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

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## Highlights

- Performances of 46 cover crop species assessed in Reunion Island over three years.
- Plant height and leaf appearance rate were traits maximizing ground cover.
- Weed control provided by pure and mixed cover crops was similar.
- Weed control was more efficient with species with high biomass and height.

## Abstract

Cover crops 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 experiments in different pedo-climatic environments. Our study was based on a set of 10 trials including 46 species of cover crops performed from 2016 to 2018 in three sites in Reunion Island. Our aim was to identify and measure plant traits of cover crops that maximize ground cover and weed control under a tropical climate. We characterized two traits of interest (mean ground cover and rate of increase in ground cover) and compared the family, area of origin and life cycle of the cover crops. The ability of cover crops to cover the soil increased with rate of increase in height and leaf appearance rate and tended to decrease with thermal time for emergence. Accordingly, weed control efficiency (low weed cover and dry mass) was positively correlated with ground cover, height and biomass. Using functional traits to characterize plant species enabled us to identify cover crops that could be used in tropical agrosystems as an alternative to herbicides, for instance, on sugarcane in Reunion Island.

**Keywords:** functional traits; cover plants; companion plants; weeds; Reunion Island; sugarcane

## 1. Introduction

Weeds are a major biotic constraint to tropical agriculture (FAO, 2017) as they can reduce both the quality and quantity of the crop yield, as well as increase the crop production costs (Oerke, 2006; FAO, 2017). Weeds not only compete with the main crop for light, water and nutrient resources (Cordeau and Moreau, 2017), but are alternative hosts for crop pests and pathogens (FAO, 2017). Weeds grow fast all year round thanks to the favorable climate in most tropical areas. As a result, large quantities of chemical inputs are used with herbicides representing a large proportion of the active ingredients (Oerke and Dehne, 2004).

Use of cover crops to control weeds before planting (Lu et al., 2000) or as a companion crop during crop growth (Vandermeer, 1992) are ways to reduce herbicide inputs in tropical agrosystems (e.g. Bhaskar et al., 2018; Mennan et al., 2000; Ranaivoson et al., 2018). Cover crops are thus increasingly used in innovative cropping systems to favor biological regulation and to deliver agro-ecosystem services such as improving soil fertility and controlling pests, weeds and erosion (Altieri et al., 2011; Kocira et al., 2020; Koohafkan et al., 2012; Snapp et al., 2005). A wide range of cover crops are available, so the choice of species 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 mechanisms underlying biological weed control using cover crops are complex. They can be direct through competition for resources, allelopathy or by providing a physical barrier to germination and emergence (Médiène et al., 2011; Teasdale et al., 2007), or indirect by enhancing seed predators or fungi that cause damping off (Cordeau and Moreau, 2017). In intensive tropical agrosystems, the process of competition especially for light is mainly put forward to explain weed control by cover crops. The other resources (high fertilization rates, high rainfall or irrigation) are seldom limiting for plant growth. The ability of a plant species to compete for light may result from its ability to access light for its own use (e.g. overgrowth ability) or to reduce access to light by its neighbors (e.g. shading). Assessing the efficiency of the processes of light interception, light conversion, and carbon allocation can be challenging when studying a wide range of cover crops.

One way of choosing and comparing possible cover crops is identifying morpho-physiognomical features, recently referred to as plant functional traits (Garnier and Navas 2012, Viole 2007), that maximize weed control. A large literature has highlighted how plant traits such as cover crop biomass (Mennan et al., 2020, Teasdale et al., 2007), height (Korres and Froud-Williams, 2002), rapid germination (Pester et al., 1999), large leaf area development (Seavers and Wright, 1999) or early light interception (Kruidhof et al., 2008) affect the interactions between the main crop and the weeds. However, the effectiveness of cover crops in weed control often depends on the composition of weed population as well as management practices (Osipitan et al., 2019).

In Reunion Island, weed pressure is a major constraint for agriculture. The aim of the 2008 Ecophyto I and 2018 Ecophyto II program is to reduce the use of herbicides in the French agricultural sector by 50% by 2025. In Reunion Island, sugarcane, the main agro-industrial

sector, plays an important economic, societal, and environmental role as it uses more than 50% of agricultural land (Agreste, 2016). The largest amount of herbicides on Reunion Island are used for sugarcane production (Antoir et al., 2016). Consequently, cover crops have a strong potential in the sugarcane sector (Mansuy et al., 2019).

The aim of this study was to perform trait-based characterization of a wide range of cover crops to assess their ability to control weeds in tropical agrosystems, using Reunion Island as a case study. Specifically, our three objectives were to use the range of cover crop species i) to identify the species with the highest ground cover in tropical climatic conditions, ii) to identify the crop traits that maximize ground cover, and iii) to assess the ability of cover crops to control weed growth.

To achieve these objectives, we conducted a set of 10 field experiments in Reunion Island from 2016 to 2018. Six were designed to assess the performance of the cover crops in response to local climate (i.e. weeds were controlled manually). The other four experiments were designed to assess the ability of cover crops to control weeds.

## 2. Materials and methods

### 2.1. Description of the trials

The trials were conducted in three experimental stations in Reunion Island between February and June (warm season and beginning of the cool season) from 2016 to 2018. Table 1 lists the locations and give the details on each trial. Soil characteristics at the three sites are listed in Supplementary Information A Table A1. Two main types of trials were performed: trials to choose the cover crop that grows best in the local climate (hereafter 'cover crop trial'), and trials to test which cover crop is best at weed control (hereafter 'weed control trial'). In the cover crop trials, weeds were removed manually after sowing and throughout the trial. Four cover crop trials were performed in La Mare (50 m asl, 2016 to 2018), one in Bassin Plat (160 m asl, 2016) and one in Colimaçons (800 m asl, 2016). Each trial comprised 12 m<sup>2</sup> or 16 m<sup>2</sup> plots containing pure cover crops. The growth period of the cover crops ranged from 2.5 to 4 months depending on the trial due to logistic reasons. In the weed control trials, weeds were not removed after sowing to assess competition between the cover crops and the weeds. Three weed control trials were performed in La Mare (2016, 2017) and one in Bassin Plat (2017) in plots ranging from 20 to 100 m<sup>2</sup>. The growth period of the cover crops was two months. In all weed control trials, the plots containing the cover crops were located next to control plots containing natural weed flora. The dominant weed flora present in La Mare and Bassin Plat are listed in Supplementary Information Table A2. In all sites, the daily average temperature ( $T_{MEAN}$ ) was measured. Five of the trials were fertilized at sowing while the other five were not fertilized. Fertilizer applications are described in Table 1. All the trials were irrigated except at Colimaçons, where precipitation was  $> 120 \text{ mm month}^{-1}$  during the growth period. Prior to sowing, the plots were tilled down to 15 cm using tines and herbicide was applied. Seeds were sown manually in lines with 40 cm interrow spacing at a depth of 2-5 cm. The sowing density for each species is listed

in Supplementary Information Table A3 and was determined from the literature, advice from suppliers and in-house expertise. The experimental design of each trial is given in Figs. A1 to A10.

## 2.2. Cover crop species

A total of 46 cover crop species were tested in the different trials. Details on the cover crop species used in each experiment are listed in Tables A3, A4 and A5. The species included Asteraceae ( $n=2$ ), Brassicaceae ( $n=3$ ), Fabaceae ( $n=32$ ), Poaceae ( $n=8$ ) and Polygonaceae ( $n=1$ ) plants. Among them, 21 are temperate and 25 are tropical species. Species were annual ( $n=36$ ) or perennial ( $n=10$ ). Their growth habit (creeping, erect or vines) is detailed in Table A4. In some cover crop trials (see the experimental design in Supplementary Information Figs A1 to A10), several cultivars were used in the same trial but in the analyses, they were considered as the same species. In the weed control trials, 18 cover crop mixtures were also tested (Table 1), the mixtures are detailed in Table A5, each mix included two species.

## 2.3. Measurements

Cover crop traits and phenology were measured in the different trials (Table 2). Ground cover by crops (COV, %) was measured in each plot weekly using a visual notation method described in Supplementary Information Table A6 and already used in previous studies (Mansuy et al., 2019; Mathieu & Marnotte, 2000; Marnotte et al., 1984). This method makes it possible to assess the soil cover of individual species in multi-species crops (e.g. cover crops and weeds). Between two measurement dates, ground cover was linearly extrapolated each day. Then, we calculated a mean ground cover (COV<sub>MEAN</sub>, %) as the average interpolated COV from sowing to the end of the trial. This mean cover was used to estimate the capacity of species to cover the soil durably. The maximum cover (COV<sub>MAX</sub>, %) was defined as the maximum value of cover reached by the species concerned. A rate of increase in ground cover per day (COV<sub>RATE</sub>, % d<sup>-1</sup>) was calculated as the COV<sub>MAX</sub> divided by the number of days needed to reach it after sowing. Additionally, for each species, the height and number of leaves of five individuals per plot were measured weekly and averaged per date. From these measurements, a rate of increase in height (H<sub>RATE</sub>, cm d<sup>-1</sup>) and a leaf appearance rate (Leaf<sub>RATE</sub>, n d<sup>-1</sup>) were calculated from emergence to flowering as the ratio between plant height or leaf number and the number of days since sowing. Regarding phenology measurements, the thermal times for emergence (Emergsdd, °d) and flowering (Flosdd, °d) were calculated as the sum of daily T<sub>MEAN</sub> from sowing to the point at which 50% of plants had emerged or flowered. Finally, to measure aboveground dry mass (ABV<sub>DM</sub>) in weed control trials, all weeds and cover crops in three 50x50cm squares inside each plot were cut at ground level after two months of growth, i.e., at the end of the weed control experiment, separated before weighing and dried at 60 °C for 2 days.

**Table 1.** Cover crop and weed control trials. The cover crop species used in the different trials are listed in Table A3. For each trial, the site, latitude, longitude, altitude, soil type (WRB classification), year, average temperature ( $T_{MEAN}$ ), number of species, plot area, sowing date, trial duration, fertilization regime are given.

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 <sup>-1</sup> )	Manual weed control	Trial ID
Cover crop trials	La Mare	-20.9	55.53	50 m	Nitisol	2016	23.0	31	16 m <sup>2</sup> (x1)	30/03	3.5 months	NPK (36-82-60)	no	1
						2017	23.2	28		13/04	4 months			2
						2018	22.7	26		27/04	4 months			3
							25.7		12 m <sup>2</sup> (x1)	20/02				
							22.0	15		12/04	3 months	no	yes	4
							23.6			13/06				
	Bassin Plat	-21.32	55.49	160 m	Andic Cambisol	2016	24.0	18	16 m <sup>2</sup> (x1)	04/03	2.5 months	NPK (36-77-48)	no	5
	Colimaçon	-21.13	55.3	800 m	Andic Cambisol	2016	20.5	18	16 m <sup>2</sup> (x1)	16/03				6
Weed control trials	La Mare	-20.9	55.53	50 m	Nitisol	2016	24.1	6 (+9)	36 m <sup>2</sup> (x1)	04/04	2 months	NPK (30-80-60)	no	7
						2016	24.4	8	100 m <sup>2</sup> (x1)	31/03				8
						2017	24.2	6 (+6)	20 m <sup>2</sup> (x4)	13/04				9
	Bassin Plat	-21.32	55.49	160 m	Andic Cambisol	2017	25.3	4 (+3)	24 m <sup>2</sup> (x4)	03/03				

In addition to cover crop traits, in the weed control trials, we assessed two weed control efficiency indices in terms of weed ground cover (WCE<sub>Cov</sub>) and biomass (WCE<sub>DM</sub>). Like for cover crop traits, a mean ground cover index for weed over time (COV<sub>Weed</sub>) was calculated in each plot in each trial. Then for each plot containing cover crops, we assessed the WCE<sub>Cov</sub> as follows:

$$WCE_{Cov} = 1 - \frac{COV_{Weed,cc}}{\langle COV_{Weed,pure} \rangle}$$

where COV<sub>Weed,cc</sub> is the mean ground cover by weeds in plots with cover crops and  $\langle COV_{Weed,pure} \rangle$  is the average COV<sub>Weed</sub> in control plots (pure weeds) in each trials. Similarly, the WCE<sub>DM</sub> was calculated based on final weed dry mass (DM<sub>Weed</sub>) in control plots and in plot planted with cover crops:

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

where DM<sub>Weed,cc</sub> is the aboveground weed dry mass in plots with cover crops and  $\langle DM_{Weed,pure} \rangle$  is the average aboveground weed dry mass in control plots in each trials. All experimental data are available online on CIRAD dataverse (<http://dx.doi.org/10.18167/DVN1/H0V2G>).

**Table 2.** Traits and variables measured in the trials and used in the study. The identification of each trial (Trial ID) in which measurements were made is given. 0-1 indicates that the variable values ranged from 0 to 1.

	Index	Units	Description	Trial ID
	COV <sub>MEAN</sub>	%	Mean ground cover	All trials
	COV <sub>RATE</sub>	% d <sup>-1</sup>	Rate of increase in ground cover per day between sowing and maximum cover	All trials
	COV <sub>MAX</sub>	%	Maximum ground cover	All trials
Crop traits	H <sub>RATE</sub>	cm d <sup>-1</sup>	Rate of increase in height per day from emergence to maximum height	1,2,4,5,6,9,10
	Leaf <sub>RATE</sub>	leaf d <sup>-1</sup>	Leaf appearance rate per day	1,2,4,5,6,9,10
	Emerg <sub>SDD</sub>	°d	Thermal time for emergence since planting	1,2,5,6
	Flo <sub>SDD</sub>	°d	Thermal time for flowering since planting	1,2,5,6
	ABV <sub>DM</sub>	kgDM m <sup>-2</sup>	Aboveground dry mass at the end of the trial	9,10
Weed control	WCE <sub>Cov</sub>	0-1	Weed control efficiency index based on weed cover	7,8,910
	WCE <sub>DM</sub>	0-1	Weed control efficiency index based on weed dry mass	9,10

## 2.4. Data analyses

First, we tested for a bias in the COV<sub>MEAN</sub> and COV<sub>RATE</sub> data in the cover crop trials between the different factors tested in this study (Supplementary Information B, Table B1): location of the site, average daily temperature (T<sub>MEAN</sub>), fertilization regime, cover crop genus, family, area of origin, life cycle and growth habit (Chi-square test using the chisq.test R function). A variance analysis based on a mixed linear model was performed on cover crop traits using the crop life cycle and the combined crop family x area of origin as fixed effects and the trial identification as random effect (R package nlme, Pinheiro et al., 2020). To ensure the normality of residues, all crop traits were transformed using the Box-Cox power transformation (R package MASS, Venables and Ripley 2002). Then a post hoc analysis on crop traits were done using the non-parametric Dunn test with respect to area of origin, life cycle and family (R package dunn.test, Dinno 2017). A variance analysis based on a mixed linear model was also performed on WCE<sub>COV</sub> and WCE<sub>DM</sub> using the crop mixture type and the combined crop family x area of origin as fixed effects, separately, each time with the trial identification as random effect. Post hoc analyses on weed control efficiencies were done using the non-parametric Dunn test. Finally, correlations between individual traits were assessed with a Spearman correlation ( $\rho_{SPEAR}$ , R package Hmisc, Harrell et al., 2020 and corrrplot, Wei and Simko, 2017) on all individual data points, without taking into account for site or species. For visual purposes, polynomial smooth regressions were added in the figures using the loess R function. Additional packages were used for plotting (ggplot2, Wickham, 2016 and ggrepel, Slowikowski, 2020). All data analyses were performed with R 4.0 (R Development Core Team, 2020).

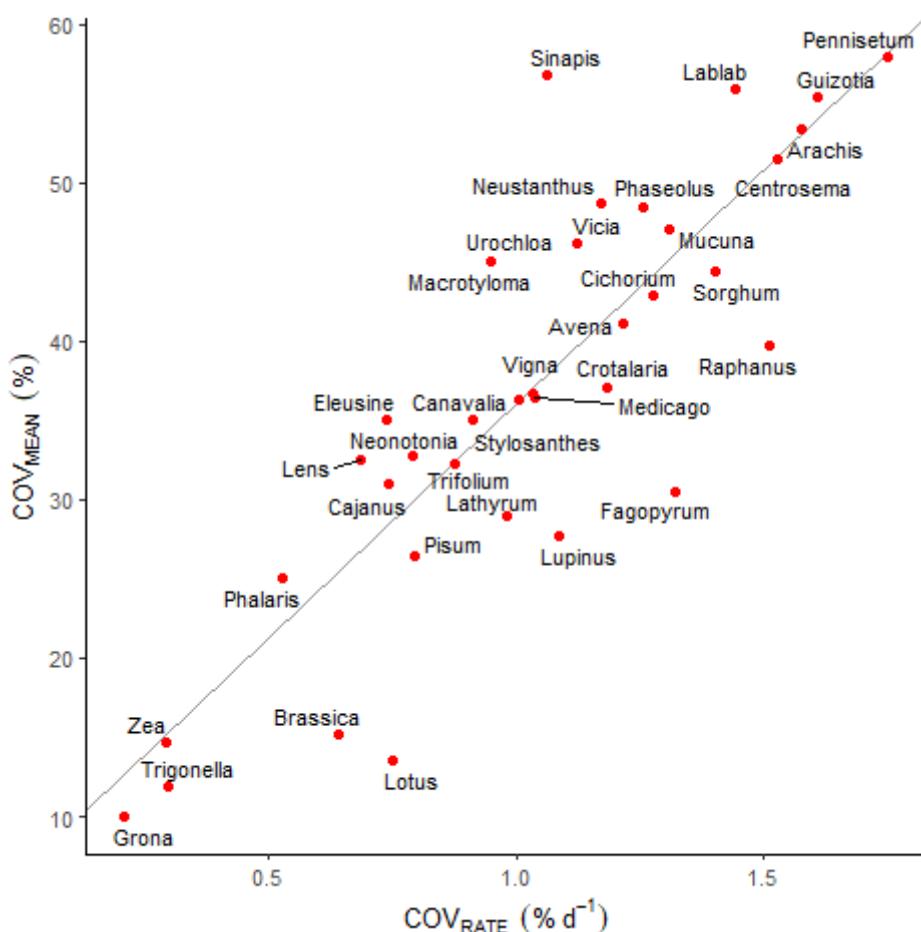
## 3. Results

### 3.1. Analyses of bias in the cover crop trials

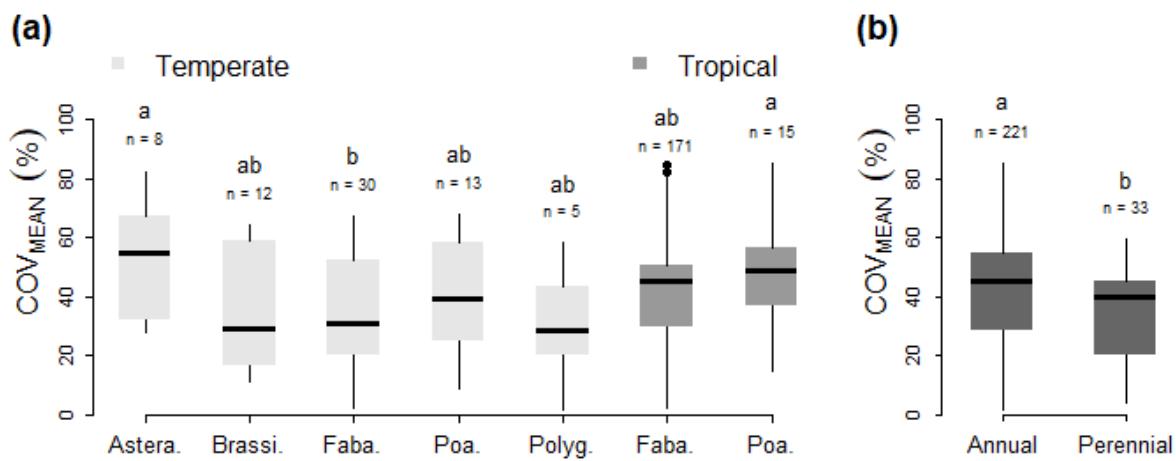
Due to the unbalanced design, possible biases related to the pedo-climatic contexts as well as to the choice of genus studied were assessed. No bias was found between the location of the site, average temperature and the genus, family, area of origin, life cycle and growth habit of the cover crops (Table B1), except for a small bias between the area of origin and T<sub>MEAN</sub> (with 62% of tropical cover crops grown at 23 °C versus 51% for temperate species, Table B2). On the contrary, the fertilization regime introduced a bias in the analyses notably in the area of origin and family of the cover crop (Table B3). In the same site (La Mare) but in different years, COV<sub>MEAN</sub> was higher in trials with no fertilization than in trial including fertilization at the level of the cover crop species (Fig. B1), highlighting the fact climate played a more important role in driving the growth of cover crops than fertilization in our trials. A strong bias was also observed between cover crop growth habits and other factors such as the genus, family, area of origin or life cycle of the cover crop (Table B1). In particular, all vines and creeping species were Fabaceae whereas erect species were found in all families, including Fabaceae (Table B4). Consequently, the growth habit factor could not be tested independently of all other factors, even within Fabaceae.

### 3.2. Ground cover dynamics in the cover crop trials

The performance of cover crops varied greatly depending on the genus of the cover crop (Fig. 1).  $\text{COV}_{\text{MEAN}}$  ranged from 10% to 60%, and  $\text{COV}_{\text{RATE}}$  ranged from 0.2%  $\text{d}^{-1}$  to 1.7%  $\text{d}^{-1}$  on average. Even if these two traits were linearly correlated ( $r = 0.84$ ,  $n = 34$ ,  $p < 0.0001$ ), some genera had a high  $\text{COV}_{\text{MEAN}}$  with a moderate  $\text{COV}_{\text{RATE}}$  (e.g. *Sinapis*) and conversely, a high  $\text{COV}_{\text{RATE}}$  with a moderate  $\text{COV}_{\text{MEAN}}$  (e.g. *Raphanus*).  $\text{COV}_{\text{MEAN}}$  was significantly influenced by the life cycle ( $F_{1,239} = 14.9$ ,  $p = 0.0001$ ) and the combined crop family x area of origin factor ( $F_{6,239} = 3.5$ ,  $p = 0.0024$ , Table B5, Fig. 2). Area of origin had no effect on  $\text{COV}_{\text{MEAN}}$  within the Poaceae or Fabaceae species (Fig. 2a). In temperate species,  $\text{COV}_{\text{MEAN}}$  was higher in Asteraceae species than in Fabaceae ( $p = 0.0134$ ), and the other families were between the two. In both tropical and temperate crop species, Fabaceae and Poaceae had similar  $\text{COV}_{\text{MEAN}}$ .  $\text{COV}_{\text{RATE}}$  response to life cycle and combined crop family x area of origin was similar to  $\text{COV}_{\text{MEAN}}$  (Table B5, B6; Fig. B2). Variations in other crop traits ( $H_{\text{RATE}}$ ,  $\text{Leaf}_{\text{RATE}}$ ,  $\text{EmergsDD}$  and  $\text{FlosDD}$ ) as a function of the family, area of origin and life cycle are detailed in Fig. B2.



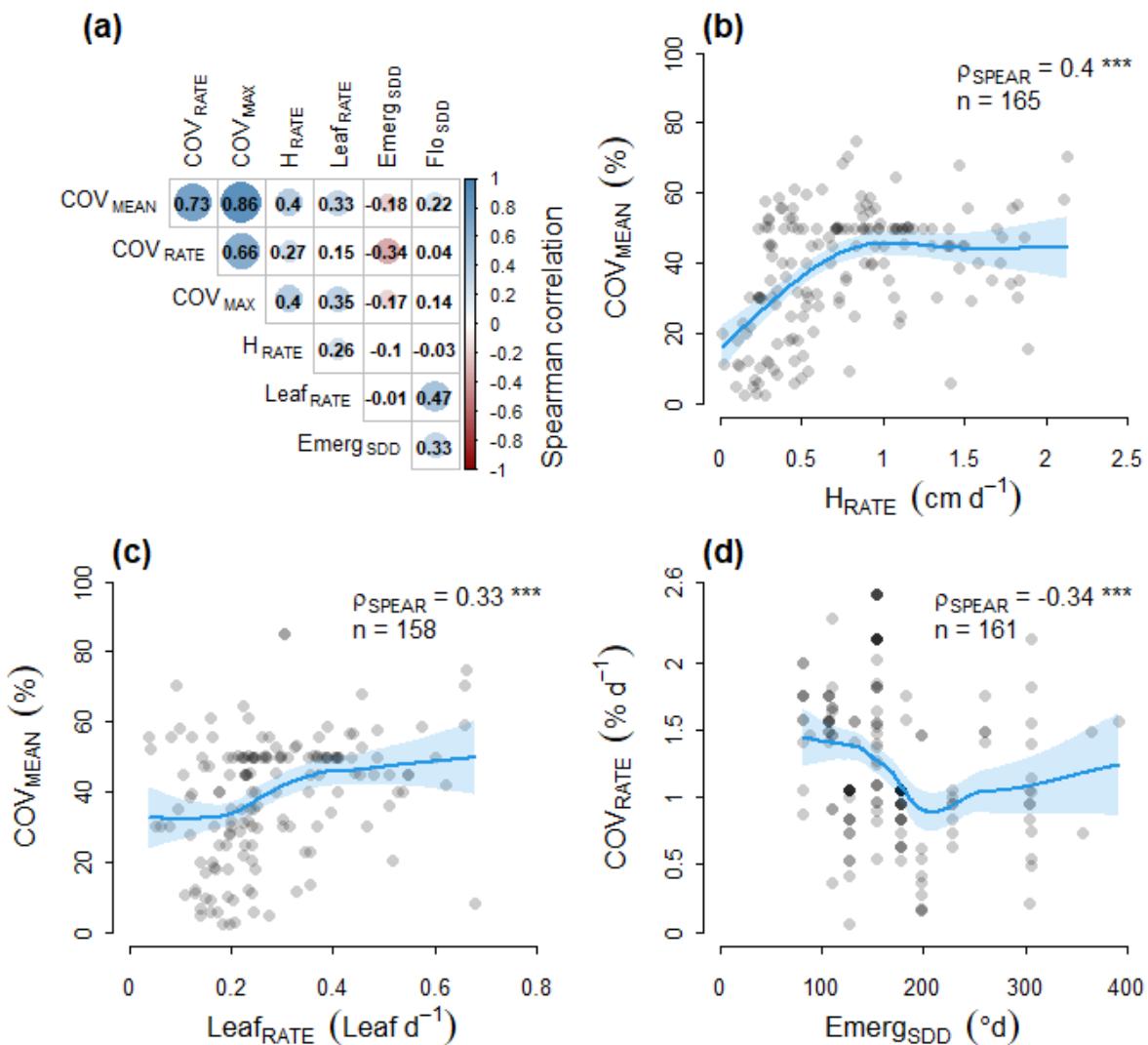
**Fig. 1.** Scatter plot of average mean ground cover ( $\text{COV}_{\text{MEAN}}$ , %) and rate of increase in ground cover ( $\text{COV}_{\text{RATE}}$ , %  $\text{d}^{-1}$ ) of the cover crop genus in the six cover crop trials. Each point is associated with the name of the genus concerned. The gray line represents the regression line.



**Fig. 2.** Mean ground cover (COV<sub>MEAN</sub>) of the cover crop used in the cover crop trials depending on the crop family and area of origin (temperate or tropical) on one hand (a) and the life cycle in the other hand (annual or perennial, b). Crop families are abbreviated for Asteraceae (Astera.), Brassicaceae (Brassica.), Fabaceae (Faba.), Poaceae (Poa.) and Polygonaceae (Polyg.). The differences between combinations of factors were tested using a Dunn test and indicated by letters a and b. The number of samples in each category is indicated by “n”.

### 3.3. Correlation between cover crop traits and ground cover

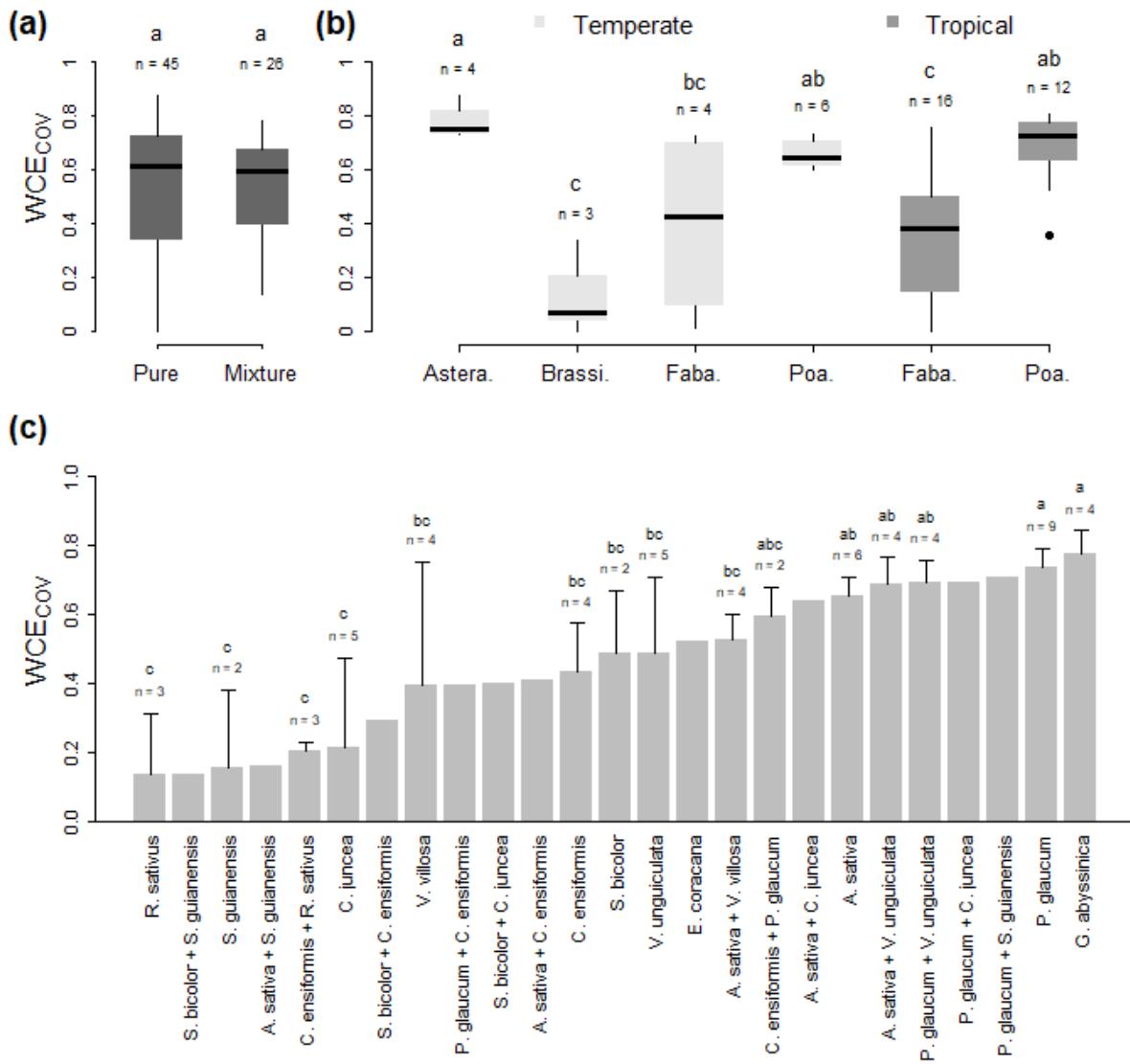
Considering all cover crops (Fig. 3), a significant positive correlation was shown between the two ground cover indices COV<sub>MEAN</sub> and COV<sub>RATE</sub> ( $\rho_{SPEAR} = 0.73$ ,  $n = 254$ ,  $p < 0.0001$ ). Additional significant correlations were found between ground cover performance and other plant traits. COV<sub>MEAN</sub> was positively correlated with H<sub>RATE</sub> ( $\rho_{SPEAR} = 0.4$ ,  $n = 165$ ,  $p < 0.0001$ ), Leaf<sub>RATE</sub> ( $\rho_{SPEAR} = 0.33$ ,  $n = 158$ ,  $p < 0.0001$ ) and FlosDD ( $\rho_{SPEAR} = 0.22$ ,  $n = 135$ ,  $p = 0.0114$ ) and negatively correlated with EmergSDD ( $\rho_{SPEAR} = -0.18$ ,  $n = 161$ ,  $p = 0.0210$ , Fig. 3). Based on a visual assessment, COV<sub>MEAN</sub> reached its maximum values when H<sub>RATE</sub>  $> 0.8 \text{ cm d}^{-1}$  (Fig. 3b). COV<sub>MEAN</sub> increased slightly with Leaf<sub>RATE</sub> and reached maximum values when the Leaf<sub>RATE</sub> was higher than 0.4 leaf  $\text{d}^{-1}$  (Fig. 3c). The highest COV<sub>RATE</sub> was also found when EmergSDD was less than 150 °d (Fig. 3d). Other significant correlations found between plant traits are shown in Fig. 3a. FlosDD was highly correlated with Leaf<sub>RATE</sub> ( $\rho_{SPEAR} = 0.47$ ,  $n = 96$ ,  $p < 0.0001$ ) and less with EmergSDD ( $\rho_{SPEAR} = 0.33$ ,  $n = 136$ ,  $p < 0.0001$ ). Leaf<sub>RATE</sub> and H<sub>RATE</sub> were slightly but significantly correlated ( $\rho_{SPEAR} = 0.26$ ,  $n = 153$ ,  $p = 0.0014$ ). The correlations between ground cover variables and H<sub>RATE</sub> were still significant when only Fabaceae species or non-Fabaceae cover crops were considered (Fig. B3). Nonetheless, Leaf<sub>RATE</sub> and FlosDD were positively correlated with COV<sub>MEAN</sub> in Fabaceae crops ( $\rho_{SPEAR} = 0.5$ ,  $n = 122$ ,  $p < 0.0001$  and  $\rho_{SPEAR} = 0.29$ ,  $n = 120$ ,  $p = 0.0015$ , respectively) but no correlations were found in non-Fabaceae crops (Fig. B3).



**Fig 3.** Spearman correlation ( $\rho_{\text{SPEAR}}$ ) between cover crop traits in the cover crop trials (a). Significant positive and negative correlations are in blue and red circles, respectively. Relations between mean ground cover ( $\text{COV}_{\text{MEAN}}$ ) and rate of increase in height ( $H_{\text{RATE}}$ ) and leaf appearance rate ( $\text{Leaf}_{\text{RATE}}$ ) are detailed in (b) and (c). The relation between the rate of increase in ground cover ( $\text{COV}_{\text{RATE}}$ ) and thermal time for emergence ( $\text{Emerg}_{\text{SDD}}$ ) is presented in (d). In each case, the number of samples is indicated ( $n$ ) and a smooth regression was added using a polynomial smooth regression (blue line) with confidence interval (area shaded in light blue).

### 3.4. Weed control by pure versus mixed cover crops

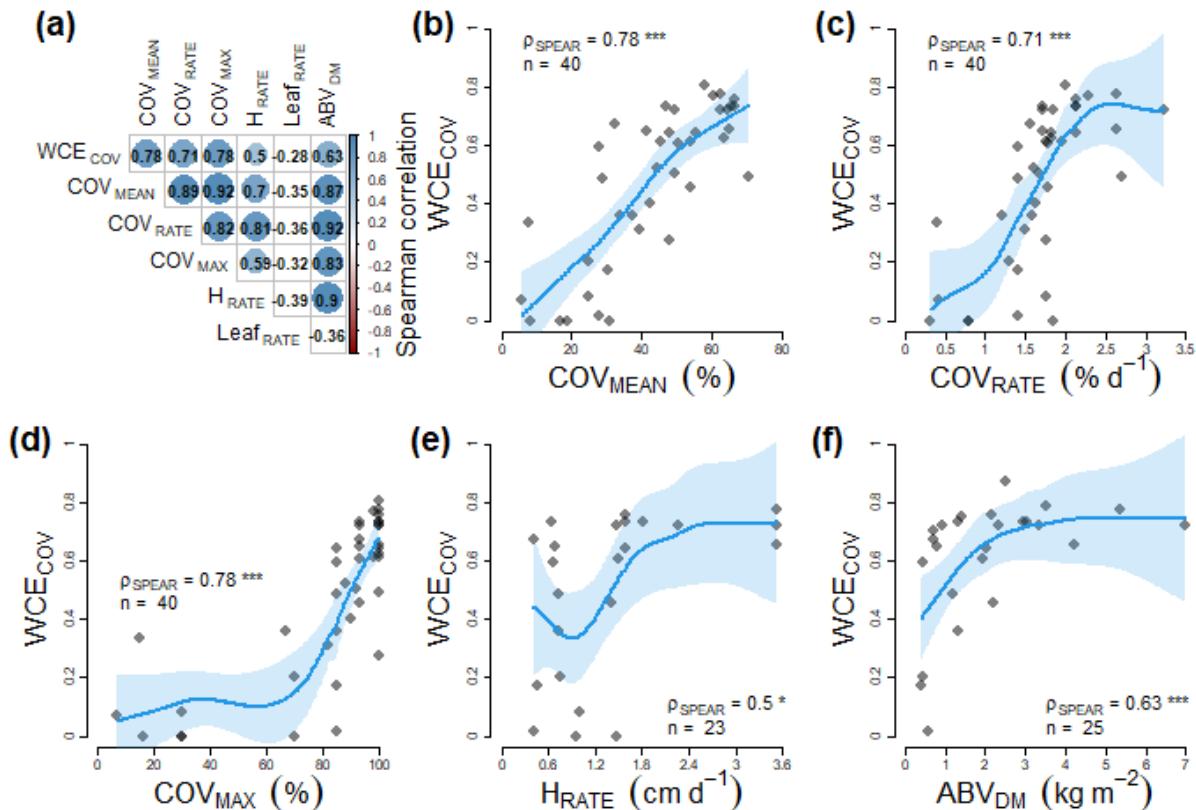
Considering both pure and mixed stand, weed control efficiency indices based on weed cover ( $WCE_{cov}$ ) and dry mass ( $WCE_{DM}$ ) were linearly correlated ( $r = 0.67$ ,  $n = 39$ ,  $p < 0.0001$ ). No difference in mean  $WCE_{cov}$  and  $WCE_{DM}$  were found between pure and mixed stands of cover crop (Table B7, Fig. 4a, Fig. B4a). Nonetheless, variance in  $WCE_{DM}$  was significantly lower in mixed stands than in pure stands ( $sd = 0.17$  and  $0.35$ , in pure and mixed stands respectively,  $F_{15,27} = 0.24$ ,  $p$ -value = 0.006) but no statistical difference was found for  $WCE_{cov}$  ( $sd = 0.20$  and  $0.27$ , respectively,  $F_{25,44} = 0.59$ ,  $p = 0.155$ ). In pure crops,  $WCE_{cov}$  and  $WCE_{DM}$  were significantly influenced by the combined area of origin and crop family factor (Table B7,  $p = 0.0001$ ). In temperate species,  $WCE_{cov}$  was higher in pure stand with Asteraceae species than Fabaceae species (Fig. 4b, Table B8,  $p = 0.0136$ ), similarly to  $WCE_{DM}$  (Fig. B4). In tropical species,  $WCE_{cov}$  was higher in pure stand with Poaceae species than Fabaceae species (Fig. 4b, Table B8,  $p = 0.0002$ ), similarly to  $WCE_{DM}$  (Fig. B4). No difference in weed control were found between tropical and temperate species within crop family. The cover crops with the highest  $WCE_{cov}$  were *Guizotia abyssinica*, *Pennisetum glaucum* and *Avena sativa*, as well as mixtures including these species (Fig. 4c). On the contrary, *Stylosanthes guianensis*, *Raphanus sativus* and *Crotalaria juncea* and mixtures including these species had low  $WCE_{cov}$ . Other species such as *Canavalia ensiformis*, *Vicia villosa* and *Vigna unguiculata* displayed intermediate weed control efficiency. Due to the high variability of weed control efficiency among cover crops, we have found no significant correlation between the level of infestation (weed cover or weed dry mass) in the neighboring control plots and weed control efficiency ( $WCE_{cov}$  or  $WCE_{DM}$ ).



**Fig. 4.** Weed control efficiency in terms of weed cover (WCE<sub>cov</sub>) in pure cover plots or a mixture of two cover crops (a), depending on crop family and area of origin in pure plots (b) or depending on cover crop species (c) in the four weed control trials. Crop families are abbreviated for Asteraceae (Astera.), Brassicaceae (Brassi.), Fabaceae (Faba.) and Poaceae (Poa.). The difference between factors was tested using Dunn's test and is indicated by letters a, b and c. The number of samples in each category is indicated by "n". When cover crop plots were repeated in (c), standard error was added.

### 3.5. Weed control and crop traits

In pure stands, WCE<sub>Cov</sub> was positively correlated with COV<sub>MEAN</sub> ( $\rho_{SPEAR} = 0.78$ ,  $p = 0.0002$ ), COV<sub>RATE</sub> ( $\rho_{SPEAR} = 0.40$ ,  $p < 0.0001$ ), COV<sub>MAX</sub> ( $\rho_{SPEAR} = 0.78$ ,  $p = 0.0003$ ) as well as H<sub>RATE</sub> ( $\rho_{SPEAR} = 0.50$ ,  $p = 0.0001$ ) and ABV<sub>DM</sub> ( $\rho_{SPEAR} = 0.63$ ,  $p < 0.0001$ , Fig. 5). Similar correlations were found for WCE<sub>DM</sub> (Fig. B5). The crop trait with the highest correlation with WCE<sub>DM</sub> was COV<sub>RATE</sub> ( $\rho_{SPEAR} = 0.83$ ,  $n = 20$ ,  $p < 0.0001$ , Fig. B5). On the contrary, correlations between weed control efficiency and leaf appearance rate were not significant.



**Fig. 5.** Spearman correlation between cover crop traits in pure stand in the weed control trials (a). Significant positive and negative correlations are in blue and red circles, respectively. Change in weed control efficiency based on weed cover (WCE<sub>Cov</sub>) in pure crops depending on cover crop traits: mean ground cover (COV<sub>MEAN</sub>, b), rate of increase in ground cover (COV<sub>RATE</sub>, c), maximum ground cover (COV<sub>MAX</sub>, d), rate of increase in height (H<sub>RATE</sub>, e) and aboveground dry mass (ABV<sub>DM</sub>, f) are detailed. The number of samples (n) and the Spearman correlation coefficient ( $\rho_{SPEAR}$ ) are indicated. Polynomial smooth regression between weed control and crop traits were added (blue line) with confidence interval (area shaded in light blue).

## 4. Discussion

### 4.1. Study bias and limits

Due to the particular design of the study, our results need to be evaluated taking into account possible biases related to the pedo-climatic contexts as well as to the choice of species studied. Although the location of the study site and temperature caused little systematic bias at the scale of the categories studied, conclusions concerning species should be limited to species found in all three study sites. Further, as is true in any site-specific study, here species performance is linked to the pedo-climatic context in Reunion Island. Despite the fact that the fertilization regime introduced a bias in the analyses, species comparison at the same site with or without fertilization suggest that climate played a more important role in the growth of cover crops than fertilization. Additionally, the majority of cover crops studied in the cover crop trials were Fabaceae ( $n=208$ ) compared to other crop families ( $n=55$ ). This imbalance could bias the correlations found between plant traits and ground cover dynamics. Nonetheless, the majority of correlations remained unchanged when only Fabaceae crops or non-Fabaceae crops were considered (e.g.  $H_{RATE}$  and  $COV_{MEAN}$ ) except for the relation between ground cover and Leaf $RATE$  and Flosdd.

### 4.2. Cover crop performance and weed control

The increasing interest of producers and researchers in cover crops may have been encouraged by the many positive aspects attributed to cover cropping such as improving soil fertility and controlling pests, weeds and erosion (Altieri et al., 2011; Kocira et al., 2020; Koohafkan et al., 2012; Snapp et al., 2005). In particular, cover crops provide direct weed control during their establishment by competing with weeds for light, water, nutrients and space (Blanco-Canqui et al., 2015), as well as releasing allelochemical compounds into the environment (Farooq et al., 2011). Additionally, cover crop residues left on the soil surface can directly limit the germination and growth of weeds in the following cash crop (Mirsky et al. 2011; Ryan et al. 2011; Teasdale and Mirsky 2015). Most importantly, they can help prevent the buildup of weed plant populations thereby reducing future weed pressure.

In intensive tropical agrosystems, the hypothesis of competition particularly 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 consequence, in this study we chose to focus on the rate of increase in ground cover ( $COV_{RATE}$ ) to identify species with early canopy closure and the mean ground cover over time ( $COV_{MEAN}$ ) to optimize ground cover over many months. Our results showed that weed control by cover crops was improved using species with a high ground cover rate at the beginning of the growth ( $COV_{RATE}$ ) and high ground cover over time ( $COV_{MEAN}$ ). These observations confirm previous reports that species with early canopy closure generally show better weed suppression (Baraibar et al., 2018; Hayden et al., 2012). Additionally, in our study, cover crops with higher biomass also controlled weeds better, underlining 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 have

highlighted the relation between cover crop biomass and weed control (e.g. Bhaskar et al., 2018; Florence et al., 2019; Osipitan et al., 2019; Schappert et al, 2019). Nevertheless, cover crop biomass is not always a good predictor of weed control (Baraibar et al., 2018; Kunz et al., 2016) and some authors like Dorn et al. (2015) suggest that rapid plant development after sowing is more important than the final biomass. The results of our study do not allow us to disentangle the effect of early canopy closure ( $\text{COV}_{\text{RATE}}$ ) and biomass, because the two traits were highly correlated and the correlations with weed control were similar in both cases. Nonetheless, our results suggest that early canopy closure must reach a threshold to effectively control weeds.

Some authors 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; Finney et al., 2016; Florence and McGuire, 2020; Schappert et al., 2019; Smith et al., 2014). In our study, average weed control efficiency by pure and mixed cover crop species was similar. Nevertheless, the standard deviation of weed control by pure cover crops was larger than the one of mixtures when considering weed biomass. In particular, depending on the species, a single cover crop might not be able to buffer rapidly changing environmental conditions (Wendling et al., 2019). Therefore, many studies have investigated the adaptability of mixtures (Hajjar et al., 2008; Tilman et al., 2001). On average in the literature, mixtures were shown to be less effective than the most efficient single sown cover crops (e.g. Smith et al., 2020). Nevertheless, combinations of species may increase resilience against weather conditions, which is an advantage in achieving efficient long-term weed control (Lawson et al. 2015).

When aiming to identify cover crop species adapted to new environments, assessing the efficiency of weed control may be challenging if a wide range of cover crops and mixtures is used, particularly due to the variability of plant performance related to soil and climate variability. However, plant traits could be considered as indicators of plant-driven processes thus making it possible to compare wide ranges of cover crops. In the current study, many crop traits were correlated with weed control efficiency but also with each other. Among them, the maximum ground cover was highly correlated with both mean ground cover over time and weed control efficiency. Being easy to measure, it is therefore a relevant trait to compare wide ranges of species under similar tropical conditions than Reunion Island.

#### **4.3. Plant traits and weed control**

Trait-based approaches have a high potential to identify the most suitable cover crops and traits to control weeds (Damour et al., 2018). To use-the terminology of Tardy et al. (2015), crops that invest carbohydrates in a support structure to grow in height 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 have increased access to light and to shade neighboring plants (Garnier and Navas, 2012). This strategy is illustrated by  $\text{H RATE}$  in our study. On the contrary, plants that invest in leaf production ( $\text{Leaf RATE}$ ) with rapid growth ( $\text{COV RATE}$ ) can be either creeping or vine 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. Vine species can also smother weeds but also the main crop (Teasdale 1998). In our study, all vines and creeping crops were Fabaceae and 85% of Fabaceae were vines or creeping crops. In our study, Fabaceae crops tend to have an obstruction strategy (low H<sub>RATE</sub> and high Leaf<sub>RATE</sub>), whereas Poaceae crops tend to have a shading strategy (high H<sub>RATE</sub> and low Leaf<sub>RATE</sub>). While all species with high ground cover and biomass succeeded in controlling weeds, our results suggest that, in our tropical conditions, the ‘shading’ strategy is more efficient than the ‘obstruction’ strategy. Indeed, although Leaf<sub>RATE</sub> is a good indicator of ground cover among Fabaceae crops, we found no link with weed control. In temperate conditions, it has also been 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., 2016; Hayden et al., 2012). However, this comparison requires further investigation because Leaf<sub>RATE</sub> alone is not enough to identify an ‘obstruction’ strategy and but needs to be completed by other traits such as specific leaf area or leaf area to mass ratio (Damour et al., 2014; Tardy et al., 2015).

Previous studies reported that Poaceae were often more efficient in controlling weeds than Fabaceae legume species (Baraibar et al., 2018; Brainard et al., 2011; Ofori and Stern, 1987), in agreement with our results. Nevertheless, the ground covering ability of Poaceae and Fabaceae species was similar in our study, suggesting other mechanisms are involved in weed control. The limited weed control displayed by Fabaceae could also be explained by low competition for soil resources. Legumes are N<sub>2</sub>-fixing species known to have less developed roots than grasses and cereals (Corre-Hellou et al., 2007; Greenwood et al., 1982; Thorup-Kristensen, 2001). While root traits are the subject of increasing study in cover crops (Fort et al., 2012; Roumet et al., 2006; Tardy et al., 2017, Wendling et al., 2016), there is still a need to better understand the relation between soil resource-acquisition strategies and weed control. Moreover, our results also show that the inter-specific variability of crop traits or weed control is remarkably high within crop family, highlighting how the identity of the species will determine its performance, in comparison to crop origin or family.

#### **4.4. Cover crops in Reunion Island**

While the use of species with shading competition strategies could be very efficient to control weeds in crop rotations, in intercropping systems, their ability to be in the top layer in the canopy could have detrimental effects on the yield of the main crop. In our climatic context in Reunion Island, where sugarcane is the main crop, the use of erect species with high cover and biomass, like *Pennisetum glaucum*, *Guizotia abyssinica* or *Avena sativa* would be particularly useful in fallow periods (3-4 months) before replanting of sugarcane. To avoid competition in the case of a sugarcane-crop association, the choice should focus on creeping or vines species that compete strongly with weeds without producing lianas (such as *Vigna unguiculata* and *Canavalia ensiformis*). As cover crop performance varies greatly with climatic conditions and management practices (Osipitan et al., 2020), the species we chose 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 crops to control weeds.

## 5. Conclusion

Our aim was to identify cover crop species and traits that optimize ground cover and weed control in tropical agrosystems, based on a set of ten trials performed in Reunion Island. Few differences were found in ground cover depending on the life cycle or crop family, but large differences were found depending on crop species. The ability of the cover crop to cover the soil rapidly and durably increased with an increase in the height or in the leaf appearance rate (in Fabaceae species) while ground cover ability tended to decrease with thermal time for emergence. No average difference in weed control was found between pure and mixed cover crops. Nonetheless, weed control was more efficient using species with a high rate of increase in ground cover and height or a lot of aboveground biomass. While cover crops can be chosen based on traits to maximize weed control, weed traits will also influence plant-weed interactions. Consequently, the traits of the weed community should also be taken into account to choose the most suitable cover crops depending on natural flora.

## Author statement

A.C. and P.M. Supervision, Project administration; P.T. and E.H. Conceptualization, Methodology, Investigation; M.C., A.N., P.V., S.A. and A.M.: Investigation, Formal analysis, Data curation; M.C. and A.N. Writing - Original Draft; All authors Writing - Review & Editing

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## Supplementary Information A: Complementary Material & Methods

**Table A1.** Soil characteristics in the 0-30 cm soil layer in the trials.

Site	pH	Organic C (g kg <sup>-1</sup> )	Organic N (g kg <sup>-1</sup> )	P (mg kg <sup>-1</sup> )	K (cmol+ kg <sup>-1</sup> )	CEC (cmol kg <sup>-1</sup> )
La Mare	6.1	19.0	1.73	97,5	0,49	11,7
Bassin Plat	6.5	19.1	1.80	50.3	1.40	12.8
Colimaçon	6.4	27.1	2.48	79.5	0.83	16.3

**Table A2.** Weed flora in the weed control trial sites (measured in 2017).

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

**Table A3.** Species composition in each trial and sowing density (SD) of pure crops. The trial IDs are detailed in Table 1 in the main text.

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

*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 A4.** List of cover crop species used in the different trials. The family, life cycle (A=annual, P=perennial), area of origin (Tr=tropical, Tm=temperate) and the growth habit (E=erect, C=creeping, V=vines) of each species are described.

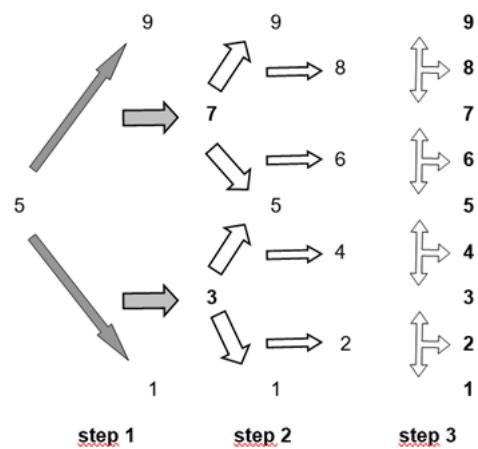
Family	Species	Cycle	Zone	Growth habit
Asteraceae	<i>Cichorium endivia</i> L.	A	Tm	E
	<i>Guizotia abyssinica</i> (L.f.) Cass.	A	Tm	E
Brassicaceae	<i>Brassica carinata</i> A.Braun	A	Tm	E
	<i>Raphanus sativus</i> L.	A	Tm	E
	<i>Sinapis alba</i> L.	A	Tm	E
Fabaceae	<i>Arachis hypogaea</i> L.	A	Tr	C
	<i>Cajanus cajan</i> (L.) Huth	P	Tr	E
	<i>Canavalia ensiformis</i> (L.) DC.	A	Tr	V
	<i>Canavalia gladiata</i> (Jacq.) DC.	A	Tr	V
	<i>Centrosema pascuorum</i> Mart. ex Benth.	A	Tr	V
	<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	C
	<i>Lablab purpureus</i> (L.) Sweet	A	Tr	V
	<i>Lathyrus sativus</i> L.	A	Tm	V
	<i>Lens nigricans</i> (M.Bieb.) Webb & Berthel.	A	Tm	V
	<i>Lotus corniculatus</i> L.	A	Tm	C
	<i>Lupinus albus</i> L.	A	Tm	E
	<i>Macrotyloma axillare</i> (E.Mey.) Verdc.	P	Tr	V
	<i>Medicago sativa</i> L.	P	Tm	E
	<i>Mucuna pruriens</i> (L.) DC.	A	Tr	V
	<i>Neonotonia wightii</i> (Wight & Arn.) J.A.Lackey	P	Tr	V
	<i>Neustanthus phaseoloides</i> (Roxb.) Benth.	P	Tr	V
	<i>Phaseolus lunatus</i> L.	A	Tr	V
	<i>Pisum sativum</i> L.	A	Tm	C
	<i>Stylosanthes guianensis</i> (Aubl.) Sw.	P	Tr	E
	<i>Trifolium hybridum</i> L.	P	Tm	C
	<i>Trifolium incarnatum</i> L.	A	Tm	C
	<i>Trifolium pratense</i> L.	P	Tm	C
	<i>Trifolium repens</i> L.	P	Tm	C
	<i>Trigonella foenum-graecum</i> L.	A	Tm	E
	<i>Vicia villosa</i> Roth	A	Tm	V
	<i>Vigna radiata</i> (L.) R.Wilczek	A	Tr	V
	<i>Vigna subterranea</i> (L.) Verdc.	A	Tr	C
	<i>Vigna unguiculata</i> (L.) Walp.	A	Tr	V
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	E
	<i>Zea mays</i> L.	A	Tr	E
Polygonaceae	<i>Fagopyrum esculentum</i> Moench	A	Tm	E

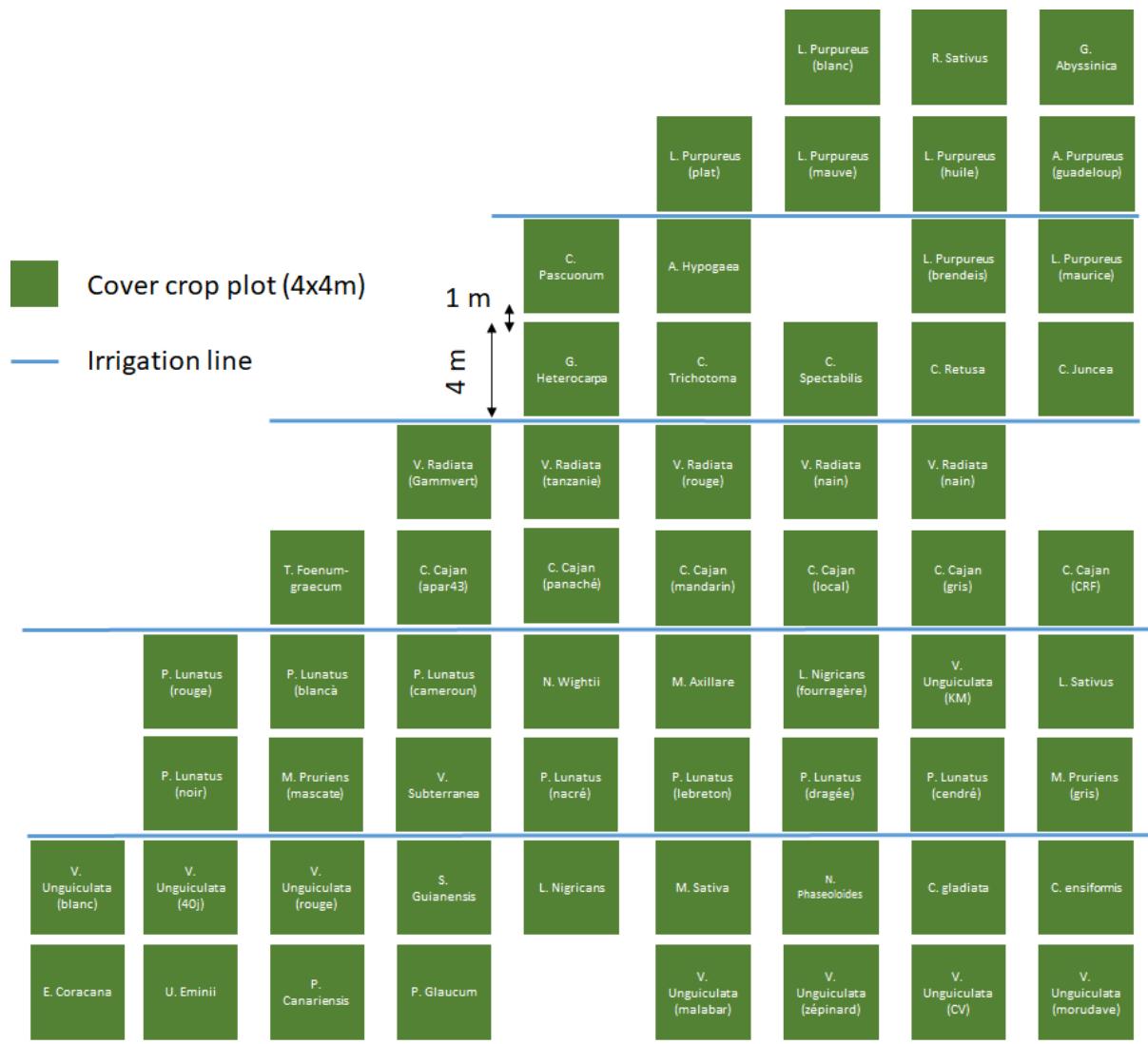
**Table A5.** Mixture of two species tested in the weed control trials. The trial IDs are detailed in Table 1 in the main text. In case of a mixture, the sowing density was half the density used for pure crops.

Mixture of species		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

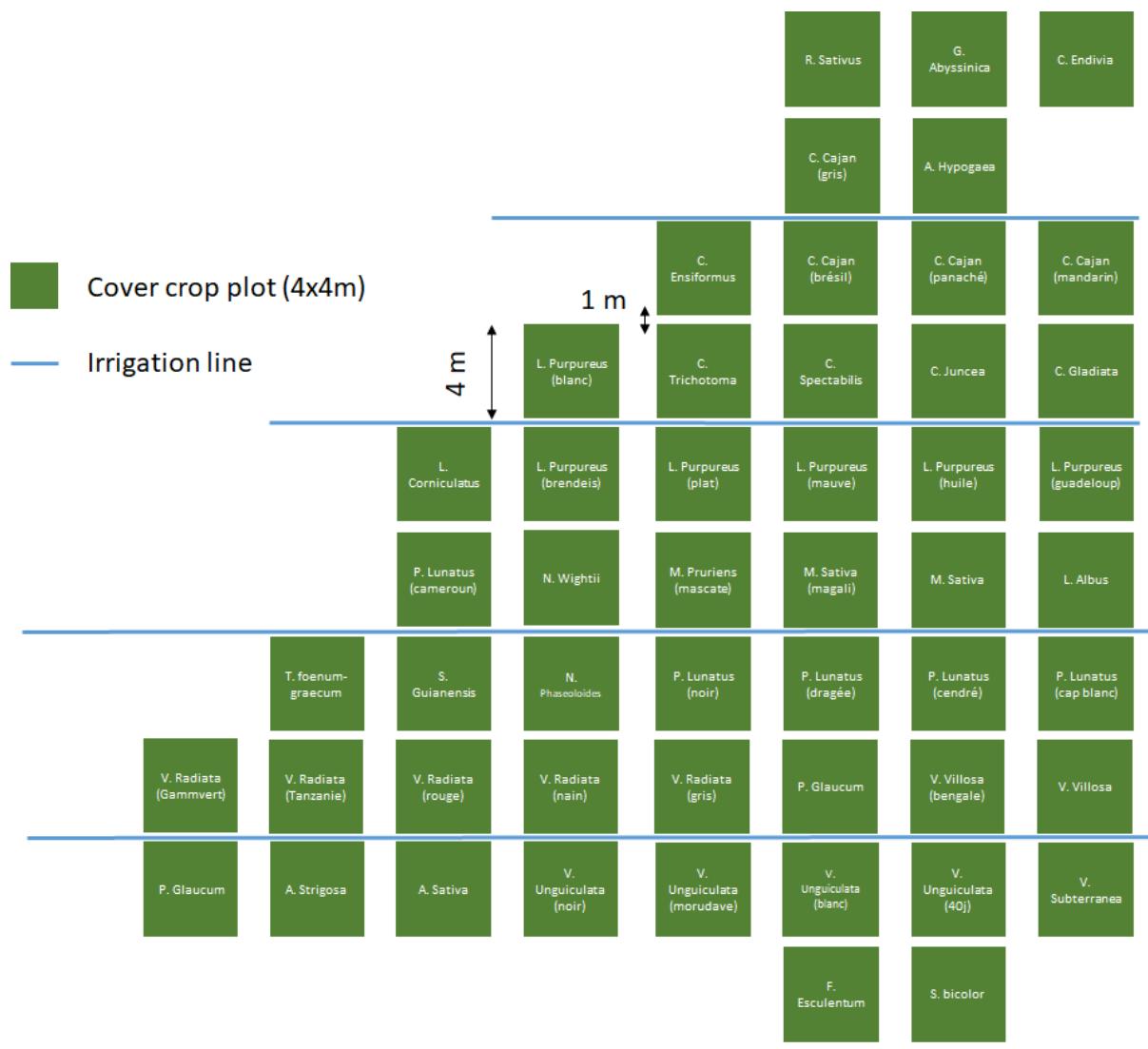
**Table A6.** Notation methods used to assess ground cover by plants (weeds or cover crops). The choice of notation was made by following a multi-step decision tree. At each step, the decision has to be taken if we estimate it to be above or below a value (e.g. 50% cover in the first step, at least one individual per m<sup>2</sup> in the second step, etc).

Notation	Equivalence in percentage	coverage
1	1	Species present but rare
2	7	Less than one individual per m <sup>2</sup>
3	15	At least one individual per m <sup>2</sup>
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

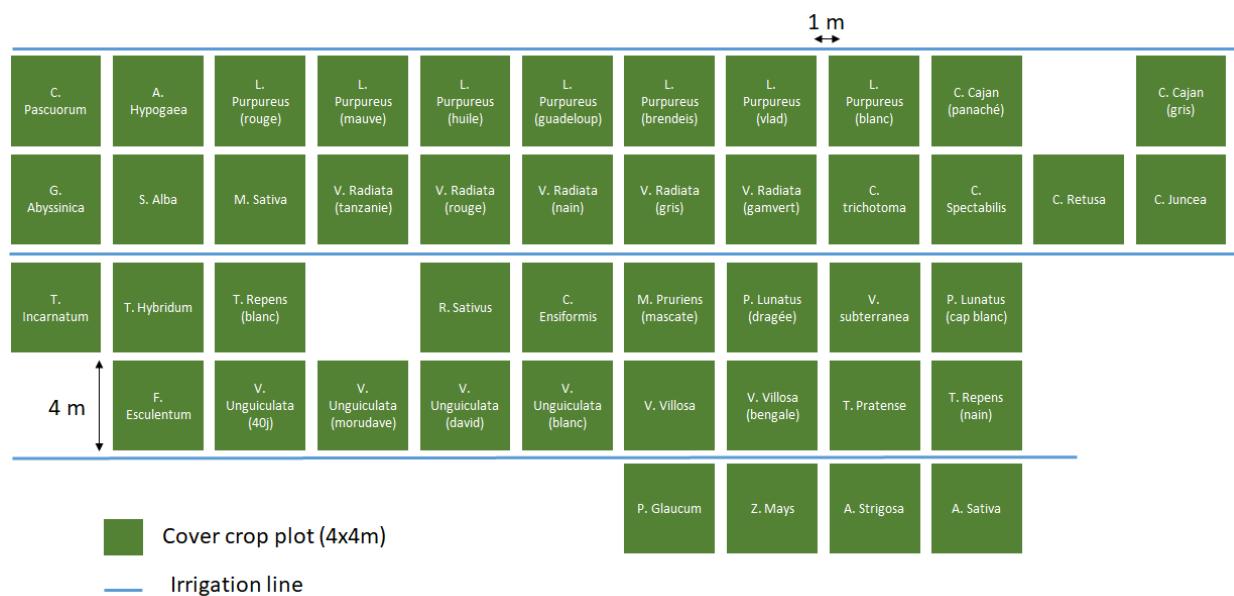




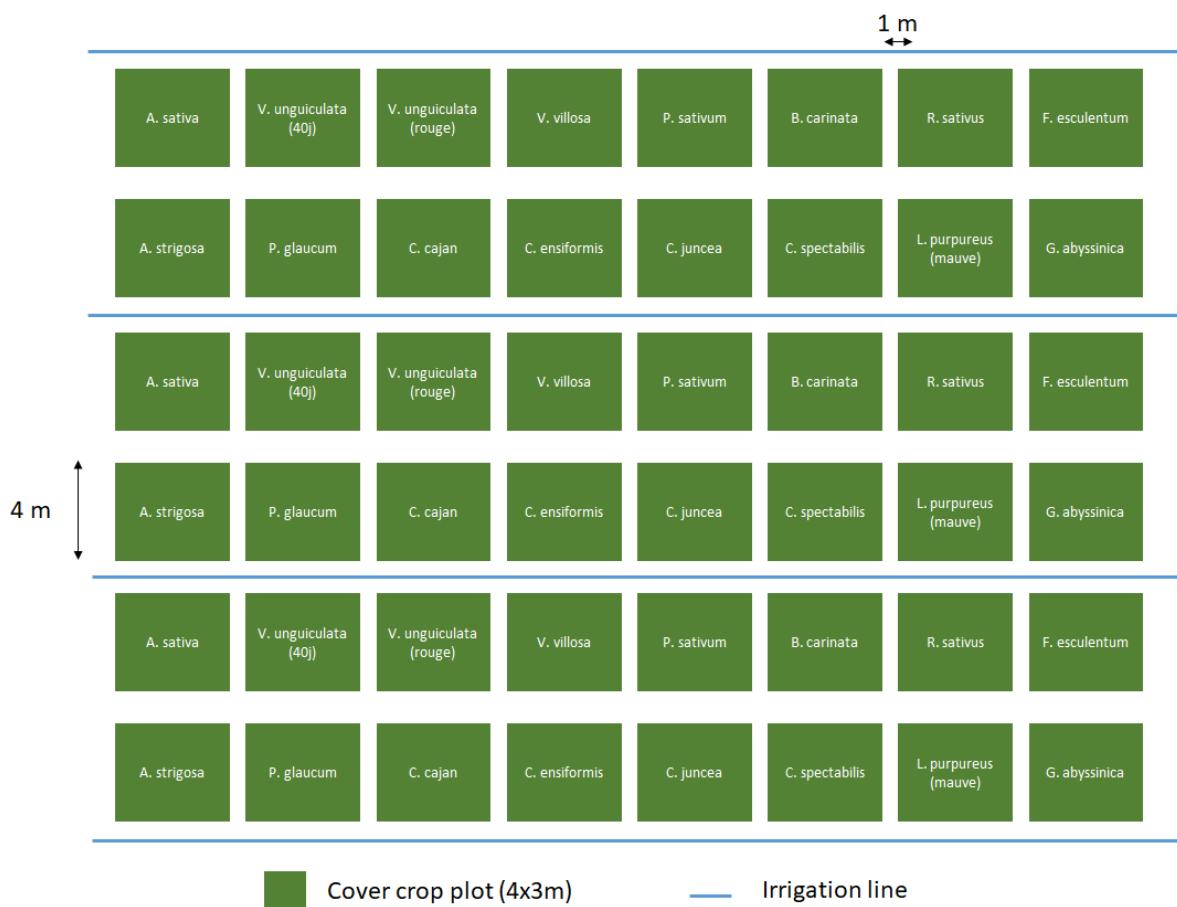
**Fig A1.** Experimental design of the cover crop trial ID 1 in La Mare 2016.



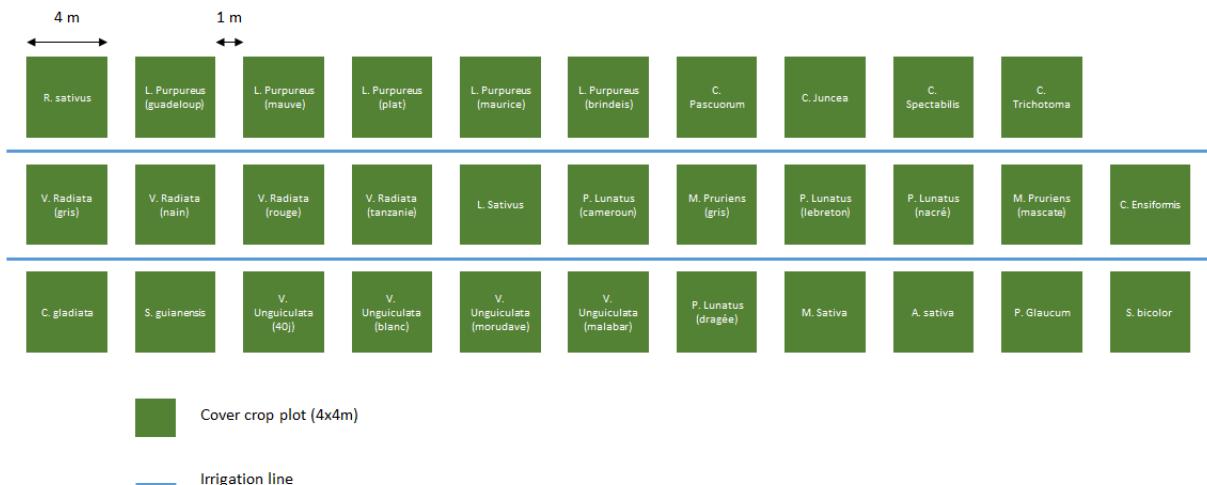
**Fig A2.** Experimental design of the cover crop trial ID 2 in La Mare 2017



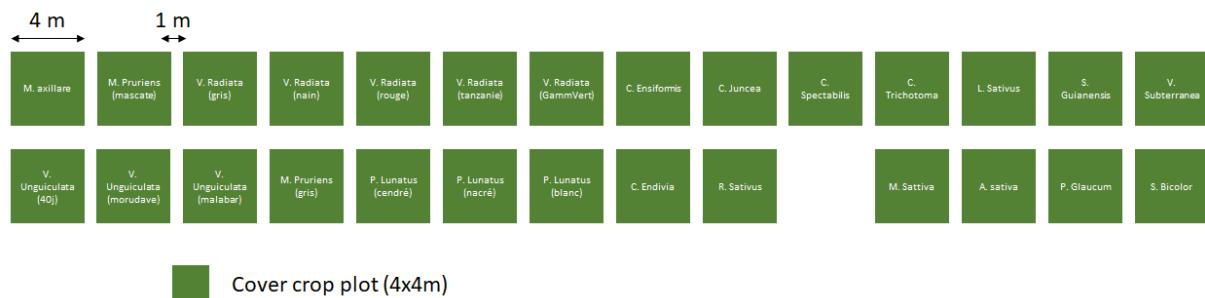
**Fig A3.** Experimental design of the cover crop trial ID 3 in La Mare 2018



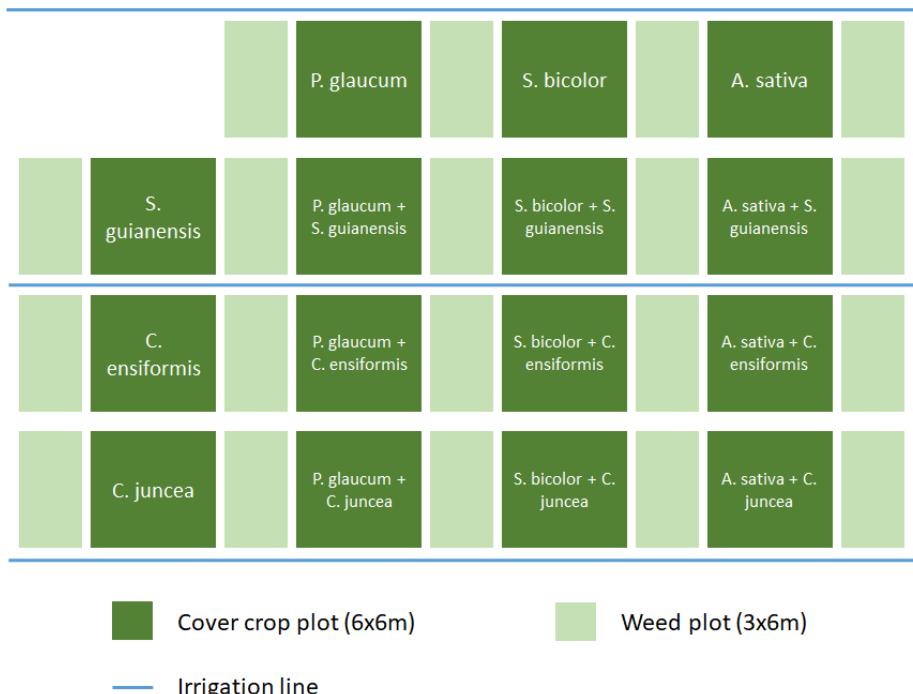
**Fig A4.** Experimental design of the cover crop trial ID 4 in La Mare 2018



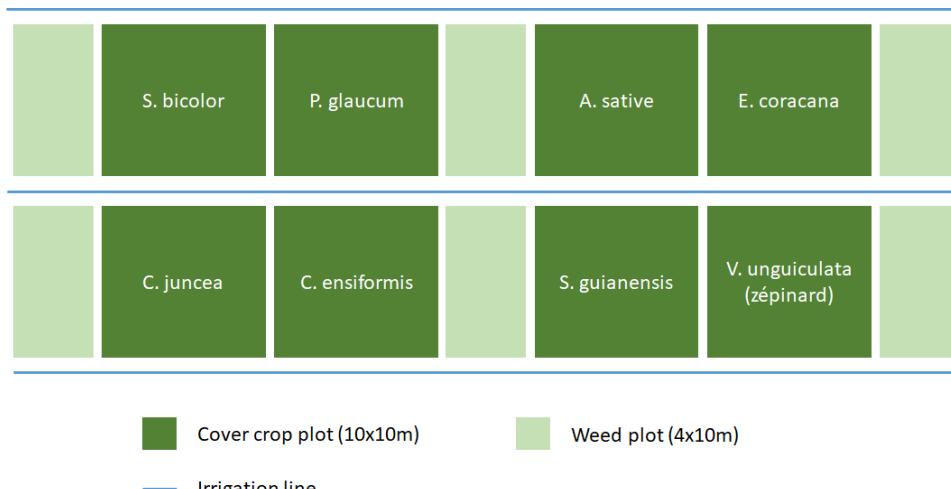
**Fig A5.** Experimental design of the cover crop trial ID 5 in Bassin Plat 2016



**Fig A6.** Experimental design of the cover crop trial ID 6 in Colimaçon 2016



**Fig A7.** Experimental design of the weed control trial ID 7 in La Mare 2016



**Fig A8.** Experimental design of the weed control trial ID 8 in La Mare 2016

A. sativa + V. villosa	C. juncea	A. sativa + C. juncea	V. unguiculata	A. sativa + V. unguiculata	P. glaucum + V. unguiculata	
G. abyssinica + C. juncea	A. sativa	V. villosa	P. glaucum + C. juncea	G. abyssinica	P. glaucum	
A. sativa + V. unguiculata	A. sativa	V. unguiculata	C. juncea	P. glaucum + V. unguiculata	P. glaucum + C. juncea	
A. sativa + C. juncea	P. glaucum	V. villosa	G. abyssinica	A. sativa + V. villosa	G. abyssinica + C. juncea	
P. glaucum + V. unguiculata	A. sativa	A. sativa + C. juncea	G. abyssinica	P. glaucum + C. juncea	A. sativa + V. unguiculata	
V. unguiculata	C. juncea	G. abyssinica + C. juncea	V. villosa	P. glaucum	A. sativa + V. villosa	
A. sativa + V. unguiculata	A. sativa	V. unguiculata	G. abyssinica + C. juncea	V. villosa	P. glaucum + V. unguiculata	
C. juncea	A. sativa + C. juncea	P. glaucum	A. sativa + V. villosa	G. abyssinica	P. glaucum + C. juncea	

**Fig A9.** Experimental design of the weed control trial ID 9 in La Mare 2017

C. juncea	C. ensiformis + P. glaucum	R. sativus	P. glaucum	C. juncea + R. sativus	C. ensiformis + P. glaucum	C. juncea + R. sativus	C. juncea
P. glaucum	C. ensiformis	C. juncea + P. glaucum	C. juncea	C. juncea	C. juncea + P. glaucum	C. ensiformis + R. sativus	P. glaucum
C. juncea + R. sativus	C. juncea + P. glaucum	C. ensiformis + P. glaucum	R. sativus + C. ensiformis	C. ensiformis + R. sativus	C. ensiformis	C. ensiformis + P. glaucum	C. ensiformis
R. sativus	C. ensiformis + R. sativus	C. ensiformis	C. juncea + R. sativus	R. sativus	P. glaucum	C. juncea + P. glaucum	R. sativus

█ Cover crop plot (4x6m)     
 █ Weed plot (2x6m)     
 — Irrigation line

**Fig A10.** Experimental design of the weed control trial ID 10 in Bassin Plat 2017.

## Supplementary Information B: Complementary Results

**Table B1.** Chi-square test on available COV<sub>MEAN</sub> data contingency table between site location, average temperature (T<sub>MEAN</sub>), fertilization regime, cover crop genus, family, area of origin, life cycle and growth habit in the cover crop trials. The chis-square value is indicated with degree of freedom (df). P. values are abbreviated by ns, \*, \*\*, \*\*\* when > 0.05, lower than 0.05, 0.01 and 0.001, respectively.

	Genus	Family	Area of origin	Life cycle	Growth habit
Location	X <sup>2</sup> <sub>df=70</sub> = 48.0 ns	X <sup>2</sup> <sub>df=8</sub> = 3.5 ns	X <sup>2</sup> <sub>df=2</sub> = 5.1 ns	X <sup>2</sup> <sub>df=2</sub> = 2.2 ns	X <sup>2</sup> <sub>df=8</sub> = 5.7 ns
T <sub>MEAN</sub>	X <sup>2</sup> <sub>df=140</sub> = 90.8 ns	X <sup>2</sup> <sub>df=16</sub> = 16 ns	X <sup>2</sup> <sub>df=4</sub> = 11.4 *	X <sup>2</sup> <sub>df=4</sub> = 6.5 ns	X <sup>2</sup> <sub>df=8</sub> = 10.9 ns
Fertilization	X <sup>2</sup> <sub>df=36</sub> = 59.9 **	X <sup>2</sup> <sub>df=4</sub> = 11.6 *	X <sup>2</sup> <sub>df=1</sub> = 18.7 ***	X <sup>2</sup> <sub>df=1</sub> < 0.1 ns	X <sup>2</sup> <sub>df=2</sub> = 9.5 **
Genus		X <sup>2</sup> <sub>df=144</sub> = 1052 ***	X <sup>2</sup> <sub>df=36</sub> = 263 ***	X <sup>2</sup> <sub>df=36</sub> = 250 ***	X <sup>2</sup> <sub>df=72</sub> = 470 ***
Family			X <sup>2</sup> <sub>df=4</sub> = 90.6 ***	X <sup>2</sup> <sub>df=4</sub> = 8.4 ns	X <sup>2</sup> <sub>df=8</sub> = 108 ***
Area of origin				X <sup>2</sup> <sub>df=1</sub> < 0.1 ns	X <sup>2</sup> <sub>df=2</sub> = 46.7 ***
Life cycle					X <sup>2</sup> <sub>df=2</sub> = 22.4 ***

**Table B2.** Proportion of data available in each area of origin depending on average air temperature (T<sub>MEAN</sub>) in the cover crop trials.

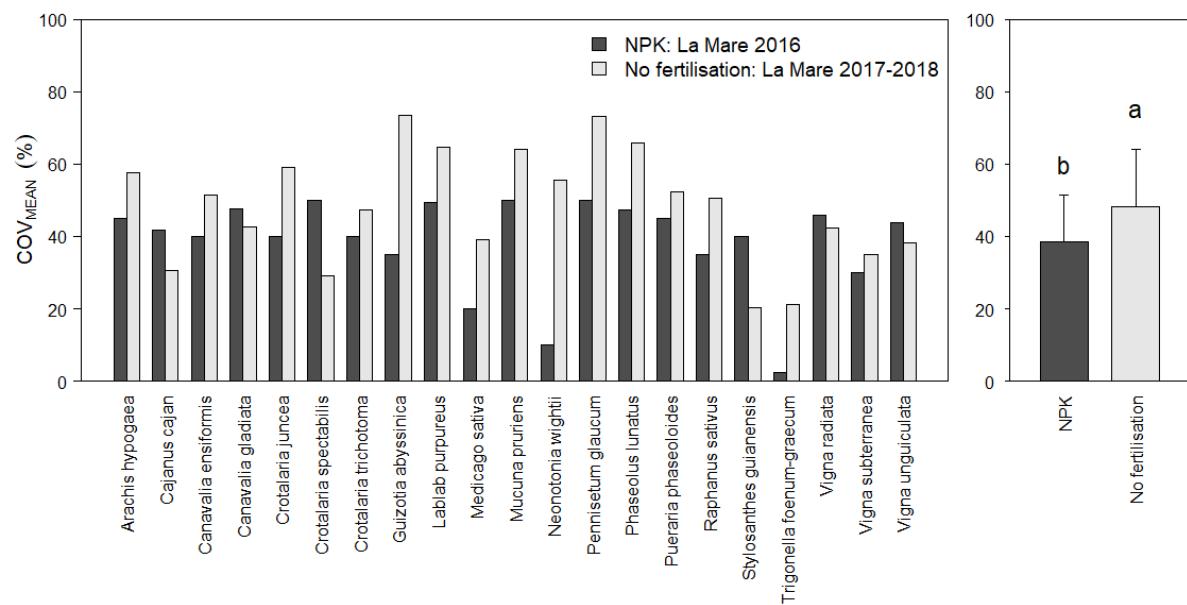
	T <sub>MEAN</sub>				
Area of origin	20°C	22°C	23°C	24°C	26°C
Temperate	7%	12%	51%	18%	12%
Tropical	11%	4%	62%	19%	4%

**Table B3.** Proportion of data available in each area of origin and growth habit depending on the fertilization regime in the cover crop trials.

Fertilization regime	Area of origin		Growth habit				
	Temperate species	Tropical species	Asteraceae	Brassicaceae	Fabaceae	Poaceae	Polygonaceae
Fertilized	25%	56%	25%	25%	53%	0.4%	0%
Not fertilized	75%	44%	75%	75%	47%	0.6%	100%

**Table B4.** Proportion of data available in each crop family depending on the growth habit in the cover crop trials.

	Growth habit			Area of origin	
	Erect	Vines	Creeping	Temperate	Tropical
Asteraceae	8%			12%	
Brassicaceae	12%			18%	
Fabaceae	46%	100%	100%	44%	91%
Poaceae	29%			19%	9%
Polygonaceae	5%			7%	



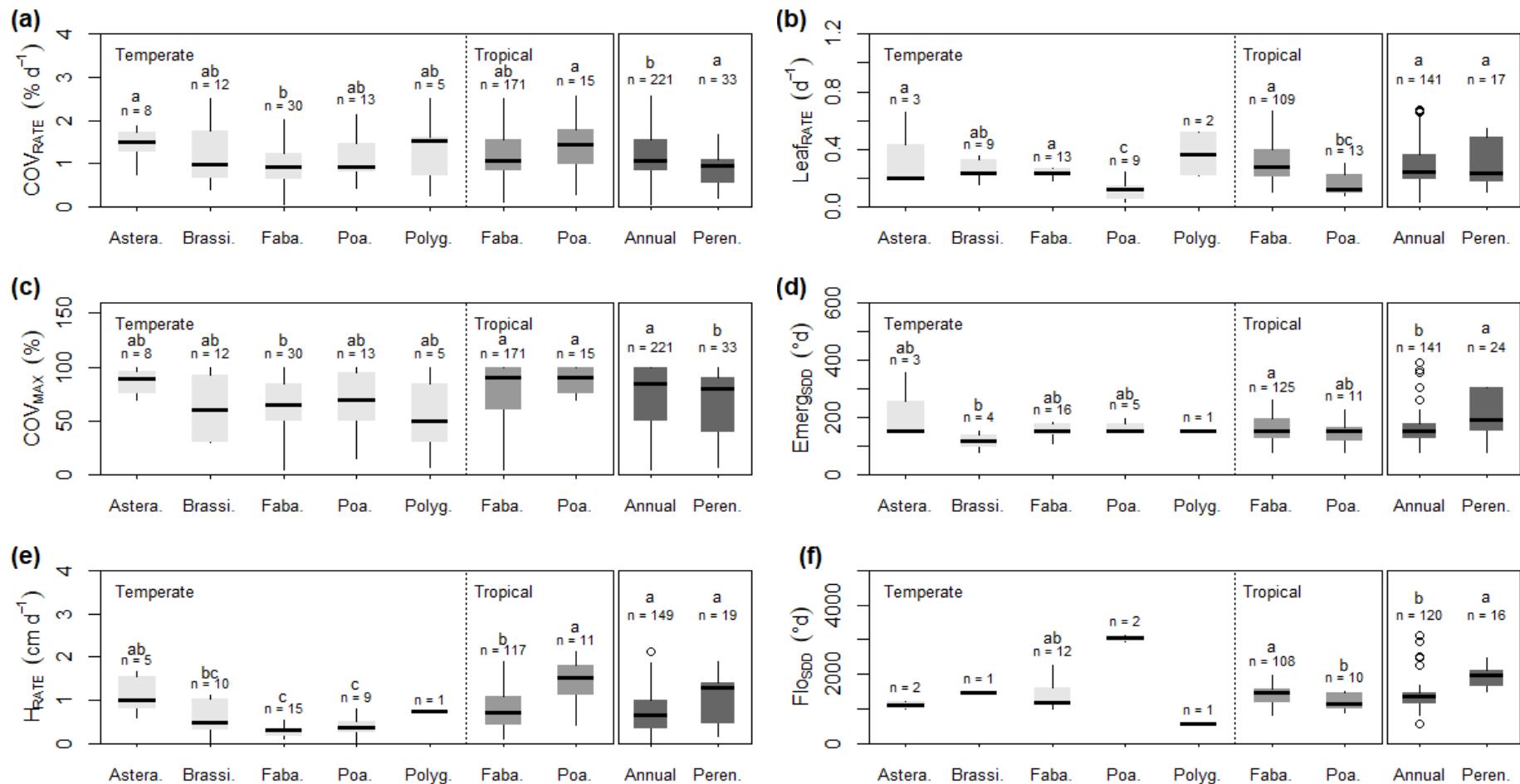
**Fig B1.** Comparison of mean ground cover (COV<sub>MEAN</sub>) for different cover crops in the fertilized cover crop trial in La Mare 2016 and the cover crop trials with no fertilization in La Mare 2017 and 2018 (left). The average COV<sub>MEAN</sub> across species depending on fertilization regime in La Mare is presented on the right. The difference between fertilization regime was tested using a Dunn test and indicated by letters a and b.

**Table B5.** Variance analysis on crop traits in the cover crop trials using a mixed linear model with the crop life cycle and the combined crop family x area of origin as fixed effects, and the trial identification as random effect. To ensure the normality of residues, all crop traits were transformed using the Box-Cox power transformation (MASS package, boxcox function).

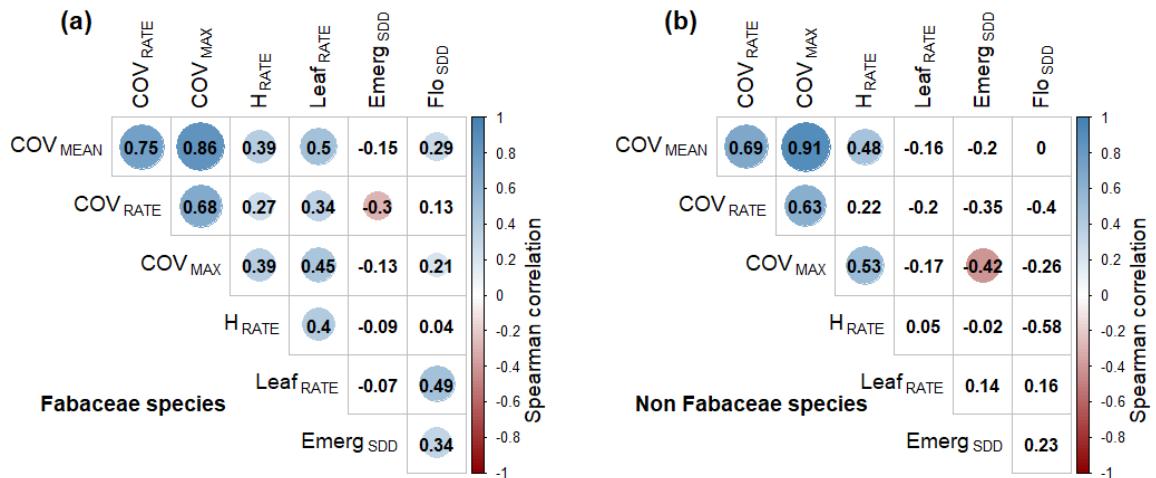
Crop trait	Life cycle			Family x area of origin		
	F	df	p	F	df	P
COV <sub>MEAN</sub>	14.9	1,239	0.0001	3.5	6,239	0.0024
COV <sub>RATE</sub>	12.8	1,239	0.0004	3.0	6,239	0.0071
COV <sub>MAX</sub>	11.4	1,239	0.0009	2.4	6,263	0.0307
H <sub>RATE</sub>	3.6	1,154	0.0589	11.2	6,154	<0.0001
Leaf <sub>RATE</sub>	0.8	1,144	0.3604	8.7	6,144	<0.0001
Emerg <sub>SDD</sub>	9.5	1,154	0.0024	1.2	6,154	0.3317
Flo <sub>SDD</sub>	49.4	1,125	<0.0001	10.6	6,125	<0.0001

**Table B6.** Pairwise comparisons of cover crop traits in the cover crop trials depending on combined crop family x area of origin factors using a non-parametric Dunn test. All pairwise were tested but only the significative comparisons are described. Crop families are abbreviated: Asteraceae (Astera.), Brassicaceae (Brassica.), Fabaceae (Faba.), Poaceae (Poa.) and Polygonaceae (Polyg.). Area of origin is abbreviated: temperate (Temp.) and tropical (Trop.).

Crop trait	Factor		Z	P.value
COV <sub>MEAN</sub>	Astera. Temp.	Faba. Temp.	2.21	0.0134
	Faba. Temp.	Poa. Trop	-2.27	0.0114
COV <sub>RATE</sub>	Astera. Temp.	Faba. Temp.	2.63	0.0043
	Faba. Temp.	Poa. Trop	-2.59	0.0049
COV <sub>MAX</sub>	Faba. Temp.	Faba. Trop.	-3.38	0.0004
	Faba. Temp.	Poa. Trop	-2.66	0.0039
H <sub>RATE</sub>	Astera. Temp.	Faba. Temp.	3.55	0.0002
	Faba. Temp.	Faba. Trop.	-4.18	<0.0001
	Astera. Temp.	Poa. Temp.	2.64	0.0041
	Faba. Trop.	Poa. Temp.	2.27	0.0116
	Brassica. Temp.	Poa. Trop.	-3.19	0.0007
	Faba. Temp.	Poa. Trop.	-5.43	<0.0001
	Faba. Trop.	Poa. Trop.	-3.20	0.0007
	Poa. Temp.	Poa. Trop.	-3.99	<0.0001
Leaf <sub>RATE</sub>	Astera. Temp.	Poa. Temp.	2.04	0.0205
	Brassica. Temp.	Poa. Temp.	2.35	0.0094
	Faba. Temp.	Poa. Temp.	2.88	0.0019
	Faba. Trop.	Poa. Temp.	4.32	<0.0001
	Faba. Temp.	Poa. Trop.	2.25	0.0124
	Faba. Trop.	Poa. Trop.	3.85	<0.0001
	Poa. Temp.	Polyg. Temp.	-2.22	0.0131
Emerg <sub>SDD</sub>	Brassica. Temp.	Faba. Trop.	-2.01	0.0223
Flo <sub>SDD</sub>	Astera. Temp.	Poa. Temp.	-2.52	0.0057
	Faba. Temp.	Poa. Temp.	-2.45	0.0072
	Faba. Trop.	Poa. Temp.	-2.29	0.0111
	Faba. Trop.	Poa. Trop.	2.18	0.0146
	Poa. Temp.	Poa. Trop.	3.04	0.0012
	Poa. Temp.	Polyg. Temp.	2.79	0.0026



**Fig B2.** Rate of increase in ground cover (COV<sub>RATE</sub>, a), leaf appearance rate (Leaf<sub>RATE</sub>, b), maximum ground cover (COV<sub>MAX</sub>, c), thermal time for emergence (Emerg<sub>SDD</sub>, d), rate of increase in height (H<sub>RATE</sub>, e) and thermal time for flowering (Flos<sub>SDD</sub>, f) of cover crop used in the cover crop trials depending on the crop family and area of origin (temperate or tropical) on one hand and the life cycle in the other hand (annual or perennial). Crop families are abbreviated: Asteraceae (Astera.), Brassicaceae (Brassi.), Fabaceae (Faba.), Poaceae (Poa.) and Polygonaceae (Polyg.). Life cycle is abbreviated: perennial (Peren.). The number of samples in each category is indicated by “n”. The differences between combinations of factors were tested using a Dunn test and indicated by letters a, b and c.



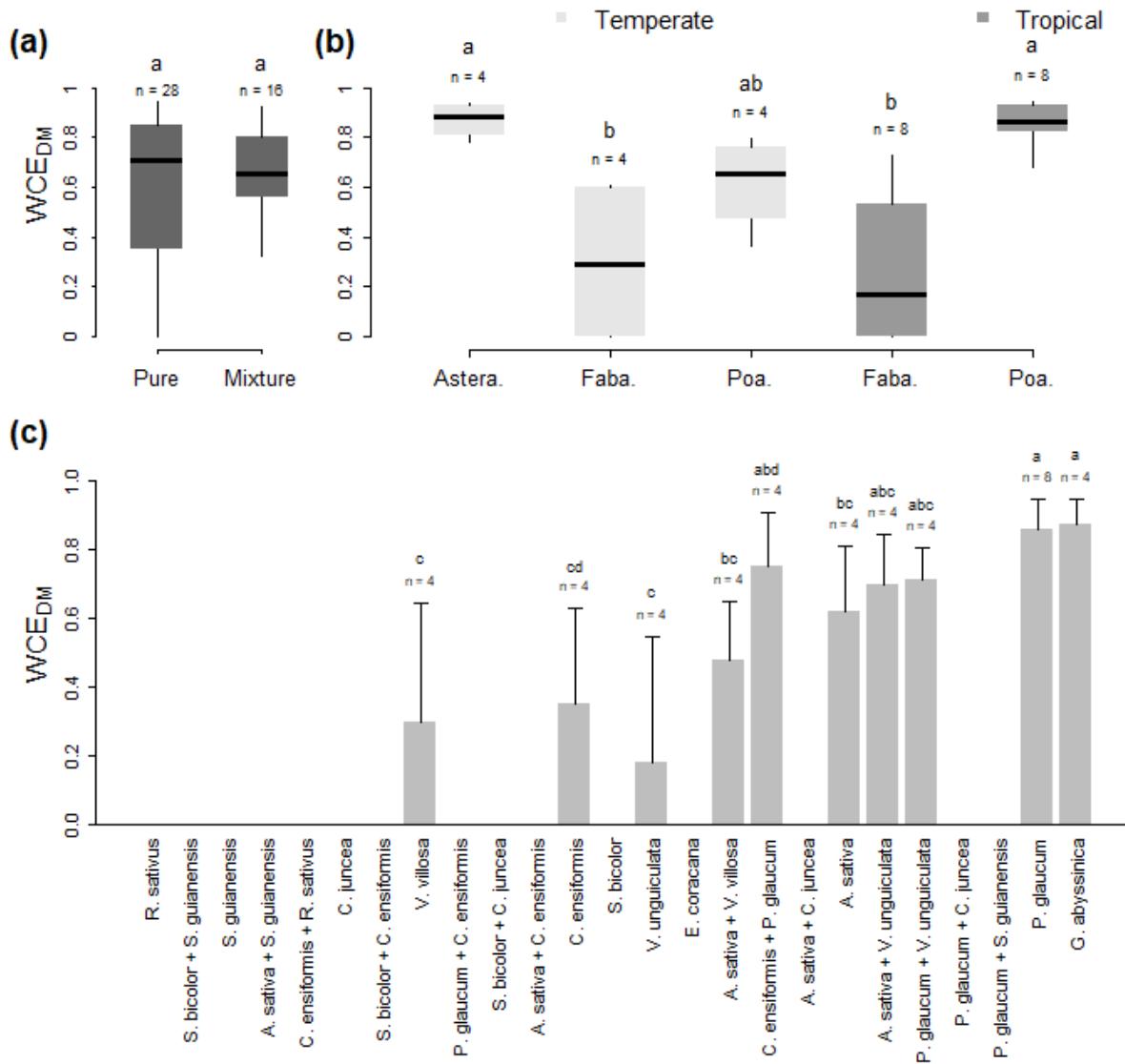
**Fig B3.** Spearman correlation between cover crop traits in the Fabaceae (a) or non-Fabaceae species (b) in the cover crop trials. In Fabaceae, the number of individuals was 201 for COV<sub>MEAN</sub>, COV<sub>RATE</sub> and COV<sub>MAX</sub>, and 132, 122, 141 and 120 for H<sub>RATE</sub>, Leaf<sub>RATE</sub>, Emerg<sub>SDD</sub> and Flo<sub>SDD</sub>, respectively. In non-Fabaceae, the number of individuals was 53 for COV<sub>MEAN</sub>, COV<sub>RATE</sub> and COV<sub>MAX</sub>, and 36, 36, 24 and 16 for H<sub>RATE</sub>, Leaf<sub>RATE</sub>, Emerg<sub>SDD</sub> and Flo<sub>SDD</sub>, respectively.

**Table B7.** Variance analysis on weed control efficiency in terms of ground cover (WCE<sub>Cov</sub>) or dry mass (WCE<sub>DM</sub>) in the weed control trials using a mixed linear model with the crop type (pure or mixture) or the combined crop family x area of origin within pure crops as fixed effects, and the trial identification as random effect.

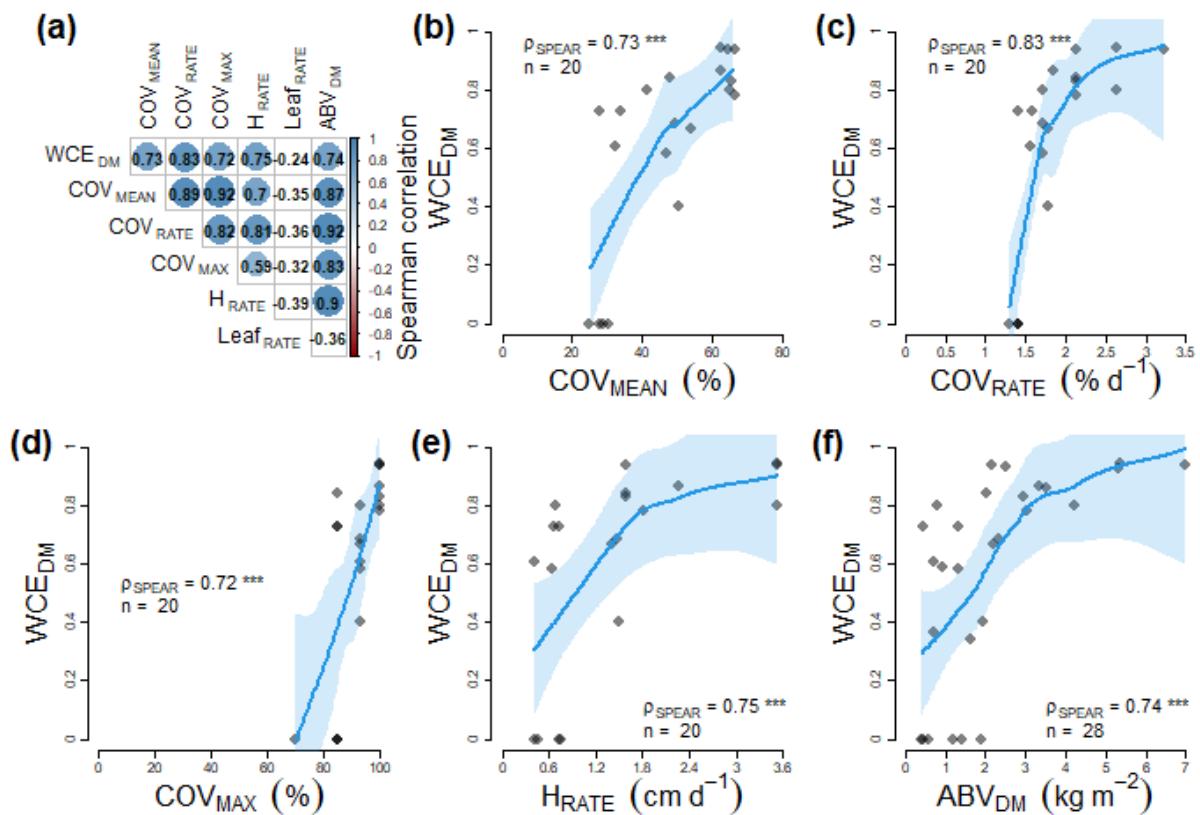
<b>Crop trait</b>	<b>Crop type (pure vs. mixture)</b>			<b>Family x area of origin (pure)</b>		
	F	df	p	F	df	P
WCE <sub>Cov</sub>	0.03	1,66	0.8652	8.34	5,36	<0.0001
WCE <sub>DM</sub>	0.78	1,41	0.3807	9.88	4,22	0.0001

**Table B8.** Pairwise comparisons of weed control efficiency in the weed control trials depending on combined crop family x area of origin factors using a non-parametric Dunn test. All pairwise were tested but only the significative comparisons are described. Crop families are abbreviated: Asteraceae (Astera.), Brassicaceae (Brassica.), Fabaceae (Faba.), Poaceae (Poa.) and Polygonaceae (Polyg.). Area of origin is abbreviated: temperate (Temp.) and tropical (Trop.).

<b>Crop trait</b>	<b>Factor</b>		<b>Z</b>	<b>P.value</b>
WCE <sub>Cov</sub>	Astera. Temp.	Brassica. Temp.	3.28	0.0005
	Astera. Temp.	Faba. Temp.	2.21	0.0136
	Astera. Temp.	Faba. Trop.	3.45	0.0003
	Brassica. Temp.	Poa. Temp.	-2.23	0.0130
	Faba. Trop.	Poa. Temp.	-2.08	0.0186
	Brassica. Temp.	Poa. Trop.	-2.96	0.0015
	Faba. Trop.	Poa. Trop.	-3.49	0.0002
WCE <sub>DM</sub>	Astera. Temp.	Faba. Temp.	2.55	0.0054
	Astera. Temp.	Faba. Trop.	2.98	0.0014
	Faba. Temp.	Poa. Trop.	-2.92	0.0018
	Faba. Trop.	Poa. Trop.	-3.62	0.0001



**Fig. B4.** Weed control efficiency in terms of weed dry mass (WCE<sub>DM</sub>) in pure cover plots or a mixture of two cover crops (a), depending on crop family and area of origin in pure plots (b) or depending on cover crop species (c) in the four weed control trials. Crop families are abbreviated for Asteraceae (Astera.), Brassicaceae (Brassica.), Fabaceae (Faba.) and Poaceae (Poa.). The difference between factors was tested using Dunn's test and is indicated by letters a, b and c. The number of samples in each category is indicated by "n".



**Fig B5.** Spearman correlation between cover crop traits in pure stand in the weed control trials (a). Significant positive and negative correlations are in blue and red circles, respectively. Change in weed control efficiency based on weed dry mass (WCE<sub>DM</sub>) in pure crops depending on cover crop traits: mean ground cover (COV<sub>MEAN</sub>, b), rate of increase in ground cover (COV<sub>RATE</sub>, c), maximum ground cover (COV<sub>MAX</sub>, d), rate of increase in height (H<sub>RATE</sub>, e) and aboveground dry mass (ABV<sub>DM</sub>, f) are detailed. The number of samples (n) and the Spearman correlation coefficient ( $\rho_{\text{SPEAR}}$ ) are indicated. Polynomial smooth regression between weed control and crop traits were added (blue line) with confidence interval (area shaded in light blue).