



HAL
open science

Species choice and spatial arrangement in soybean-based intercropping: Levers that drive yield and weed control

Timothée Cheriére, Mathieu Lorin, Guénaëlle Corre-Hellou

► To cite this version:

Timothée Cheriére, Mathieu Lorin, Guénaëlle Corre-Hellou. Species choice and spatial arrangement in soybean-based intercropping: Levers that drive yield and weed control. *Field Crops Research*, 2020, 256, pp.1-10. 10.1016/j.fcr.2020.107923 . hal-03233728

HAL Id: hal-03233728

<https://hal.inrae.fr/hal-03233728>

Submitted on 22 Aug 2022

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.



Distributed under a Creative Commons Attribution - NonCommercial 4.0 International License

1 **Species choice and spatial arrangement in soybean-based intercropping: levers that drive yield and**
2 **weed control.**

3

4 Timothée Cheriére, Mathieu Lorin, Guénaëlle Corre-Hellou

5 USC 1432 LEVA, École Supérieure d'Agriculture (ESA), INRAE, SFR 4207 QUASAV, 55 rue Rabelais, F-
6 49007 Angers, France

7

8 Corresponding author: g.hellou@groupe-esa.com

9

10 **Highlights**

- 11 • The species intercropped with soybean affected soybean production and weed control
- 12 • Soybean yield and weed control are related to the associated crop biomass and height
- 13 • The higher the soybean production was, the larger the weed biomass was
- 14 • The spatial arrangement only affected soybean production, not weed control
- 15 • Alternate-row limit the trade-off in sorghum and buckwheat intercrops

16

17 **Abstract**

18 Soybean is prone to weed infestations and yield variability. With the proposition of using
19 intercropping to overcome these problems, this study explored the effects of combinations of
20 different associated crop species and spatial arrangements on grain production and weed control.

21 In a two-year field experiment in western France, soybean was intercropped with buckwheat, lentil,
22 sorghum and sunflower in two spatial arrangements: within-row intercropping and alternate-row
23 intercropping, to investigate their effects on weed control and soybean production.

24 The results showed that the highest soybean yield occurred in the intercropping with lentil, followed
25 by sorghum and sunflower, and finally buckwheat, but this effect varied by year. The opposite
26 species order was obtained for weed control, revealing a trade-off between soybean production and
27 weed control. We also demonstrated that associated species height was related to soybean yield and

28 weed control. Alternate-row intercropping helped to increase soybean production without
29 compromising weed control for sorghum and buckwheat, which have small height difference with
30 soybean.

31 Finally, our paper showed that combining associated species choice and spatial arrangement allows
32 farmers to manage the trade-off between soybean yield and weed control.

33 **Key words:**

34 Intercropping

35 Cropping systems diversification

36 Soybean

37 Spatial pattern

38

39 **1. Introduction**

40 Intercropping - the growing of two or more crops in the same field for a significant part of their life
41 cycles (Willey, 1979) - is gaining an increasing interest in Europe. Several studies have demonstrated
42 the multiple benefits of intercropping such as a better weed control and improvement of
43 productivity and yield stability compared to sole crops, especially in low input systems (Lithourgidis
44 et al., 2011; Raseduzzaman and Jensen, 2017). Thus, intercropping could be proposed as a tool to
45 facilitate the introduction of a crop known for its yield variability and low competitive ability against
46 weeds notably when there are few mechanical or chemical solutions available. Legumes are well
47 known for their potential positive impact on crop rotations and their improvement of cropping
48 system sustainability (Nemecek et al., 2008) but are also known for their low competitiveness toward
49 weeds and their high yield variability. Soybean (*Glycine max* (L.) Merr.), producing protein-rich grain,
50 is still rarely cultivated in France (about 154 000 ha in 2018; Agreste, 2020). The development of
51 early cultivars, the global increase in temperatures (Moriondo et al., 2010) and a favourable market
52 for locally produced protein crops (Martin, 2015) are opportunities to increase its production area,
53 even in regions where it has not been cultivated in the past. However, soybean has been shown to

54 have the second most variable yield among the major legume crops of Western Europe (Cernay et
55 al., 2015). In addition, Oerke, (2006) demonstrated that weed competition was the main biotic
56 source of soybean yield losses, before pathogens, animal pests and viruses.

57 While pea- and faba bean-cereal intercropping have been the subjects of numerous studies,
58 intercropping soybean with another species is an innovative practice that has received little attention
59 in Europe. Moreover, previous studies dealing with cereal-grain legume intercrops often focused on
60 one particular species combination and tried to optimize it (Carton, 2017; Yu et al., 2016, 2015). The
61 originality of our approach is to explore a wide range of associated species, with different
62 competitive abilities, imposing different levels of competition to soybean and weeds. This approach
63 should help better understand how grain yield and weed control can be altered in intercrops
64 depending on the competitive ability of the associated crop. The level of crop biomass and crop
65 height are expected to influence the level of inter-species competition – crop-crop and crop-weeds –
66 and, as a consequence, change soybean yield and weed control obtained. In previous studies on
67 cereal-grain legumes intercrops, the difference in plant height between the two species was usually
68 low and there is a lack of references for intercropped species having very contrasted heights in
69 temperate agricultural conditions.

70 In addition to the choice of the associated species, other technical levers can influence the level of
71 competition and therefore the expected soybean production and weed control. Some options have
72 been extensively studied, including through meta-analysis for cereal-grain legume intercropping:
73 relative density and relative sowing time (Echarte et al., 2011; Yang et al., 2017; Yu et al., 2015) and
74 fertilisation (Gomez and Gurevitch, 1998; Pelzer et al., 2014). Amongst the different spatial
75 arrangements - the way crops are mixed together in intercropping (Andrews and Kassam, 1976) –
76 row intercropping is particularly relevant for mechanised agriculture where farmers may be
77 constrained by available farm machinery for their intercrop management choices. Combining crops
78 within the same row or sowing them one row out of two may affect the competition between crops
79 and has been rarely compared. In addition, no consensus can be drawn from the available literature

80 concerning the effects of within-row and alternate-row intercropping on productivity and weed
81 control (Chapagain and Riseman, 2014; Kermah et al., 2017; Martin and Snaydon, 1982). Given the
82 diversity of species used in these studies, we argue that there might be an interaction between
83 species and spatial arrangement. Hence, using a diversity of crops in both spatial arrangements
84 should clarify the effect of spatial arrangement on intercrops performances when varying the level of
85 competition.

86 The objective of this work was to study soybean grain production, associated crop yield and weed
87 control obtained from soybean-based intercropping as affected by species choice, spatial
88 arrangement and their combination through field experiments carried out in western France in 2018
89 and 2019.

90 **2. Materials & Methods**

91 **2.1 Site and soil**

92 The experiments were carried out in 2018 and 2019 in Brain-sur-l'Authion, France (47°28'N, 0°23'W).
93 Over ten years (2008 to 2017), the mean annual rainfall was 660 mm on the experimental site, and
94 the mean annual air temperature was 12°C. The air temperature, rainfall and irrigation recorded
95 during the time of the experiments are shown in Figure 1. In 2018, the second half of May and June
96 were particularly humid and warm compared to the normal. In 2019, late May and early June were
97 cooler than in 2018, and early June temperatures were below normal. We thus have experienced
98 contrasted early growth conditions. In both years, July was warmer than the 10-year average.

99 Two different fields were used for the experiments, one per year. In both fields, the soil was at least
100 90 cm deep. The topsoil (0-30 cm) of the field used in 2018 was a sandy loam with 7.7% clay, 18.3%
101 silt, 24.9% fine sand and 49.1% coarse sand. The organic matter content was 1.2%, and the pH of the
102 soil in water was 7.3. In 2019, the soil texture was also sandy loam, with 16.9% clay, 21.5% silt, 24%
103 fine sand and 37.6% coarse sand. There was 1.9% organic matter, and the pH of the soil in water was
104 7.9. Soil mineral nitrogen content in the 0-90 cm soil layer before sowing was 84 kg ha⁻¹ in 2018 and
105 94 kg ha⁻¹ in 2019. In both years, P, K and Mg were present in the soil with values above the locally

106 recommended thresholds of fertilisation for these elements. The preceding crop was a spring barley

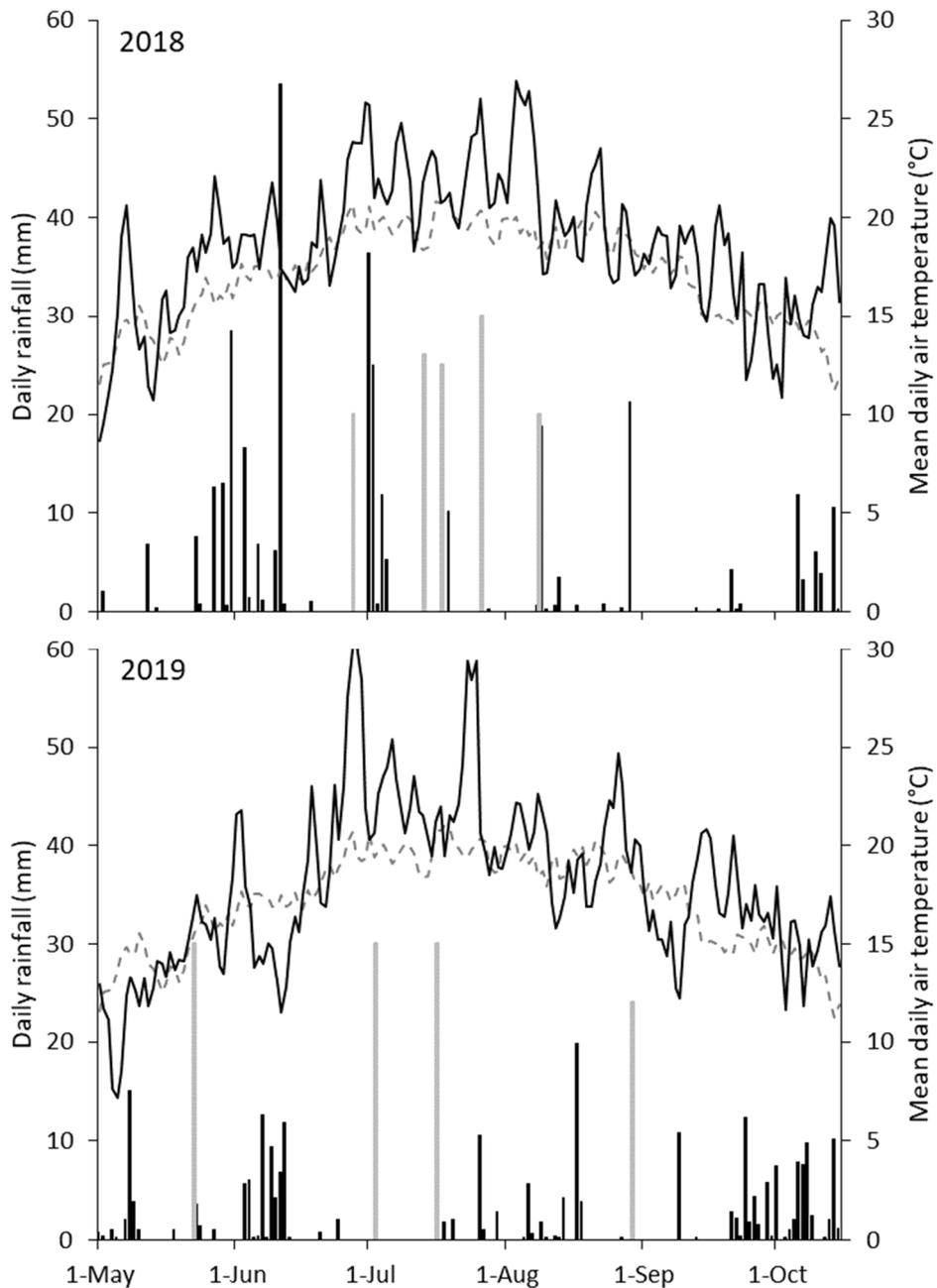


Figure 1: Mean daily air temperature and daily rainfall recorded in 2018 and 2019 in Brain-sur-l'Authion, France (47°28'N, 0°23'W). Black bars in histogram correspond to rainfall while grey ones correspond to irrigation. Black continuous line represents the mean daily temperature for the cropping season and the grey dashed line, the mean daily air temperature over a ten-years period, from 2008 to 2017.

107 in 2018 and winter wheat in 2019. In both fields, a mustard-faba bean cover crop was sown in July
108 after the harvest of the preceding crop and mechanically destroyed in March before soil preparation.

109 **2.2 Experimental design**

110 Soybean cv. Sirelia, a very early maturing cultivar (maturity group 000; recommended for the local
111 pedoclimatic conditions) with an indeterminate growth habit, was chosen to be intercropped with
112 four crops. The four intercrop species were selected from different families for their differences in
113 morphology and competitive ability (amount of biomass produced, height, growth habit) and
114 nitrogen fixation capacity, in order to obtain different levels of competition. The ability to complete
115 their cropping cycle at the same time as soybean was also a major criterion for cultivar choice. These
116 crops were buckwheat (*Fagopyrum esculentum* Moench cv. Harpe), lentil (*Lens culinaris* Medik. cv.
117 Rosana), grain sorghum (*Sorghum bicolor* (L.) Moench cv. RGT Iggloo) and sunflower (*Helianthus*
118 *annuus* L. cv. SY Valeo). These four crops will hereafter be referred to as “associated crops”.

119 All five crops were grown as sole crops, and soybean was intercropped with each of the four
120 associated crops in two spatial arrangements: mixed within-row, where both crops were randomly
121 sown within the same row (i.e.: there was no specific pattern between plants within the rows), and in
122 alternate-row, with each crop being sown in every other row. The intercropping systems were
123 designed following the replacement principle, with 50% of the sole soybean crop density replaced
124 with 50% of the sole associated crop density.

125 The seeding rates for the sole crops were based on the densities recommended by local agricultural
126 institutes to farmers. The sole crop seeding densities were 68, 168, 350, 42 and 7.2 seeds m⁻² for
127 soybean, buckwheat, lentil, sorghum and sunflower, respectively. The soybean seeds were
128 inoculated with *Bradyrhizobium japonicum* (strain G49; Force 48 Inoculum Soja NPPL®, Euralis
129 Semences). Due to the regular presence of leguminous crops in the fields used for the study, decision
130 was made not to inoculate lentil. Later on, nodule presence was confirmed for soybean and lentil.

131 Before sowing, the soil of the experimental fields was tilled to completely destroy the cover crop and
132 get rid of any weed present in the field. On May 16th 2018 and May 15th 2019, the five sole crops, the
133 eight intercrops and a bare soil treatment were sown in a randomized complete block design with 4
134 replicates in each year. The bare soil treatment received exactly the same mechanical treatment as
135 the other ones; the seed-drill went through “bare soil” plots, without seeds. The plots were 18.0 m

136 long by 1.44 m wide, with four rows sown 36 cm apart. A north-south row orientation was
137 maintained for both years. The crops were managed without fertilizers, fungicides, insecticides nor
138 chemical or mechanical weed control, except for the seed treatments present on sunflower and
139 sorghum seeds. Irrigation was provided for all treatments at once when needed, based on visual
140 observation of the state of the crops, mainly soybean, and soil (Figure 1).

141 **2.3 Measurements and analysis**

142 Soybean, associated crop and weed above-ground biomass samples were taken in every plot at
143 soybean flowering (R1; Fehr and Caviness, 1977) and soybean maturity (R8) from the two central
144 rows and from inter-rows over one meter long (1 m x 0.72 m). In 2018, R1 occurred on July 4th and R8
145 occurred on September 19th. In 2019, R1 occurred on July 8th and R8 on September 25th. All samples
146 were dried at 70°C for 48 hours before weighing. At soybean maturity, crop samples were threshed
147 using a stationary thresher (Type 350C-S.R.C. sas, Mayet, France) before drying. The soybean grain
148 samples were ground down to 120 µm (universal cutting mill “Pulverisette 19”; variable-speed rotor
149 mill “Pulverisette 14”–Fritsch, Idar-Oberstein, Germany) and then analysed through isotope ratio
150 mass spectrometry for their total N content.

151 At soybean flowering, the names of the main weeds present in the field were recorded, based on a
152 rapid visual assessment of plant number and size. Also, crop height was recorded for five randomly
153 chosen plants of each crop species per plot. Height was measured as the longest distance from the
154 soil to the highest standing part of the plant, meaning that prostrated plants would not be
155 straightened up before measurement.

156 **2.4 Calculations and statistical analysis**

157 The soybean seed protein content was calculated by multiplying the soybean grain nitrogen content
158 by 5.5, a conversion factor suggested by Mariotti et al. (2008).

159 Statistical analysis were conducted on crop yields, crop biomasses at flowering and weed biomasses
160 at flowering and harvest using linear mixed models with the lme4 package in R software (Bates et al.,
161 2015; R Core Team, 2019). For each year separately, we used the following linear mixed model:

162
$$y_{ijk} = \mu + \alpha_i + \beta_j + \alpha\beta_{ij} + B_k + \epsilon_{ijk}$$

163 where μ is the intercept, α_i , the main effect of the i^{th} associated crop species and β_j , the main effect
164 of the j^{th} spatial arrangement and $\alpha\beta_{ij}$, the associated crop species by spatial arrangement
165 interaction, which are all fixed factors. B_k correspond to the k^{th} block, the random factor and ϵ_{ijk} is the
166 residual error of y_{ijk} . ϵ_{ijk} and B_k are assumed to be independent from each other and normally
167 distributed around 0 with unknown variance parameters.

168 ANOVA was performed on the fixed part of the model to determine the significance of each factor
169 and their interaction. To deal with the few missing data points, Type II sum of squares was used for
170 the ANOVA (Langsrud, 2003).

171 To check the model assumptions, the residuals were tested for normality with the Shapiro test and
172 for homoscedasticity through the Bartlett test. When the assumptions were not met, transformation
173 using the Box-Cox procedure was performed (Box and Cox, 1964). In the situations where
174 homoscedasticity and normality of the residuals were not met after the Box & Cox transformation,
175 Kruskal-Wallis test was used. Post hoc comparison of the different factors was performed with
176 Tukey's HSD.

177 To go beyond species and spatial arrangement effects and to investigate mechanisms responsible for
178 the grain production and weed control variations, relationships between soybean yield and weed
179 biomass as response variable and crop characteristics (crop above-ground biomass, associated crop
180 proportion in the mixture) as explanatory variables were tested using a simple linear mixed model.
181 For all models, the explanatory variable was the fixed part of the model and Block was the random
182 part. Relationships were investigated within experimental years considering all measured
183 intercropping treatments and repetitions. The response variables were tested without
184 transformation and log transformed. The residuals were inspected to assess the normality and
185 heteroscedasticity of their distribution. The marginal R^2 of the model, representing the variance
186 explained by the fixed part of the model, was calculated using the `r.squaredGLMM` function based on
187 Nakagawa et al. (2017). The model with the highest marginal R^2 was selected.

188 To compare the grain production and weed control obtained from intercropping to those obtained
 189 from the sole soybean crop, three indices were calculated: the soybean production, the weed control
 190 and the associated crop production indices. Following the recommendations of Jensen et al. (2020),
 191 all indices were calculated, for a given year, from the average of the values obtained from the four
 192 blocks. Thus, soybean production index was obtained by dividing the averaged soybean yield in a
 193 given intercrop by the average yield of soybean in the sole crop. Similarly, weed control index was
 194 calculated as 1 minus the averaged above-ground weed biomass at harvest in a given intercrop
 195 divided by the averaged weed biomass at harvest in the soybean sole crop. The associated crop
 196 production index was, for a given associated crop, the ratio of its averaged yield in a given intercrop
 197 to its averaged yield in the corresponding sole crop. Thus, whether it is for crop yields or weed
 198 control, the higher the indices, the better the situation.

199 **3. Results**

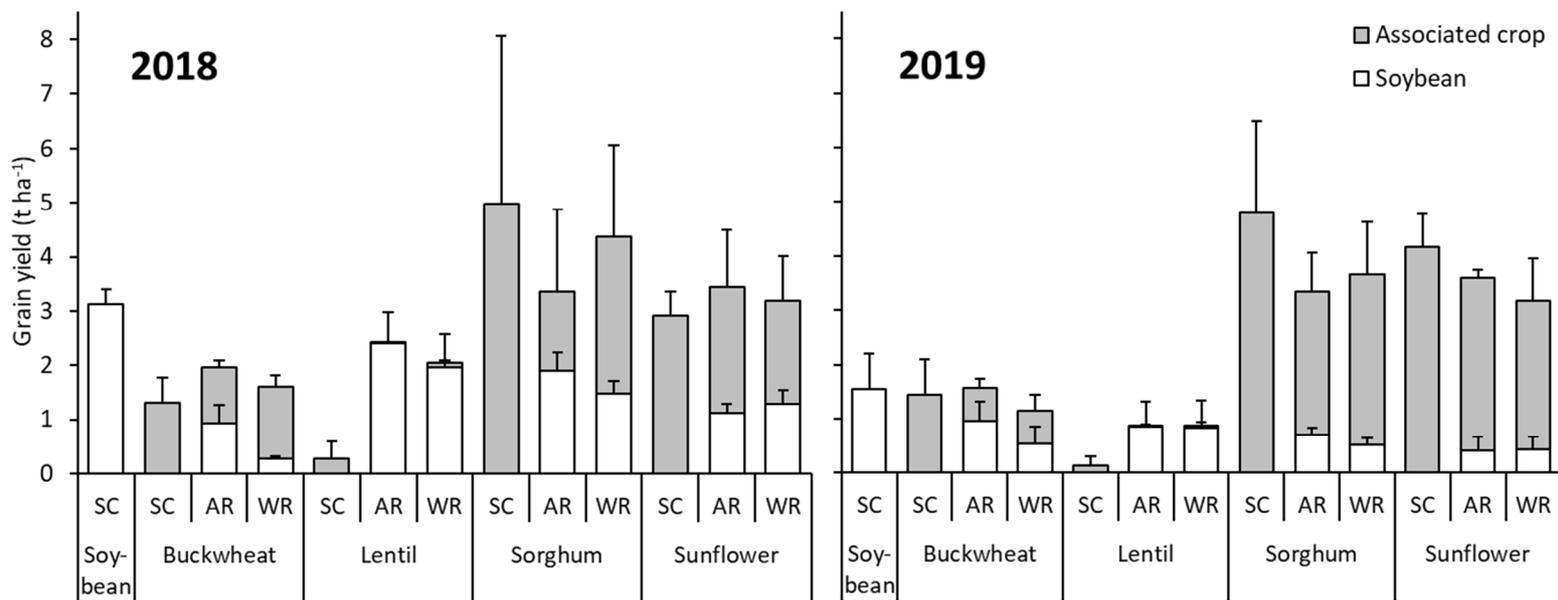


Figure 2: Grain yields of soybean, buckwheat, lentil, sorghum and sunflower in sole crops (SC) and intercropping in two spatial arrangements: alternate-row intercropping (AR) and within-row intercropping (WR). In the cumulated histograms, error bars represent the standard deviation.

200 **3.1 Soybean productivity**

201 The soybean sole crop yielded 3.12 t ha⁻¹ in 2018 and 1.56 t ha⁻¹ in 2019 (Figure 2). In the
 202 intercropping treatments, the soybean yield ranged from 0.26 to 2.40 t ha⁻¹ in 2018 and from 0.40 to

203 0.95 t ha⁻¹ in 2019. The choice of the associated crop species significantly affected soybean yield in
 204 both years (Table 1). Soybean yield was the highest with lentil in both years and the lowest with
 205 buckwheat in 2018 and sunflower in 2019. Spatial arrangement also had an effect on soybean yield,
 206 but this effect was significant only in 2018 (Table 1). Alternate-row intercropping increased soybean
 207 yield by 31% compared to that in within-row intercropping in 2018.

208 Soybean yield decreased with the increase in associated crop above-ground dry matter measured at
 209 soybean flowering (Figure 3). The relationship linking soybean yield to the associated crop biomass
 210 explained more variance in 2018 than in 2019 (Figure 3). Buckwheat in 2018 and sunflower in 2019
 211 had the highest crop biomass (Table 2) and entailed the higher yield reduction. As early as flowering,
 212 soybean biomass was affected by buckwheat growth in within-row intercropping in 2018 (Table 2). In
 213 both years, lentil produced the smallest amount of biomass at soybean flowering and displayed the
 214 highest soybean yield.

215 **Table 1: Species and spatial arrangement effects on soybean yield within intercropping treatments.**
 216 Significance levels are: * <0.05, ** <0.01 and *** <0.001. Different letters amongst species or spatial
 217 arrangements indicate significant differences with Tukey-HSD (p< 0.05).

	Soybean yield (t ha ⁻¹)	
	2018	2019
Species significance	<0.001 ***	0.028 *
Lentil-soybean	2.18 a	0.84 a
Sorghum-soybean	1.69 ab	0.61 ab
Sunflower-soybean	1.22 b	0.42 b
Buckwheat-soybean	0.6 c	0.74 ab
Spatial arrangement significance	0.010 *	0.128
Alternate-row	1.62 a	0.73
Within-row	1.24 b	0.58
Interaction significance	0.211	0.378

218 The protein content of soybean seeds was high and rather stable, on average 40.9 (±2.3) % in 2018
 219 and 34.6 (±3.4) % in 2019. Neither the intercropped species nor the spatial arrangement had a
 220 significant impact on soybean protein content. As a consequence, the total protein production was
 221 closely related to the soybean yield.

222

223

224

225

226 **Table 2: Soybean, associated crop and weed biomasses at soybean flowering.** Mean and standard deviation
 227 (in brackets) values are presented. SC stands for sole crop, AR for alternate-row and WR for within-row.
 228 Significance levels are shown for each factor and their interaction: N.S. stands for non-significant ($\alpha > 0.05$).
 229 Small bald letters distinguish treatments which are significantly different according to Tukey's HSD and capital
 230 bald letters identify species with significant differences according to Tukey's HSD. † Non-significant according
 231 to Kruskal-Wallis test.

		2018							
		Soybean (t ha ⁻¹)		Associated crop (t ha ⁻¹)			Weeds (t ha ⁻¹)		
Soybean	SC	2.497	(0.42)					0.597	(0.33)
Buckwheat- soybean	AR	1.039	(0.17)	ab	2.850	(0.63)	A	0.307	(0.07)
	WR	0.417	(0.21)	b	3.154	(0.99)		0.330	(0.24)
Lentil- soybean	AR	1.452	(0.19)	a	0.765	(0.18)	C	0.687	(0.21)
	WR	1.395	(0.35)	a	0.540	(0.14)		0.561	(0.28)
Sorghum- soybean	AR	1.153	(0.39)	a	1.625	(0.65)	B	0.525	(0.21)
	WR	1.441	(0.42)	a	1.812	(0.46)		0.417	(0.10)
Sunflower- soybean	AR	1.142	(0.27)	ab	1.647	(0.95)	BC	0.595	(0.54)
	WR	1.560	(0.32)	a	1.333	(0.28)		0.545	(0.27)
Species		< 0.001		< 0.001			N.S.		
Spatial arrangement		N.S.		N.S.			N.S.		
Interaction		0.013		N.S.			N.S.		
		2019							
Soybean	SC	0.995	(0.20)					2.241	(0.99)
Buckwheat- soybean	AR	0.738	(0.16)		1.876	(0.47)	BC	0.740	(0.51)
	WR	0.419	(0.10)		1.861	(0.99)		0.929	(0.94)
Lentil- soybean	AR	0.690	(0.25)		1.100	(0.16)	C	1.067	(0.42)
	WR	0.582	(0.18)		1.509	(0.83)		0.905	(0.25)
Sorghum- soybean	AR	0.612	(0.10)		2.36	(0.43)	B	0.898	(0.36)
	WR	0.678	(0.03)		2.328	(0.53)		1.026	(0.34)
Sunflower- soybean	AR	0.508	(0.17)		4.767	(0.56)	A	0.510	(0.15)
	WR	0.506	(0.11)		3.503	(0.86)		0.832	(0.32)
Species		N.S.		< 0.001			-		
Spatial arrangement		N.S.		N.S.			-		
Interaction		N.S.		N.S.			N.S.†		

232

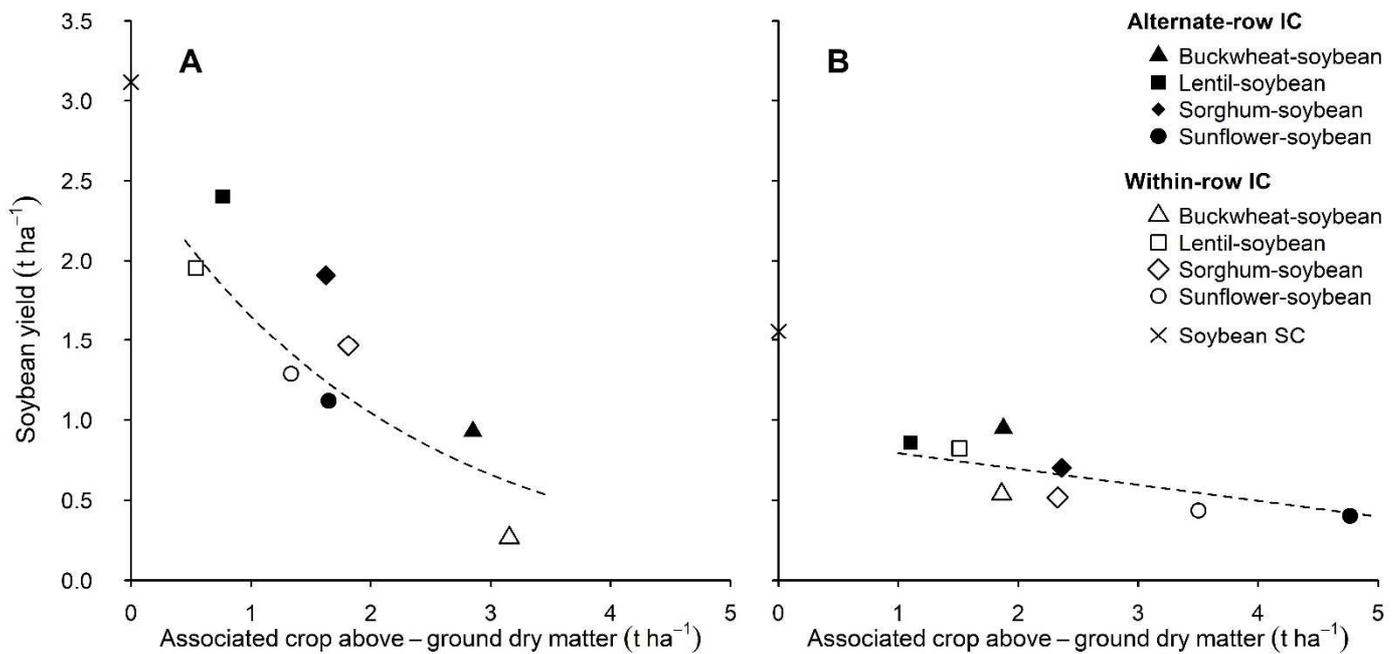


Figure 3: Soybean yield as a response to associated crop dry matter at soybean flowering. IC stands for intercropping, and SC stands for sole crop. **A** corresponds to 2018 and **B** to 2019. Each symbol corresponds to the averaged values of each treatment. The dashed lines represent the regressions fitted with all intercropping measurements. The soybean sole crop was not included in the regression calculation. In 2018, $\log(Y) = -0.459 * X + 0.962$ ($R^2 = 0.443$; p -value < 0.001); in 2019, $Y = -0.099 * X + 0.892$ ($R^2 = 0.122$; p -value = 0.023).

233 3.2 Weed biomass

234 At crop maturity, the weed potential measured on bare soil was similar in both years, with values of
 235 6.32 and 6.68 t ha⁻¹ in 2018 and 2019, respectively. The main weed species occurring in both years
 236 were lamb's quarters (*Chenopodium album* L.) and lady's thumb (*Polygonum persicaria* L.). The weed
 237 biomass in the soybean sole crop reached 2.29 t ha⁻¹ in 2018 and 3.94 t ha⁻¹ in 2019. In the
 238 intercropping treatments, weed biomass varied greatly by treatment from 0.32 to 3.90 t ha⁻¹ in 2018
 239 and from 1.37 to 4.29 t ha⁻¹ in 2019.

240 The choice of the species intercropped with soybean had an effect on weed biomass measured at
 241 crop harvest in the intercropping treatments which was significant both years (Table 3). The lentil-
 242 soybean intercrop had a significantly higher weed biomass in both years than the other intercropping
 243 treatments. Sorghum and sunflower intercropped with soybean had comparable weed control
 244 abilities, while buckwheat significantly lowered weed biomass in 2018 compared to the other crops,
 245 but this was not the case in 2019. Spatial arrangement had no significant effect on weed biomass at
 246 harvest (Table 3).

247 At soybean flowering, no significant effects of species, spatial arrangement, nor their interactions
 248 were found on the weed biomass (Table 2). The effect of associated species occurred after flowering.

249 **Table 3: Species and spatial arrangement effects on weed dry matter at crop maturity within intercropping**
 250 **treatments.** Significance levels are: * <0.05, ** <0.01 and *** <0.001. Different letters amongst species or
 251 spatial arrangements indicate significant differences with Tukey-HSD ($p < 0.05$).

	Weed dry matter (t ha ⁻¹)	
	2018	2019
Species significance	<0.001 ***	<0.001 ***
Lentil-soybean	3.55 a	4.18 a
Sorghum-soybean	1.3 b	2.11 b
Sunflower-soybean	1.66 b	1.6 b
Buckwheat-soybean	0.34 c	2.52 b
Spatial arrangement significance	0.419	0.516
Alternate-row	1.68	2.47
Within-row	1.75	2.73
Interaction significance	0.080	0.705

252 Overall, weed dry matter decreased with the increasing accumulation of dry matter by crops
 253 measured at soybean flowering (Figure 4). Low crop biomass (about 2 t ha⁻¹) was associated with a

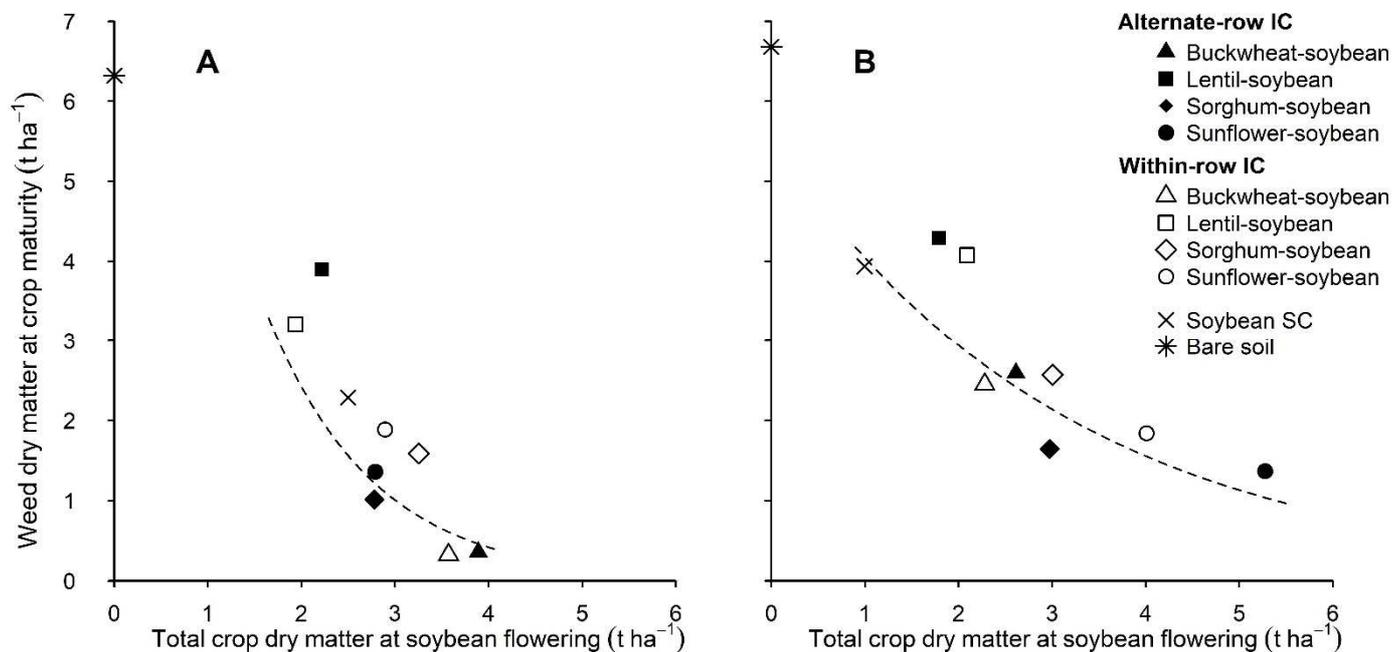


Figure 4: Weed dry matter at crop maturity as a response to total crop dry matter at soybean flowering. Total crop dry matter corresponds to above-ground dry matter of soybean summed with the associated crop above-ground dry matter in intercropping treatments or to soybean above-ground dry matter for sole soybean crop. IC stands for intercropping and SC for sole crop. **A** corresponds to 2018 and **B** to 2019. Each symbol corresponds to the averaged values of each treatment. The dashed lines represent the regressions fitted with all intercropping measurements. Soybean sole crop was included for the regression calculation but not bare soil. In 2018, $\log(Y) = -0.877 * X + 2.637$ ($R^2 = 0.411$; p -value < 0.001) and in 2019, $\log(Y) = -0.318 * X + 1.716$ ($R^2 = 0.359$; p -value < 0.001).

254 low competitive ability of lentil-soybean intercropping in both years. The other intercropping
 255 combinations had higher weed control ability due to their higher crop biomass. The buckwheat-
 256 soybean intercrops produced less total biomass in 2019 than in 2018, 4.89 and 3.73 t ha⁻¹
 257 respectively, while the sunflower-soybean intercrops showed the opposite trend with an average of
 258 2.84 t ha⁻¹ in 2018 and 4.64 t ha⁻¹ in 2019. Thus, the level of weed control for a given intercropping

259 treatment differed between years based on the level of crop biomass. In addition, the weed biomass
 260 decreased as the associated crop dry matter proportion in the total crop biomass at soybean
 261 flowering increased (Figure 5). In 2018, the associated crop dry matter proportion varied from 28% to
 262 88% in lentil-soybean within-row and buckwheat-soybean within-row, respectively. In 2019, the
 263 range was smaller, from 62% in lentil-soybean alternate-row intercrop to 90% in sunflower-soybean
 264 alternate-row intercrop.

265 3.3 Trade-off between soybean production and weed control

266 When considering within-row intercropping, soybean production appeared to be related to weed
 267 control (Figure 6A). Specifically, the higher the level of weed control, the stronger the reduction of

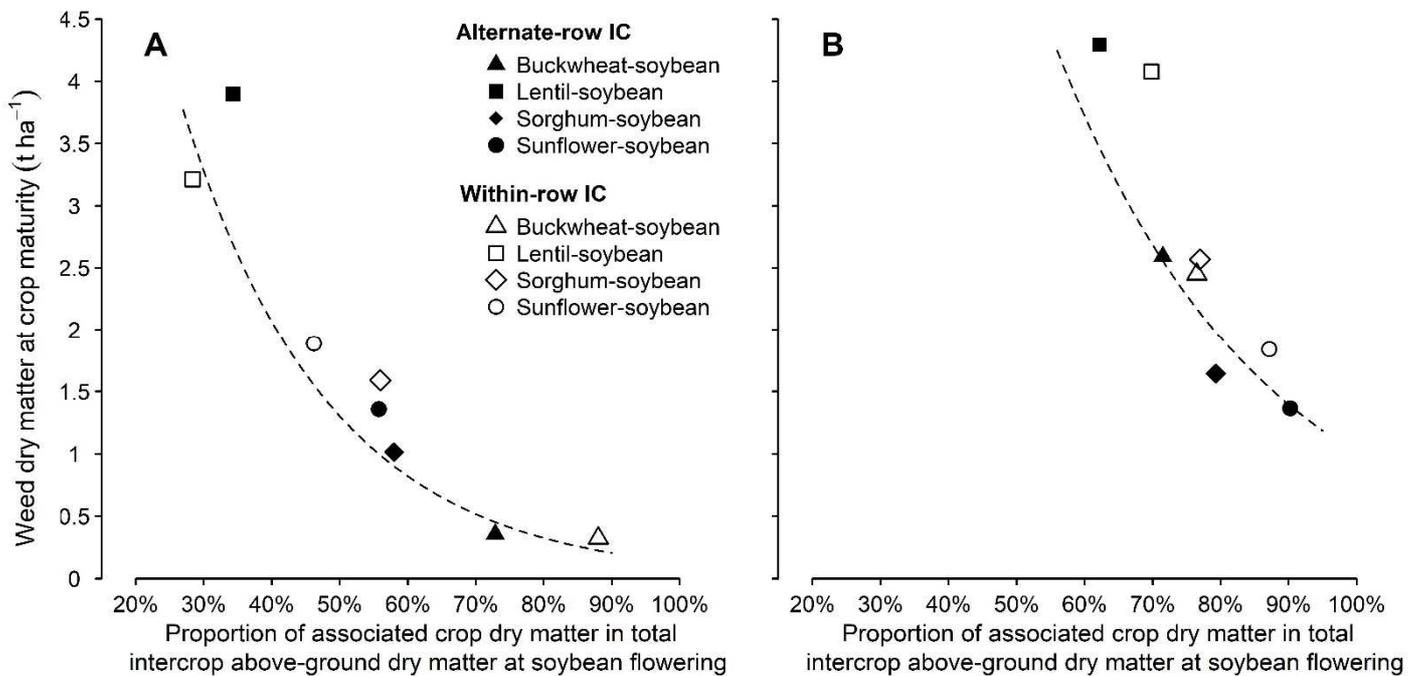


Figure 5: Response of weed dry matter at crop maturity to associated crop dry matter proportion of the total intercropped dry matter at soybean flowering. IC stands for intercropping. **A** corresponds to 2018 and **B** to 2019. Each symbol corresponds to the averaged values of each treatment. The dashed lines represent the regressions fitted for all intercropping measurements. In 2018, $\log(Y) = -4.619 * X + 2.574$ ($R^2 = 0.591$; p -value < 0.001); in 2019, $\log(Y) = -3.270 * X + 3.276$ ($R^2 = 0.254$; p -value = 0.003).

268 soybean grain yield. However, in the case of alternate-row intercropping, two situations were
 269 observed. On the one hand, sunflower-soybean alternate-row and lentil-soybean alternate-row
 270 followed approximately the same trend as within-row intercropping. On the other hand, alternate-
 271 row sorghum-soybean and alternate-row buckwheat-soybean had higher soybean production indices

272 than their respective within-row intercropping treatments, with similar weed control indices (Figure
 273 6A).

274 As shown in figure 2, associated crops production was different between species. In intercrops, the
 275 associated crop yielded, on average, 0.04 t ha⁻¹ for lentil, 0.90 t ha⁻¹ for buckwheat, 2.54 t ha⁻¹ for
 276 sorghum and 2.56 t ha⁻¹ for sunflower. Statistical comparison of associated crop yields did not reveal
 277 interaction between spatial arrangement and species both years. Spatial arrangement had a
 278 significant effect in 2018 only, with the associated crops producing in within-row intercropping an
 279 average of 38% more than in alternate-row intercropping.

280 Associated crop production index ranged from 0.08 to 1.07 in 2018 and from 0.19 to 0.77 in 2018
 281 (Figure 6B). The treatments with a high reduction in the soybean grain production index had high

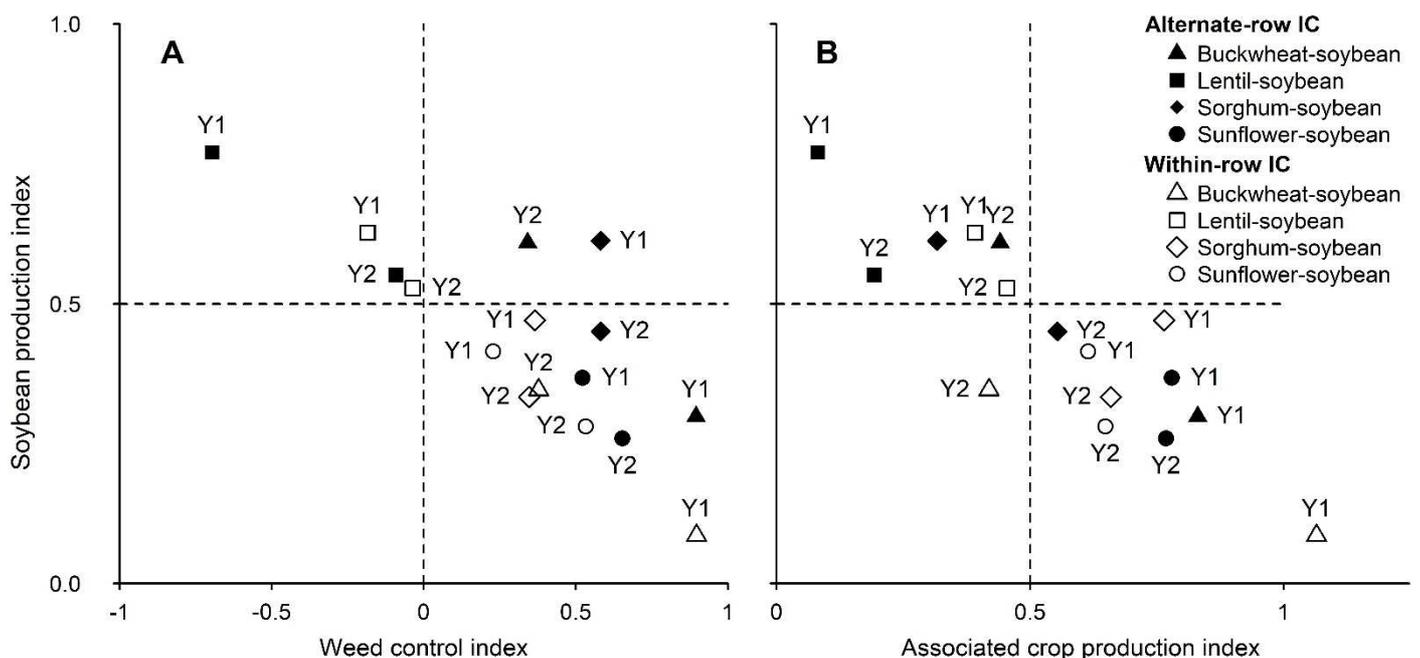


Figure 6: Soybean production of intercropping treatments in relation to weed control (A) and to the associated crop productivity (B). The soybean production index value was obtained as the ratio of the soybean yield in a given intercropping treatment to the soybean yield in the sole crop. The weed control index value is 1 minus the ratio of final weed biomass within a given intercropping treatment divided by that in soybean sole crop. Associated crop production index corresponds to the yield of the associated crop in a given intercropping divided by the yield of the corresponding sole crop. Each symbol corresponds to the averaged values of each treatment. IC stands for intercropping, AR for alternate-row intercropping and WR for within-row intercropping. Points labelled Y1 correspond to 2018 and Y2 to 2019.

282 associated crop production index. Thus, as weed control increased in the intercropping treatments,
 283 soybean grain production decreased, but the associated crop production index increased.

284 3.4 Crop height in relation to soybean productivity and weed control

285 Crop heights at soybean flowering averaged over all treatments were 55 (± 5) and 43 (± 7) cm for
 286 soybean, 117 (± 10) and 85 (± 11) cm for buckwheat, 31 (± 3) and 28 (± 3) cm for lentil, 83 (± 5) and 80
 287 (± 4) cm for sorghum and 119 (± 7) and 106 (± 7) cm for sunflower in 2018 and 2019, respectively. As
 288 shown in Figure 7A, lentil was thus the only crop smaller than soybean, the other ones were on the
 289 contrary taller, up to 67 cm for sunflower. We found significant (p -value < 0.001 in 2018 and p -value
 290 < 0.01 in 2019) negative correlation between soybean production index and the height difference
 291 between the associated crop (Figure 7A) while weed control index increased as maximum canopy
 292 height increased (Figure 7B).

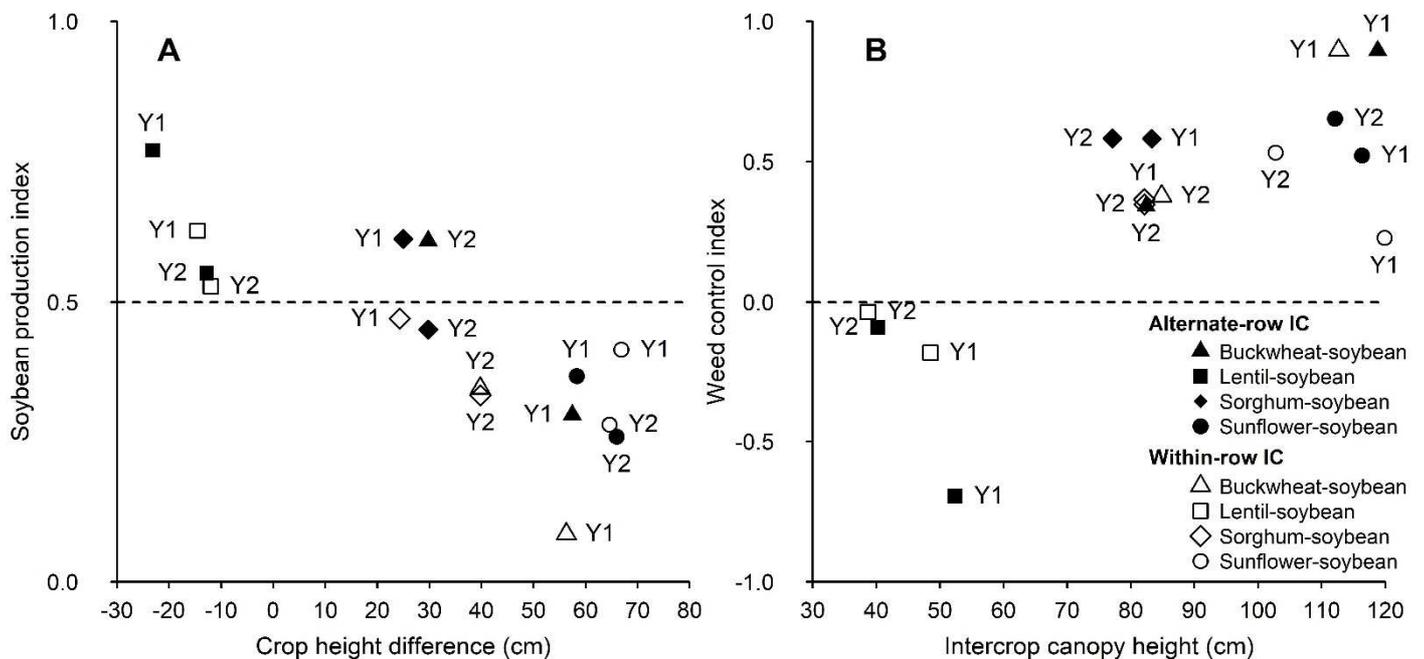


Figure 7: Soybean production in relation to crop height difference within intercrops (A) and weed control in relation to intercrop canopy height (B). The soybean production index value was obtained as the ratio of the soybean yield in a given intercropping treatment to the soybean yield in the sole crop. The weed control index value is 1 minus the ratio of final weed biomass within a given intercropping treatment divided by that in soybean sole crop. Height difference was calculated the following way: Associated crop height – Soybean height. Each symbol corresponds to the averaged values of each treatment. IC stands for intercropping, AR for alternate-row intercropping and WR for within-row intercropping. Points labelled Y1 correspond to 2018 and Y2 to 2019.

294 **4. Discussion**

295 Our study highlighted that soybean yield and weed suppression depended on management options.
296 The choice of the intercropped species and the spatial arrangement are key levers for influencing the
297 level of competition between species and, consequently, grain production and weed control. Thanks
298 to the range of contrasted species studied, we observed a strong negative correlation between
299 soybean yield and weed suppression. A key result is that the trade-off between soybean production
300 and weed control can be, in some situations, managed through spatial arrangement. Also, it appears
301 that the level of biomass and height of the associated species influenced soybean production and
302 weed control.

303 **4.1 Weed control**

304 Weed control by intercropping depends on the total biomass of the mixture. Our results showed that
305 a high total intercrop biomass in the first part of the crop cycle (up to soybean flowering) was
306 associated with a low final weed biomass. A fast growth in early stages is often considered as a
307 strong advantage in weed-crop competition but such correlations have been mainly investigated in
308 sole crops (e.g. Pérez et al., 2006), in intercrops with companion crops (Hiltbrunner et al., 2007; Lorin
309 et al., 2015) or in studies dealing with cover crops (Finney et al., 2016; MacLaren et al., 2019). The
310 use of highly contrasted species allowed us to cover a wide range of crop biomass and demonstrate
311 its effect on weed control. Another result is that the level of biomass accumulation by the associated
312 species appears crucial; indeed, weed biomass was negatively strongly correlated to the percentage
313 of the associated crop in total intercrop biomass, which is in line with previous studies including
314 cover crops (MacLaren et al., 2019).

315 Among the studied species, buckwheat was the most competitive species in relation to a fast early
316 growth ; this species is known for its high ability to compete early for growth resources (Falquet et
317 al., 2015). Lentil, the least competitive against weeds, had a low biomass production and a short
318 canopy. Moreover, due to its ability to fix a great part of its own nitrogen requirements by N₂
319 fixation, a large amount of soil N was probably available for weeds. Previous studies have

320 demonstrated that the low competitive ability of legumes for soil N contribute to their low
321 competitive ability against weeds (Corre-Hellou et al., 2011).

322 Canopy height has been shown to be an important factor in plant competition for light (Violle et al.,
323 2009). This crop trait is especially determinant in weed-crop competition when weed community is
324 dominated by tall weed species. Sunflower canopy height, being superior to the two dominant weed
325 species maximum height (Kleyer et al., 2008), gave it a competitive advantage over both
326 *Chenopodium album* and *Polygonum persicaria* while sorghum and buckwheat had this advantage on
327 *Polygonum persicaria* only. Lentil, being shorter than the two dominant weed species could not
328 compete for light with them.

329 Despite our hypothesis that within-row mixtures would provide a more regular soil shading than
330 alternate-rows of crops, especially for crops with low sowing densities, no effect of spatial
331 arrangement was found on weed control. In fact, regardless of the species, intercrops biomass was
332 not affected by spatial arrangement at soybean flowering, which in turn did not influence weed
333 growth. Hence, weed biomass accumulation was probably more related to the ability of associated
334 species to produce biomass and capture resources all along the cropping cycle than an early change
335 in canopy structure.

336 **4.2 Soybean production**

337 We demonstrated that weed growth was affected by the associated crop, and the same was true for
338 soybean. A level of biomass higher than 1.5 t ha⁻¹ for the associated crop at soybean flowering
339 entailed soybean yields in intercrops below 50% of soybean sole crop yield. Thus, soybean, known to
340 have slow early growth at the beginning of its cropping cycle (Hock et al., 2006; Jannink et al., 2000),
341 was easily outcompeted by an early fast-growing crop such as buckwheat in 2018 and to a lesser
342 extent in 2019, especially in within-row intercropping (Table 2). An associated crop with relatively
343 slow early growth will probably be better tolerated by soybean than one with early vigour. Our result
344 showed also that the crops with the largest difference in height with soybean at flowering did impact

345 the most soybean production. Very high differences in heights were obtained in soybean-sunflower
346 intercrop. A large part of light is certainly intercepted by such a dominant species (Geier et al., 1996).
347 Unlike weed control, soybean production was affected by the spatial arrangement. Globally, soybean
348 was more productive in alternate-row. Thus, resource acquisition by soybean might be improved by
349 the spatial separation of soybean from the associated crop. In contrast, the associated crop yield
350 tended to be higher in within-row intercropping, suggesting that soybean was generally less
351 competitive than the associated crop. Like Martin and Snaydon (1982), we argue that the spatial
352 separation of crops reduced the competitive advantage of the most competitive crop in the
353 intercropping system by allocating a given space with corresponding resources to each species,
354 thereby delaying interactions (positive or negative) until one species was able to reach the resource
355 pool of the other.

356 **4.3 Interactions between grain productions and weed control**

357 As detailed above, associated crop biomass and height are involved in competition against both
358 weeds and soybeans, thus contributing to weed control but impeding soybean production. This is in
359 line with the trade-off between soybean production and weed control we highlighted. Such trade-
360 offs have not yet been demonstrated through a range of species in intercropping systems except in
361 systems integrating cover crops (Finney et al., 2017). den Hollander et al. (2007) highlighted a trade-
362 off between weed control and leek production in leek intercropped with different clover species. In
363 their study, they linked the reduction in leek biomass to clover species height which was also
364 involved in weed control. In winter oilseed rape-living mulch intercrops, Lorin (2015) also highlighted
365 the importance of the living mulch crop biomass growth rate as a key indicator for the delivery of
366 weed control and grain production.

367 Nonetheless, our results also revealed that the soybean production could be improved by spatial
368 separation of crops without compromising weed control, for soybean intercropped with sorghum
369 and buckwheat. Thus, spatial arrangement can be a lever to modulate the level of antagonisms
370 between soybean production and weed control. However, we argue that crop characteristics may

371 play an important part in the success of spatial arrangement implementation. Indeed, for soybean-
372 sorghum and sorghum-buckwheat intercrops, the differences in height were moderate. By contrast,
373 in soybean-sunflower intercrop, the sunflower was much taller than soybean and exhibited a strong
374 and similar competition on soybean whatever the spatial arrangement. These results suggest that
375 response to spatial arrangement is dependent on the level of differences in crop height between
376 species and crop early competitiveness. The analysis of the distance between values of different
377 traits between species and the plasticity of traits in response to crop management options could help
378 to understand performances and trade-offs occurring in intercrops (Damour et al., 2014; Gaba et al.,
379 2015; Malézieux et al., 2009).

380 There was also an antagonistic relationship between soybean production and associated crop
381 production, as shown by the values of the production indices (Figure 6). However, this can be seen as
382 positive for farmers because the associated crop can improve the total yield and potentially the
383 income at the field level and provide some sort of production insurance in the case of a low yield
384 from the main crop.

385 **4.4 Soybean intercropping management for grain production and weed control**

386 From our results, some recommendations can be made as regard to intercrops design. For weed
387 control, overall intercrop biomass should be maximized and canopy height should be as high as
388 possible. Hence, an additive design should be favoured (e.g. Gomez and Gurevitch, 1998). Soybean,
389 should be favoured by being separated in space (alternate-row) from a more competitive associated
390 crop, ideally being the tallest crop of the mix and could be fostered by increasing the soybean density
391 proportion in the mixture. The associated crop should be added in sufficient density if a grain harvest
392 is expected, but less in proportion than soybean to avoid strong competition with it (Bedoussac et al.,
393 2015; Yu et al., 2016). Also, it should be producing as much biomass as possible, with a height inferior
394 or equal to that of soybean. Other levers can be used: inter-row width is expected to delay or
395 increase crop interactions (Elmore and Jackobs, 1984) and sowing soybean first can give a head start

396 to soybean, for higher tolerance to the associated crop competitiveness (Yu et al., 2016). Cultivar choice
397 can also play a role in associated crop tolerance (Hauggaard-Nielsen and Jensen, 2001).

398 Despite the potential benefits on yield, the intercropping of soybean with another legume crop is not
399 recommended unless chemical weed control can be applied. Further research on intercrops
400 composed of two grain legumes crops should be conducted to use the existing variability among
401 legumes for early growth (Dayoub et al., 2017; Hiltbrunner et al., 2007).

402 Given that many legumes crops present the same problems than soybean, the results obtained in
403 this study should be rather easily transferred to other crops. However, the difficulties encountered
404 with other intercrops also have to be addressed such as machinery issues for sowing, harvesting and
405 grain sorting.

406 **5. Conclusion**

407 Soybean production and weed control are both driven by the associated crop biomass production
408 and as a consequence are antagonists. Nonetheless, relevant combinations of different management
409 options, amongst which spatial separation of crops in alternate rows and the choice of an associated
410 specie with comparable height, can help modulate these antagonistic relationships and obtain higher
411 soybean yield while maintaining weed control. The identification of these management options
412 requires further investigation of the competition between different cropping system components in
413 terms of their respective crop traits.

414 **Acknowledgements**

415 The authors would like to thank the technical staff of the lab for their contribution in data collection
416 and the anonymous reviewers for their comments which helped improve the manuscript. We are
417 most grateful to PLATIN' (PLATeau d'Isotopie de Normandie) core facility for all elemental and
418 isotopic analysis used in this study.

419 **Funding**

420 This work was funded by Regional Council (Pays de la Loire) in interaction with H2020 European
421 projects diverIMPACTS and Diversify.

422 **References**

- 423 Agreste, 2020. MÉMENTO 2019. Paris, France.
- 424 Andrews, D.J., Kassam, A.H., 1976. The Importance of Multiple Cropping in Increasing World Food
425 Supplies, in: Papendick, I.R., Sanchez, P.A., Triplett, G.B. (Eds.), Multiple Cropping. pp. 1–10.
426 <https://doi.org/10.2134/asaspecpub27.c1>
- 427 Bates, D., Mächler, M., Bolker, B., Walker, S., 2015. Fitting Linear Mixed-Effects Models Using lme4. *J.*
428 *Stat. Softw.* 67, 1–48. <https://doi.org/10.18637/jss.v067.i01>
- 429 Bedoussac, L., Journet, E.-P., Hauggaard-Nielsen, H., Naudin, C., Corre-Hellou, G., Jensen, E.S., Prieur,
430 L., Justes, E., 2015. Ecological principles underlying the increase of productivity achieved by
431 cereal-grain legume intercrops in organic farming. A review. *Agron. Sustain. Dev.* 35, 911–935.
432 <https://doi.org/10.1007/s13593-014-0277-7>
- 433 Box, G.E.P., Cox, D.R., 1964. An Analysis of Transformations. *J. R. Stat. Soc. Ser. B* 26, 211–252.
- 434 Carton, N., 2017. Interactions induites par l'association du lupin avec une céréale, effets sur les
435 adventices et conséquences sur la productivité. Doctoral dissertation. Angers.
- 436 Cernay, C., Ben-Ari, T., Pelzer, E., Meynard, J., Makowski, D., 2015. Estimating variability in grain
437 legume yields across Europe and the Americas. *Sci. Rep.* 5, 11171.
438 <https://doi.org/10.1038/srep11171>
- 439 Chapagain, T., Riseman, A., 2014. Barley–pea intercropping: Effects on land productivity, carbon and
440 nitrogen transformations. *F. Crop. Res.* 166, 18–25. <https://doi.org/10.1016/j.fcr.2014.06.014>
- 441 Corre-Hellou, G., Dibet, A., Hauggaard-Nielsen, H., Crozat, Y., Gooding, M., Ambus, P., Dahlmann, C.,
442 von Fragstein, P., Pristeri, A., Monti, M., Jensen, E.S., 2011. The competitive ability of pea–
443 barley intercrops against weeds and the interactions with crop productivity and soil N
444 availability. *F. Crop. Res.* 122, 264–272. <https://doi.org/10.1016/j.fcr.2011.04.004>
- 445 Damour, G., Dorel, M., Quoc, H.T., Meynard, C., Risède, J.-M., 2014. A trait-based characterization of
446 cover plants to assess their potential to provide a set of ecological services in banana cropping
447 systems. *Eur. J. Agron.* 52, 218–228. <https://doi.org/10.1016/j.eja.2013.09.004>

448 Dayoub, E., Naudin, C., Piva, G., Shirliffe, S.J., Fustec, J., Corre-Hellou, G., 2017. Traits affecting early
449 season nitrogen uptake in nine legume species. *Heliyon* 3, e00244.
450 <https://doi.org/10.1016/j.heliyon.2017.e00244>

451 de Vida, F.B.P., Laca, E.A., Mackill, D.J., Fernández, G.M., Fischer, A.J., 2006. Relating rice traits to
452 weed competitiveness and yield: a path analysis. *Weed Sci.* 54, 1122–1131.
453 <https://doi.org/10.1614/WS-06-042R.1>

454 den Hollander, N.G., Bastiaans, L., Kropff, M.J., 2007. Clover as a cover crop for weed suppression in
455 an intercropping design II. Competitive ability of several clover species. *Eur. J. Agron.* 26, 104–
456 112. <https://doi.org/10.1016/j.eja.2006.08.005>

457 Echarte, L., Maggiora, A. Della, Cerrudo, D., Gonzalez, V.H., Abbate, P., Cerrudo, A., Sadras, V.O.,
458 Calviño, P., 2011. Yield response to plant density of maize and sunflower intercropped with
459 soybean. *F. Crop. Res.* 121, 423–429. <https://doi.org/10.1016/j.fcr.2011.01.011>

460 Elmore, R.W., Jackobs, J.A., 1984. Yield and Yield Components of Sorghum and Soybeans of Varying
461 Plant Heights when Intercropped 1. *Agron. J.* 76, 561–564.
462 <https://doi.org/10.2134/agronj1984.00021962007600040012x>

463 Falquet, B., Gfeller, A., Pourcelot, M., Tschuy, F., Wirth, J., 2015. Weed Suppression by Common
464 Buckwheat: A Review. *Environ. Control Biol.* 53, 1–6. <https://doi.org/10.2525/ecb.53.1>

465 Fehr, W.R., Caviness, C.E., 1977. Stages of soybean development. *Spec. Rep.* 87, 3–11.

466 Finney, D.M., Murrell, E.G., White, C.M., Baraibar, B., Barbercheck, M.E., Bradley, B.A., Cornelisse, S.,
467 Hunter, M.C., Kaye, J.P., Mortensen, D.A., Mullen, C.A., Schipanski, M.E., 2017. Ecosystem
468 Services and Disservices Are Bundled in Simple and Diverse Cover Cropping Systems. *Agric.*
469 *Environ. Lett.* 2, 170033. <https://doi.org/10.2134/aerl2017.09.0033>

470 Finney, D.M., White, C.M., Kaye, J.P., 2016. Biomass Production and Carbon/Nitrogen Ratio Influence
471 Ecosystem Services from Cover Crop Mixtures. *Agron. J.* 108, 39–52.
472 <https://doi.org/10.2134/agronj15.0182>

473 Gaba, S., Lescouret, F., Boudsocq, S., Enjalbert, J., Hinsinger, P., Journet, E.-P., Navas, M.-L., Wery, J.,

474 Louarn, G., Malézieux, E., Pelzer, E., Prudent, M., Ozier-Lafontaine, H., 2015. Multiple cropping
475 systems as drivers for providing multiple ecosystem services: from concepts to design. *Agron.*
476 *Sustain. Dev.* 35, 607–623. <https://doi.org/10.1007/s13593-014-0272-z>

477 Geier, P.W., Maddux, L.D., Moshier, L.J., Stahlman, P.W., 1996. Common Sunflower (*Helianthus*
478 *annuus*) Interference in Soybean (*Glycine max*). *Weed Technol.* 10, 317–321.

479 Gomez, P., Gurevitch, J., 1998. Weed community responses in a corn-soybean intercrop. *Appl. Veg.*
480 *Sci.* 1, 281–288. <https://doi.org/10.2307/1478958>

481 Hauggaard-Nielsen, H., Jensen, E., 2001. Evaluating pea and barley cultivars for complementarity in
482 intercropping at different levels of soil N availability. *F. Crop. Res.* 72, 185–196.
483 [https://doi.org/10.1016/S0378-4290\(01\)00176-9](https://doi.org/10.1016/S0378-4290(01)00176-9)

484 Hiltbrunner, J., Liedgens, M., Bloch, L., Stamp, P., Streit, B., 2007. Legume cover crops as living
485 mulches for winter wheat: Components of biomass and the control of weeds. *Eur. J. Agron.* 26,
486 21–29. <https://doi.org/10.1016/j.eja.2006.08.002>

487 Hock, S.M., Knezevic, S.Z., Martin, A.R., Lindquist, J.L., 2006. Soybean row spacing and weed
488 emergence time influence weed competitiveness and competitive indices. *Weed Sci.* 54, 38–46.
489 <https://doi.org/10.1614/WS-05-011R.1>

490 Jannink, J.-L., Orf, J.H., Jordan, N.R., Shaw, R.G., 2000. Index Selection for Weed Suppressive Ability in
491 Soybean. *Crop Sci.* 40, 1087–1094. <https://doi.org/10.2135/cropsci2000.4041087x>

492 Jensen, S.M., Svensgaard, J., Ritz, C., 2020. Estimation of the harvest index and the relative water
493 content – Two examples of composite variables in agronomy. *Eur. J. Agron.* 112, 125962.
494 <https://doi.org/10.1016/j.eja.2019.125962>

495 Kermah, M., Franke, A.C., Adjei-Nsiah, S., Ahiabor, B.D.K., Abaidoo, R.C., Giller, K.E., 2017. Maize-
496 grain legume intercropping for enhanced resource use efficiency and crop productivity in the
497 Guinea savanna of northern Ghana. *F. Crop. Res.* 213, 38–50.
498 <https://doi.org/10.1016/j.fcr.2017.07.008>

499 Kleyer, M., Bekker, R.M., Knevel, I.C., Bakker, J., Thompson, K., Sonnenschein, M., Poschlod, P., van

500 Groenendael, J.M., Klimeš, L., Klimešová, J., Klotz, S., Rusch, G.M., Hermy, M., Adriaens, D.,
501 Boedeltje, G., Bossuyt, B., Dannemann, A., Endels, P., Götzenberger, L., Hodgson, J.G., Jackel, A.-
502 K., Kühn, I., Kunzmann, D., Ozinga, W.A., Römermann, C., Stadler, M., Schlegelmilch, J.,
503 Steendam, H.J., Tackenberg, O., Wilmann, B., Cornelissen, J.H.C., Eriksson, O., Garnier, E., Peco,
504 B., 2008. The LEDA Traitbase: a database of life-history traits of the Northwest European flora. *J.*
505 *Ecol.* 96, 1266–1274. <https://doi.org/10.1111/j.1365-2745.2008.01430.x>

506 Langsrud, O., 2003. ANOVA for unbalanced data: Use Type II instead of Type III sums of squares. *Stat.*
507 *Comput.* 13, 163–167. <https://doi.org/http://dx.doi.org/10.1023/A:1023260610025>

508 Lithourgidis, A.S., Dordas, C.A., Damalas, C.A., Vlachostergios, D.N., 2011. Annual intercrops: An
509 alternative pathway for sustainable agriculture. *Aust. J. Crop Sci.* 5, 396–410.
510 <https://doi.org/1835-2707>

511 Lorin, M., 2015. Services écosystémiques rendus par des légumineuses gélives introduites en tant
512 que plantes de service dans du colza d’hiver : évaluation expérimentale et analyse
513 fonctionnelle. Doctoral dissertation. ParisTech.

514 Lorin, M., Jeuffroy, M.-H., Butier, A., Valantin-Morison, M., 2015. Undersowing winter oilseed rape
515 with frost-sensitive legume living mulches to improve weed control. *Eur. J. Agron.* 71, 96–105.
516 <https://doi.org/10.1016/j.eja.2015.09.001>

517 MacLaren, C., Swanepoel, P., Bennett, J., Wright, J., Dehnen-Schmutz, K., 2019. Cover Crop Biomass
518 Production Is More Important than Diversity for Weed Suppression. *Crop Sci.* 59, 733–748.
519 <https://doi.org/10.2135/cropsci2018.05.0329>

520 Malézieux, E., Crozat, Y., Dupraz, C., Laurans, M., Makowski, D., Ozier-Lafontaine, H., Rapidel, B.,
521 Tourdonnet, S., Valantin-Morison, M., 2009. Mixing plant species in cropping systems: concepts,
522 tools and models. A review. *Agron. Sustain. Dev.* 29, 43–62.
523 <https://doi.org/10.1051/agro:2007057>

524 Mariotti, F., Tomé, D., Mirand, P.P., 2008. Converting Nitrogen into Protein—Beyond 6.25 and Jones’
525 Factors. *Crit. Rev. Food Sci. Nutr.* 48, 177–184. <https://doi.org/10.1080/10408390701279749>

526 Martin, M.P.L.D., Snaydon, R.W., 1982. Intercropping Barley and Beans I. Effects of Planting Pattern.
527 Exp. Agric. 18, 139–148. <https://doi.org/10.1017/S0014479700013612>

528 Martin, N., 2015. Domestic soybean to compensate the European protein deficit: illusion or real
529 market opportunity? OCL 22, D502. <https://doi.org/10.1051/ocl/2015032>

530 Moriondo, M., Bindi, M., Kundzewicz, Z.W., Szwed, M., Chorynski, A., Matczak, P., Radziejewski, M.,
531 McEvoy, D., Wreford, A., 2010. Impact and adaptation opportunities for European agriculture in
532 response to climatic change and variability. Mitig. Adapt. Strateg. Glob. Chang. 15, 657–679.
533 <https://doi.org/10.1007/s11027-010-9219-0>

534 Nakagawa, S., Johnson, P.C.D., Schielzeth, H., 2017. The coefficient of determination R^2 and intra-
535 class correlation coefficient from generalized linear mixed-effects models revisited and
536 expanded. J. R. Soc. Interface 14, 20170213. <https://doi.org/10.1098/rsif.2017.0213>

537 Nemecek, T., von Richthofen, J.-S., Dubois, G., Casta, P., Charles, R., Pahl, H., 2008. Environmental
538 impacts of introducing grain legumes into European crop rotations. Eur. J. Agron. 28, 380–393.
539 <https://doi.org/10.1016/j.eja.2007.11.004>

540 Oerke, E.-C., 2006. Crop losses to pests. J. Agric. Sci. 144, 31–43.
541 <https://doi.org/10.1017/S0021859605005708>

542 Pelzer, E., Hombert, N., Jeuffroy, M.-H., Makowski, D., 2014. Meta-Analysis of the Effect of Nitrogen
543 Fertilization on Annual Cereal-Legume Intercrop Production. Agron. J. 106, 1775–1786.
544 <https://doi.org/10.2134/agronj13.0590>

545 R Core Team, 2019. R: A language and environment for statistical computing. R Foundation for
546 Statistical Computing, Vienna, Austria. URL <https://www.R-project.org/>.

547 Raseduzzaman, M., Jensen, E.S., 2017. Does intercropping enhance yield stability in arable crop
548 production? A meta-analysis. Eur. J. Agron. 91, 25–33.
549 <https://doi.org/10.1016/j.eja.2017.09.009>

550 Violle, C., Garnier, E., Lecoœur, J., Roumet, C., Podgeur, C., Blanchard, A., Navas, M., 2009.
551 Competition, traits and resource depletion in plant communities. Oecologia 160, 747–755.

552 <https://doi.org/10.1007/s00442-009-1333-x>

553 Willey, R.W., 1979. Intercropping-its importance and research needs: Part 1. Competition and yield
554 advantages. *F. Crop Abstr.* 32, 1–10.

555 Yang, F., Liao, D., Wu, X., Gao, R., Fan, Y., Raza, M.A., Wang, X., Yong, T., Liu, W., Liu, J., Du, J., Shu, K.,
556 Yang, W., 2017. Effect of aboveground and belowground interactions on the intercrop yields in
557 maize-soybean relay intercropping systems. *F. Crop. Res.* 203, 16–23.
558 <https://doi.org/10.1016/j.fcr.2016.12.007>

559 Yu, Y., Stomph, T.-J., Makowski, D., van der Werf, W., 2015. Temporal niche differentiation increases
560 the land equivalent ratio of annual intercrops: A meta-analysis. *F. Crop. Res.* 184, 133–144.
561 <https://doi.org/10.1016/j.fcr.2015.09.010>

562 Yu, Y., Stomph, T.-J., Makowski, D., Zhang, L., van der Werf, W., 2016. A meta-analysis of relative crop
563 yields in cereal/legume mixtures suggests options for management. *F. Crop. Res.* 198, 269–279.
564 <https://doi.org/10.1016/j.fcr.2016.08.001>

565