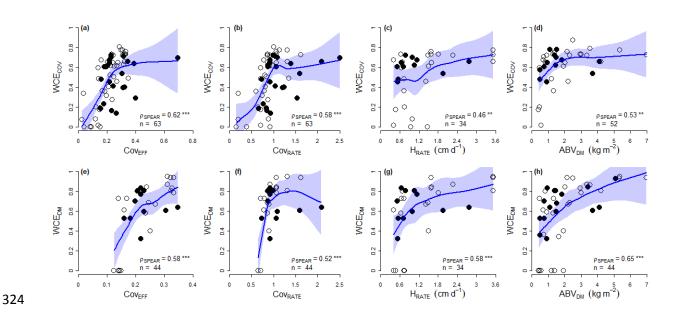


Fig. 6. Change in weed control efficiency based on weed coverage (WCE_{COV}) and dry mass (WCE_{DM}) depending on cover plant traits: coverage efficiency (Cov_{EFF}, a, e), growth rate in coverage (Cov_{RATE}, b, c), growth rate in height (H_{RATE}, e,g) and aerial dry mass (ABV_{DM}, d,h). The number 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.

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4. Discussions

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4.1. Cover plant performance and weed control

The increasing interest of producers and researchers in cover plants might have been 338 encouraged by the many positive aspects which are attributed to cover cropping. In particular, 339 cover plants provide direct weed control during their establishment by competing with weeds 340 341 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 342 residues retained on the soil surface can directly limit germination and growth of weeds in the 343 344 following cash crop (Mirsky et al. 2011; Ryan et al. 2011; Teasdale and Mirsky 2015). Most 345 importantly, they can help prevent the buildup of weed plant populations and therefore reduce 346 future weed pressure.

In intensive tropical agrosystem, the hypothesis of competition especially for light is mainly 347 348 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 349 on the coverage growth rate (Cov_{RATE}) to identify species with early canopy closure and the 350 351 coverage efficiency over time (Cov_{EFF}) to optimize ground cover over many months. Our results highlight how weed control by cover plant was improved with species with high coverage rate 352 at the beginning of the growth and high coverage efficiency over time. Such observations 353 confirm previous conclusion that species with early canopy closure generally show better weed 354 355 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 356 resources. High biomass production can increase the effect of competition (den Hollander et 357 358 al., 2007; Tobin et al., 2012) and many studies highlighted this relation between cover plants 359 biomass and weed control (e.g. Bhaskar et al., 2018; Florence et al., 2019; Osipitan et al., 2019; Schappert et al, 2019). Nevertheless, cover plant biomass is not always a good predictor of 360 361 weed control (Baraibar et al., 2018; Kunz et al., 2016) which make some authors like Dorn et 362 al. (2015) suggesting that rapid plant development after sowing is more important than the final 363 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; Finnay et al., 2016; Schappert et al., 2019; 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.

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381 **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 (Damour et al., 2016, 2014; Garnier and Navas, 2012; Tardy et al., 2015; Tixier et al., 2011).

389 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 390 "shading" competition strategy, with no physical action on neighbours. Their ability to develop 391 support structures in height allows them to be in the top layers of the canopy, and therefore to 392 increase access to light and to shade neighbouring plants. On the contrary, plants which invest 393 in leaf production with rapid growth can be either creeping or twining species. They have an 394 "obstruction" competition strategy conferred by their ability to cover the soil and to avoid the 395 germination and the emergence of weeds. When they are twining species, they also can smother 396 weeds but also the main crop (Teasdale 1996). 397

While all species with high coverage and biomass succeeded in controlling weeds, our results 398 highlight how the 'shading' strategy appeared more efficient than the 'obstruction' strategy in 399 our tropical conditions. The positive correlation between height and plant coverage was also 400 401 observed in previous studies in tropical conditions (Tardy et al., 2015). In temperate conditions, 402 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 403 et al., 2012). Previous studies highlighted how Poaceae were often more efficient to control 404 weeds than Fabaceae legume species (Baraibar et al., 2018; Brainard et al., 2011; Ofori and 405 406 Stern, 1987), similarly to our results. Nevertheless, soil cover by Poaceae and Fabaceae species 407 were similar in our study, suggesting additional mechanisms involved in weed control. The low 408 weed control by Poacea could be explained a low competitiveness for soil resources. Legumes 409 are known to have less developed roots than grasses. Previous studies have shown that the speed 410 of progression of deep roots as well as root density are lower in legumes than in cereals (Corre-Hellou et al., 2007; Greenwood et al., 1982; Thorup-Kristensen, 2001). 411

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4.3. Trait-based selection in Reunion

While the use of species with shading competition strategies could be very efficient to control 414 weeds in crop rotations (Liebman and Dyck, 1993), their ability to be in the top layer in the 415 416 canopy could have detrimental effects on main crop yield in crop mixtures. In that second case, 417 it is necessary to find a trade-off between the ability of the cover plant to compete with weeds 418 for light and their impact on main crop.

In Reunion, sugarcane plantations represent more than 50% of agricultural land (Agreste, 2016) 419 420 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 421 422 (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 423 424 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 425 weed control in this study. 426

Moreover, to reduce quantitatively the use of herbicide, sugarcane intercropping with cover 427 428 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 429 after harvest, which make it sensitive to competition with weeds (Marion and Marnotte, 1992). 430 To avoid competition, the choice should more focus on particular creeping or twining species 431 which still showed high competition with weeds. In our study, Vigna unguiculata and 432 Canavalia ensiformis have shown relatively high coverage and efficient weed control, despite 433 having low growth rate in height. Such Fabaceae species have also the advantage to fix nitrogen 434 from the atmosphere to deliver it to the main crop when it decomposes. Moreover, despite being 435 semi-twining species, lianas were not observed in our climatic conditions for these two species. 436

The use of cover plants in rotation or intercropping with sugarcane is an increasing practices 437 worldwide (Soares et al., 2017 in Brazil; Ali et al., 2018 and Teshome et al., 2015 in Africa; 438 Paungfoo-Lonhienne et al., 2017 in Australia; Hemwong et al., 2009 in Asia). As cover plant 439 performance will strongly vary with climatic conditions, the species selection performed in this 440 study will only be valid in similar climatic areas. Nevertheless, the selection of traits that 441 improve weed control should not depend on local climatic variability, highlighting the high 442 potential of trait-based approaches to identify the most suitable plants and traits to control 443 weeds. 444

445

446 **5.** Conclusion

447 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. 448 449 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 450 451 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 452 453 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 454 identify adapted to crop rotation or intercropping in the case of sugarcane plantations in 455 Reunion, as an alternative to herbicides. While trait-based selection of cover plants appeared 456 promising, weed traits will also influence plant-weed interactions. Consequently, future 457 458 researches should focus on weed traits and their link with the harmfulness of natural flora.

460 Acknowledgements

- 461 We thank the Conseil Régional de La Réunion, the French ministry of agriculture and food, the
- 462 European Union (Feader program, grant n°AG/974/DAAF/2016-00096 and Feder program,
- 463 grant n°GURTDI 20151501-0000735) and the Cirad for funding, within the framework of the
- 464 project "Services et impacts des activités agricoles en milieu tropical" (Siaam). We are grateful
- to J. Fournier, T. Lizekne, R Bernard, J Courtois, MV Latchoumy, Y Marin, JM Gueno, G.
- 466 Gauvin and JC Ribotte for their involvement in field measurements.

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642 Supplementary materials

Table S1. List of cover plant species used in the different trials. The family, life cycle (A=annual,
P=perennial, Bi=biennal, 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
Actorococo	Cichorium endivia L.	Bi	Tm	E
Asteraceae	Guizotia abyssinica (L.f.) Cass.	А	Tm	E
	Brassica carinata A.Braun	А	Tm	E
Brassicaceae	Raphanus sativus L.	А	Tm	E
	Sinapis alba L.	А	Tm	E
	Arachis hypogaea L.	А	Tr	Cr
	Cajanus cajan (L.) Huth	Р	Tr	E
	Canavalia ensiformis (L.) DC.	А	Tr	semi-Tw
	Canavalia gladiata (Jacq.) DC.	А	Tr	semi-Tw
	Centrosema pascuorum Mart. ex Benth.	А	Tr	Tw
	Crotalaria juncea L.	А	Tr	E
	Crotalaria retusa L.	А	Tr	E
	Crotalaria spectabilis Roth	А	Tr	E
	Crotalaria trichotoma Bojer	А	Tr	E
	Grona heterocarpa (L.) H.Ohashi & K.Ohashi	A	Tr	Cr
	Lablab purpureus (L.) Sweet	А	Tr	Tw
	Lathyrus sativus L.	А	Tm	Tw
	Lens nigricans (M.Bieb.) Webb & Berthel.	А	Tm	Tw
	Lotus corniculatus L.	А	Tm	Cr
	Lupinus albus L.	А	Tm	E
	, Macrotyloma axillare (E.Mey.) Verdc.	Р	Tr	Tw
Fabaceae	Medicago sativa L.	Р	Tm	E
	Mucuna pruriens (L.) DC.	А	Tr	Tw
	Neonotonia wightii (Wight & Arn.) J.A.Lackey	Р	Tr	Tw
	Neustanthus phaseoloides (Roxb.) Benth.	Р	Tr	Tw
	Phaseolus lunatus L.	А	Tr	Tw
	Pisum sativum L.	А	Tm	Cr
	Stylosanthes guianensis (Aubl.) Sw.	Р	Tr	semi-E
	Trifolium hybridum L.	Р	Tm	Cr
	Trifolium incarnatum L.	А	Tm	Cr
	Trifolium pratense L.	V	Tm	Cr
	Trifolium repens L.	V	Tm	Cr
	Trigonella foenum-graecum L.	А	Tm	E
	Vicia villosa Roth	А	Tm	Tw
	Vigna radiata (L.) R.Wilczek	А	Tr	Tw
	Vigna subterranea (L.) Verdc.	А	Tr	Cr
	Vigna unguiculata (L.) Walp.	А	Tr	semi-Tw
	Avena sativa L.	А	Tm	E
	Avena strigosa Schreb.	A	Tm	E
	Eleusine coracana (L.) Gaertn.	A	Tr	E
	Pennisetum glaucum (L.) R.Br.	A	Tr	E
Poaceae	Phalaris canariensis L.	A	Tm	E
	Sorghum bicolor (L.) Moench	A	Tr	E
	Urochloa eminii (Mez) Davidse	P	Tr	semi-E
	Zea mays L.	A	Tr	E
Polygonaceae	Fagopyrum esculentum Moench	A	Tm	E

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647 Crotalaria zanzibarica Benth. synonym of Crotalaria trichotoma Bojer

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

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

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

651 *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. 653

	Collection trial	Weed control trial	Sowing density
Species	ID	ID	(kg/ha)
Cichorium endivia L.	2,5		7
Guizotia abyssinica (L.f.) Cass.	1,2,3,6	9	10
Brassica carinata A.Braun	6		6
Raphanus sativus L.	1,2,3,4,5,6	10	10
Sinapis alba L.	3		10
Arachis hypogaea L.	1,2,3,		150
Cajanus cajan (L.) Huth	1,2,3,6		10
Canavalia ensiformis (L.) DC.	1,2,3,4,5,6	7,8,10	40
Canavalia gladiata (Jacq.) DC.	1,2,4		40
Centrosema pascuorum Mart. ex Benth.	1,4		15
Crotalaria juncea L.	1,2,3,4,5,6	7,8,9,10	40
Crotalaria retusa L.	1		25
Crotalaria spectabilis Roth	1,3,4,5,6		20
Crotalaria trichotoma Bojer	1,2,3,4,5		25
Grona heterocarpa (L.) H.Ohashi & K.Ohashi	1		20
Lablab purpureus (L.) Sweet	1,2,3,4,6		50
Lathyrus sativus L.	1,4,5		50
Lens nigricans (M.Bieb.) Webb & Berthel.	1		80
Lotus corniculatus L.	2		8
Lupinus albus L.	2		150
Macrotyloma axillare (E.Mey.) Verdc.	1,5		4
Medicago sativa L.	1,2,3,4,5		25
Mucuna pruriens (L.) DC.	1,2,3,4,5		35
Neonotonia wightii (Wight & Arn.) J.A.Lackey	1,2		25
Neustanthus phaseoloides (Roxb.) Benth.	1,2		20
Phaseolus lunatus L.	1,2,3,4,5		80
Pisum sativum L.	6		100
Stylosanthes guianensis (Aubl.) Sw.	1,2,4,5	7,8	8
Trifolium hybridum L.	3	7,0	15
Trifolium incarnatum L.	3		15
Trifolium pratense L.	3		8
Trifolium repens L.	3		10
Trigonella foenum-graecum L.	1,2,		35
Vicia villosa Roth	2,3,6	9	20
Vigna radiata (L.) R.Wilczek	1,2,3,4,5	5	10
Vigna subterranea (L.) Verdc.	1,2,3,5		90
Vigna unguiculata (L.) Walp.	1,2,3,4,5,6	9	15
		7,8,9	90
Avena sativa L. Avena strigosa Schreb.	2,3,4,5,6	7,0,9	40
Eleusine coracana (L.) Gaertn.	2,3,6 1	8	3
Pennisetum glaucum (L.) R.Br.	1 1,2,3,4,5,6	8 7,8,9,10	3 20
Phalaris canariensis L.	1,2,3,4,5,0	1,0,3,10	4
Sorghum bicolor (L.) Moench	-	70	
Urochloa eminii (Mez) Davidse	1,2,4,5	7,8	11 8
	1 3		8 15
Zea mays L.			
Fagopyrum esculentum Moench	2,3,6		40

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

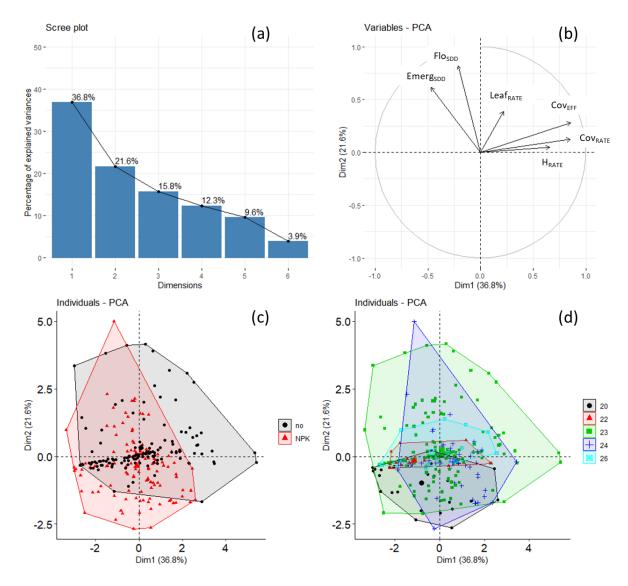
Species I	mixture	Weed control trial ID		
Avena sativa	Canavalia ensiformis	7		
Avena sativa	Crotalaria juncea	7,9		
Avena sativa	Stylosanthes guianensis	7		
Avena sativa	Vicia villosa	9		
Avena sativa	Vigna unguiculata	9		
Canavalia ensiformis	Pennisetum glaucum	10,7		
Canavalia ensiformis	Raphanus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

Famille	Espèces	Bassin Plat	La Mare
Aizoaceae	Trianthema portulacastrum L.	x	
Amaranthaceae	Amaranthus sp	х	Х
Asteraceae	Acanthospermum hispidum DC.	х	
Asteraceae	Bidens pilosa L.	х	х
Cleomaceae	Cleome viscosa L.		Х
Commelinaceae	Commelina benghalensis L.	х	
Convolvulaceae	Ipomoea eriocarpa R.Br.	х	х
Convolvulaceae	Ipomoea hederifolia L.		х
Convolvulaceae	Ipomoea obscura (L.) Ker-Gawler	х	Х
Convolvulaceae	Ipomoea triloba L.		Х
Convolvulaceae	Merremia aegyptia (L.) Urb.		х
Cyperaceae	Cyperus rotundus L.	х	х
Euphorbiaceae	Euphorbia heterophylla L.	х	х
Euphorbiaceae	Euphorbia hirta L.	х	х
Euphorbiaceae	Euphorbia hyssopifolia L.	х	х
Euphorbiaceae	Phyllanthus amarus Schumach. & Thonn.	х	
Fabaceae	Desmanthus virgatus (L.) Willd.	х	х
Fabaceae	Mimosa pudica L.		х
Fabaceae	Senna occidentalis (L.) Roxb.		х
Lamiaceae	Leucas lavandulifolia Sm.	х	
Malvaceae	Malvastrum coromandelianum (L.) Garcke	х	
Papaveraceae	Argemone mexicana L.	х	
Plantaginaceae	Plantago lanceolata L.	х	
Poaceae	Brachiaria decumbens Stapf		х
Poaceae	Dactyloctenium aegyptium (L.) P.Beauv.	х	
Poaceae	Eleusine indica (L.) Gaertn.	х	
Poaceae	Panicum maximum Jacq.	х	
Portulacaceae	Portulaca oleracea L.	х	х
Sapindaceae	Cardiospermum microcarpum Kunth	х	Х
Solanaceae	Nicandra physalodes (L.) Gaertn.	х	
Solanaceae	Solanum americanum Mill.		Х

Table S4. Weed flora in the sites with weed control trials (measured in 2017).

Notation	Equivalence in percentage	coverage	9	9	~
1	1	Species present but rare		∑∕ ⇒ °	ĵþ>
2	7	Less than one individual per m ²		7	\sim
3	15	At least one individual per m^2		$\sum \Longrightarrow 6$	jĘ>
4	30	30 % of coverage	5	5	$\hat{\Delta}$
5	50	50 % of coverage		$// \implies 4$	ļ->
6	70	70 % of coverage		3 1	Ŷ
7	85	High coverage		$\downarrow \downarrow \implies 2$	Ę>
8	93	Very little apparent soil	1	1	
9	100	Full coverage	step 1	step 2	step 3

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



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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.

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