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1 **Weed regulation by crop and grassland competition: critical biomass level and**  
2 **persistence rate**

3

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24 **Abstract**

- 25 1. It is widely agreed that competition regulates plant populations and shapes  
26 communities. Many studies have suggested that crop and grassland competition  
27 can be used for cost-effective sustainable weed control. However, effective weed  
28 management requires a precise knowledge of the effects of agronomic practices  
29 and there is a lack of quantitative indicators to compare and predict the success of  
30 weed biocontrol by competition.
- 31 2. We studied weed abundance dynamics over a 12-year period in crop-grassland  
32 rotations (rotation treatments consisted of maize, wheat and barley crops,  
33 alternating with temporary grassland maintained for three or six years in the  
34 rotation and fertilised with two different levels of nitrogen). In addition to  
35 classical statistical analysis of the different aforementioned rotation treatments,  
36 we also modelled weed abundance as a function of the crop and grassland  
37 competition, expressed here by biomasses harvested in the preceding years.
- 38 3. We show that weed abundance decreases over the years in grassland and  
39 subsequent crops only if the grassland receives sufficient nitrogen fertiliser. Our  
40 model had a much greater explanatory power than the rotation treatments. This  
41 model estimates a critical biomass level above which weeds are suppressed in  
42 subsequent years, and below which they tend to thrive. This critical biomass level  
43 was 24.3 and 4.7 tonnes ha<sup>-1</sup> of dry matter for crops and grassland, respectively,  
44 highlighting the greater competitiveness of grasslands than of crops. Several clear  
45 differences between weed functional groups emerged.
- 46 4. *Synthesis and applications* - This new modelling approach directly links the  
47 interannual dynamics of weed populations to current and previous biomass  
48 production levels. This approach facilitates the development of environment-

49 friendly weed management strategies and paves the way for comparisons of the  
50 competitiveness against weeds of crops and grassland under various pedoclimatic  
51 conditions and agronomic practices.

52

53 **Keywords:** weed management, weed ecology, weed biocontrol, weed modelling, weed  
54 population dynamics

55

## 56 **1. Introduction**

57 Most food and feed production systems worldwide make use of synthetic  
58 herbicides for weed management. In this context, herbicide use has resulted in serious  
59 environmental and ecological problems (Boutin et al., 2014). Highly effective  
60 environment-friendly alternatives to chemical weed control, such as the use of crop and  
61 grassland competition with weeds, could potentially reconcile agricultural production and  
62 environment quality and play a key role in ensure global food security in the future (Petit  
63 et al., 2018; Gaba et al., 2018).

64 Many previous studies have shown how the manipulation of agronomic practices  
65 (e.g. seed rate, crop cultivar and row spacing and direction) to improve the  
66 competitiveness of the crop can help to control weeds (Sardana et al., 2017). Other studies  
67 have suggested that grassland is more efficient than crops for weed suppression (Meiss et  
68 al., 2010b; Schuster et al., 2018). However, several studies have shown that, in dry  
69 conditions (Miller et al., 2015) or at high grazing intensities (Schuster et al., 2016), the  
70 introduction of grassland into the rotation can have deleterious effects on weed control.  
71 Assessments of the competitiveness of crops and grassland against weeds would help to  
72 explain these divergent results, but quantitative indicators for predicting the success of

73 weed biocontrol and comparing competitiveness between studies are lacking.  
74 Furthermore, such studies are often based on a snapshot characterisation of the effects of  
75 crop or grassland competition on weeds, with very few considering the impact over  
76 multiple years.

77 It is difficult to gain a comprehensive understanding of the dynamics of crop and  
78 grassland competition against weeds, not only due to the interactions between the  
79 grassland or crop and all the intrinsic components of the weed species (e.g. life cycle, leaf  
80 and root type, growth habit; Gaba et al., 2014), but also due to the interactions between  
81 weeds, environment (e.g. time of emergence, growth rate, seed production; Cirillo et al.,  
82 2018) and the management (i.e. farmer's decisions) to which fields are subjected (e.g.  
83 tillage regime, fertilisation rates, crop rotation; Colbach et al., 2014).

84 We studied weed abundance dynamics in crop-grassland rotations over a 12-year  
85 period, to determine whether and how weed abundance during the crop and grassland  
86 phases of the rotation changes with the duration and fertilisation of grasslands. We also  
87 developed a statistical model with an explicit translation of cultivated plant  
88 competitiveness against weeds. We adjusted this model according to weed abundance  
89 data and tested the hypothesis that the effects of the duration and fertilisation of grassland,  
90 and of rotation schemes and weather conditions over the years can be measured as  
91 variations in grassland and crop biomass production, used as an indicator of competitive  
92 potential. Finally, we characterised the effects of weed traits on the competitiveness of  
93 crops and grassland.

94

## 95 **2. Materials and Methods**

96

97 *2.1 Description of the site, management and rotation treatments*

98           The long-term study of cropping systems including temporary grasslands analysed  
99 here is part of SOERE ACBB (Observatory and Experimental System for Environmental  
100 Research - Agroecosystems, Biogeochemical Cycles, and Biodiversity) and is located at  
101 INRA, Lusignan, France (46°25'13" N; 0°07'29" E, 151 m above sea level). This site has  
102 an oceanic climate with a summer drought, a mean air temperature of 12°C and a mean  
103 annual precipitation of 750 mm. The soil is a rubefied brown earth on clay, with traces of  
104 ferruginous shell.

105           This experiment was started in 2005 and conducted over 12 years. The treatments  
106 studied are rotations of maize, wheat and barley alternating with grassland. The  
107 grasslands were sown in mid-September with a mixture of three grass species: perennial  
108 ryegrass (*Lolium perenne* cv. Milca: 5 kg.ha<sup>-1</sup>), tall fescue (*Festuca arundinacea* cv. Soni:  
109 10 kg.ha<sup>-1</sup>) and orchard grass (*Dactylis glomerata* cv. Ludac: 12 kg.ha<sup>-1</sup>). Grasslands were  
110 mowed to a height of 5 to 7 cm and harvested three to five times per year, depending on  
111 climate and biomass production, and the cut grass was removed from the field. The first  
112 cut took place in the spring (April). Grasslands were fertilised after each cut (see Kunrath  
113 et al. 2015 for more details). The weed species present was described in  
114 Weed\_traits\_SuppInfo and their management have been described elsewhere (Doisy  
115 2015). Briefly here, in order to control weed invasion, post-emergence herbicide was  
116 applied on annual crops every year during April. No herbicide was applied on grasslands,  
117 except once during grassland installation in 2005.

118           The five rotation treatments were distributed in four blocks of individual plots of  
119 4000 m<sup>2</sup> each (for more details see [http://www.soere-acbb.com/demarche-](http://www.soere-acbb.com/demarche-experimentale)  
120 [experimentale](http://www.soere-acbb.com/demarche-experimentale)). The rotation treatments consisted of: cereal-based rotation with repeated  
121 maize/wheat/barley sequences (C); a crop-grassland rotation, in which the cereal

122 sequence was followed by three years of grassland (G3C); a grassland-cropping rotation,  
123 beginning with six years of grassland receiving high ( $\sim 230 \text{ kg ha}^{-1} \text{ year}$ ) or low ( $\sim 30 \text{ kg}$   
124  $\text{ha}^{-1} \text{ year}$ ) levels of nitrogen fertiliser (G6C and -G6C, respectively) followed by the cereal  
125 sequence; and a continuous grassland with high levels of nitrogen fertilization, as defined  
126 above, (G).

127

## 128 *2.2 Data collection*

### 129 *2.2.1 Field sampling to estimate weed abundance*

130 In each experimental unit, from 2005 to 2017, weed abundance was determined  
131 in the cereal fields in April, before post-emergence herbicide application, and then again  
132 in early autumn, before crop harvest. In the grasslands, weed abundance was determined  
133 before the first cut (April). In each plot, 13 points were sampled at 12 m intervals along  
134 two 72 m transects laid out in an “X” pattern starting 5 m from the edge of the field. At  
135 each point, the abundance of each weed species was estimated with the Barralis scale  
136 adapted for an area of  $0.25 \text{ m}^2$ , with classes “0” to “4” corresponding to, one, two to five,  
137 six to 12 and more than 12 individual weeds, respectively. When weed abundances were  
138 measured twice a year, we used the maximum abundance by species observed for each  
139 measurement point on both dates. Hereafter, the density per point for a group of weed  
140 species is the sum of the lowest abundance values of the Barralis interval for the species  
141 present at each point, expressed per  $\text{m}^2$ .

142

### 143 *2.2.2 Field sampling to estimate crop and grassland biomass*

144 Biomass production in the fields was estimated by harvesting with an  
145 experimental harvester equipped with an on-board weighing system (Haldrup, Germany),

146 and drying to constant weight in an oven at 70°C to determine dry matter content per unit  
147 area (DM t ha<sup>-1</sup>). We estimated biomass production just before harvest, for both grassland  
148 and crops, at three different sampling points per field. Each sample covered an area of at  
149 least 7.50 m<sup>2</sup>, corresponding to the passage of a harvester with a 1.5 m cutting bar over a  
150 distance of 5 m. The length of the sampling area was increased if smaller amounts of  
151 biomass were produced or if biomass production was heterogeneous. The cutting bar was  
152 set at a height of 5 to 7 cm (the same height as for the mowing of grassland plots).

153

### 154 2.2.3 Weather data

155 Yearly rainfall, mean air temperatures and thermal amplitude data at a height of 2  
156 m were measured at the experimental site and are available from the Climatik database  
157 maintained by INRA AgroClim.

158

### 159 2.3 Data management and general modelling procedures

160 The abundance of weeds in a field plot was summarised as the sum of the  
161 abundances, expressed per m<sup>2</sup>, at the 13 sampling points. We modelled this total  
162 abundance by a negative binomial distribution with a log link (Bates et al., 2015). We  
163 compared the models with Akaike's information criterion (AIC) in R regression packages  
164 (Sakamoto and Akaike, 1978). We checked that the residuals were not autocorrelated  
165 over time, using acf in the R package itsadug (van Rij et al. 2017). The significance of  
166 differences between factor levels, such as the different rotations and crops in place,  
167 according to the models obtained, was assessed in pairwise comparisons with an alpha  
168 risk of 0.05, with Holm–Bonferroni adjustment, as implemented in the R package lsmeans  
169 (Lenth, 2015). The relevance of the models for describing the variability in the data was  
170 assessed with Fisher's "goodness of fit" test (Fisher, 1924).



171

## 172 2.4 Basal model of weed control by crop and grassland biomass

173 We propose a model connecting weed abundance to the biomass harvested in  
174 previous years and show how this model can be transformed into a generalised linear  
175 model that is easy to fit with statistical software. We assume that, for each year, if the  
176 harvested biomass  $B$  (i.e. the total of the three to five harvests over the year for grassland,  
177 and above-ground biomass at harvest for the crops; i.e. grains plus leaves and stems) is  
178 above a crop-specific critical level,  $S_c$ , then weed abundance,  $W$ , tends to decrease the  
179 following year. By contrast, the weed flora was assumed to increase if the cultivated  
180 biomass (crop and grassland) was below  $S_c$ . We account for this effect by considering the  
181 estimated abundance of weeds emerging in year  $T$ , ( $\widehat{W}_T$ ), to be proportional to a power  
182 of the  $S_c/B$  ratios of the preceding years.

183 We also considered ratios to have a decreasing impact on weed density over time  
184 (years), and we accounted for this decrease by modulating the ratios by a power  
185 coefficient inversely proportional to the number of years elapsed:

$$186 \quad \widehat{W}_T \propto \left(\frac{S_{c(T-1)}}{B(T-1)}\right)^a \times \left(\frac{S_{c(T-2)}}{B(T-2)}\right)^{\frac{a}{2}} \times \dots \times \left(\frac{S_{c(0)}}{B(0)}\right)^{\frac{a}{T}} = \prod_{t=1}^T \left(\frac{S_{c(T-t)}}{B(T-t)}\right)^{\frac{a}{t}}$$

187 This can be expressed logarithmically, to obtain a linear formulation:

$$188 \quad \log(\widehat{W}_T) = I + \sum_{t=1}^T \frac{a}{t} \log\left(\frac{S_{c(T-t)}}{B(T-t)}\right)$$

189 where  $I$  is an intercept corresponding to the logarithm of a basal level of weeds. In the  
190 above equation, the biomass over time and the inverse of time are separable:

$$191 \quad \log(\widehat{W}_T) = I + a \sum_{t=1}^T -\frac{\log(B(T-t))}{t} + \sum_c \left( a \cdot \log(S_c) \sum_{t=1}^T \frac{1_c(t)}{t} \right)$$

192 where  $1_c(t)$  is the indicator function for the presence of crop  $c$  in year  $t$ . The terms of this  
193 linear expression are identifiable with the terms of a negative binomial regression with a  
194 logarithmic link:

$$195 \quad W_T \sim NB(\iota + \alpha k + \Gamma N)$$

196 - where  $\iota$  is the intercept of the regression corresponding to  $I$  in the initial linear  
197 expression. We use this intercept to account for the block of plots,  $P$ , and the  
198 current crop in the plot,  $C$ , which we subsequently treat as random effects.

$$199 \quad \iota(P, C) = \iota_P + \iota_C$$

200 -  $k$  accounts for previously harvested biomasses:  $k = -\sum_{t=1}^T \frac{\log(B(T-t))}{t}$ , the  
201 sum of the log of the harvested biomasses inversely weighted by the time  
202 elapsed, multiplied by  $\alpha = a$ , the corresponding coefficient in the regression.

203 -  $N$  is a vector of crop factors corresponding to the sum of the inverse of the  
204 time elapsed since the presence of the crop:  $N_c = \sum_{t=1}^T \frac{1_c(t)}{t}$ , multiplied by  $\Gamma$ ,  
205 the vector of the corresponding regression coefficients for each crop, with  
206  $\Gamma_c = a \cdot \log(S_c)$ .

207 Once  $k$  and  $N$  have been calculated, the model can be fitted, with, for example, the `glm.nb`  
208 function of the R package MASS. The critical biomass level for each crop  $c$  is the  
209 exponential of the ratio of the regression coefficients:

$$210 \quad S_c = \exp\left(\frac{\Gamma_c}{\alpha}\right)$$

211 As the order of the cash crops in the rotation was always the same, it was not  
212 possible to determine critical biomass levels for individual crops. We simply  
213 distinguished grassland from cash crops, grouping maize, wheat and barley together to  
214 obtain a common  $S_c$  for these crops. The time required to reduce the impact of a given

215 year under a given threshold is directly proportional to the coefficient  $\alpha$  in the regression  
216 (see supplementary materials “alpha\_visualization\_SuppInfo.docx”).

217 We report the confidence intervals for  $S_c$  according to the exponentiation of  
218 Fieller's confidence interval for a ratio of parameters (Fieller, 1954). The significance of  
219 the difference between parameter values estimated with different models was assessed by  
220 a million draws from the estimated normal distribution (for  $\alpha$ ) or transformed multinormal  
221 distributions of  $\Gamma_c$  and  $\alpha$  (for  $S_c$ ), with comparison of the draws obtained, in pairs, for two  
222 different models or crops. If one of the parameters was greater than the other 95% of the  
223 time, we considered the parameters significantly different.

224

## 225 *2.5 Variants of the basal model*

226 We ran the model on subgroups of weeds defined on the basis of their common  
227 traits. Weeds were successively split into groups (see *Weed\_traits\_SuppInfo*) according  
228 to their life cycle (annual vs. perennial), taxonomic group (monocots vs. dicots), root  
229 structure (fibrous roots vs. tap roots), and growth habit  
230 (upright/climbing/rosette/creeping).

231 We used several indicators to characterise the quality of the predictions from the  
232 various models fitted: the root mean square error of prediction (RMSE) and bias, as  
233 implemented in the hydroGOF package (Zambrano-Bigiarini, 2014), and Pseudo- $R^2$  and  
234 Spearman's rank correlation as implemented in the Hmisc package (Frank and Harrell,  
235 2016). Data assembly, consolidation and analysis were performed in R software for  
236 statistical computing version 3.1.3 (R Development Core Team, 2015). Detailed  
237 statistical codes are provided (*CBL\_PaperScript\_R\_SuppInfo* and  
238 *CBL\_functions\_R\_SuppInfo*).

239

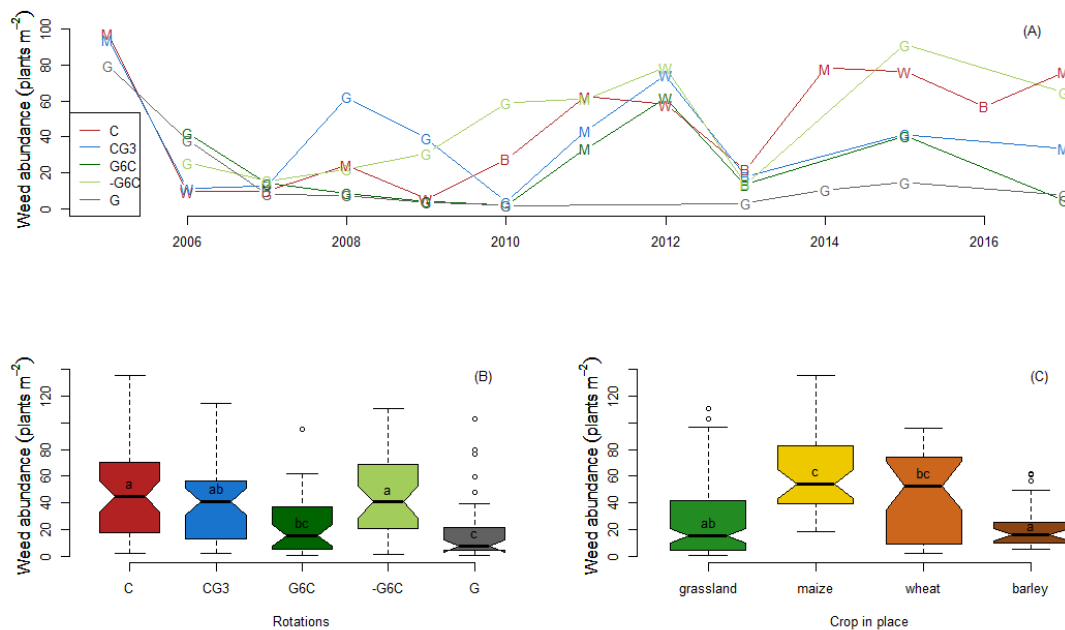
## 240 **3. Results**

241

### 242 *3.1 Effects of grassland duration and fertilisation on weed abundance*

243 Weed abundance differed considerably between the crop-grassland rotations  
244 studied, and seemed to follow different trajectories over the years according to the  
245 management system (Figure 1A). Over the last 10 years of the study, mean weed  
246 abundance was systematically lower in the continuous grassland than in the cereal-based  
247 rotation (rotation treatments G vs. C). Mean weed abundance was generally lower in the  
248 rotation treatment including six years of well-fertilised temporary grassland than in the  
249 cereal-based rotation (Figure 1B, rotation treatments G6C vs. C). By contrast, six years  
250 of temporary grassland with low levels of nitrogen fertilisation in the rotation resulted in  
251 higher weed abundances, similar to those obtained in the rotation without grasslands  
252 (Figure 1B, rotation treatments -G6C and C, respectively). Rotation treatments including  
253 well-fertilised grassland maintained over a period of six years had lower weed abundance  
254 than rotation treatments including well-fertilised grassland maintained over only three  
255 years (rotation treatments G6C vs. CG3). Weed abundance declined progressively over  
256 successive years of the grassland phase in rotation treatments receiving high levels of  
257 nitrogen fertiliser (rotation treatments CG3, G6C and G, years 2005-10) but not in the  
258 rotation treatment in which the grassland received low levels of nitrogen fertiliser  
259 (rotation -G6C) (Figure 1A). We assessed the statistical significance of the differences in  
260 weed abundance between these rotation treatments by modelling weed abundance per  
261 field as a function of both the rotation treatment and the crop or grassland in place,  
262 controlling for the plot block (Figure 1B and 1C). As the statistical model includes the  
263 effect of the crop in place, the significance of the effect of rotation treatments reported  
264 here goes beyond the differences in crop type (i.e., grassland or cereal crop). Crop type

265 also had a strong effect on weed abundance: weed abundance in maize and wheat crops  
266 was, on average, about three times higher than that in grassland and barley crops (Figure  
267 1C).  
268



269  
270 Figure 1. Weed abundance (mean number of plants.m<sup>-2</sup>) dynamics (A), and distribution,  
271 by rotation (B) and crop in place (C) during the 12 years of the experiment. The uppercase  
272 letters in panel (A) indicate the crop in place: G=grassland, M=maize, W=wheat and  
273 B=barley; each point corresponding to the mean abundance over the fields of a rotation.  
274 Rotation codes in panel (B): C corresponds to a repeated three-year cereal rotation, G  
275 corresponds to continuous grassland and three or six indicates the number of years of  
276 well-fertilised grassland and the negative sign (-) corresponds to grassland with a lower  
277 level of fertilisation. Different lowercase letters (a, b, c) in panels (B) and (C) indicate  
278 significant differences between rotation systems and crops in place in pairwise  
279 comparisons, after Holm–Bonferroni adjustment ( $P < 0.05$ ). The boxplots indicate the  
280 median (dark line), the 25 and 75% percentiles (limits of the coloured box), and the

281 confidence interval for the median based on an assumption of asymptotic normality of  
282 the median (notch). The length of the whiskers corresponds to the minimum of either the  
283 distance to the extremes or 1.5 times the length of coloured box, with possible outliers  
284 shown as points.

285

286 We evaluated the weed-suppressing effect of well-fertilised grasslands in the  
287 crops following the temporary grassland, by analysing three years in which the crops were  
288 identical in the different rotations. In 2011-2013, all rotations had similar cereal crops in  
289 place (except rotation treatment G, the permanent grassland), and all these crops followed  
290 a period of grassland phase except for the rotation including only cereal crops. During  
291 this three-year period, only rotation treatment G6C, in which the cereal crop followed six  
292 years of well-fertilised grassland had a significantly lower weed abundance, 25 to 50%  
293 lower than the values obtained for the other rotations (Figure 1A and Table 1). During the  
294 next three years (2014 to 2016), grassland was reintroduced in rotation treatments CG3,  
295 G6C and -G6C. During this period, weed abundance was lowest in the continuous  
296 grassland (G). Well-fertilised grasslands left in place for three or six years (CG3 and G6C)  
297 had similar intermediate weed abundances. Finally, weed abundance was higher and  
298 similar in the cereal crops (G) and in grassland with a low level of nitrogen fertilisation  
299 (-G6C; Table 1).

300

301 Table 1. Effects of rotations on weed abundance (GLM coefficient “Estimate”) in three  
302 year periods of cereal crops after grassland (2011-2013) or grassland after crops (2014-  
303 2016), with weed abundance in the cereal crop-only rotation as the reference.

| Rotation | Cereal crop<br>after<br>grassland<br>(2011-2013) | Grassland<br>after cereal<br>crop<br>(2014-2016) |
|----------|--|--|
|----------|--|--|

| C*   | 0 a      | 0 a      |
|------|----------|----------|
| CG3  | -0.141 a | -0.682 b |
| G6C  | -0.396 b | -0.724 b |
| -G6C | -0.064 a | 0.124 a  |
| G    | -1.789 c | -1.866 c |

304 For rotation codes, C corresponds to the repeated three-year cereal crop rotation, G  
305 corresponds to well-fertilised grassland left in place for 3 or 6 years and to grassland with  
306 lower levels of fertilisation and \* is the reference rotation. Different lowercase letters (a,  
307 b, c) indicate significant differences between rotations in pairwise comparisons with  
308 Holm–Bonferroni adjustment ( $P < 0.05$ ).

309

### 310 *3.2 Comparison of models explaining weed abundance*

311 As rotation treatment had a strong impact on weed abundance over the years, we  
312 attempted to model directly the impact on weed abundance of nitrogen fertilisation,  
313 grassland duration (i.e., age of grassland) and the crop in place. Strong variability was  
314 also observed between years. We therefore also took the major weather variables (i.e.,  
315 mean precipitation and temperature, and the thermal amplitude of each year) into account.  
316 Hypothesising that biomass production might suppress weeds, we compared the  
317 explanatory power of the biomass produced in the previous year with that of the  
318 aforementioned explanatory factors (AIC differences, Table 2). The biomass of the  
319 crop/grassland in the previous year (model 9) largely outperformed all other predictive  
320 factors, even combined (model 10).

321 Finally, we evaluated our proposed critical biomass model and compared it with  
322 the other models. The critical biomass model was more than 50 AIC points better than  
323 the model with based on the biomass of the crop/grassland in the previous year, and 256.4  
324 AIC points better than the model with rotation treatment as the only explicative factor.  
325 We also investigated whether the inclusion of weather data, nitrogen rates and grassland

326 age could improve the critical biomass model. These inclusions improved the model by  
 327 less than 1%, indicating limited statistical support for the use of these more complex  
 328 models ( $\leq 12.4$  AIC points; Table 2) and suggesting that previous crop/grassland biomass  
 329 production, as described in the critical biomass model, correctly integrates the impact of  
 330 the other factors on weed abundance.

331

332 Table 2. Comparison of the proposed critical biomass model with other models for  
 333 explaining weed abundance patterns in the systems studied (the proposed model without  
 334 other variables as explanatory factors is highlighted in grey).

| Model | Main explanatory factor <sup>1</sup> |  | Additional explanatory factors              |                |                  | AIC     | ▲ AIC <sup>3</sup> | Gof    |
|-------|--------------------------------------|--|---|----------------|------------------|---------|--------------------|--------|
|       |                                      |  | Weather data                                | Nitrogen rates | Age of grassland |         |                    |        |
| 1     |                                      |  | Yes   | -              | Yes              | *2765.0 | 268.8              | 0.009  |
| 2     |                                      |  | -   | Yes            | Yes              | 2768.2  | 265.6              | 0.116  |
| 3     |                                      |  | -   | -              | Yes              | 2772.1  | 261.7              | 0.124  |
| 4     | Critical biomass model <sup>2</sup>  |  | Yes   | Yes            | Yes              | 2772.4  | 261.4              | 0.088  |
| 5     |                                      |  | -   | Yes            | -                | 2772.5  | 261.3              | 0.208  |
| 6     |                                      |  | -   | -              | -                | 2775.4  | 256.4              | 0.217  |
| 7     |                                      |  | Yes   | Yes            | -                | 2777.5  | 256.3              | 0.167  |
| 8     |                                      |  | Yes   | -              | -                | 2781.0  | 252.4              | 0.179  |
| 9     |                                      |  | Biomass of crop/grassland the previous year |                | -                | -       | -                  | 2832.4 |
| 10    | -                                    |  | Yes   | Yes            | Yes              | 2989.1  | 44.7               | 0.151  |
| 11    | -                                    |  | -   | -              | Yes              | *3012.3 | 21.5               | 0.012  |
| 12    | Rotation treatment                   |  | -   | -              | -                | 3033.8  | -                  | 0.068  |
| 13    | -                                    |  | Yes   | -              | -                | 3034.4  | -0.6               | 0.195  |
| 14    | -                                    |  | -   | Yes            | -                | 3035.6  | -1.8               | 0.146  |
| 15    | Biomass for the year concerned       |  | -   | -              | -                | 3039.3  | -5.5               | 0.165  |

335 <sup>1</sup>Explanatory factor: in addition, all models took into account the crop in place and plot  
 336 as categorical random cofactors; \* indicates a model not fitted with these random  
 337 variables, in which these variables were treated as fixed effects.

338 <sup>2</sup> See the Materials and Methods section for more information.

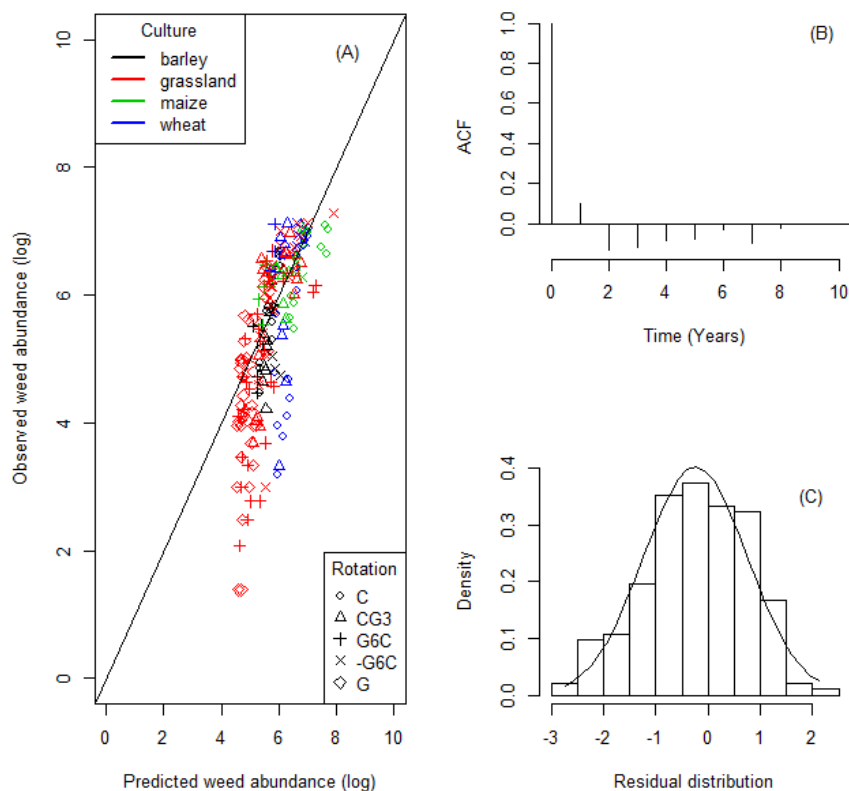


339 <sup>3</sup>▲AIC: difference in AIC relative to the model with rotation treatment as an explanatory  
340 factor (model 12).

341

### 342 3.3 Evaluation and consistency of the critical biomass model

343 The weed abundances predicted by our critical biomass model closely matched  
344 the observed values (Figure 2A), with a good  $R^2$  (0.57) and correct ranking (Spearman's  
345 correlation coefficient of 0.75). The bias test revealed a tendency toward overestimation  
346 of 4.2% and the mean prediction error (root-mean-square deviation, RMSE) was about  
347 21% (Table 3). No autocorrelation of the residuals over time was detected (Figure 2B),  
348 and the residuals displayed no major deviation from a normal distribution (Figure 3C).  
349 The statistical estimates can thus be considered accurate.



350

351 Figure 2. Assessment of the model. Predicted vs. observed weed abundances (log scale)  
352 for the crop-grassland rotation treatments (A), autocorrelation (autocorrelation and cross-  
353 correlation function, ACF) of the residuals over time (B) and distribution of the residuals  
354 of the model (C). Each point represents the weed abundance (over an area of 13 m<sup>2</sup>) per  
355 plot and per year on a logarithmic scale. For rotation codes, C corresponds to a repeated  
356 three-year cereal rotation, G corresponds to continuous grassland and three or six  
357 indicates the number of years of well-fertilised grassland and the negative sign (–)  
358 corresponds to grassland with a lower level of fertilisation.

359

360 According to the critical biomass model of weed abundance, in the studied crop-  
361 grassland rotations, the estimated critical levels of biomass corresponding to a  
362 stabilisation of weed abundance were 24.3 and 4.7 tonnes dry matter.ha<sup>-1</sup> for crop and  
363 grassland, respectively (Table 3: General). Comparison with actual above-ground  
364 biomass over the study — average of 12.1 ton.ha<sup>-1</sup> for crops (range: 2.7-26.7) and 7.1  
365 ton.ha<sup>-1</sup> for grassland (range: 0.2-16.6) — highlighted the difficulty reaching the critical  
366 biomass level (CBL) for cereal crops, whereas grassland biomass values were generally  
367 above the CBL.

368

### 369 *3.4 Weed trait group responses to previous crop and grassland biomass production*

370 We then investigated whether weeds with different traits were affected differently  
371 by the crop and grassland, by fitting the critical biomass model separately to the  
372 abundances of different groups of weeds (Table 3). The “critical biomass model” could  
373 generally be fitted to the abundances of the different weed trait groups but no convergence  
374 of fit could be achieved for weeds with a climbing growth habit.

375 For all weed traits, the grassland CBL was significantly lower than the cereal crop  
376 CBL. The biomass required for weed suppression was two to 10 times higher for cereal  
377 crops than for grassland (Table 3). The differences in CBL between weed trait groups  
378 were smaller in grassland than in cereal crops. For example, the CBL for cereal crops was  
379 almost four times higher for annual weeds than for perennial weeds, whereas the CBL for  
380 grassland was 20% lower for annual than for perennial weeds. Consequently, the  
381 confidence intervals for grassland critical biomasses also largely overlapped for the  
382 different weed trait groups, although some groups had significantly different grassland  
383 CBLs. For example, the CBL for monocots in grassland was estimated to be twice that  
384 for dicots. The largest difference in crop critical biomass levels was observed for root  
385 type, with crop critical biomass levels for tap-rooted weeds only one sixth those for weeds  
386 with fibrous roots. By contrast, grassland CBLs for tap-rooted weeds were half those for  
387 weeds with fibrous roots, revealing opposite control potentials for grassland and crops for  
388 these weed groups. Dicots were more easily outcompeted than monocots by both crops  
389 and grassland.

390 In the critical biomass model, the time required to reduce the impact of a given  
391 year under a given threshold is directly proportional to alpha (hereafter called persistence  
392 rate). For example, a year with a harvested biomass of 14 ton ha<sup>-1</sup> and a critical biomass  
393 of 10 ton ha<sup>-1</sup> would result in a large decrease in weed abundance in the following years.  
394 This effect would decrease over time and lead to a variation of estimated weed counts of  
395 less than 5% after seven years with a persistence rate of 1, whereas it would take three  
396 times longer (21 years) to achieve the same result with a persistence rate of 3 (see also  
397 alpha\_visualisation\_SuppInfo). The estimated persistence rate did not differ significantly  
398 between weed trait groups except for perennial life cycle and rosette growth habit, which  
399 had persistence rates about twice those of the other weed groups.

400

401 Table 3. Critical levels of biomass production required to modify (to decrease if higher

402 and to increase if lower) weed abundance the following year, persistence of the effect

403 over time (*a*) and indicators of model quality, as a function of weed trait group.

| Type            | Trait group | Critical biomass level                                   |                   | Persistence rate    | Quality indicator |                        |
|-----------------|-------------|--|-------------------|---------------------|-------------------|------------------------|
|                 |             | Ton ha <sup>-1</sup> [confidence intervals] <sup>1</sup> |                   | <i>a</i>            | Gof               | NRMSE (%) <sup>2</sup> |
|                 |             | Crop   | Grassland         |                     |                   |                        |
| Life cycle      | Perennial   | 11.0 [8.2-16 ] bc  | 5.5 [4.2-7.2] a   | 0.80 [0.55-1.10] ab | 0.052             | 22.8                   |
|                 | Annual      | 44.0 [19->99] efg  | 4.4 [2.7-6.9] ad  | 0.37 [0.21-0.52] cd | 0.062             | 22.8                   |
| Taxonomic group | Monocot     | 56.0 [21->99] ef   | 6.4 [4.0-10 ] ah  | 0.45 [0.23-0.67] cd | 0.018             | 17.3                   |
|                 | Dicot       | 16.0 [8.1-45 ] bgi                                       | 3.2 [1.4-5.4] d   | 0.42 [0.19-0.66] cd | 0.210             | 20.4                   |
| Root type       | Tap-root    | 14.0 [8.3-26 ] bci                                       | 3.4 [2.0-5.0] d   | 0.55 [0.32-0.79] ac | 0.170             | 14.2                   |
|                 | Fibrous     | 86.0 [24->99] e  | 7.0 [3.9-13 ] ach | 0.35 [0.16-0.54] cd | 0.026             | 17.1                   |
| Growth habit    | Rosette     | 8.5 [6.1-12 ] ch   | 4.7 [3.7-5.9] ad  | 0.97 [0.69-1.20] b  | 0.030             | 29.2                   |
|                 | Upright     | 48.0 [23->99] efg  | 4.6 [2.9-7.0] ad  | 0.39 [0.22-0.56] cd | 0.045             | 15.8                   |
|                 | Creeping    | 110.0 [0.9->99]  | 4.2 [0.2-18 ]     | 0.21 [ < 0-0.45] d  | 0.086             | 18.3                   |
| General         | -           | 24.0 [15 - 45 ] fgi                                      | 4.7 [3.5-6.4] ad  | 0.49 [0.34-0.65] c  | 0.217             | 21.0                   |

404 <sup>1</sup> Significance of the difference ( $p < 0.05$ ) between critical biomass levels or persistence

405 rates are indicated by different letters after the confidence interval.

406 <sup>2</sup> NRMSE: normalised root mean square error: the root mean square error expressed as a

407 percentage of the difference between the maximum and the minimum observed values.

408

#### 409 4. Discussion

410 In this 12-year field trial, grassland was more competitive against weeds than

411 cereal crops, but this effect was dependent on the grassland receiving sufficient nitrogen

412 fertiliser. Our model suggests that biomass production mediates this conditional

413 suppressive effect and estimates separate critical biomass levels (CBLs) for crops and

414 grassland that must be exceeded for weed suppression in subsequent years. These CBL

415 estimates highlight significant variations of cereal crop and grassland competitiveness

416 according to the traits of the weeds present. The lasting effects of composition are

417 additional to those of the crop in place and are modulated by an estimated persistence rate  
418 that differs between weed types.

419

#### 420 *4.1 Factors affecting weed abundance*

421 Weed abundances were lower in grassland than in the maize and wheat phases of  
422 the rotations, despite the use of herbicides only during the years in which cereals were  
423 grown. This result is consistent with the results of Meiss et al. (2010a), and consistent  
424 with grasslands having a greater weed-filtering effect than annual crops. Barley had a low  
425 weed abundance similar to that of grassland, probably due to the reported allelopathic  
426 activity of barley (Jabran, 2017). In addition to these overall effects of the crop in place  
427 on emerged weeds, provided adequate amounts of fertiliser were supplied (i.e., high dry  
428 matter production), weed abundance was lower in older grasslands and in subsequent  
429 crops, as reported in previous studies (e.g., Schuster 2016; Schuster 2018). We also found  
430 that lower levels of nitrogen fertilisation in grassland led to an increase in weed  
431 abundance over time. This implies that the mere introduction of grassland for a few years  
432 is not sufficient to reduce weed abundance in arable land, and that adequate nitrogen  
433 fertilisation is the determinant factor for such a reduction. Nevertheless, it should be borne  
434 in mind that the grassland investigated here was a mixture of three grass species  
435 (perennial ryegrass, tall fescue and orchard grass) and care must be taken when trying to  
436 extrapolate these results to other types of grassland, consisting of monocultures of these  
437 species or mixtures of widespread grassland species, grasses or leguminous plants.

438

#### 439 *4.2 Biomass produced as an integrative trait for competitiveness against weeds*

440           The model developed here integrates different rotations and amounts of nitrogen  
441 fertilizer into a single meaningful biological variable: biomass production in previous  
442 years. Competitiveness, expressed as crop/grassland biomass, may affect different phases  
443 of the weed life cycle, including seed germination and emergence, plant survival and  
444 vegetative growth, and seed production and survival (Colbach et al., 2014). The  
445 abundances reported here were reconstituted from abundance classes susceptible to  
446 threshold effects, but these effects should be limited by the use of 13 samples per plot. In  
447 any case, the use of more precise data would improve the fit of the model.

448           One remarkable feature of our model is its handling of multiannual history. The  
449 multiplicative impact of previous years on weed abundance is consistent with former  
450 observations that the geometric mean growth rate is more appropriate than the arithmetic  
451 mean for describing long-term changes in weed abundance in variable growing conditions  
452 (Freckleton and Watkinson, 1998). However, this mean is weighted here by the inverse  
453 of the number of years elapsed, and persistence rate could be interpreted as the number  
454 of years characterising the persistent influence of a given year on the dynamics of the  
455 group of weeds considered. This decrease over time in the impact of crop and grassland  
456 competition in a given year may depend on the persistence of both the weed seed bank  
457 and vegetative organs. Strikingly, perennial weeds had significantly higher estimated  
458 persistence rates, consistent with previous observations suggesting that perennial  
459 vegetative organs play an important role in weed persistence (Herben et al., 2014). The  
460 high persistence rate of rosette weeds was also striking, rosettes weeds are not only  
461 perennial (Weed\_traits\_SuppInfo) but also have, during their vegetative phase, leaves  
462 attached just above soil level below cutting height, thus at least partly escaping defoliation  
463 at mowing. Nevertheless, additional studies are required to disentangle the components  
464 of persistence rate: persistence of the seeds, vegetative organs and asexual reproduction.

465

466 *4.3 Crop and grassland biomass competitiveness and weed traits*

467 Overall, in our crop-grassland rotations, cereal crop biomass did not reduce weed  
468 abundance efficiently, with estimated critical levels higher than biomass production in  
469 most years. Previous studies reported that crop competition reduced weed growth and  
470 fecundity but did not completely prevent weed seed production (Chauhan et al., 2017).  
471 As a consequence, weeds tend to thrive in subsequent years in monocrop systems.  
472 However, the results of our crop-grassland rotations may be specific to seed rate, row  
473 spacing and direction conditions, as previous studies have demonstrated that a modulation  
474 of the competitive ability of crops through these factors to achieve effective weed control  
475 (Sardana et al., 2017). Further studies are required to determine the impact of such  
476 agronomic practices on “critical biomass levels”.

477 The greater effectiveness of grassland biomass against weeds may be due to the  
478 year-round ground cover in grassland and the absence of soil tillage, preserving a living  
479 and perennial weed-suppressing mulch (Wiens et al., 2006). Furthermore, a closed  
480 canopy is achieved more quickly after mowing in grasslands than during the  
481 establishment of cereal crops, resulting in greater resistance to invaders (Milbau et al.,  
482 2003).

483 Fitting the “critical biomass model” separately for each group of weeds as a  
484 function of their traits revealed large differences in critical biomass levels between weeds,  
485 consistent with previous reports that the traits of weeds are closely related to their  
486 competitiveness (Schwartz et al., 2016). Overall, our results are consistent with former  
487 observations that grassland suppresses dicot weeds more effectively than monocot weeds,  
488 as monocots higher survival rates and grow back more rapidly after grassland cutting  
489 (Meiss et al. 2008), an effect possibly reinforced by the use of dicot-specific herbicides

490 in our monocotyledon crops. Our model did not adjust for the climbing growth habit,  
491 consistent with a lower susceptibility of weeds with this growth habit to competition, as  
492 previously reported (Schuster et al., 2016). Such weeds may grow over the crop and  
493 grassland canopy with the help of special structures (e.g. tendrils hooks, twining stems  
494 and leaves), enabling them to absorb sunlight with limited competition (Kissmann and  
495 Groth, 1997). We also expected perennial plants to be more easily controlled by cereal  
496 crops than annual plants, because tillage and weeding could be carried out before the  
497 sowing of the crop. Rosette weeds were not very competitive in cereal crops, probably  
498 due to their lower levels of access to light relative to upright weeds in these tall, very  
499 dense crops. By contrast, critical biomass levels in grasslands were very similar for weeds  
500 with these two habits, and the greater competitiveness of rosettes relative to plants with  
501 erect growth habits in grassland may also be enhanced by their lower sensitivity to  
502 repeated mowing (Meiss et al., 2008).

503

## 504 **5. Conclusion**

505 This study highlights the importance of crop/grassland competitiveness for weed  
506 control. Well-fertilised grasslands are particularly competitive and produce sufficient  
507 amounts of biomass to outcompete weeds. The critical biomass model developed here  
508 can be used to calculate an intuitive metric of this competitiveness with a simple statistical  
509 procedure, paving the way for comparisons of crop and grassland competitiveness against  
510 weeds under various pedoclimatic conditions and agronomic practices. It makes use of a  
511 limited set of readily available variables, such as crop and grassland rotation schemes and  
512 biomass production in previous years. In addition to providing a powerful indicator of  
513 crop/grassland competitiveness against weeds, this model could potentially be used to



514 predict weed abundance and to develop environment-friendly weed management  
515 strategies.

516

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523

## 524 **6. Author contributions**

525

526 FG, XC and SM set up and oversighted the long term study; SM and XC designed the  
527 weed survey and XC, DD, SM and MS collected the data with the SOERE-ACBB  
528 technical staff; MS, SM, FG, CB and DD conceived the ideas; CB and MS designed the  
529 data analysis methodology, analyzed the data and conceived the model; MS and CB led  
530 the writing of the manuscript. FG, SM, AM and XC contributed critically to the drafts.  
531 All authors gave final approval for publication.

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