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# 1 **The response of weed and crop species to shading: which parameters explain** 2 **weed impacts on crop production?**

3

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## 19 **Highlights**

- 20 - Virtual experiments were run for diverse regions, cropping systems and weed floras
- 21 - Plant-morphology and shade-response parameters were related to crop production
- 22 - The same parameter values promote crop and weed species in mixed canopies
- 23 - Successful species reduce leaf thickness and are taller and wider per unit biomass
- 24 - There is a trade-off between yield promotion and weed suppression traits

## 25 **Abstract**

26 Crops compete with weeds for light, and choosing competitive crop species contributes to managing  
27 weeds. The objective was to identify which crop and weed parameters related to competition for light  
28 drive weed harmfulness for crop production. In a previous experiment, we measured parameters to  
29 characterize species potential plant morphology in unshaded conditions and species response to shading  
30 for a range of 60 crop and annual weed species. Here, we integrated the measured parameter values into  
31 an existing simulation model that uses an individual-based 3D representation of crop-weed canopies to  
32 predict weed dynamics and crop production from pedoclimate and cropping system information. The  
33 model, i.e. FLORSYS, was used to run virtual experiments in seven French and Spanish regions, with  
34 272 cropping systems varying in terms of crop rotations, herbicide use and tillage intensity etc. A series

35 of statistical methods (RLQ, fourth corner analysis, Principal Component Analysis, Pearson correlation  
36 coefficients, analysis of variance) were used to identify the key weed and crop parameters that drive  
37 crop yield loss and other weed harmfulness indicators. The weed species that caused the highest yield  
38 loss had a large leaf area at emergence. When young, they presented a large specific leaf area and a  
39 uniform leaf area distribution along plant height. They were also taller per unit plant biomass and their  
40 populations were more homogeneous in terms of plant width. At later stages, harmful weed species  
41 presented a smaller interception area to herbicides, with thicker leaves located lower on the plant. When  
42 shaded, harmful weed species shifted their leaves upwards and decreased their plant width per unit  
43 biomass. Weed-suppressive crop species had a large specific leaf area, wider plants per unit biomass,  
44 and a uniform leaf area distribution along plant height. When shaded, they increased their plant height  
45 and width per unit biomass. There was a trade-off between parameters driving potential crop production  
46 and those minimizing weed-inflicted yield losses.

47

48 **Keywords.** Weed damage; trait; photosynthetically active radiation PAR; yield loss; yield gap; ideotype

49

## 50 **1 Introduction**

51 When herbicide use is reduced due to environmental and health issues, crops are more often confronted  
52 to competition with weeds. In temperate climates with high-input crop management, the main resource  
53 for which crops and weed compete is light. As a consequence, choosing light-competitive crop species  
54 and varieties is a major lever for non-chemical weed management (Drews et al., 2009; Paynter and Hills,  
55 2009; Mhlanga et al., 2016). Once emerged, species competitiveness for light depends on how much  
56 light a species intercepts and how little it leaves to competing species. In terms of growth, this translates  
57 into three questions: how fast a species occupies empty space, how much space it occupies, and how it  
58 avoids shading or reacts to shade.

59 Field trials can investigate the effects of cultural techniques that drive canopy structure (e.g. crop  
60 species, cultivar, sowing density and interrow width) on weed biomass and/or crop production  
61 (Kristensen et al., 2006; Olsen et al., 2006; Drews et al., 2009; Paynter and Hills, 2009). These  
62 experiments though often focus on one or a few crop and/or weed species in a single location,  
63 disregarding long-term effects, thus lacking in genericity. Consequently, mechanistic models have been  
64 developed to describe processes in detail (e.g. light interception, absorption and transformation) at the  
65 scale of crop canopies or single plants within these canopies (Renton and Chauhan, 2017). The earliest  
66 of the crop-weed competition models considered bispecific homogeneous crop-weed canopies based on  
67 detailed ecophysiological functions driving crop-weed competition for light and other resources  
68 (Spitters and Aerts, 1983; Wilkerson et al., 1990; Kropff and Spitters, 1992). These were later updated  
69 to 3D individual-based bispecific competition models (Brainard and Bellinder, 2004). Conversely, the  
70 earliest multiannual weed dynamics model simplified competition processes to include weed seed bank

71 processes and impacts of cultural techniques (Cousens et al., 1986; Ballaré et al., 1987; Debaeke, 1988).  
72 The combination of the two approaches led to individual-based three-dimensional models combining  
73 simplified 3D plant representation with multiannual species dynamics and detailed effects of cultural  
74 techniques. Such models are the best compromise to represent heterogeneous crop-weed canopies and  
75 test contrasting cropping systems with different weed floras and pedoclimatic conditions (Colbach et  
76 al., 2014a).

77 The process-based FLORSYS model follows this principle. It simulates multi-specific and multi-cohort  
78 weed dynamics and their impact on crop production as a function of cropping systems and pedoclimate,  
79 at a daily scale over several years or decades (Gardarin et al., 2012; Munier-Jolain et al., 2013; Colbach  
80 et al., 2014b; Munier-Jolain et al., 2014). The 3D multispecies crop-weed canopy consists of individual  
81 plants whose leaf area is distributed inside cylinders, predicting light availability in each 3D pixel  
82 ("voxel") (Munier-Jolain et al., 2013; Munier-Jolain et al., 2014). In addition to light availability, plant  
83 dimensions and leaf area are driven by species parameters determining early growth, potential plant  
84 morphology and shading response (Colbach et al., 2014b; Colbach et al., in revision). Shading response  
85 is a key process in plant-plant interaction, particularly in multispecies heterogeneous canopies where  
86 morphological plasticity allows weeds to avoid shade cast by crops (Cavero et al., 2000). The latter  
87 model as well as earlier crop-weed competition models (Kropff et al., 1992) have already been used to  
88 identify pertinent weed state variables (e.g. weed biomass) linked to crop yield loss, similarly to what  
89 was already attempted in field trials (Regnier and Stoller, 1989; Pike et al., 1990; Cavero et al., 1999).

90 Previous models worked with state variables describing crops, weeds and canopies, which vary with  
91 plant stage as well as cultural and pedoclimatic conditions. Conversely, in the present study, we worked  
92 with generic universally valid parameters that describe plant properties intrinsic to a species, focusing  
93 on those crucial for plant-plant interaction, i.e. those related to plant morphology and shade response.  
94 This switch from site-dependent to intrinsic species properties is essential to draw generic conclusions  
95 valid in a large range of situations. The objective of the study was to use the FLORSYS model to run a  
96 multi-site, multi-annual and multi-species simulation (i.e. a virtual field network) in order to investigate  
97 (1) which annual weed species and weed parameters drive crop yield loss due to crop-weed competition  
98 for light and other weed impacts on crop production, (2) which crop species parameters reduce this  
99 competition-driven yield loss, and (3) at which plant stages the parameter values are crucial for the  
100 outcome. The final aim was to identify crop ideotypes (i.e. theoretical ideal crop plants that combine all  
101 the characteristics required to reach one or several goals in a production situation, Martre et al., 2015)  
102 for arable cropping systems in order to promote weed suppression by crop competition.

103

## 104 **2 Material and methods**

### 105 **2.1 The "virtual-field" model FLORSYS**

#### 106 ***2.1.1 Weed and crop life cycle***

107 FLORSYS is a virtual field on which cropping systems can be experimented with a large range of virtual  
108 measurements of crop, weed and environmental state variables. The structure of FLORSYS is presented  
109 in detail in previous papers (Gardarin et al., 2012; Munier-Jolain et al., 2013; Colbach et al., 2014b;  
110 Munier-Jolain et al., 2014; Mézière et al., 2015).

111 The input variables of FLORSYS consist of (1) a description of the simulated field (daily weather, latitude  
112 and soil characteristics); (2) all the crops and management operations in the field, with dates, tools and  
113 options; and (3) the initial weed seed bank, which is either measured on soil samples or estimated from  
114 regional flora assessments (Colbach et al., 2016). These input variables influence the annual life cycle  
115 of annual weeds and crops, with a daily time-step. Pre-emergence stages (surviving, dormant and  
116 germinating seeds, emerging seedlings) are driven by soil structure, temperature and water potential.  
117 Post-emergence processes (e.g. photosynthesis, respiration, growth, shade response) are driven by light  
118 availability and air temperature. At plant maturity, weed seeds are added to the soil seed bank; crop  
119 seeds are harvested to determine crop yield. Crop-weed competition was considered for light only in the  
120 present FLORSYS version. The model is currently parameterized for 25 frequent and contrasting annual  
121 weed species, 11 cash crop species (sold for profit) and 15 cover and forage crop species (grown for  
122 services and not for sale), including several varieties of wheat, field bean and pea (section [A.2](#) of the  
123 supplementary material online).

#### 124 ***2.1.2 The parameters driving morphology and shading response***

125 Early post-emergence growth, potential plant morphology and response to shading by neighbours are  
126 key processes that drive crop-weed competition and that determine how fast plants occupy space once  
127 they emerge, how much space they occupy and how they try to capture light when surrounded by  
128 neighbour plants. In FLORSYS (which considers water and nutrient conditions to be non-limiting), these  
129 processes are driven by temperature and light. Species strategies are described by 145 parameters  
130 measured either in field trials (Munier-Jolain et al., 2014) or in garden plot experiments (Colbach et al.,  
131 in revision). Early post-emergence plant growth in the absence of shading is driven by two parameters  
132 per species, i.e. leaf area at emergence and plant relative growth rate, which determine how fast a species  
133 occupies the field after emergence (Table 1, and section B online). Potential plant morphology in  
134 unshaded conditions depends on eight parameters per species and stage for 11 plant stages. These  
135 parameters determine plant dimensions, its leaf area and leaf area distribution along plant height. A  
136 further five parameters per species and stage drive species response to shading, determining whether  
137 shaded plants invest more into plant height versus width or into leaf versus stem biomass, and whether  
138 they shift their leaves upwards or downwards.

139

140 **2.1.3 Effect of cultural techniques**

141 Life-cycle processes depend on the dates, options and tools of management techniques (tillage, sowing,  
142 herbicides, mechanical weeding, mowing, harvesting), in interaction with weather and soil conditions  
143 on the day the operations are carried out (section A.3 online). For instance, weed plant survival  
144 probabilities are calculated deterministically depending on management operations, biophysical  
145 environment as well as weed morphology and stage; the actual survival of each plant is determined  
146 stochastically by comparing this probability to a random probability.

147

148 **2.1.4 Indicators of weed impact on crop production**

149 FLORSYS simulates crop yield as well as a set of indicators assessing weed impacts on crop production  
150 (Mézière et al., 2015) (see section A.4 online). Here, we investigated (1) crop grain yield loss which is  
151 the difference in yield in weed-including vs weed-free simulations relative to yield in weed-free  
152 simulations, (2) harvest pollution by weed seeds and debris resulting from weed biomass and seeds  
153 harvested with the crop grain, and (3) field infestation by weed biomass during crop growth. In addition,  
154 (4) annual weed seed production in crops was examined, as a proxy for the risk of future weed  
155 infestations. Finally, (5) potential crop yield was analysed, predicted by the weed-free simulations. To  
156 make yields of different crop species comparable, yield in MJ/ha (instead of t/ha) was preferred,  
157 multiplying the grain yield in t/ha by its energy content (see details in Lechenet et al., 2014).

158

159 **2.1.5 Domain of validity**

160 FLORSYS was previously evaluated with independent field data on weed short and long-term dynamics  
161 at French national scale, over a large range of existing arable cropping systems. It showed that crop  
162 yields, daily weed species densities and, particularly, densities averaged over the years were generally  
163 well predicted and ranked as long as a corrective function was added to keep weeds from flowering  
164 during winter at more southern latitudes (Colbach et al., 2016). A further critical analysis of yield loss  
165 was carried out in a previous simulation study covering the same regions as and cropping systems that  
166 were used here (Colbach and Cordeau, 2018). They concluded that the model's prediction quality was  
167 adequate for the model's purpose, i.e. to predict orders of magnitude and to rank situations in terms of  
168 cropping systems and crop species. Higher crop yield losses than those reported in previous field studies  
169 mostly resulted from the simulation plan. This does not adapt practices to simulated weed floras and  
170 interannual weather variability (as farmers or trial managers would do), in order to discriminate the  
171 effect of crop species and management practices on weeds from the effect of weeds on the choice of  
172 crops and practices (Colbach and Cordeau, 2018).

173

## 174 **2.2 The simulated field network**

175 A virtual field network was simulated combining (1) a large number of contrasting cropping systems  
176 from several regions, (2) different weather series, and (3) presence or absence of weeds. Several sources  
177 were used to gather data on contrasting cropping systems from six French regions (Burgundy, Paris  
178 region, Aquitaine, Poitou-Charentes, Lorraine, Picardie) and one Spanish region (Catalonia). These  
179 systems were all already used in previous simulation studies (find the detailed list of sources and  
180 references in Colbach and Cordeau, 2018) and were reused here, focusing on different factors and  
181 impacts, to tackle our new research questions. In total, 272 arable cropping systems were simulated with  
182 FLORSYS (section C online). They included both conventional and organic systems, with a tillage  
183 intensity varying from no-till to annual mouldboard ploughing. Rotations were mainly based on cereals  
184 (wheat, barley, maize) and oilseed rape, with occasional legume crops (lucerne, faba bean etc), non-  
185 legume broadleaved crops (sunflower, flax etc) and temporary grassland, with proportions and crop  
186 species depending on regions.

187 Two series of simulations were run. The first simulated the cropping systems starting with a typical  
188 regional weed seed bank consisting of the 25 annual weed species currently included in FLORSYS  
189 (section A.2 online). The second series ran without an initial weed seed bank. Comparing series 1 and 2  
190 gave the weed impact on crop production and led to calculating a crop yield loss due to weeds.

191 In each series, each cropping system was simulated over 27 years (running from summer to summer),  
192 repeating the basic rotational pattern (e.g. oilseed rape/wheat/barley) over time. For each region, a  
193 typical soil (texture etc.) was based on soil analyses from locations inside the simulated regions (section  
194 C.2 online). Daily weather variables were recorded by INRA weather stations in the different regions  
195 (INRA Climatik platform) and by the experimental station La Tallada in Catalonia. Each system was  
196 repeated 10 times with 10 different weather series consisting of 28 randomly chosen weather (calendar)  
197 years from its region of origin, using the same 10 series for each system of a given region.

198

## 199 **2.3 Statistics**

200 First, we analysed which weed parameters drive crop yield loss and other indicators of weed harmfulness  
201 for crop production. RLQ analyses were used to identify significant relationships between weed-impact  
202 indicators and weed species parameters, using the library ade4 (Chessel et al., 2004) of R (R Core Team,  
203 2016). The RLQ analysis was initially developed to analyse correlations between cultural techniques (R  
204 matrix) and species traits (Q matrix) via weed species densities (L matrix). Here, we used annual  
205 indicator values of yield loss, harvest pollution and field infestation from the 27 simulated years and 10  
206 weather repetitions for the R matrix. The Q matrix consisted of the 145 parameters of Table 1 for the 25  
207 weed species in FLORSYS. These parameters discriminate species for their ability to compete for light.  
208 The L matrix comprised the plant density of each weed species for each of the 27 years and the 10  
209 repetitions, using the maximums of the daily weed species densities between crop sowing and harvest.

210 Only parameter-indicator relationships significant at  $p=0.05$  after a 4<sup>th</sup> corner analysis were considered,  
211 using the `fourthcorner()` function of R. This analysis tests whether species are distributed independently  
212 of their effect on indicators and of their traits, retaining for each indicator  $\times$  trait combination the highest  
213 p values of models permuting either indicators or traits. To check whether weed species could be  
214 aggregated into functional groups in terms of impact on crop production related to plant morphology  
215 and shading response, species were grouped based on a Ward ascendant hierarchy classification using  
216 the `hclust()` function of R according to the Euclidian distances separating coordinates of species in the  
217 RLQ multidimensional space.

218 Then, we analysed which crop parameters reduce weed-caused crop yield loss and other weed  
219 harmfulness indicators. A Principal Component Analysis (PCA) was carried out on annual yield  
220 potential (i.e. yield from weed-free simulations), crop yield loss (relative yield difference in weed-free  
221 vs. weed-infested simulations) and annual weed seed production as a proxy for the risk of future weed  
222 harmfulness. Among the 145 parameters of Table 1, those most correlated to the PCA axes were  
223 projected onto the PCA correlation circle. Analyses were carried out with the FactoMineR package of  
224 R.

225 Finally, to evaluate the relative contribution of crop species and cropping systems on weed harmfulness,  
226 crop yield loss and weed seed production were both analysed with linear models as a function of crop  
227 species, cropping system, region, weather repetition, time since simulation onset as well as interactions  
228 between factors, using PROC GLM of SAS. Cropping systems and weather repetitions were nested  
229 within regions. Mean crop yield loss and weed seed production were compared per crop, with a least-  
230 significant difference test.

## 231 **3 Results**

### 232 **3.1 Weed harmfulness**

#### 233 ***3.1.1 Which weed species drive weed harmfulness***

234 At the annual scale, the three actual immediate weed harmfulness indicators, i.e. crop grain yield loss,  
235 harvest pollution and field infestation, were correlated (Pearson correlation coefficients ranging from  
236 0.65 to 0.73,  $p<0.0001$ , section D.1 online). Conversely, there was no correlation at all between actual  
237 immediate and potential future harmfulness, i.e. weed seed production (Pearson correlations ranging  
238 from 0.04 to 0.06,  $p<0.0001$ ). When focusing on actual immediate weed harmfulness, it appeared that  
239 weed species were the most discriminated by harvest pollution (longest arrow on Figure 1.A) and the  
240 least by yield loss (shortest arrow) though all three harmfulness indicators were orientated into the same  
241 direction, along the left-hand side of axis 1. This axis explained almost all of the variance of the indicator  
242 values (97.7%, section D.2.2 online), a large part of the trait-value variance (61.6%) and nearly the entire  
243 cross-variance between the traits and the indicators (98.0% of axis 1 in Figure 1).

244 Weed species could be clustered into several groups, depending on their contribution to weed  
245 harmfulness averaged over all cropping systems, crops, years and weather repetitions (Figure 1.B). The

246 most harmful ones were *Galium aparine* (GALAP) and *Avena fatua* (AVEFA). The second most  
247 harmful group, especially in terms of yield loss and harvest pollution, consisted of six species including  
248 *Alopecurus myosuroides* (ALOMY), *Chenopodium album* (CHEAL), *Echinochloa crus-galli*  
249 (ECHCG), *Geranium dissectum* (GERDI), *Panicum milleaceum* (PANMI), and *Stellaria media*  
250 (STEME). Three other clusters included the species that were the least harmful in terms of harvest  
251 pollution (*Senecio vulgaris*, SENVU; *Sonchus asper*, SONAS; *Veronica persica*, VERPE), crop yield  
252 loss (*Abutilon theophrasti*, ABUTH; *Ambrosia artemisiifolia*, AMBEL; *Poa annua*, POAAN) and field  
253 infestation (*Mercurialis annua*, MERAN, *Fallopia convolvulus*, POLCO, *Polygonum persicaria*,  
254 POLPE), respectively. The remaining seven species located at the centre of the graph presented an  
255 intermediate harmfulness.

### 256 **3.1.2 Which weed parameters drive weed harmfulness?**

257 The parameters determining the potential morphology and shading response of the most harmful weed  
258 species are shown in Figure 1.C. The most harmful weed species irrespective of crops, cropping systems,  
259 years and weather repetitions had a high initial leaf area at emergence (LA0 at the left-hand side of  
260 Figure 1.C); in unshaded conditions, they presented a high specific leaf area at early stages (SLA0 and  
261 SLA1), and they were taller per unit plant biomass from the end of vegetative stage onwards (HM7,  
262 HM8, HM9, HM10). In the most harmless weed species, plant width increased with plant biomass  
263 (b\_WM9, b\_WM10 on the right-hand side of Figure 1.C). Harmless species also had a larger  
264 interception area per unit leaf biomass at later stages, with a high specific leaf area from flowering  
265 onwards (SLA8, SLA9, SLA10), with leaves mostly located at the top of the plant (RLH6, RLH7).  
266 When shaded, harmful species shifted their leaves upwards in mature plants (mu\_RLH10 at the left)  
267 whereas species that increased their plant width per unit biomass (mu\_WM8, mu\_WM9, mu\_WM10 on  
268 the right) were harmless.

269 There were few differences between the weed parameters driving the three types of investigated weed  
270 harmfulness. Generally, harvest pollution was the most driven by parameters increasing plant height  
271 (HM7, HM8, HM9, HM10 at the left top quadrant) and placing leaves above the combine cutting, i.e.  
272 shifting leaves upwards in shaded mature plants (mu\_RLH10). Yield loss was the most driven by  
273 parameters that ensured a large light interception and shading area very early via a large leaf area both  
274 in absolute value and per unit of leaf biomass (LA0, SLA0, SLA1 on the left-hand side of the first axis).  
275 Finally, weeds with a larger interception area per unit leaf biomass, with a high specific leaf area (SLA8,  
276 SLA9, SLA10 in the upper right quadrant) and increased plant width per unit biomass when shaded  
277 (mu\_WM8, mu\_WM9, mu\_WM10) contributed the least to field infestation.

278 Conversely, only one parameter relevant for weed seed production could be identified. This proxy for  
279 future weed harmfulness was the highest in species that increased their plant width per unit biomass  
280 when shaded, particularly at early stages (mu\_WM2, Pearson correlation coefficient identified by  
281 fourth-corner analysis = 0.24, section D.2.1 online).

282 Though many indicator-trait correlations were identified by the RLQ analyses, the correlation  
283 coefficients were generally low (below 0.30, section D.2.1 online). This, together with the relative low  
284 variance of the trait values accounted for by the two RLQ axes (a total of 58.5%, compared to 99.9%  
285 for indicator values, section D.2.2 online), shows that trait combinations rather than single trait values  
286 drive weed species impact.

### 287 **3.2 Which crop parameters reduce weed harmfulness?**

288 Crops differed more in terms of potential yield than weed suppression. The Principal Component  
289 Analysis (PCA) showed that the situations (cropping system x year x weather repetition) that maximised  
290 potential yield were generally not those that minimized weed harmfulness as the two categories were  
291 perpendicular on the PCA variable graph (Figure 2.A). But, this also means that there were situations  
292 that reconciled both high yield potential and low yield loss due to weeds. Moreover, the two harmfulness  
293 indicators, i.e. yield loss and weed seed production, were also perpendicular when switching PCA axes  
294 (Figure 2.C), indicating that the situations with a low yield loss did not necessarily present a low weed  
295 seed production.

296 Crop species and varieties were roughly ranked along the second axis of the PCA (Figure 2.B) which  
297 was driven almost entirely by potential yield (Figure 2.A). Averaged over all cropping systems, years  
298 and weather repetitions, wheat (TRZAX) was potentially the most productive crop (toward the top of  
299 the second PCA axis), followed by sunflower (HELAN) and maize (ZEAMX). The species with the  
300 lowest potential yield (toward the bottom of the second axis) were flax (LIUUT), winter barley (HORVX  
301 and soybean (GLXMA). The difference between species was greater than the difference among cultivars  
302 of a given species. The middle group consisted of field bean (VICFX), sorghum (SORVU), pea (PIBSX)  
303 and oilseed rape (BRSNN).

304 The crop species differed much less in terms of weed suppression, here illustrated by weed-related crop  
305 yield loss and annual weed seed production (as a proxy for future weed-borne crop yield loss). Indeed,  
306 species were roughly at the centre of the first PCA axis which was driven by the two weed-harmfulness  
307 indicators (Figure 2.A and B). Plotting the third vs the first PCA axis made it a bit easier to see crop  
308 differences, as the third axis allowed to separate the two harmfulness indicators (Figure 2.C). This graph  
309 showed that crops differed a little bit more in terms of yield loss than weed seed production as the crops  
310 were distributed along the  $y=-x$  line (i.e. the direction of the yield loss arrow) with little variability along  
311 the  $y=x$  line (i.e. the direction of the weed seed production arrow) (Figure 2.D). Averaged over all  
312 cropping systems, years and weather repetitions, maize (ZEAMX) and oilseed rape (BRSNN) were the  
313 crops with the lowest crop yield loss (left upper quadrant). Conversely, flax (LIUUT), spring pea  
314 (PIBSX) and barley (HORVX) presented the highest yield loss (lower right quadrant).

315

### 3.2.1 *Crop species is not the main driver of yield loss*

316 The analysis of variance confirmed that crop species was not the main driver of crop yield loss in this  
317 simulation study (Table 2.A). Yield loss mostly depended on cropping system (partial  $R^2 =$   
318  $0.49=0.27+0.05+0.17$  out of total  $R^2$  of 0.68), albeit in interaction with weather (partial  $R^2 = 0.17$ ) and  
319 crop species (partial  $R^2 = 0.05$ ). Crop species explained three times less variability than cropping system  
320 (partial  $R^2 = 0.16 = 0.10+0.05+0.01$ ), and part of this depended on cropping system (partial  $R^2 = 0.05$ ).  
321 Using a method that accounted for the main driver of weed harmfulness (i.e. cropping systems) allowed  
322 to better discriminate crops in terms of yield loss and, particularly, weed seed production (Table 2.B).  
323 The general ranking was the same as the one observed in the PCA of Figure 2.D. Among the species  
324 with enough situations, the crops with the highest yield loss due to weeds were legumes, i.e. pea and  
325 soybean. Conversely, early-sown broadleaved crops (oilseed rape) and summer crops (maize and  
326 sunflower) presented the lowest yield loss. Autumn-sown cereals (wheat, triticale) were intermediate,  
327 except for the Caphorn wheat cultivar, which presented a very high yield loss.  
328 The crop ranking for weed seed production as a proxy for the risk of future yield loss was very different  
329 (Table 2.B). The crops with the lowest weed seed production were early-sown crops, i.e. wheat and  
330 oilseed rape, those with the highest weed seed production were late-sown crops, i.e. sunflower and  
331 soybean. Interestingly, the crops and varieties with the highest yield loss presented very low (wheat cv  
332 Caphorn) or moderate weed seed production (pea).

334

### 3.2.2 *Which crop parameters drive potential yield and weed harmfulness?*

336 The projection of the crop parameters driving potential plant morphology and shading response onto the  
337 PCA axes allowed to identify the key parameters driving yield potential (along the first PCA axis, Figure  
338 2.A), crop yield loss (along the  $y=-x$  line, Figure 2.C) and, to a lesser degree, weed seed production  
339 (along the  $y=x$  line in Figure 2.C). In the absence of shading, the crops with the highest potential yield  
340 invested in leaf biomass to the detriment of stem biomass, particularly at earlier stages (LBR0-LBR4 at  
341 the top of second PCA axis, Figure 2.A), with an uneven leaf distribution along plant height (b\_RLH8-  
342 b\_RLH10 at the top of second axis). High-potential crop species were more homogeneous in terms of  
343 plant height which depended less on plant biomass, particularly at late stages (b\_HM8-b\_HM10 at the  
344 bottom of second axis). When shaded, the high-potential crops were able to etiolate, producing taller  
345 plants per unit biomass, particularly during the vegetative stage ( $\mu_{HM5}-\mu_{HM8}$ ), but they kept a  
346 uniform leaf area distribution along plant height, particularly at early stages ( $\mu_{RLH0}-\mu_{RLH5}$  at  
347 the bottom of second axis).  
348 The optimal crop morphology and shading response for limiting yield loss was different. When  
349 unshaded, crops with the lowest yield loss were those with thinner leaves, maximising their leaf area per  
350 unit leaf biomass, particularly at early stages (SLA0-SLA4 in the left upper quadrant of Figure 2.C),  
351 with wider plants per unit biomass during vegetative stages (WM4-WM7), particularly for plants with  
352 a lower biomass (b\_WM6-b\_WM7 in the right lower quadrant), and a uniform leaf area distribution

353 along plant height (b\_RLH5-b\_RLH7). When shaded, the crops with the lowest yield loss were able to  
354 occupy even more space, by increasing their plant width per unit biomass at early stages (mu\_WM2-  
355 mu\_WM4 in the left upper quadrant) and, even more importantly, their plant height per unit biomass,  
356 both at early (mu\_HM3-mu\_HM4 in the left upper quadrant) and late stages (mu\_HM8-mu\_HM9 in the  
357 left upper quadrant). It was impossible to identify individual key crop parameters related to weed seed  
358 production (Figure 2.C).

359

### 360 **3.3 Crop ideotypes and weed "harmtypes"**

361 The most relevant crop parameters could be combined into crop ideotypes, i.e. the optimal combination  
362 of parameter values to maximise yield in weed-free (i.e. potential yield) or weed-infestation situations  
363 (i.e. actual yield) (Figure 3). Except for the shade response resulting in increased height per unit biomass  
364 (mu\_HM), the parameters that maximise one or the other type of yield were not the same or even  
365 contrary (leaf area distribution b\_RLH). In both situations, though, the relevant parameters aimed at two  
366 effects, i.e. occupying the field space before any other plant and reacting to shade once neighbour plants  
367 start to compete for space and light.

368 Early space occupation was also the main success of the generalist weed species that were harmful in  
369 all crops, cropping systems and regions (Figure 4). Even more interesting, several parameters that made  
370 species successful in multispecies canopies were the same for both crops and weeds (SLA, b\_WM,  
371 b\_RLH). However, later in the weed life-cycle (at the time when foliar herbicides were sprayed in the  
372 simulations), inconspicuous weeds with a lower leaf area per unit leaf biomass (smaller SLA) and plant  
373 width per unit biomass (smaller mu\_WM), were more harmful. Harvest pollution was very much related  
374 to weed morphology at harvest itself, which explains why weed species contributed more to this  
375 pollution when their leaf area was concentrated at the top of the plant. Conversely, no generalized  
376 parameter profile could be identified for weed seed production, which is a proxy for weed harmfulness  
377 for future crops, indicating that this function depends much more on cropping system and regional  
378 conditions.

379

## 380 **4 Discussion**

### 381 **4.1 A novel approach to determine crop ideotypes and weed "harmtypes"**

382 The present simulation-based approach allowed us to determine crop ideotypes maximising yield  
383 potential and minimizing weed-caused crop yield loss as well as weed "harmtypes" most harmful for  
384 crop production in large range of contrasting cropping systems and regions. The study also demonstrated  
385 that the crop parameters driving the yield potential were not those driving yield-loss reduction and that  
386 none of the investigated crop species answered to all requirements of the crop ideotypes. Both for crop  
387 ideotypes and weed "harmtypes", it was all about early field occupation and later shade response though

388 the exact features depended on the goal (i.e. yield potential vs weed suppression, current or future  
389 harmfulness). Weed "harmtypes" also included characteristics that would allow the plants to avoid late-  
390 season herbicides.

391 The novelty of our approach consisted in combining detailed measurements on plant morphology and  
392 shading response carried out on individual plants in controlled conditions (Colbach et al., in revision)  
393 with a simulation study to test the different species and cultivars in a multi-annual and multi-site virtual  
394 farm field network. Tardy et al. (2015; 2017) similarly used detailed individual-plant measurements but  
395 combined them with expert knowledge to define the characteristics of the ideotypes for weed-  
396 suppressive cover crop species in banana cropping systems. They then identified the best species within  
397 the panel of experimented cover crop species as the one with characteristics the closest to those of the  
398 ideotype.

399 Most authors usually worked with canopy or weed state variables such as early ground cover or canopy  
400 closure, plant height, leaf area index, weed density or leaf area, either in fields (Regnier and Stoller,  
401 1989; Pike et al., 1990; Cavero et al., 1999; Paynter and Hills, 2009; Reiss et al., 2018) or in simulations  
402 (Kropff et al., 1992). These variables are specific to cropping systems and pedoclimate, which makes it  
403 more difficult to draw generic conclusions, particularly as these studies worked with a single crop  
404 species and a very limited number of species (three or less). Conversely, we worked here with  
405 parameters that described species-intrinsic performances and were closer to processes driving  
406 competition for light, which allowed us to identify pertinent parameters and to go further in  
407 understanding crop-weed competition. For instance, most studies report that taller cultivars are more  
408 weed-suppressive than shorter cultivars (section 4.2). Here, we demonstrated that crop plant width per  
409 unit plant biomass is the key morphological trait in unshaded conditions and that plant height per unit  
410 plant biomass is an efficient response strategy when shaded (i.e. in the presence of weeds). The drawback  
411 is that these parameters are difficult to measure and not among those that are routinely measured by  
412 plant breeders (Zhao et al., 2006).

413 Experimental studies also have trouble to measure the attainable yield as it is notoriously difficult to  
414 achieve a continuously totally weed-free situation in fields, particularly when monitoring many fields at  
415 a time (Colbach et al., submitted). As in our study, yield-gap analyses thus often estimate the attainable  
416 yield from simulations (Grassini et al., 2015). In contrast to these studies, we used simulations to both  
417 estimate attainable yield and actual yield. This ensured that any difference between these two yields was  
418 due to the limiting factors that we aimed to investigate, i.e. weeds, and not due to errors in field  
419 observations used for simulation inputs on one hand, actual yield on the other hand.

## 420 **4.2 Simulation results consistent with field observations**

421 Our results are conditional on the prediction quality of FLORSYS which was shown to be adequate in a  
422 previous study (section 2.1.5). This evaluation concluded that FLORSYS correctly predicted and ranked  
423 weed species densities but could not assess the harmfulness of individual weed species for crop  
424 production. Coverage by the literature on this topic is scant. Some establish harmfulness thresholds for

425 different weed species in a single crop (e.g. see review by Caussanel, (1989) or link weed densities  
426 observed in field communities to yield loss in different crop types (Milberg and Hallgren, 2004).  
427 Extension services establish harmfulness scores based on expert opinion, usually also for a given crop  
428 (CETIOM, 2008) or aggregate qualitative knowledge (<http://www.infloweb.fr>). Among the weed  
429 species present both in literature and here, *A. fatua* and *G. aparine* were among the most harmful species,  
430 *A. myosuroides* and *S. media* among the second most harmful species, *F. convulvus*, *V. persica* and *V.*  
431 *hederifolia* among the least harmful ones (Caussanel, 1989; Wilson and Wright, 1990). Other authors  
432 though found different results. For instance, *G. aparine* was deemed rather harmless in Sweden (Milberg  
433 and Hallgren, 2004) but that was on spring cereals whereas we established a crop-independent  
434 harmfulness ranking. Indeed, the impact of a given weed species also depends on the identity of the  
435 infested crops (Fried et al., 2017), the weed floras and, of course, on which resource crops and weeds  
436 compete for (Zimdahl, 2004). The above-cited field studies did not discriminate between competition  
437 causes whereas we exclusively focused on competition for light and our simulations ensured that there  
438 were no other abiotic or biotic stresses. Moreover, our weed species ranking was established over many  
439 contrasting cropping systems, crops, weed floras and pedoclimates. Conversely, yield-loss field studies  
440 either investigate one weed species in one crop species in bi-specific trials (Caussanel, 1989), which is  
441 an unrealistic situation disregarding weed-weed interference, or the impact of multispecific weed floras  
442 without discriminating individual species (Keller et al., 2014), which is consistent with farming  
443 situations but does not allow to draw conclusions on individual species.

444 Though many simulation and field studies analysed canopy and weed state variables related to yield loss  
445 (see Introduction), few studies investigate correlations between weed species parameters and weed  
446 harmfulness for crop production as we did here. The few exceptions confirmed our findings on which  
447 weed parameters drive harmfulness, such as the importance of early space occupation (Spitters and  
448 Aerts, 1983), plant height surpassing crop canopy (Spitters and Aerts, 1983; Fried et al., 2017), a high  
449 stem elongation rate, particularly in shaded conditions (Weinig, 2000) (consistent with our higher plant  
450 height per unit biomass, particularly at later stages when shading is more likely), or a large specific leaf  
451 area (SLA) at early stages and a small one at later stages (Storkey, 2004; Storkey, 2005) (which is  
452 identical to our results). The harmfulness of a small SLA late in the weed life-cycle seems surprising at  
453 first, but such plants are less likely to be affected by foliar herbicides, which may be applied later in the  
454 cropping season and enter via weed leaves.

455 Reports on crop parameters relevant for yield potential and weed suppressiveness are more common but  
456 they usually compare different cultivars rather than species, as we did here. Again, our results are mostly  
457 consistent with previous experimental studies. The most frequent reported feature of weed-suppressive  
458 species and cultivars is plant height (Ford and Pleasant, 1994; Christensen, 1995; Lemerle et al., 1996;  
459 Mennan and Zandstra, 2005; Østergård et al., 2008; Drews et al., 2009; Fried et al., 2017; Jha et al.,  
460 2017) which is consistent with our height efficiency. A large leaf area, leaf area index or light  
461 interception area also increase weed suppression (Ford and Pleasant, 1994; Christensen, 1995; Lindquist

462 and Mortensen, 1998; Drews et al., 2009) which is consistent with our large specific leaf area and wider  
463 plants per unit plant biomass. Some parameters reported in literature required a more detailed plant  
464 description than we used here, such as leaf inclination (Drews et al., 2009). Conversely, other features  
465 used in literature are not actual parameters but the result of several processes such as rapidly shading  
466 canopies or high ground cover (Holt, 1995; Drews et al., 2009). Both are though consistent with our  
467 results demonstrating the need of an early space occupation by crops.

### 468 **4.3 Can weed-suppressive crop ideotypes contribute to weed** 469 **management**

470 Choosing crop species and cultivars that tolerate or suppress weeds is expected to be a major lever for  
471 integrated crop protection (see introduction). The present study identified the features that make species  
472 and cultivars "generalist winners", i.e. that produce a high yield in weed-free situations or that are weed-  
473 suppressive, regardless of the cropping system and pedoclimate. But, even if some of the crop species  
474 studied here were better than others, none of them combined all the parameter values minimizing weed  
475 impacts on crop production, far less those reconciling low weed impact with high potential production.  
476 This frequently reported antagonisms (Sardana et al., 2017) may correspond to the theoretical trade-off  
477 between community performance and competitiveness (Denison et al., 2003): crop plants with traits that  
478 maximize their competition towards weeds compete among themselves in the absence of weeds,  
479 reducing their overall performance in resource capture and biomass production. However, Denison et al  
480 (2003) concluded that "there is no reason to expect the structure of natural ecosystems [...] to be a  
481 reliable blueprint for agricultural ecosystems". The antagonism between yield potential and weed  
482 suppression is thus not inevitable as shown by recent varietal improvement (section **Error! Reference**  
483 **source not found.**).

484 Even when focusing on the sole weed suppression aspect, there was a trade-off between crop species  
485 that minimize weed-caused crop yield loss and those that limit weed seed production, i.e. the risk of  
486 future yield loss. For instance, pea presented a high weed-caused crop yield loss but a low weed seed  
487 production, which partially explains, in addition to the use of different herbicides and the absence of  
488 mineral nitrogen fertilization, why pea is a very interesting diversification crop in winter rotations  
489 resulting in an impressive reduction of weed infestation (Chauvel et al., 2001). This again demonstrates  
490 the necessity to combine crop/cultivar choice with all other cropping-system components.

491 The present study focused on parameters driving crop-weed competition for light, albeit in a large range  
492 of crops and cropping systems. But, as the lower-input crop management and weed management  
493 strategies required by new farming policies must be robust to hazards resulting from climate change, it  
494 will be necessary to similarly consider crop and weed parameters related to competition for nitrogen and  
495 water or those to frost damage. Indeed, other parameter-based studies have shown the importance of,  
496 e.g., photosynthesis response to temperature or photosynthetic pathway (Spitters and Aerts, 1983). The  
497 same applies to parameters that drive crop and weed phenology and, for weeds, seed persistence. This

498 is essential when aiming to tailor advice to particular crops and cropping systems as the most successful  
499 weeds were shown to be those mimicking crops in terms of emergence and maturity dates (Fried et al.,  
500 2008; Fried et al., 2009).

501 Down-scaling the present approach to investigate intra-species variability in crop robustness to weeds  
502 is a promising avenue. The goal is not only to assist the choice of the best varieties to sow, but also to  
503 identify key selection criteria to focus on, in order to create new high-yielding crop varieties that are  
504 robust to weed impacts (Martre et al., 2015; Rotter et al., 2015). Recent studies suggested that, at least  
505 in rice, high yield potential and improved weed-suppressive ability are compatible (Mahajan *et al.*, 2014;  
506 Mahajan *et al.*, 2015).

## 507 **5 Conclusion**

508 The present study identified generic rules on which species parameters make annual weeds harmful for  
509 crop production and crops tolerant to crop-weed competition for light, across a large range of arable  
510 cropping systems and pedoclimates. Crop and weed species that were successful in mixed canopies were  
511 shown to be similar in terms of potential plant morphology and shading response. These rules can be  
512 used as pointers for selecting crops in agroecological cropping systems aiming to regulate weeds by  
513 biological interactions. The study also demonstrated a trade-off between crop traits that promoted  
514 potential yield and those that made crops tolerate or suppress weeds. Further research is thus needed to  
515 resolve this trade-off and identify combinations of crop species traits that reconcile high potential yield  
516 and low yield loss.

517

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677

678

679 **8 Tables**

680

681 Table 1. Species parameters for characterizing initial growth, potential plant morphology and response to shading (based on Colbach et al., in revision). For  
 682 each species, there are 11 values for each potential-morphology and shading-response parameter, corresponding to 11 BBCH<sup>§</sup> stages ranging from emergence  
 683 (0) to death (10). Ranges of variation correspond to the 25 weed species and 33 crop species investigated by Colbach et al.

Parameter name	Relative advance of growth stage at the time of parameter measurement	Unit	Median [min,max] <sup>§</sup>
<b>A. Initial growth (without neighbour shading or self-shading)</b>			
RGR	Relative growth rate	cm <sup>2</sup> ·cm <sup>-2</sup> ·°Cday <sup>-1</sup>	0.0172 [0.0055, 0.0461]
LA0	Leaf area at emergence	cm <sup>2</sup>	0.179 [0.01, 3.10]
<b>B. Potential morphology (morphology variables in unshaded conditions)</b>			
SLA	Specific Leaf Area (total leaf area vs total leaf biomass <sup>&amp;</sup> ) - <i>Leaf area efficiency</i>	cm <sup>2</sup> ·g <sup>-1</sup>	153 [10, 1204]
LBR	Leaf biomass ratio (leaf biomass vs total above-ground biomass) – <i>Leafiness</i>	none	0.75 [0, 1]
HM	Specific (allometric) plant height – <i>Height efficiency</i> (height vs. total above-ground biomass ratio)	cm·g <sup>-1</sup>	20 [1.2, 838]
b_HM	Shape parameter b for specific plant height – <i>Height efficiency of heavy vs light plant</i>	none	0.27 [0.0005, 0.99]
WM	Specific (allometric) plant width – <i>Width efficiency</i> (width vs. total above-ground biomass ratio)	cm·g <sup>-1</sup>	22 [0.82, 3464]
b_WM	Shape parameter b for specific plant width – <i>Width efficiency of heavy vs light plant</i>	none	0.37 [0.02, 1.70]
RLH	Median relative leaf height (relative plant height below which 50% of leaf area are located)	cm cm <sup>-1</sup>	0.48 [0.20, 0.81]
b_RLH	Shape parameter for leaf distribution along plant height – <i>Unevenness of leaf distribution</i>	none	2.7 [0.24, 58]
<b>C. Response to shading (variation in morphology variables with shading intensity)</b>			
mu_SLA	Response of specific leaf area to shading	none	0.48 [-0.56, 1.72]
mu_LBR	Response of leaf biomass ratio to shading	none	-0.01 [-0.66, 1.02]
mu_HM	Response of specific height to shading	none	0.43 [-0.53, 2.27]
mu_WM	Response of specific width to shading	none	0.27 [-1.53, 1.87]
mu_RLH	Response of median relative leaf height to shading	none	0.01 [-1.00, 1.39]

684 <sup>§</sup> The BBCH-scale is a generic scale applying to both mono and dicotyledonous weed species to identify their growth stages (Hess et al., 1997)

685 <sup>§</sup> Median, minimum and maximum values over all crop and weed species. For B and C, these are over all stages

686 <sup>&</sup> All biomass-based units refer to dry plant or leaf biomass

687 Table 2. Which factors influence crop yield loss the most?

688 A. Analysis of variance of yield loss as a function of simulation factors with PROC GLM of SAS.  
 689 Cropping systems and weather repetitions were nested within regions. All factors were significant at  
 690  $p=0.0001$

Factors	Partial R <sup>2</sup>	
	Crop grain yield loss	Weed seed production
Years since simulation onset (log10-transformed)	0.03	0.00
Crop species	0.10	0.01
Region	0.04	0.01
Cropping system (within region)	0.27	0.27
Weather repetition (within region)	0.01	0.00
Crop species x cropping system (within region)	0.05	0.09
Crop species x weather repetition (within region)	0.01	0.00
Cropping system x weather repetition (within region)	0.17	0.05
TOTAL	0.68	0.44

691  
 692 B. Comparison of means. Variation in yield loss relative to mean loss. Numbers followed by the same  
 693 letter are not significantly different at  $p=0.05$ . Crops between brackets are based on a too small number  
 694 of situations and reflect the effect of cropping system and region rather than the crop species

Crop species		N	Variation in	
			Crop grain yield loss (%) <sup>§</sup>	Weed seed production (seeds/m <sup>2</sup> )
Maize	ZEAMX	17342	-31.4 a	5682 d
Oilseed rape	BRSNN	10452	-26.8 b	-26853 b
(Field bean)	(VICFX cv Gladice)	210	-15.8 c	-26365 abc
Sunflower	HELAN	3127	-1.7 d	43898 f
Spring barley	HORVX	1421	-0.6 de	-1540 d
Wheat	TRZAX cv Cézanne	18187	0.4 e	-12321 c
Triticale	TTLSS	655	0.5 e	8209 de
Wheat	TRZAX cv Orvantis	3939	0.9 e	-33635 a
Soybean	GLXMA	689	4.3 f	61057 g
Pea	PIBSX cv Enduro	446	7.7 fgh	-2250 cd
(Sorghum)	(SORVU)	241	7.8 fgh	32872 f
(Flax)	(LIUUT)	258	8.2 fgh	-21315 bc
Barley	HORVX	6901	8.6 g	17 d
Wheat	TRZAX cv Caphorn	3028	11 h	-40991 a
Spring pea	PIBSX	4340	26.9 i	13537 e

695 <sup>§</sup>Yield loss is 100 (yield in weed-free – yield in weed-infested simulation)/(yield in weed-free  
 696 simulation)  
 697

698 **9 Figure captions**

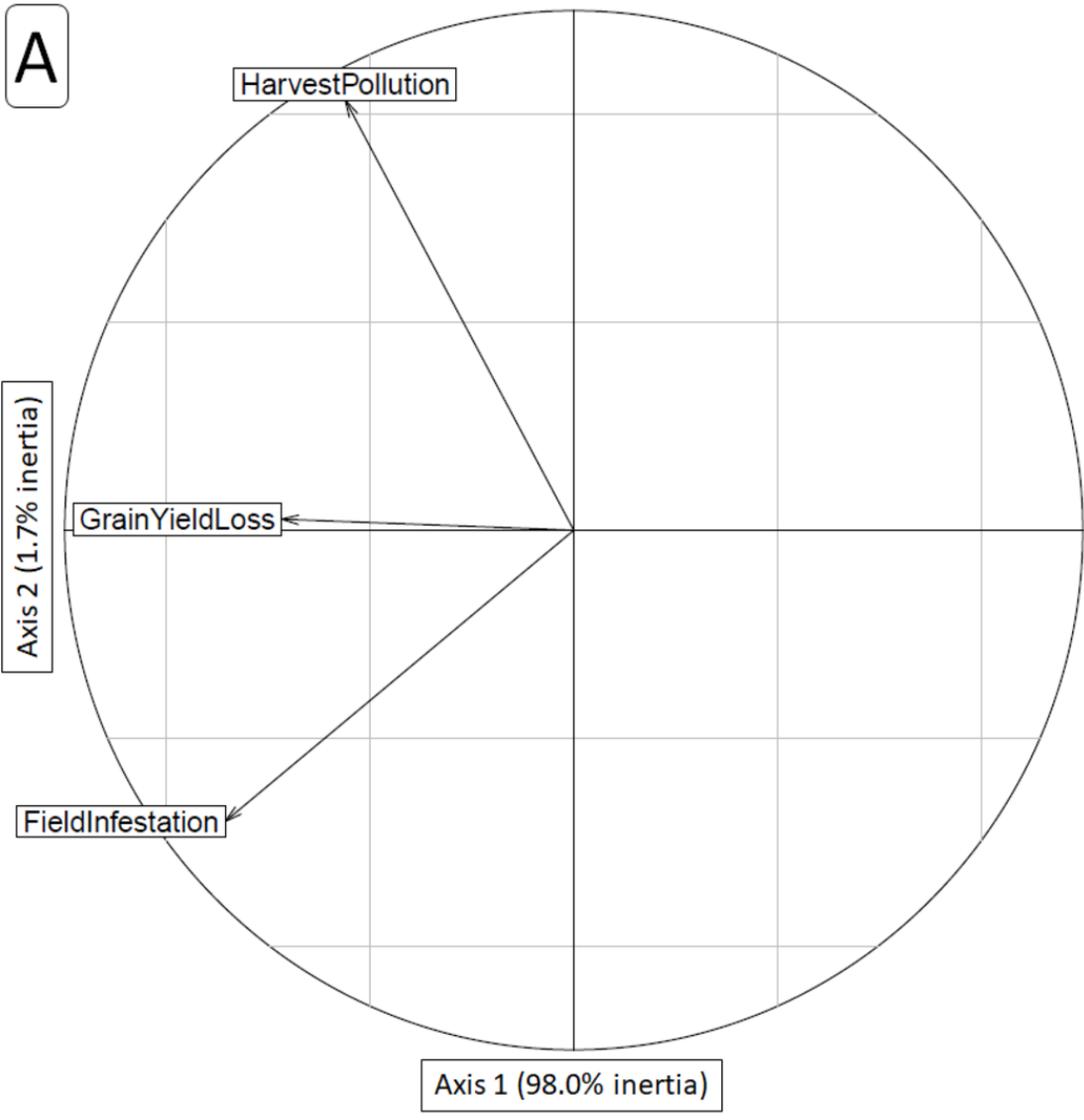
699 Figure 1. The weed species (shown with EPPO codes) and species traits that explain weed harmfulness  
700 for crop production, irrespective of crops and cropping systems. Synthetic representation of the RLQ  
701 results with weed-impact indicators and weed plant density in simulated fields as matrix R and L,  
702 respectively, and parameters driving morphology and shading as matrix Q. A. Weed-impact indicators  
703 with correlation circle, B. Weed species, clustered into groups, following a Ward ascendant hierarchy  
704 classification, C. species parameters, with those positively or negatively correlated to weed harmfulness  
705 for crop production in respectively red and green; parameters in gray are not significantly correlated to  
706 weed harmfulness based on fourth-corner analysis (LA0 is hidden behind SLA0, mu\_RLH6 and 7 behind  
707 mu\_RLH10). For the meaning of species parameters, see Table 1. (Nathalie Colbach © 2018)

708  
709 Figure 2. Annual crop performance in terms of weed-caused crop yield loss (100 t/t), weed seed  
710 production (seeds/m<sup>2</sup>) and potential yield (MJ/ha), and the correlation with crop parameters driving  
711 potential plant morphology and shading response. Principal Component Analysis (PCA) on annual  
712 performance indicators. A and C: arrows show performance variables, with a projection of the most  
713 correlated crop parameters. B and D: dots show annual performance of 272 cropping systems x 27 years  
714 x 10 weather repetitions as symbols and crop species (EPPO codes) at the center of 95% ellipses. For  
715 the meaning of the crop parameters, see Table 1. (Nathalie Colbach © 2018)

716  
717 Figure 3. Schematic representation of crop ideotypes in terms of potential plant morphology and shade  
718 response for maximising potential yield and limiting weed-caused yield loss across a large range of  
719 contrasting cropping systems and pedoclimates. Based on crop parameters shown to increase potential  
720 yield in weed-free simulations (A) and decrease yield loss (B) by Principal Component Analysis of  
721 Figure 2. Parameters describing plant morphology in unshaded conditions drive space occupation before  
722 other plants (top); parameters describing shade response drive the reaction to neighbour plants (bottom)  
723 in monospecies (A) and multispecies canopies (B). For the names of the crop parameters, see Table 1.  
724 (Nathalie Colbach © 2018)

725  
726 Figure 4. Schematic representation of weed "harmtypes" in terms of potential plant morphology and  
727 shade response that drive immediate harmfulness for the current crop irrespective of cropping system  
728 and pedoclimate. Based on weed parameters shown to increase yield loss, field infestation, harvest  
729 pollution (A), only yield loss and field infestation (B), only harvest pollution (C) by RLQ analysis of  
730 Figure 1. Parameters describing plant morphology in unshaded conditions drive space occupation before  
731 other plants (top); parameters describing shade response drive the reaction to neighbour plants in  
732 multispecies canopies (bottom). For the names of the crop parameters, see Table 1. (Nathalie Colbach  
733 © 2018)

A



**B**

Axis 2 (1.7% inertia)

5

0

-5

-10

-10

-5

0

5

Axis 1 (98.0% inertia)

GALAP

D

AVEFA

GERDI

STEME

ALOMY

ECHCG

CHEAL

PANMI

MATIN

CAPBP

VERHE

AMARE

SOLNI

POLAV

DIGSA

POAAN

VERPE

DATST

DIGSA

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POLCO

MERAN

POLPE

ABOTH

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CAPBP

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AMARE

SOLNI

POLAV

DIGSA

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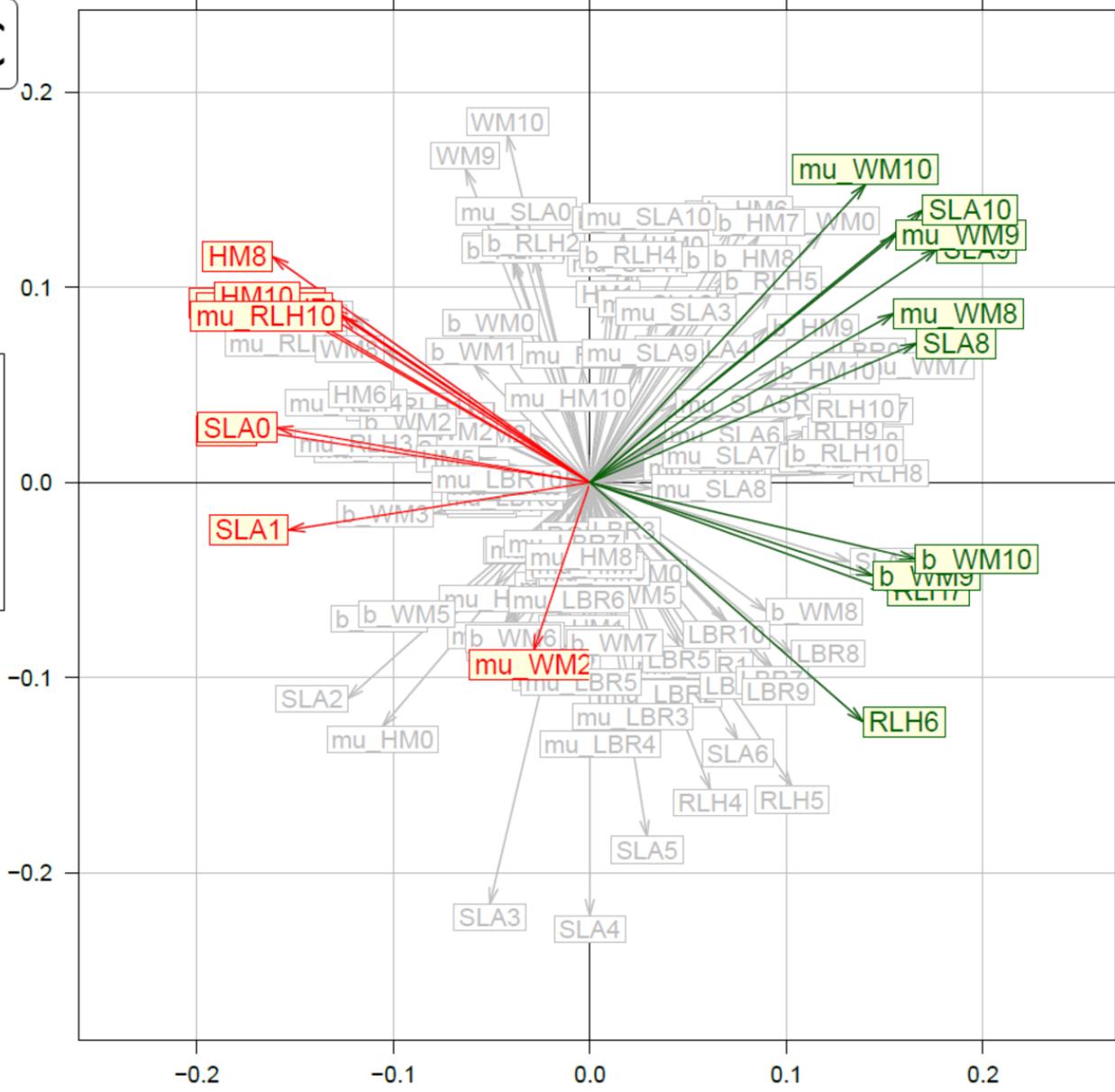
ABOTH

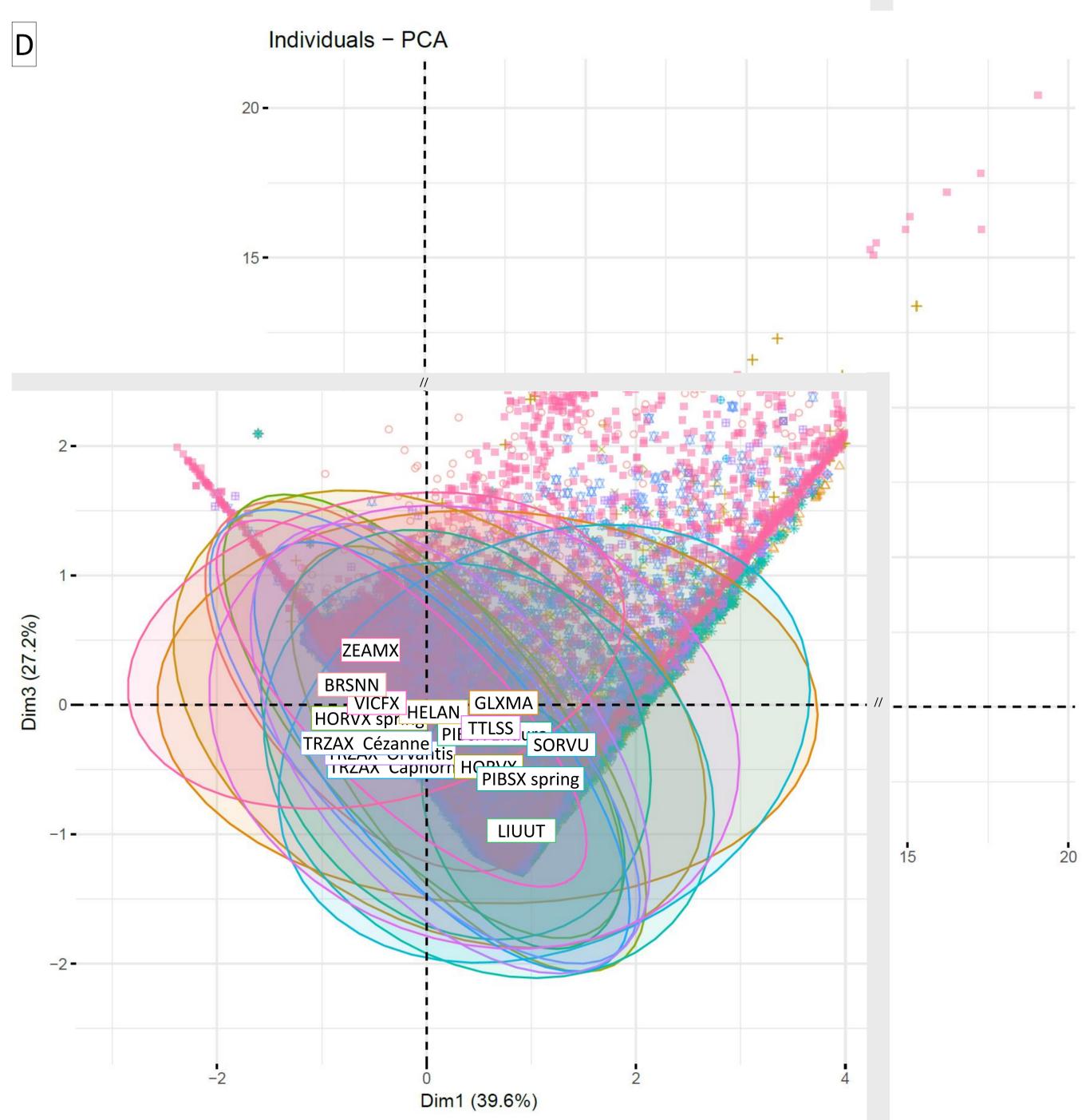
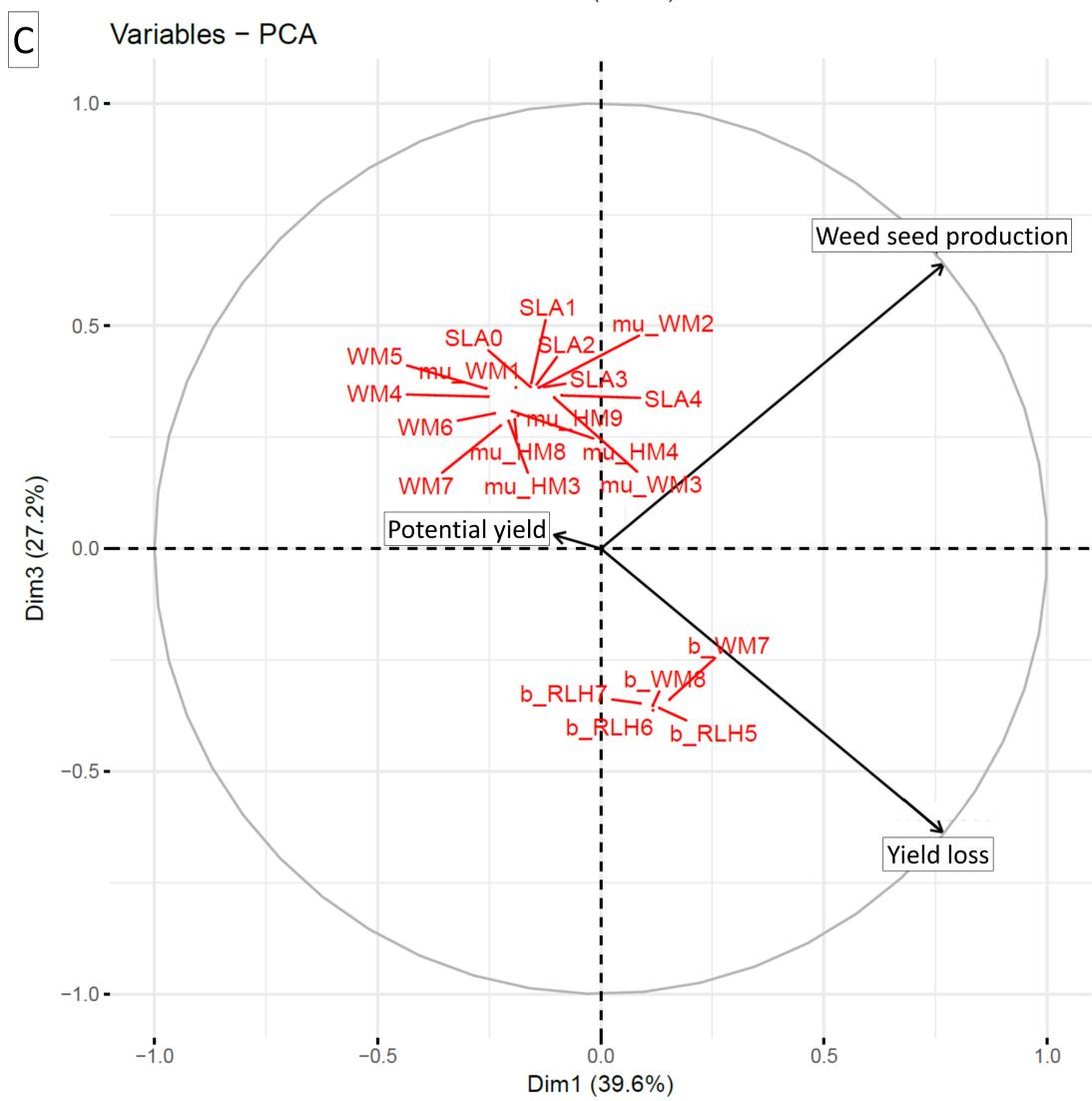
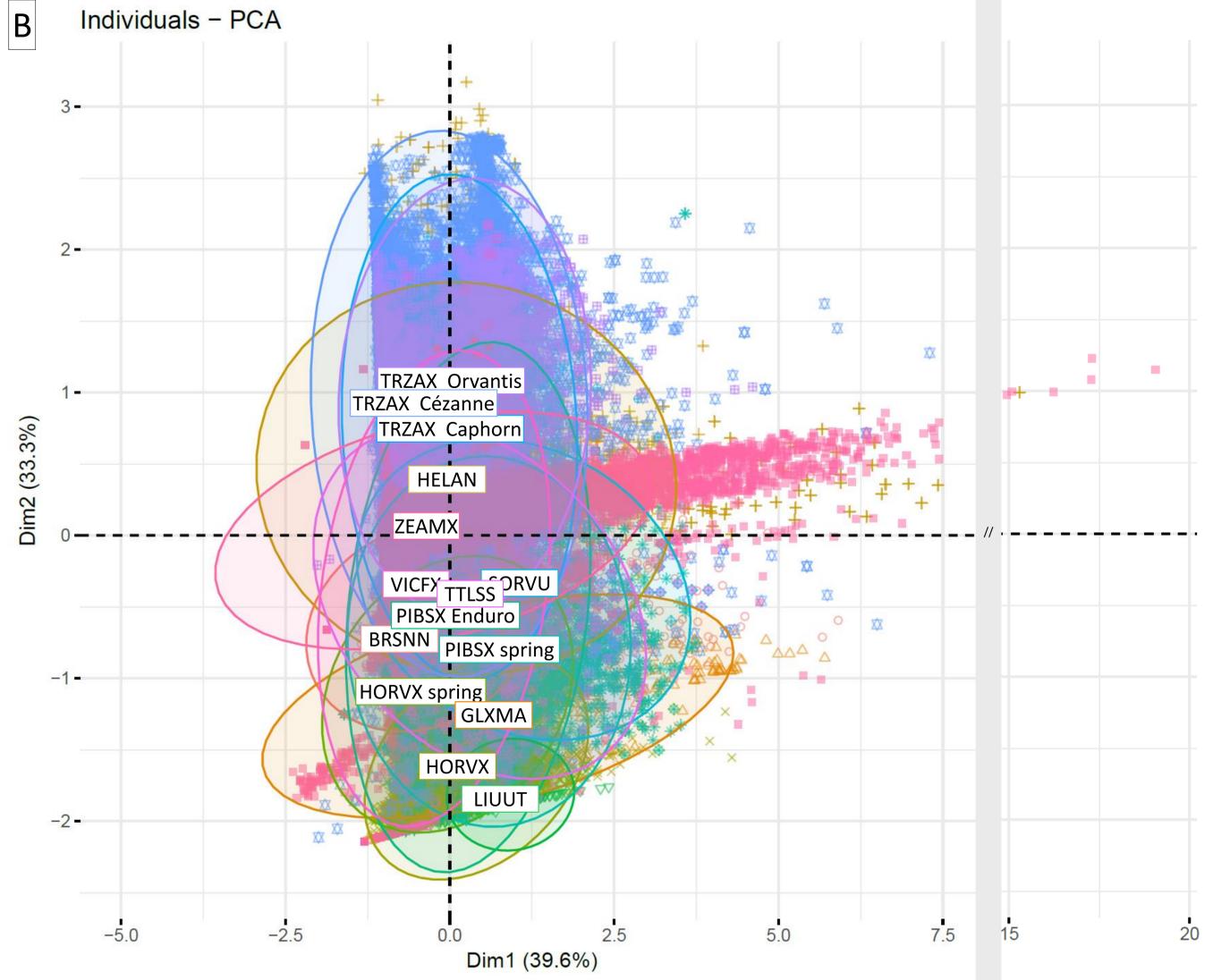
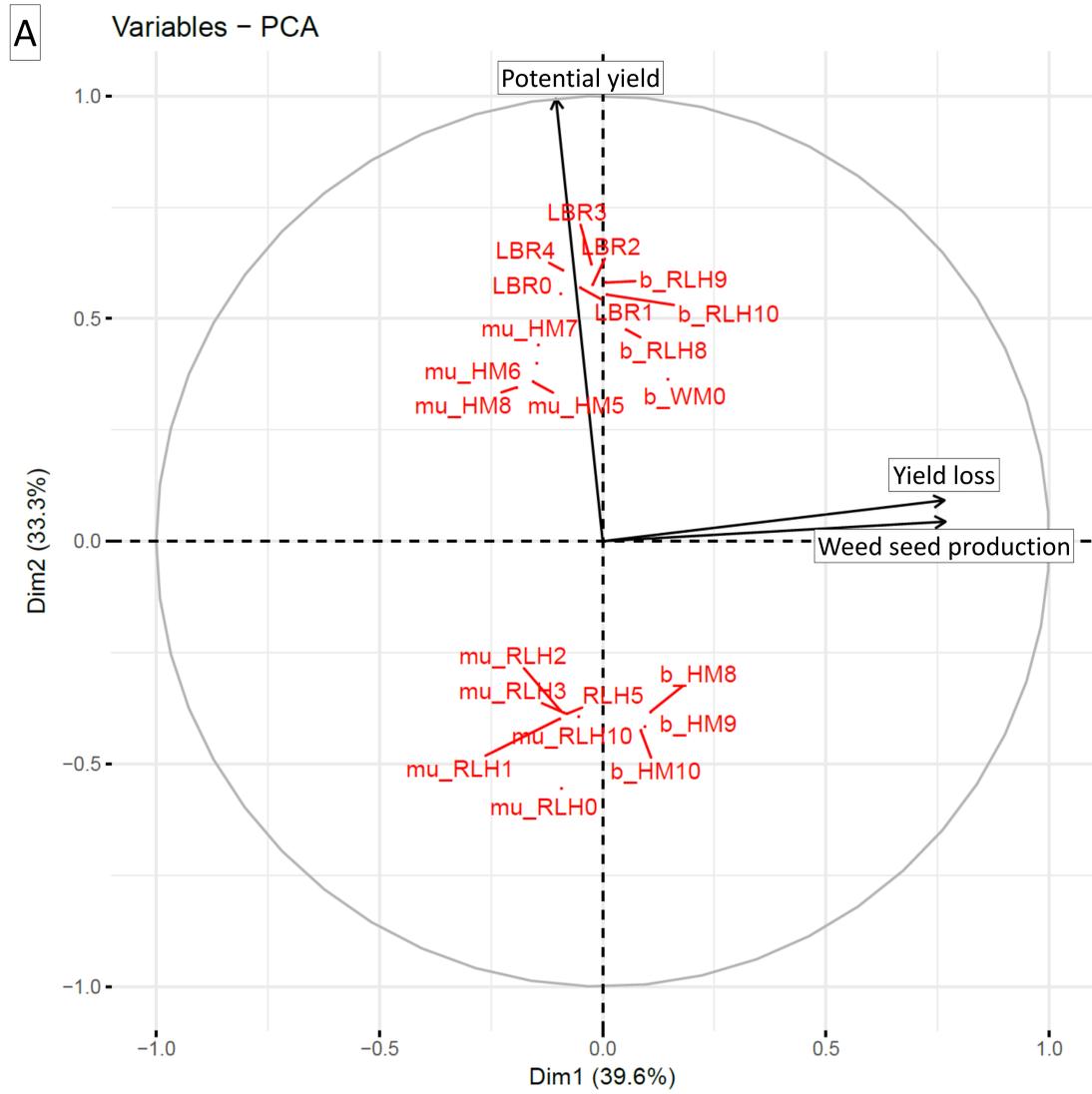
AMBEL

**C**

Axis 2 (1.7% inertia)

Axis 1 (98.0% inertia)

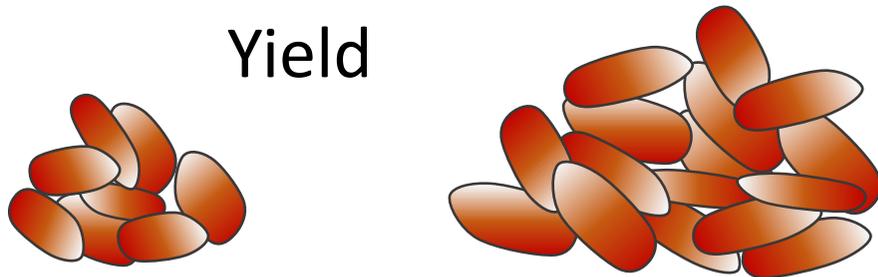
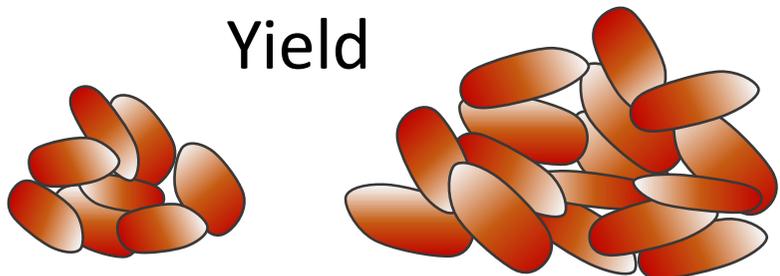




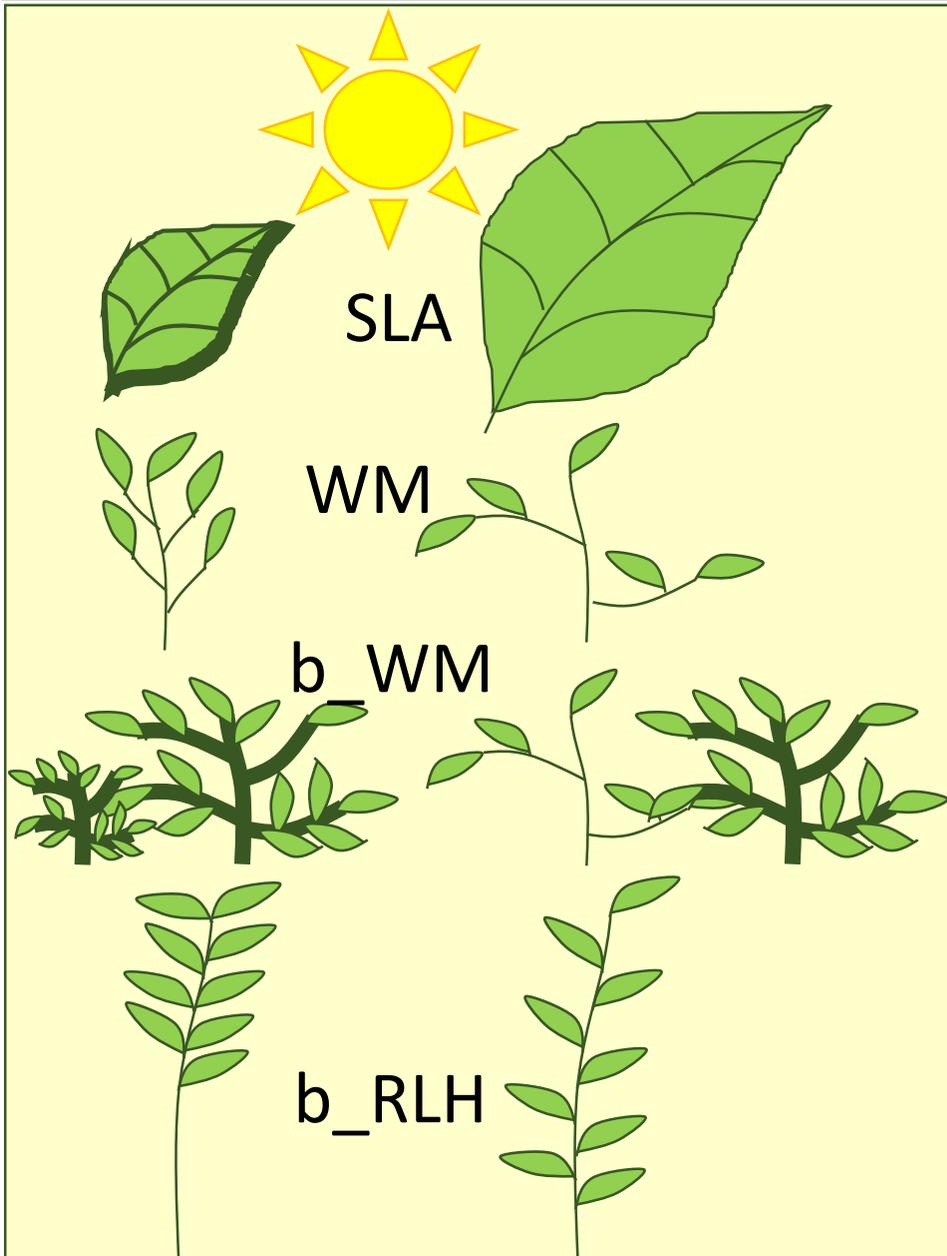
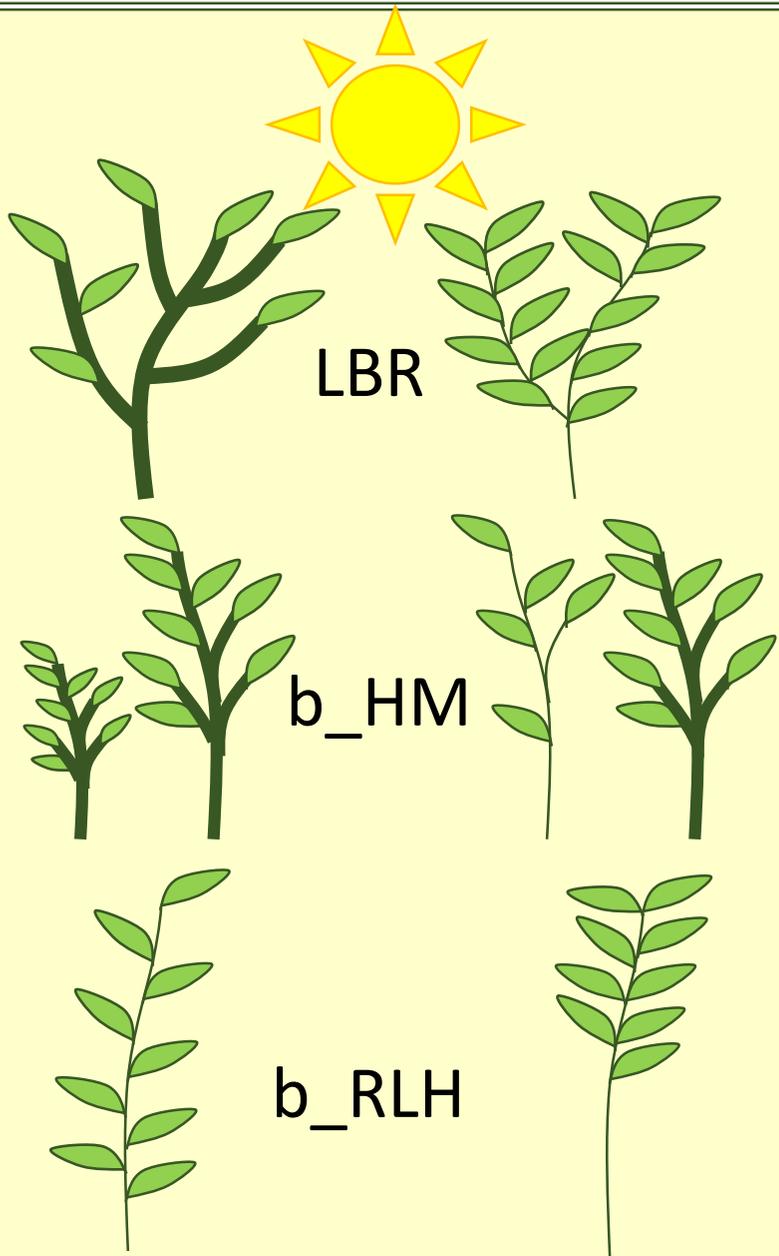
# A. Without weeds

# B. With weeds

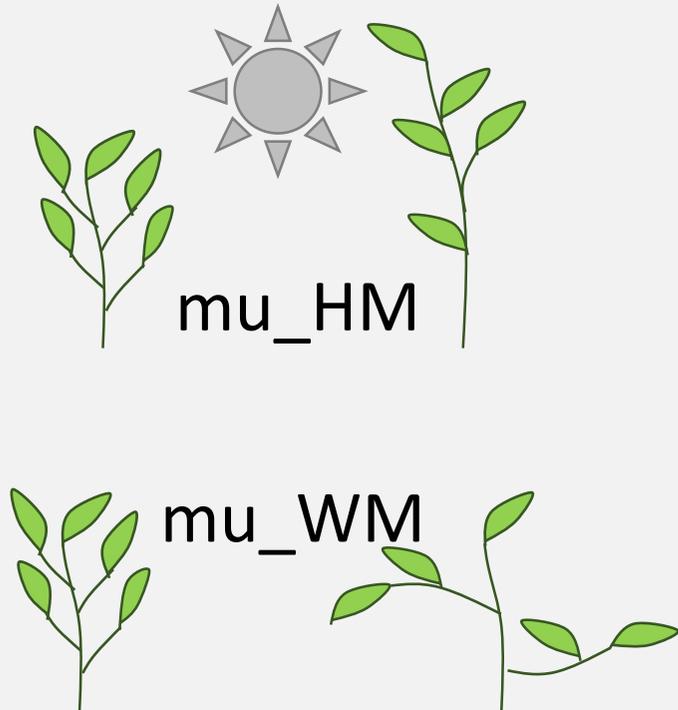
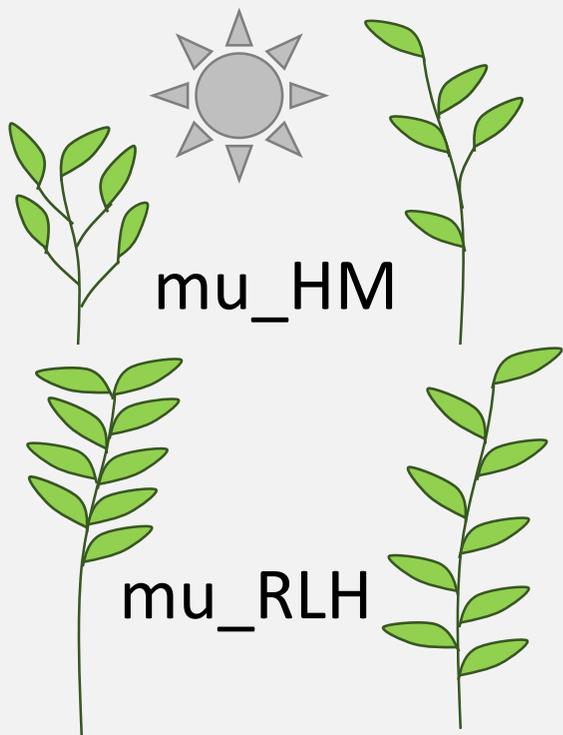
Yield



Occupy space before any other



React to neighbours

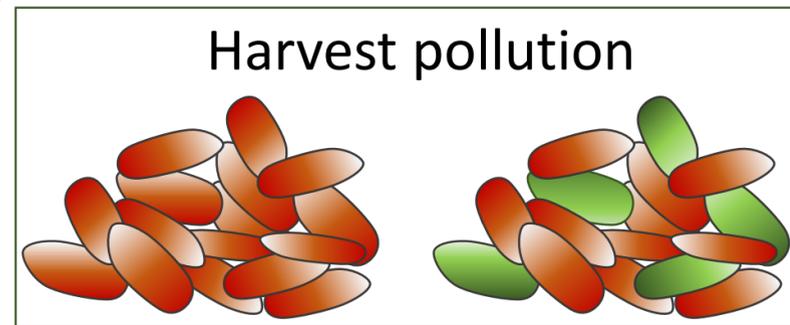
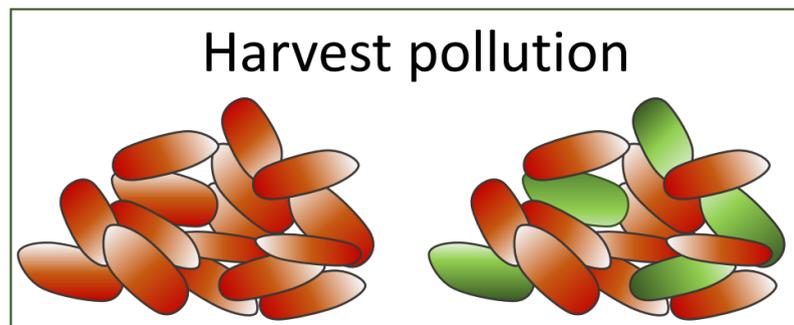
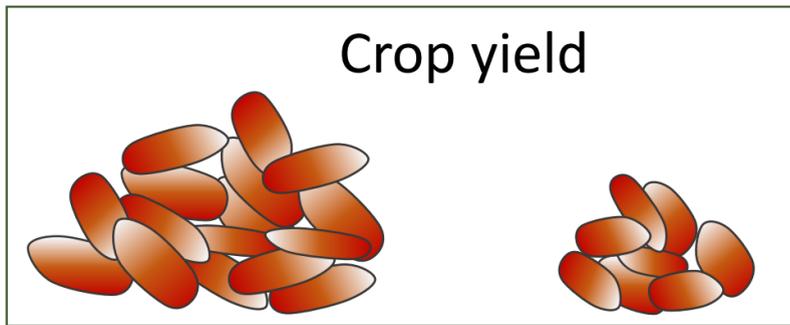
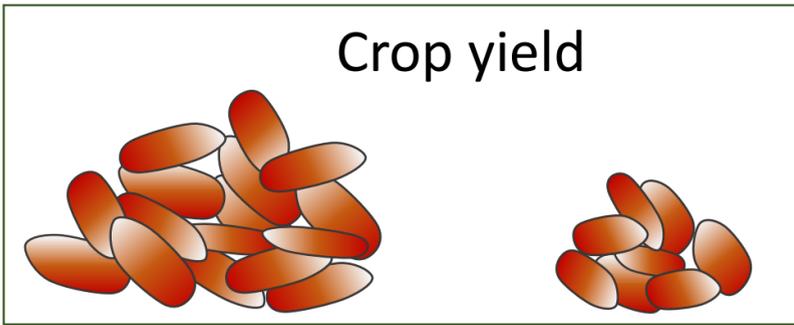


# A. During crop cycle

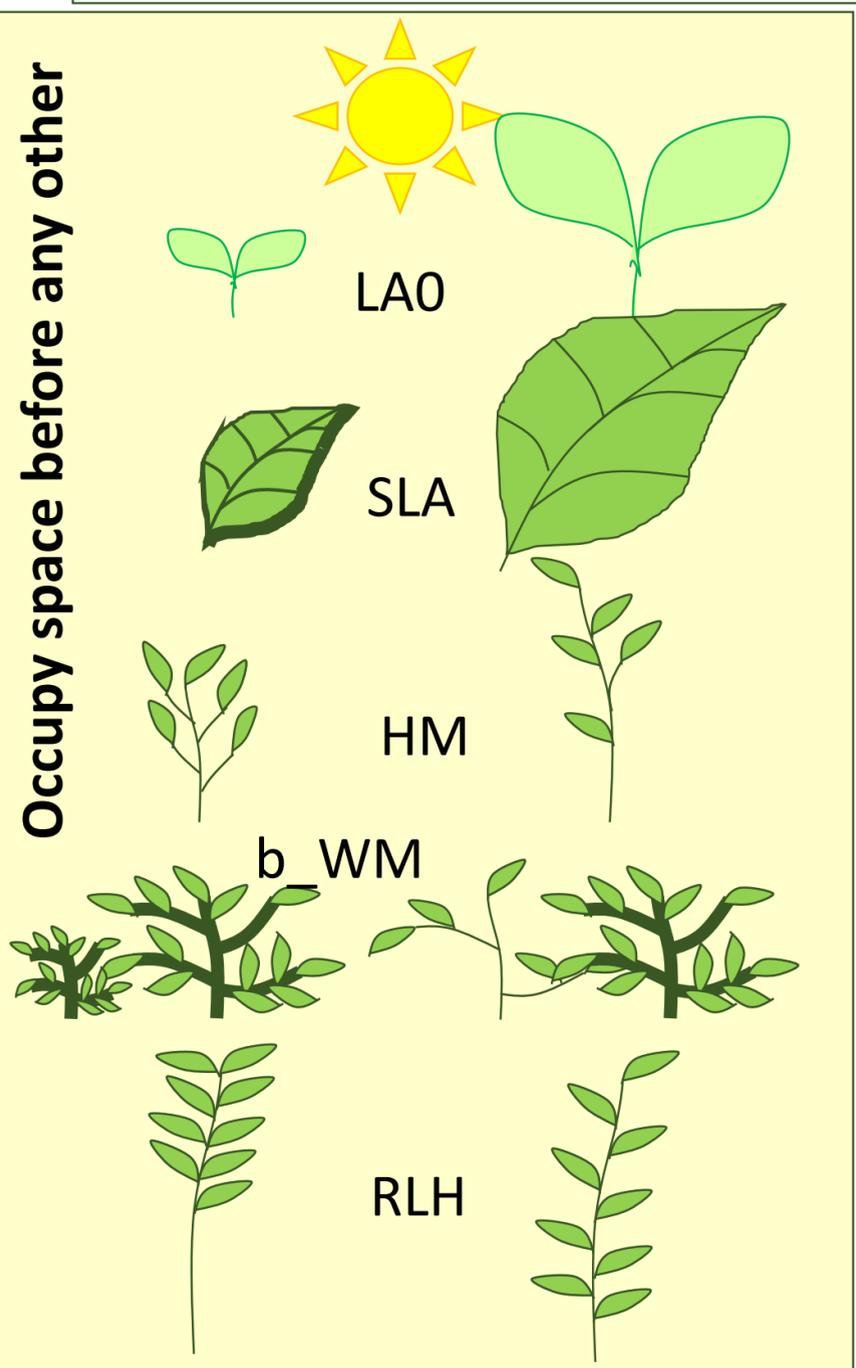
# B. Before harvest

# C. At harvest

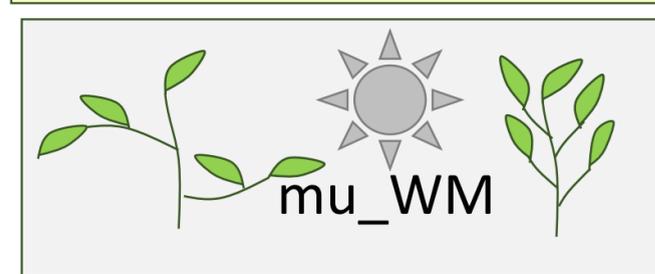
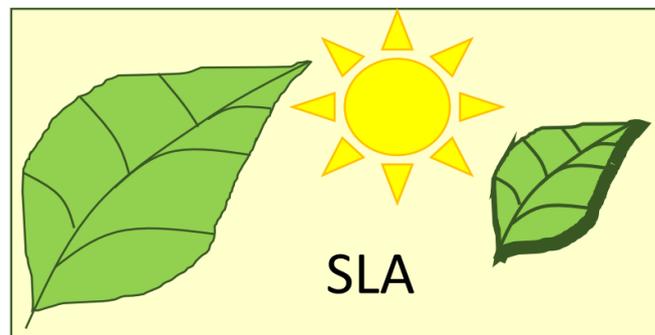
Weed harmfulness criteria



Occupy space before any other



Decrease herbicide interception area



Shift biomass above cutting height

