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1 **Short title:** Cover crop mixture and weed control in Reunion Island

2 **Weed control under increasing cover crops diversity in tropical summer and winter.**

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12

13 **Author contributions:** Conceptualization and Methodology: AN, PM, PT and MC; Data
14 collection AN, JH, PV, MS and PT; Data curation and formal analysis: AN, PM, AR, SA and
15 MC; Writing – Original Draft: AN, PM, MC ; Writing – Review & Editing: all authors ;
16 Supervision and Project administration: MC and PM.

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24 **Abstract:**

25 **Description of the subject.** Weed pressure is a main biotic constraint in tropical agriculture. Cover crop
26 mixtures have increased in popularity to limit weed growth through competition for shared resources,
27 but the relationship between cover crop diversity and weed suppression is still under debate.

28 **Objectives.** This study aimed to assess the impact of increasing cover crops diversity (one to four
29 species) on weed control during two growing seasons (tropical summer and winter) in Reunion Island.

30 **Methods.** Weed control was expressed regarding ground cover by weeds and weed aboveground dry
31 mass and linked to cover crop traits in the mixtures during four months of growth.

32 **Results.** While cover crops reduced weed ground cover and dry mass by 60% and 68% on average in
33 summer and winter, respectively, a higher number of cover crops species within a mixture did not
34 increase mean weed control but decreased weed control variability in summer. Additionally, cover crop
35 traits explaining weed control differed between growing seasons. In summer, weed control was mainly
36 explained by the final cover crop aboveground biomass and leaf area (depletion strategy). In contrast,
37 weed control was mainly explained by the cover crop rate of increase in ground cover (obstruction
38 strategy) in winter.

39 **Conclusions.** Using functional traits to characterize cover crop mixture enables us to identify mixture
40 of species and traits adapted to different growing conditions. Despite being limited to one service, future
41 studies could use this approach to assess the relationship between diversity and the multifunctionality
42 of cover crop mixtures.

43 **Keywords:** cover plants; mixed cropping; weed control; plant competition; tropical agriculture; Réunion

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49 **Résumé**

50 **Description du sujet.** La pression des adventices est une contrainte biotique majeure dans les systèmes
51 de culture tropicaux. Les mélanges de plantes de services ont gagné en popularité pour limiter la
52 croissance des adventices par la compétition pour les ressources, mais la relation entre la diversité des
53 plantes de services et la suppression des adventices est encore en débat.

54 **Objectifs.** Cette étude visait à évaluer l'impact de l'augmentation de la diversité des plantes de services
55 (une à quatre espèces) sur la maîtrise des mauvaises herbes pendant deux saisons de croissance (été
56 tropical et hiver) sur l'île de la Réunion.

57 **Méthodes.** Le contrôle des adventices a été exprimé en fonction de la couverture du sol et de la masse
58 sèche aérienne des adventices, et lié aux traits des plantes de services dans les mélanges pendant quatre
59 mois de croissance.

60 **Résultats.** Alors que les plantes de services ont réduit le recouvrement et la masse sèche des adventices
61 de 60% et 68% en moyenne en été et en hiver, respectivement, un nombre plus élevé d'espèces dans un
62 mélange n'a pas augmenté la maîtrise moyenne des adventices mais a diminué sa variabilité en été. De
63 plus, les traits fonctionnels des plantes de services expliquant la maîtrise des adventices différaient selon
64 les saisons. En été, la maîtrise des adventices a été principalement expliqué par la biomasse aérienne et
65 la surface foliaire des plantes de service (stratégie d' « épuisement »). En revanche, en hiver, la maîtrise
66 des adventices a été principalement expliqué par la vitesse de recouvrement des plantes de service
67 (stratégie d' « obstruction »).

68 **Conclusions.** L'utilisation de traits fonctionnels pour caractériser les mélanges de plantes de services
69 nous a permis d'identifier des mélanges d'espèces et de traits adaptés à différentes conditions de
70 croissance. Bien que limitée à un service, cette approche pourrait être utilisée dans de futures études
71 pour évaluer la relation entre la diversité et la multifonctionnalité des mélanges de plantes de services.

72 **Mots clés:** Plante de couverture; culture en mélange ; désherbage ; compétition végétale ; agriculture
73 tropicale ; Réunion

74 **1. Introduction**

75

76 Faced with climate change and environmental and public health problems, the new challenge for crop
77 science is to make current agriculture more sustainable by increasing production and limiting the use of
78 inputs (Hunter et al., 2017). In most tropical areas, weeds pressure is a main biotic constraint to
79 agriculture (FAO, 2017). It can induce a loss of yields in terms of quality and quantity (Oerke, 2006).
80 The climate is favorable for weed growth, and chemical inputs are often used to control them (Oerke et
81 al., 2004). Under new societal and environmental pressures, there is a growing need for alternatives to
82 herbicides.

83 The use of cover crops before planting (Lu et al., 2000) or during crop growth as an intercrop
84 (Vandermeer, 1992) to control weeds can be one of these alternatives (Bhaskar et al., 2018; Mennan et
85 al., 2020). These plants are increasingly used in innovative cropping systems to deliver well-
86 characterized agro-ecosystem services such as erosion control (Quinton et al., 1997), improvements in
87 soil structure and health (Snapp et al., 2005; Wortman et al., 2012; Kocira et al., 2020), pest and disease
88 regulation (Teasdale, 1996) or suppressing weeds (Bàrberi, 2002; Altieri et al., 2011; Christina et al.,
89 2021). But species cannot perform all desired services, and effectiveness depends strongly on the choice
90 of species (Snapp et al., 2005, 2005; Damour et al., 2015; McKenzie-Gopsill et al., 2022). By increasing
91 diversity in mixtures, the various services of cover crops may be enhanced and stabilized (Wortman et
92 al., 2012; Finney et al., 2016; Rouge et al., 2022). Nonetheless, several studies have failed to find
93 evidence in support of this hypothesis in annual cover-cropping systems (Smith et al., 2014, 2020;
94 Florence et al., 2019, 2020), highlighting the crucial role of species selection in crop mixture
95 (McKenzie-Gopsill et al., 2022).

96 The stability hypothesis is based on interspecific interactions between cover crops, particularly niche
97 complementarity (Vandermeer, 1992; Damour et al., 2014, 2015; Tribouillois et al., 2015) and
98 facilitation (Høgh-Jensen et al., 2010). The objective of mixtures is to efficiently share resources among
99 species (Tilman et al., 2014). Each species within a mixture can have different competitive, acquisition
100 and use of resources strategies, in terms of light interception (Tardy et al., 2015; Damour et al., 2016),

101 water absorption, or nutrients uptake (*e.g.*, nitrogen, Høgh-Jensen et al., 2010; Tardy et al., 2015;
102 Tribouillois et al., 2015) The choice of species allows orientating these strategies to determine the
103 potential performance of the mixtures (Malézieux et al., 2009; Holmes et al., 2017).

104 Approaches based on functional traits are particularly relevant to characterize the interactions among
105 cover crops within a mixture. A functional trait is defined as a morpho-physio-phenological feature,
106 which is measurable at the plant or group of plants level and impacts plant performances (Violle et al.,
107 2007). Traits can be considered an indicator of plant-driven processes and make it possible to compare
108 wide ranges of plants as, for example, cover crops. Although trait-based approaches have been
109 extensively used in natural ecosystems, applications of these approaches to agroecosystems remain
110 relatively new (Garnier et al., 2012; Damour et al., 2014, 2016; Tardy et al., 2015). However, they can
111 represent a high potential to identify the most suitable traits to study the role of mixtures or each species
112 in mixtures.

113 In Reunion Island, weed pressure is a major constraint for agriculture. Due to a growing demand for
114 viable alternatives to herbicides, the 2018 Ecophyto II program aims to reduce the use of herbicides in
115 the French agricultural sector by 50% by 2025. Cover crop mixtures appeared as an alternative to
116 herbicides in many cropping-system in Reunion Island (Christina et al., 2021). Based on the literature,
117 we hypothesized that increasing the species diversity in cover crop mixtures will enhance weed control.
118 Currently, this type of study is rare in tropical cropping-system and the weed control efficiency of
119 mixture compared to pure cover crops is still under debate. A trait-based approach makes it possible to
120 characterize the different mixtures and their ability to suppress weed growth. The objectives of this study
121 were i) to assess the weed control efficiency depending on the number of species in cover crop mixtures,
122 ii) to identify traits responsible for this control in mixtures and iii) to assess the influence of species
123 selection in the mixture. Field experiments with cover crops were performed during two growing
124 seasons in Reunion Island (tropical summer and winter), with an increasing number of cover crops from
125 one to four species in the mixture.

126

127 **2. Materials and methods**

128

129 **2.1. Experimental site**

130 The field experiment was conducted from 2019 to 2020 at the CIRAD experimental station of Bassin
131 Plat in Reunion Island (-21.323, 55.491) at an altitude of 150 m a.s.l. On average, annual precipitation
132 in this site was 850 mm year⁻¹ (data from 2002 to 2019), with mean monthly temperatures ranging from
133 20.0°C (July, austral winter) to 26.1°C (January, austral summer). During the trials, mean temperatures
134 were 25.6°C and 20.1°C in summer and winter, respectively, and average rainfall was 147 and 33 mm
135 month⁻¹ in summer and winter, respectively (Table S1). The soil type was classified as an andic cambisol
136 (WRB classification) with main characteristics in Table S2. The dominant weed flora present during the
137 two trials was listed in Table S3.

138 **2.2. Experimental design**

139 The experimental design consisted of two trials performed in austral summer (from November to March)
140 and in austral winter (from May to September) using tropical and temperate cover crop species (Table
141 1). Each trial was a complete randomized design with 13 treatments repeated three times (Figure S1,
142 Table S4). In both trials, treatments 1 to 4 were plots with one cover crop species sown, treatments 5 to
143 8 and treatments 9 to 12 were plots with mixtures of two and three species sown, respectively. Treatment
144 number 14 was a treatment with a mixture of four species sown and was repeated four times. Treatment
145 plots were associated with a total of 20 neighbor control plots where only weeds were grown without
146 intervention. Treatment plots with cover crops were 8 m² (2 m x 4 m) and weed plots were 3 m² (2 m x
147 1.5 m).

148 **2.3. Cover crop species**

149 A total of 7 cover crops species were tested in this experiment, with one common species between the
150 two trials. They were Asteraceae, Brassicaceae, Fabaceae and Poaceae plants. *Guizotia abyssinica* was
151 used in both trials because it can grow in both seasons (Tribouillois et al., 2016; Christina et al., 2021).
152 The mixtures were chosen according to the botanical family, the origin (temperate or tropical) and the

153 plant growth habit (Table 1) among a wide range of cover crop species already tested in Reunion Island
154 (Christina et al. 2021).

155

156 **Table 1.** List of cover crop species used in the summer and winter trials. Species, family, growth type
157 and origin are indicated. An identification code (ID) will be used in the study.

Species	Family	Growth	Origin	ID	Trials
<i>Canavalia ensiformis</i> (L.) DC.	Fabaceae	Twining	Tropical	Ce	Summer
<i>Pennisetum glaucum</i> (L.) R.Br.	Poaceae	Erected	Tropical	Pg	Summer
<i>Vigna radiata</i> (L.) R.Wilczek	Fabaceae	Twining	Tropical	Vr	Summer
<i>Avena strigosa</i> Schreb.	Poaceae	Erected	Temperate	As	Winter
<i>Brassica carinata</i> A.Braun	Brassicaceae	Erected	Temperate	Bc	Winter
<i>Vicia villosa</i> Roth	Fabaceae	Twining	Temperate	Vv	Winter
<i>Guizotia abyssinica</i> (L.f.) Cass.	Asteraceae	Erected	Temperate	Ga	Winter & Summer

158

159 **2.4. Experimental management**

160 Soil tillage was performed before sowing using a rototiller. The first trial was sown manually on the 12th
161 of November 2019 and harvested on the 3rd of March 2020. The second trial was sown manually on the
162 20th of May 2020 and harvested on the 4th of September 2020. Seed sowing densities were indicated in
163 Table S4. When cover crops were mixed, the sowing density of pure plots was divided by the number
164 of species. Both trials were fertilized manually at sowing with 300 kg ha⁻¹ of 15-12-24 (N-P-K). Finally,
165 both trials were irrigated with around 10 mm per week, divided into three applications. For both trials,
166 the paths between plots were maintained with brush cutter.

167 **2.5. Trait measurements**

168 Trait measurements were performed during the cover crop growth (ground cover and height) and at the
169 end of each experiment (3.5 months after sowing) for destructive measurements such as biomass and
170 specific leaf area (Table 2). The same protocol was used in both summer and winter trials. Ground cover
171 by cover crops or weeds was measured in each plot using a visual notation method described in Table
172 S5 and used in previous studies (Marnotte, 1984; Mansuy et al., 2019; Christina et al., 2021). Notations

173 were made weekly the first month and every two weeks until cover crop harvest. The ground cover was
174 assessed for each individual cover crop species in treatment plots and weeds as a whole in both treatment
175 and control plots. Between two measurement dates, the ground cover was linearly extrapolated each day
176 and the mean ground cover (COV_{MEAN} , %) was calculated from sowing to harvest. The maximum cover
177 (COV_{MAX} , %) was defined as the maximum value of cover reached by the species concerned. A rate of
178 increase in ground cover per day (COV_{RATE} , % d⁻¹) was calculated as the COV_{MAX} divided by the number
179 of days needed to reach it after sowing. Additionally, the height of 4 individuals per cover crop species
180 was measured on the same date that ground cover in each treatment plot. The rate of increase in height
181 (H_{RATE} , cm d⁻¹) was calculated as the slope of the linear regression between the height of the cover crops
182 and the number of days since sowing up to reaching the maximum height.

183 At harvest, the fresh aboveground biomass of the whole treatment and control plots was measured and
184 separated into each cover crop species and the whole weeds. A sample of each cover crop species and
185 weeds was dried at 60°C for 48 hours, and dry weights were used to assess the aboveground dry mass
186 (ADM, kg m⁻²) and the dry matter content (DMC, %) of each cover crops and weeds. For cover crops
187 samples, leaves were separated to calculate the dry leaves to aboveground mass fraction (LMF). For
188 each species in the whole trial, fresh leaves were selected from 5 individuals, leaf area was measured
189 with the EasyLeafArea software (Easlon et al., 2014), and specific leaf area was calculated based on dry
190 mass (SLA, cm² g⁻¹). The SLA was used to estimate the leaf area index of each cover crop species (LAI,
191 m² m⁻²). In each treatment plot, a mean cover crop trait was calculated for the whole mixture of cover
192 crops ($Trait_{MIX}$) and weighted by the COV_{MEAN} of each individual species, as follows:

193
$$Trait_{MIX} = \frac{\sum_1^n Trait_{CC} * COV_{MEAN}}{\sum_1^n COV_{MEAN}}$$

194 Where $Trait_{CC}$ is the trait of each cover crop and n the number of cover crops within the mixture.

195

196

197

198 **2.6. Weed control efficiency**

199 In addition to cover crop trait, two indexes were calculated to assess weed control efficiency based on
 200 weed ground cover (WCE_{COV}) and weed dry mass (WCE_{ADM}). At harvest, the WCE_{COV} was calculated
 201 in each treatment plot as:

$$202 \quad WCE_{COV} = 1 - \frac{COV_{MEAN_{weed,treatment}}}{COV_{MEAN_{weed,control}}}$$

203 Where $COV_{MEAN_{weed,treatment}}$ is the mean ground cover by weeds in the treatment plot and
 204 $COV_{MEAN_{weed,control}}$ the mean ground cover by weeds in the three nearest control plot during the whole
 205 trial. A similar equation using the weed dry mass at harvest was used for WCE_{ADM} calculation.

206

207 **Table 2.** List of cover crop traits and weed control efficiency indexes used in the study.

Traits	Description	Unit
ADM	Aboveground dry mass at harvest	Kg m ⁻²
DMC	Aboveground dry mass content at harvest	%
LMF	Leaf to aboveground mass fraction at harvest	Ø
LAI	Leaf area index at harvest	m ² m ⁻²
H _{RATE}	Rate of increase in height up to maximum height	cm d ⁻¹
COV _{RATE}	Rate of increase in ground cover up to maximum ground cover	% d ⁻¹
Efficiency indexes		
WCE _{COV}	Weed control efficiency based on mean weed ground cover	Ø
WCE _{ADM}	Weed control efficiency based on weed dry mass at harvest	Ø

208

209 **2.7. Data analyses**

210 All experimental data on this study are available online on CIRAD dataverse (Négrier et al., 2022;
 211 <https://doi.org/10.18167/DVN1/WPGRAM>). All analyses and plots were performed with R 4.0 (R
 212 Development Core Team, 2020). First, the influence of the number of cover crop species, the day after
 213 sowing and their interaction on ground cover by weeds were tested using a mixed linear analysis of
 214 variance with the plot identification as random effect in both summer and winter season, separately (lme
 215 function from nlme package, Pinheiro et al., 2022). In each season, ground cover was transformed using

216 the Boxcox function to ensure residue normality (MASS package, Venables et al., 2013). The influence
217 of the number of cover crop species on ground cover by weeds was then tested at each day after sowing
218 using a linear analysis of variance followed by a Holm p value adjustment method (Holm, 1979). The
219 influence of the number of cover crop species as well as the mixture composition on WCE_{COV} and
220 WCE_{ADM} were tested using a linear analysis of variance followed by a Least Significant Difference test
221 (LSD.test function from agricolae package, de Mendiburu, 2020).

222 For each growing season and after assessing pearson correlations among cover crop traits (R package
223 corrplot, Wei et al., 2022), structural equation models (SEM, R package piecewiseSEM, Lefcheck,
224 2016) were built to identify and mathematically characterize the direct impact of COV_{RATE} , LAI and
225 ADM on weed control efficiency. An indirect effect of LMF and COV_{RATE} on LAI and ADM were
226 accounted for when building SEM. Additionally, a correlation without causal relationship was assumed
227 between LAI and ADM. The fit of the model was evaluated using the AIC, BIC and the global goodness-
228 fit-criteria (Fisher's C test). The variables selected in the model were removed when the path coefficient
229 was not significant ($p > 0.05$).

230 In each growing season, a principal component analysis (PCA) was performed on WCE_{COV} , WCE_{ADM} ,
231 ADM, LAI, COV_{RATE} and LMF with FactoMineR (Lê et al., 2008) and factoextra (Kassambara et al.,
232 2020) R packages. The influence of the presence of absence of a given species on the two first
233 components values of the PCA was tested using a non-parametric Wilcoxon test.

234

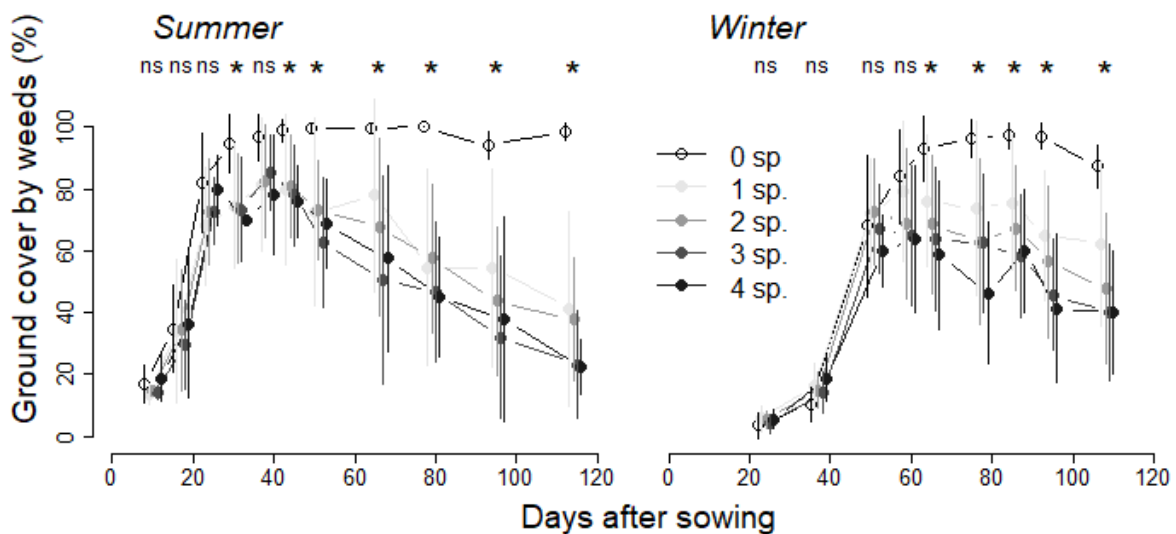
235 **3. Results**

236

237 **3.1. Time-course of weed ground cover**

238 Ground cover by weeds was significantly influenced by the interaction between the number of cover
239 crop species and the number of days after sowing, both in summer ($F_{4,595}=23.9, p<0.0001$) and in winter
240 ($F_{4,555}=17.2, p<0.0001$, Figure 1, Table S6). In control plots, ground cover by weeds increased up to
241 more than 90% and peaked at this level around 30 days and 60 days after sowing in summer and winter,
242 respectively. In the plots with cover crop, the mean ground cover by weeds across treatments reached
243 82 and 70% at the same date before decreasing to 31 and 48% at the end of the experiment, in summer
244 and winter, respectively. At the beginning of the growth, ground cover by weeds was not influenced by
245 the number of cover crop species. The difference in ground cover started to be significant after reaching
246 the peak in ground cover.

247



248

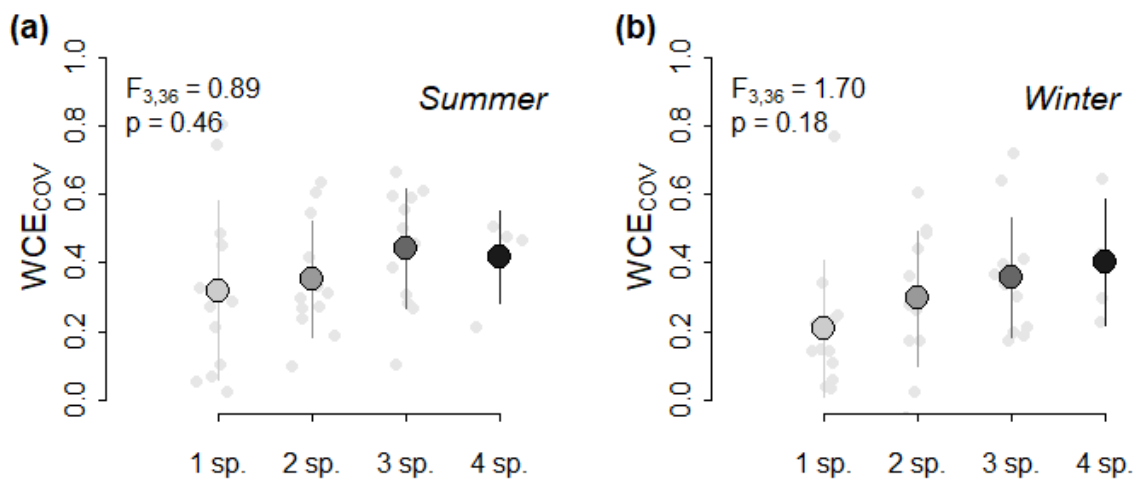
249 **Figure 1.** Time-course of ground cover by weeds depending on the number of cover crop species (sp.)
250 in the mixture in the summer and winter trials. Mean and standard error bars are represented. The effect
251 of number of cover crop species at each date of measurements was tested using a linear analysis of
252 variance and indicated as “*” when p.value was lower than 0.05 and “ns” when non-significative.

253

254

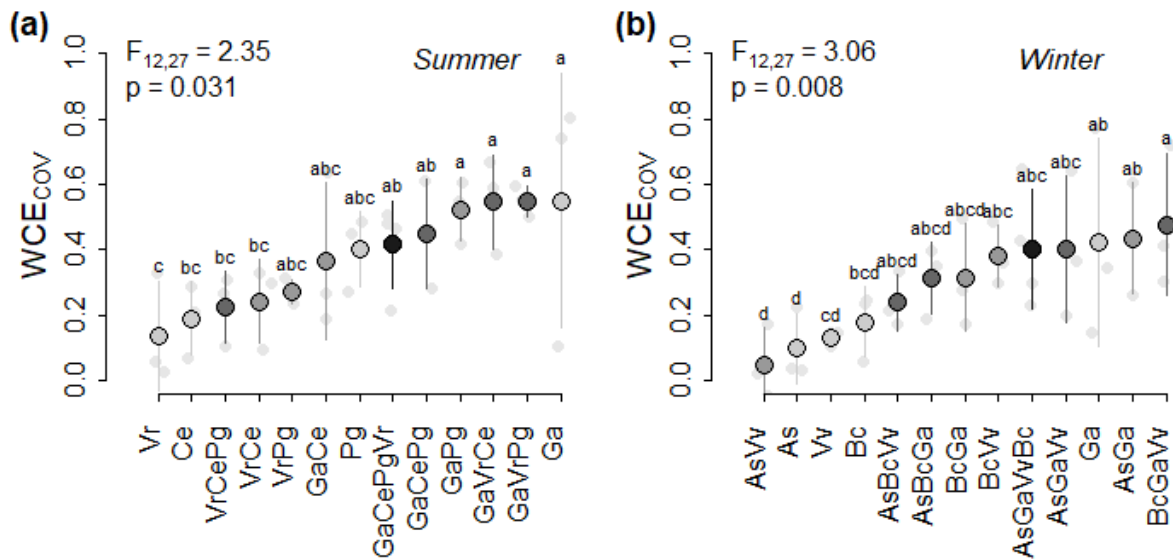
3.2. Weed control efficiency depending on mixtures

255 WCE_{COV} and WCE_{ADM} were not statistically different depending on the number of cover crop species
256 within the plot, whatever growing season (Figure 2, Figure S2, Table S7). Across all treatments, the
257 mean WCE_{COV} was 0.38 and 0.30 in summer and winter, respectively, and the mean WCE_{ADM} was 0.42
258 and 0.34 in summer and winter, respectively. In summer, the standard deviation of WCE_{COV} and
259 WCE_{ADM} reduced from 0.26 to 0.13 and from 0.40 to 0.22, respectively, with increasing species in the
260 mixture (Figure 2, Figure S2). On the contrary, the standard deviation was relatively constant across
261 treatments in winter. Nonetheless, mean WCE_{COV} was significantly influenced by some of the cover
262 crop mixtures both in summer and winter (Figure 3, Figure S3). WCE_{ADM} was also influenced by the
263 cover crop mixture but only in summer. In summer, the cover crops with the significantly lowest
264 WCE_{COV} and WCE_{ADM} were Vr and Ce pure crops and their VrCe mixtures, while the cover crops with
265 the significantly highest WCE_{COV} were Ga pure crops as well as mixtures including Ga (GaVrPg and
266 GaVrCe, Figure 3a). In winter, the cover crops with the significantly highest WCE_{COV} were also
267 mixtures and pure Ga crops (Figure 3b).



268

269 **Figure 2.** Weed control efficiency in terms of weed ground cover (WCE_{COV}) depending on the number
270 of cover crop species (sp.) in the mixture during summer (a) and winter (b) trials. The influence of the
271 number of species was tested using linear analysis of variance. F statistics, degree of freedom and p
272 value were indicated.

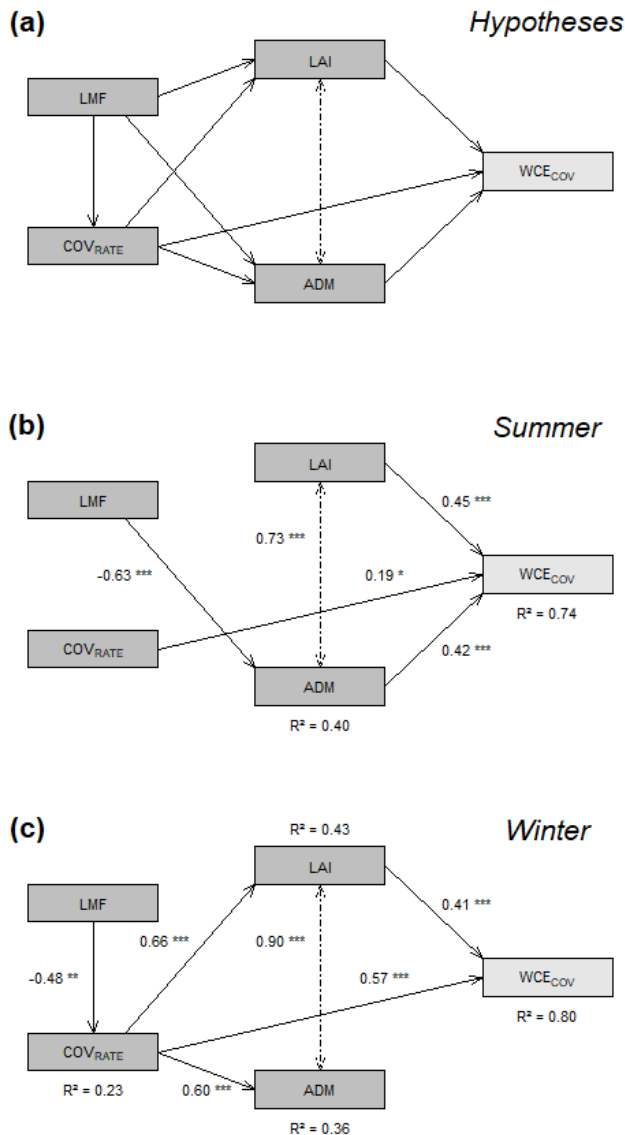


273

274 **Figure 3.** Weed control efficiency in terms of weed ground cover (WCE_{COV}) depending on cover crop
 275 mixtures. WCE_{COV} are presented in the summer (a) and winter trials (b). The influence of cover crop
 276 mixtures on WCE_{COV} was tested using linear analysis of variance. F statistics and p value were indicated.
 277 Differences between each mixture were tested using a LSD test and indicated by letters (“a,” “b,” “c”
 278 and “d”) when p-value was lower than 0.05.

279 3.3. Weed control and cover crop traits

280 Based on multiple correlations among cover crop traits (Figure S4, Figure S5), a structural equation
 281 modeling approach was performed to test the influence of the rate of increase in ground cover after
 282 sowing (COV_{RATE}) and the final cover crop(s) development (ADM and LAI at harvest) on WCE_{COV}
 283 (Figure 4a). In summer, the variation in WCE_{COV} was explained ($R^2 = 0.74$) by a direct and positive
 284 effect of LAI, ADM and COV_{RATE} and an indirect effect of LMF through ADM (Figure 4b).
 285 Nonetheless, COV_{RATE} only explained 4% of WCE_{COV} variance in summer. In winter, WCE_{COV} variance
 286 was explained ($R^2=0.80$) by a direct effect of COV_{RATE} and LAI as well as an indirect effect of COV_{RATE}
 287 through LAI and an indirect effect of LMF through COV_{RATE} (Figure 4c). The direct effect (0.47) of
 288 COV_{RATE} on WCE_{COV} was about twice as large as its indirect effect (0.27). On the contrary, ADM had
 289 no direct effect on WCE_{COV} in winter. Similar results were found using the WCE_{DM} (Figure S6). Like
 290 WCE_{COV} and WCE_{ADM} , the number of cover crop species didn’t impact cover crop traits in both growing
 291 seasons (Table S8, S9).



292

293 **Figure 4.** Structural equation model showing direct and indirect effects of cover crop traits on weed
 294 control efficiency in ground cover (WCE_{COV}). Arrows in (a) represent the initial hypothesized structural
 295 equation with variables: cover crop(s) rate of increase in ground cover (COV_{RATE} , % d^{-1}), leaf area index
 296 of the cover crop(s) (LAI , $m^2 m^{-2}$), aboveground dry mass of the cover crop(s) (ADM , $kg m^{-2}$) and leaf
 297 to aboveground mass fraction (LMF). The dashed arrows between LAI and ADM represent a correlation
 298 between these two variables without a causal relationship. The arrows in (b) and (c) represent the
 299 significant result of the analysis in summer and winter, respectively. The asterisks relate the significance
 300 levels of the coefficients ($* < 0.05$, $** < 0.01$, $*** < 0.0001$) and R^2 per predicted variables are given. The
 301 standardized estimates in the model were presented to compare the relative strengths of predictors.

302 **3.4. Weed control and cover crop species**

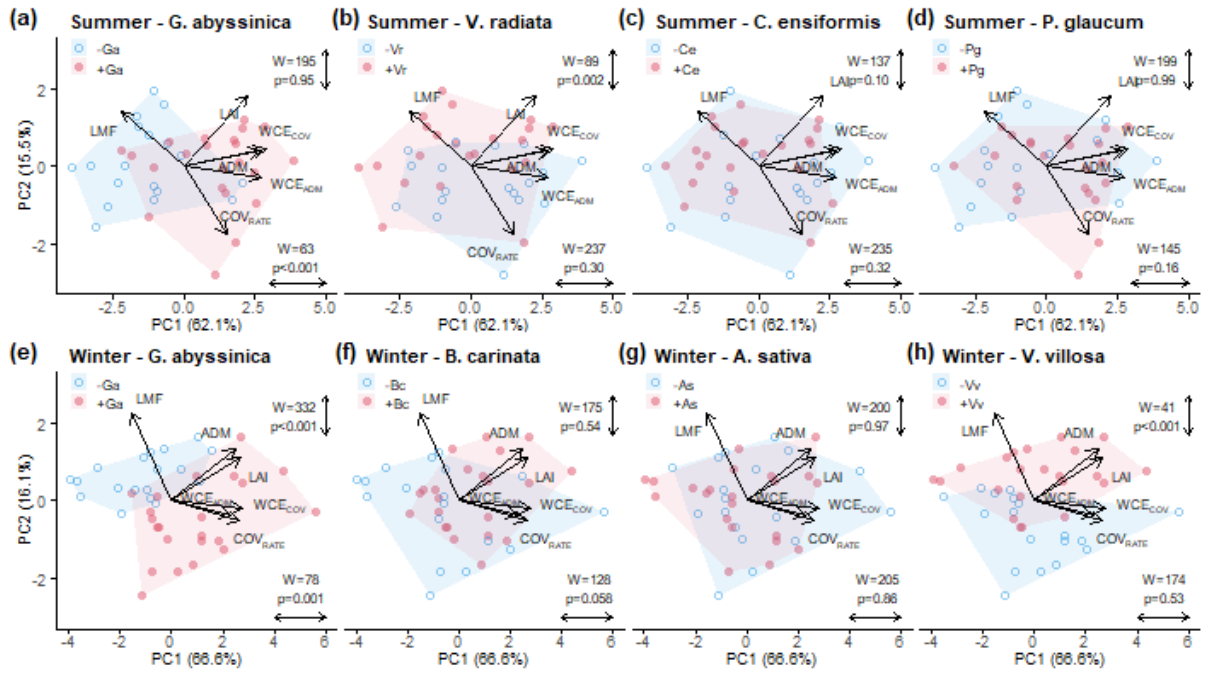
303 The PCA summarized the cover crop traits (LAI, ADM, LMF and COV_{RATE}) and weed control
304 efficiency (WCE_{COV} and WCE_{ADM}) into two axes (PC1 and PC2, Figure 5). In summer (Fig 5a,b,c,d),
305 PC1 (62.1% of the explained variance) was mainly determined by WCE_{COV}, WCE_{ADM} and ADM, while
306 COV_{RATE}, LAI and LMF mainly determined PC2 (15.5% of the explained variance). In winter (Fig
307 5e,f,g,h), PC1 (66.6% of the explained variance) was mainly determined by WCE_{COV}, WCE_{ADM} and
308 COV_{RATE}, while LMF was mainly determined PC2 (16.1% of the explained variance). The presence
309 of *C. ensiformis*, *P. glaucum*, *B. carinata*, *A. sativa* had no impact on PC1 and PC2 values (Figure 5).
310 On the contrary, the presence of *G. abyssinica* significantly increased PC1 both in summer and winter,
311 highlighting how its presence in the cover crop mixture induced an increase in WCE and ADM in
312 summer and an increase in WCE and COV_{RATE} in winter (Figure S7). The presence of *V. villosa* induced
313 an increased in PC2 (correlated with LMF) but no difference in PC1 (correlated with WCE, Figure 5h).

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319 **Figure 5.** Principal component analysis (PCA) on cover crop traits (LAI, ADM, LMF and COV_{RATE})
 320 and weed control efficiencies (WCE_{COV} and WCE_{ADM}) during summer (a,b,c,d) and winter (e,f,g,h)
 321 depending on the presence (+, red filled point) or absence (-, blue open circle) of each species in the
 322 plot: *Guizotia abyssinica* (Ga, a,b), *Vigna radiata* (Vr, b), *Canavalia ensiformis* (Ce, c), *Pennisetum*
 323 *glaucum* (Pg, d), *Brassica carinata* (Bc, f), *Avena sativa* (As, g) and *Vicia villosa* (Vv, h). For each
 324 species, the impact of the presence or absence of the species on the two first components of the PCA
 325 (PC1 and PC2) was tested using a Wilcoxon test (W with p-value) and were indicated in the bottom
 326 right and top right, respectively.

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333 **4. Discussion**

334 As any site-specific study, cover crop mixture performance was linked to the soil and climatic context
335 in our study in the South of Reunion Island. Nevertheless, this study gave enlightened perspectives on
336 weed control by cover crops in tropical summer and winter involving different crop traits and
337 competitive strategies.

338 **4.1. Cover crop mixtures and weed control**

339 Cover crops were able to reduce weed infestation in many different situations (Teasdale, 1996; Bàrberi,
340 2002; Altieri et al., 2011; Cordeau et al., 2017). Our study supports these previous observations: mean
341 weed ground cover was reduced by cover crops, regardless of the number of species in the mixture.
342 Several mechanisms have been highlighted in literature to explain weed control, such as physical
343 interference, resource competition for light, water, nutrients and space (Blanco-Canqui et al., 2015;
344 Tardy et al., 2015; Cordeau et al., 2017) or allelopathy by releasing allelochemicals into the environment
345 (Kunz et al., 2016; Sturm et al., 2018).

346 Interest in using mixtures of cover crop species has grown in recent years. The theory suggests that
347 cover crop mixtures may increase the breadth of services provided (Tilman et al., 2014; Baraibar et al.,
348 2018), as a greater weed suppression (Akemo et al., 2000; Brennan et al., 2005; Lawson et al., 2015;
349 Ranaldo et al., 2020). In our study, increasing the number of cover crop species in the mixture did not
350 increase weed control. No significant difference in weed control efficiency in terms of ground cover or
351 biomass was found between 2, 3 or 4 species mixtures compared to the pure crop. These results are
352 consistent with recent studies showing that cover crop mixtures are no more weed suppressant than the
353 best-performing pure crops (Finney et al., 2016; Baraibar et al., 2018; Osipitan et al., 2018; Schappert
354 et al., 2019; Smith et al., 2020). In particular, Florence et al., (2020) highlighted through a meta-analysis
355 in a systematic review that in 88% of cases, there is no difference between pure crops and mixtures, and
356 only in 2% of cases is the mixture better.

357 A decrease of the variability with an increase of species in the cover crop mixture was observed in
358 summer. These results suggested that diversity increases the resilience of the agrosystem, *i.e.*, there

359 would be less failure when species are mixed. Depending on the species, a single cover crop might not
360 be able to buffer rapidly changing environmental conditions (Wendling et al., 2019). Recent publications
361 showed by increasing diversity in mixtures, the different services of cover crops could be stabilized
362 (Finney et al., 2016; Elhakeem et al., 2021; Franco et al., 2021). Combining species may increase
363 resilience against weather conditions, an advantage in achieving efficient long-term weed control
364 (Lawson et al., 2015; Schappert et al., 2019). Nonetheless, previous studies did not always support this
365 hypothesis (Smith et al., 2014, 2020; Florence et al., 2019), highlighting the importance of species
366 selection. As an example, McKenzie-Gopsill et al., (2022) showed that legumes and mixtures containing
367 legumes were the least stable in terms of weed control in Canada.

368

369 **4.2. Cover crop traits and weed control**

370 In our analysis, the relation between cover crop traits and weed control in mixtures differed depending
371 on the growing season. In our tropical summer, weed control was mainly explained by aboveground
372 biomass (ADM) compared to the rate of increase in ground cover (COV_{RATE}). Plants, especially weeds,
373 grow rapidly with favorable climatic conditions (temperature, light, rainfall and nutrients). Cover crop
374 species with high biomass were more likely to control weeds in tropical summer. Many studies highlight
375 the relationship between biomass and weed control (Holmes et al., 2017; Osipitan et al., 2018; Schappert
376 et al., 2019). For example, Christina et al., (2021) showed that increasing cover crop biomass was
377 positively correlated with weed suppression in Reunion Island, as Finney et al., (2016) in central
378 Pennsylvania in the USA or MacLaren et al., (2019) in South Africa's winter rainfall region. In
379 opposition, COV_{RATE} was the most important trait for weed control in our tropical winter conditions.
380 Due to colder and drier climate conditions and a shorter photoperiod, weeds took longer to grow.
381 Consequently, cover crop species with a fast ground cover rate were more likely to control weeds. These
382 results agreed with other studies suggesting that rapid cover crop development after sowing could be
383 more important than the final cover crop biomass to prevent weed growth (Brennan et al., 2005; Hayden
384 et al., 2012; Dorn et al., 2015; Baraibar et al., 2018).

385 The scientific community does not always agree on the nature of the cover crop traits linked to weed
386 control. Our study suggests that the season (*i.e.*, climatic context) induces different weed control
387 strategies involving different cover crop traits. On the one hand, high growth in biomass can increase
388 the effect of competition (den Hollander et al., 2007; Tobin et al., 2012) through water or soil nutrients
389 (Høgh-Jensen et al., 2010; MacLaren et al., 2019) and light (Tardy et al., 2015; Damour et al., 2016). In
390 that case, cover crops have a “depletion” competition strategy towards weeds. On the other hand, cover
391 crops can invest in rapid ground cover to occupy the soil surface more quickly and avoid the germination
392 and the emergence of weeds. In that case, they have an “obstruction” competition strategy (Tardy et al.,
393 2015). In our study, cover crops which successfully controlled weeds tend to have a “depletion”
394 competition strategy in summer and an “obstruction” competition strategy in winter. Trait
395 complementarity of cover crop species in mixtures could improve weed control stability in innovative
396 cropping systems. Cover crops with interesting traits can be combined, regardless of the number of
397 species in the mixture (Osipitan et al., 2018; Schappert et al., 2019). Nonetheless, further studies are
398 needed to investigate the question of trait complementarity to understand whether weed control
399 efficiency is due to a combination of traits or the presence of a particular species in the mixture.

400

401 **4.3. Cover crops species and weed control**

402 Our results showed pure crop of *G. abyssinica* and mixtures including *G. abyssinica* control weeds better
403 than other mixtures in both seasons. In contrast, the mixtures that less controlled weeds included *C.*
404 *ensifomis* and *V. radiata* in summer and *A. strigosa* and mixtures with *V. villosa* in winter. Usually, tall
405 grasses effectively control weeds due to their rapid growth rate (Baraibar et al., 2018; Christina et al.,
406 2021) or high biomass (Franco et al., 2021; McKenzie-Gopsill et al., 2022). Previous studies also
407 reported that Poaceae were often more efficient in controlling weeds than Fabaceae species (Akemo et
408 al., 2000; Brainard et al., 2011; Baraibar et al., 2018). In our study, while mixtures including *P. glaucum*
409 were efficient in summer in most cases, except for VrPg and VrCePg mixtures, it was not the case for
410 *A. strigosa* in winter. Nonetheless, previous studies have shown that *A. strigosa* can efficiently control
411 weeds, particularly in pure crops (Khan et al., 2019; Schappert et al., 2019; Christina et al., 2021).

412 Despite increasing ADM in the mixtures, *V. villosa* didn't limit weed growth in our study (Figure S7).
413 This species did not perform with Schappert et al., (2019) nor Baraibar et al., (2018) and Hayden et al.,
414 (2012) due to its slow growth rate. This cover crop stayed alive in our trial under weeds and other cover
415 crops. It grew above the canopy only at the end of the trial, rapidly increasing its ground cover. In our
416 climatic conditions, this species is not recommended in short cover crop mixtures. Still, it can be
417 interesting for longer cover cropping when the other cover crops have finished their cycle. The poor
418 results of *V. radiata* may be explained by a germination or emergence problem as its presence in the
419 mixture significantly reduced COV_{RATE} . Finally, while *B. carinata* did not impact weed control in our
420 tropical winter, Holmes et al., (2017) highlighted a decrease in weed biomass with mixtures including
421 mustards. Globally, Brassicaceae species seem to perform well because of their rapid growth and high
422 biomass (Kunz et al., 2016), and they can dominate community biomass in mixtures (Wortman et al.,
423 2012). In our study, winter climatic conditions may not have been suitable for cold season species,
424 especially for *A. strigosa* and *B. carinata*. Thus, *G. abyssinica* seems to be a good candidate for weed
425 management in cropping systems in our tropical conditions as a pure crop or in mixtures. In this study,
426 the number of species and mixtures assessed was too limited to recommend mixtures to farmers. The
427 trait approach allowed us to identify different cover crop strategies that effectively control weeds. It is
428 necessary to transpose these strategies to a broader range of cover crop species to recommend cover
429 crop mixture depending on tropical growing seasons.

430

431 **5. Conclusion**

432 Our study aimed to assess the weed control efficiency under increasing cover crops diversity. Increasing
433 the number of cover crop species in a mixture did not increase weed control but decreased its variability
434 in summer. Combinations of species may increase resilience against climatic conditions and reduce
435 failure probability. Additionally, cover crop traits related to weed control differed according to the
436 growing season. In summer, weed control was mainly explained by cover crops aboveground biomass
437 (depletion strategy). In contrast, weed control was explained primarily by the cover crop rate of increase
438 in ground cover (obstruction strategy) in winter. Among tested species, *Guizotia abyssinica* was the best
439 specie candidate, both in pure or mixed stands and growing seasons. In addition to their ability to control
440 weeds, cover crops provide other ecosystem services in innovative cropping systems. Future studies will
441 be focused on the relation between the diversity of cover crops and the multifunctionality of cover crop
442 mixtures.

443

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449

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