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How to pit weeds against parasitic plants. A simulation study with *Phelipanche ramosa* in arable cropping systems

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Abstract

Branched broomrape (*Phelipanche ramosa* (L.) Pomel) is a parasitic plant, which causes severe yield losses in major crops worldwide. Due to its broad host range, including numerous non-parasitic weed species, the persistence of its seeds in the soil, and the poor efficiency of available management techniques, broomrape management is complex. In a previous paper, we developed a broomrape-dynamics model called PHERASYS to support the design of management strategies combining multiple techniques aiming at long-term control of broomrape. Here, the objective is to use this simulation model to (1) check the consistency of simulations vs. literature data, (2) evaluate the potential of cropping systems to manage the combination of branched broomrape and weeds, (3) investigate whether weeds can biologically regulate parasitic plants in agroecosystems. Five contrasting cropping systems including different levers known to influence broomrape dynamics were simulated with different weather series. Four simulation series were run, with or without broomrape as well as with or without weeds, to discriminate the individual effects of weeds and broomrape on crop production as well as the effect of weeds on broomrape dynamics. Simulations with PHERASYS showed that delayed sowing in combination with the use of trap and catch crops are promising for reducing broomrape infestation and yield losses in the long term. Tolerating a temporary and/or low-density weed flora in such cropping systems could improve broomrape management because spring/summer weeds could reduce broomrape seed bank by triggering broomrape germinations that would not reproduce. During cash-crop growth, weed contribution to broomrape infection would be negligible. However, these conclusions are only valid if broomrape-attaching weeds reproduce before broomrape has time to do so, which needs to be checked with field experiments for most weed species.

Keywords: branched broomrape, weed, agroecology, modelling, cropping systems, *Phelipanche ramosa*, PHERASYS, biological regulation

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39 1 Introduction

40 Broomrapes are parasitic plants that threaten major crops worldwide (Parker, 2013). As holoparasites,
41 they are unable to photosynthesize and entirely rely on host resources to survive and reproduce (Heide-
42 Jørgensen, 2013). They must germinate close to a host root, after being stimulated by its exudates
43 (Yoneyama *et al.*, 2013), to connect to its vascular system and derive the resources they need (Heide-
44 Jørgensen, 2013). Among broomrapes, branched broomrape, *Phelipanche ramosa* (L.) Pomel, is
45 particularly devastating since it is found on every continent and is able to infect crops in more than 10
46 botanical families including *Solanaceae*, *Brassicaceae* and *Asteraceae*, though it is rare in *Poaceae*
47 (Parker and Riches, 1993a; Molenat *et al.*, 2013). In France, it is a major pest of winter oilseed rape,
48 where it can cause up to 90% yield losses (Gibot-Leclerc *et al.*, 2012), and it also infects hemp,
49 sunflower and tobacco (Terres Inovia, 2018).

50 To date, the only curative method available in arable crops is the application of herbicides on herbicide-
51 resistant crops (Fernández-Aparicio *et al.*, 2016a; Données Ephy - Anses, 2018), but this technique
52 clashes with current policies aiming at reducing the use of pesticides because of their impacts on human
53 health and environment (Potier, 2014). Most herbicides efficient on broomrape are systemic herbicides
54 such as inhibitors of aromatic (glyphosate) or branched-chain amino acid synthesis (imidazolinones and
55 sulfonylureas) applied to the leaves of the crop (e.g., Eizenberg *et al.*, 2006). To date, none of these are
56 both tolerable to the host plant and lethal to the parasite. Biocontrol is a promising option to complement
57 cultural techniques, but applicable and efficient products are still under development (Fernández-
58 Aparicio *et al.*, 2016c; Cartry *et al.*, 2021). Consequently, several preventive techniques with partial
59 effects must be combined to control broomrapes (Grenz *et al.*, 2005a; Rubiales and Fernández-Aparicio,
60 2012). They must provide long-term control as broomrape seeds die off very slowly (other broomrape
61 species: Murdoch and Kebreab, 2013; branched broomrape: Pointurier *et al.*, 2019).

62 Reducing the frequency of host-crops in the rotation is the first broomrape-preventive option that comes
63 to mind. Another option is to choose varieties that stimulate fewer germination, reduce attachments
64 and/or growth of attached shoots (Gauthier *et al.*, 2012). Trap crops and catch crops deplete the
65 broomrape seed bank by inducing broomrape germination without allowing further development of the
66 parasitic plant because they are resistant (trap crop) or because they are destroyed before broomrape
67 reproduction (catch crop) (Goldwasser and Rodenburg, 2013). Flax (*Linum usitatissimum* L.) and
68 birdsfoot trefoil (*Lotus corniculatus* L.) are interesting trap-cop candidates (Parker and Riches, 1993b;
69 Molenat *et al.*, 2013), white mustard (*Sinapis alba* L.) and oilseed rape volunteers can be used as catch
70 crops during summer fallow (Molenat *et al.*, 2013). Delayed sowing is consistently reported to reduce
71 infection of winter crops such as oilseed rape (Gibot-Leclerc *et al.*, 2006b; Fernández-Aparicio *et al.*,
72 2016c) but not of summer crops (Grenz *et al.*, 2008). Evidence on tillage effects (Rubiales *et al.*, 2009a;

73 Fernández-Aparicio *et al.*, 2016c) and mineral fertilization (Goldwasser and Rodenburg, 2013) is
74 contradictory.

75 Moreover, branched-broomrape management must be thought along with non-parasitic weed
76 management (hereafter, the word "weeds" refers to non-parasitic weeds) because several dozens of weed
77 species are hosts (Boulet *et al.*, 2001; Gibot-Leclerc *et al.*, 2003; Simier *et al.*, 2013; Gibot-Leclerc *et*
78 *al.*, 2015). Weeds might increase broomrape infestation, as they serve as alternative hosts in the absence
79 of host crops. However, they can also deplete the broomrape seed bank, as some species stimulate
80 broomrape germination without supporting further parasite development (Gibot-Leclerc *et al.*, 2003).
81 Such weed species can potentially provide biological regulation of branched broomrape.

82 As a consequence, branched-broomrape management must be thought at the cropping system scale,
83 using multiple techniques and exploiting biological regulation by weeds. Therefore, simulation models
84 are essential to design cropping systems because they allow evaluating cropping system performances
85 in the long term in various pedoclimatic and floristic contexts (Bergez *et al.*, 2010; Jeuffroy *et al.*, 2014;
86 Colbach *et al.*, 2021). To our knowledge, to date only one model answers to the requirements for
87 evaluating cropping systems for branched-broomrape management. The mechanistic (process-based)
88 PHERASYS (Pointurier *et al.*, 2021a), connected to the multi-species weed dynamics model FLORSYS
89 (Colbach *et al.*, 2021), simulates branched-broomrape dynamics at a daily time-step and in 3D over the
90 years depending on cropping techniques and pedoclimate, in interaction with growth and development
91 of crops and weeds.

92 Consequently, the objective of the present study was to use PHERASYS to evaluate the potential of
93 cropping systems to manage branched broomrape (hereafter simply called "broomrape") and weeds in
94 interaction. In particular, we investigated whether weeds can contribute to biologically regulate parasitic
95 plants in agroecosystems. The simulations were also used to check the consistency of the model with
96 literature.

97 2 Materials and methods

98 This section first summarily presents the model to be used, followed by the choice of the cropping
99 systems to be tested, the simulation plan and the statistical methods needed to evaluate cropping-system
100 performance and understand the reasons for this performance.

101 2.1 The PHERASYS and FLORSYS model association

102 PHERASYS (Pointurier *et al.*, 2021a) describes broomrape dynamics from cropping system in interaction
103 with crop and weed growth as well as pedoclimate. It is a submodel of FLORSYS which simulates
104 multispecies crop and weed growth and reproduction at a daily time-step and in 3D from cropping system
105 in interaction with pedoclimate (Gardarin *et al.*, 2012; Munier-Jolain *et al.*, 2013; Colbach *et al.*, 2014;

106 Munier-Jolain *et al.*, 2014; Colbach *et al.*, 2021; Pointurier *et al.*, 2021b). This model associated can be
107 considered to be a virtual field on which cropping systems can be experimented with a large range of
108 virtual measurements of crop, weed and environmental state variables. Only the main features were
109 summarized here and additional information can be found in sections **S1** and **S2** of supplementary material
110 online.

111 2.1.1 Input variables and soil state variables

112 The user provides inputs to characterize the field (daily weather, latitude and soil characteristics), the crops
113 and cropping techniques (with their dates, tools used and options) and the initial weed seed bank (including
114 broomrape and non-parasitic weed species). These input variables drive various soil state variables (i.e.
115 structure, temperature, water potential) in 30 1-cm-thick soil layers.

116 2.1.2 Crop and weed life-cycle

117 The input variables and the soil-state variables influence the annual life cycle of annual weeds and crops,
118 with a daily time-step (Figure 1).

119 Pre-emergence stages (surviving, dormant and germinating seeds, emerging seedlings) are driven
120 by seed depth, soil structure, temperature and water potential. The crop-weed canopy is represented in
121 3D, with each crop and weed plant schematized as a cylinder (above ground) and top of a spilled cone
122 (below ground). Post-emergence processes (e.g. photosynthesis, respiration, growth, shade response)
123 are driven by light availability and air temperature. At plant maturity, weed seeds are added to the soil
124 seed bank; crop seeds are harvested to determine crop yield. Nitrogen stress is disregarded in the present
125 model version, and water stress only considered for pre-emergent processes.

126 2.1.3 Domain of validity

127 The model is currently parameterized for 26 frequent and contrasting annual weed species and 30
128 crop species, including cash crops as well as cover and forage crop species (section **S1.5** online). This
129 limits its use in conditions with dominant annual weeds. In other situations, the comparison of
130 simulations to independent field data from different French regions showed that crop yields, daily weed
131 species densities and, particularly, densities averaged over the years were generally well predicted and
132 ranked as long as a corrective function was added to keep weeds from flowering during winter at more
133 southern latitudes (Colbach *et al.*, 2016; Pointurier *et al.*, 2021b).

134 2.1.4 Parasite life-cycle

135 In parallel, the PHERASYS submodel predicts the number of broomrape individuals per host plant at
136 different stages and the biomass of broomrape shoots every day depending on biophysical processes.
137 Each day, a part of the seeds in the soil dies; non-dormant seeds can germinate only if stimulated by
138 neighbouring host-plant root exudates; the germinated seeds must attach to nearby susceptible plant
139 roots before emerging, flowering and producing new seeds. Attached broomrapes die either when they

140 have finished their life cycle, or when their host dies of old age or is destroyed by cultural operations.
141 When a broomrape produces seeds, the new broomrape seeds are dormant and are added to the
142 superficial layer of the soil seed bank.

143 2.1.5 Effect of parasitism on host plant growth and reproduction

144 Between attaching to host roots and emerging from the soil, broomrape biomass and its effect on host-
145 plant growth are negligible. Once broomrape starts to emerge, the daily net biomass produced by an
146 infected host after photosynthesis and respiration is reduced. Once the host plant reaches the rosette
147 stage, parasitism reduces biomass allocation to roots. Biomass allocation to leaves in the pathosystem is
148 not affected by parasitism. Host seed production is the most affected by infection: the larger broomrape
149 biomass is, the less biomass can be allocated to host seed production. But, as the broomrape life-cycle
150 duration is independent of host species, hosts that reproduce early suffer less from broomrape competition
151 for host resources and allow less broomrape reproduction (or even none at all).

152 2.1.6 Modelling the effects of cropping systems on broomrape dynamics

153 The different processes modelled in PHERASYS allowed integrating the effects of several cropping
154 techniques. For example, soil tillage moves seeds in the soil, which makes them more or less close to
155 stimulating root exudates and to host roots and thus determines the number of stimulated broomrape
156 seeds and attachments.

157 2.2 Simulation plan

158 To understand broomrape-weed interactions as a function of cropping system, we chose to investigate
159 in detail a small number of contrasting cropping systems differing in terms of cropping techniques that
160 potentially influence broomrape. Five cropping systems practiced by farmers in western France
161 (Colbach *et al.*, 2017a), where broomrape is the most problematic on oilseed rape (Terres Inovia, 2018),
162 were simulated (Table 1). They included a typical local system, i.e. crop rotation including wheat,
163 sunflower and oilseed rape, with mouldboard ploughing and pesticide treatments (Agreste, 2012). In
164 addition, four alternative systems implementing three techniques known to control broomrape were
165 simulated, namely diversified crop rotations, delayed sowing and reduced tillage (Fernández-Aparicio
166 *et al.*, 2016b). The crops used to diversify the rotations, flax and mustard, are known to be "trap" and
167 "catch" crops" respectively, which reduce parasite seed bank by stimulating parasite germination but
168 preclude parasite reproduction either because they are resistant to parasite attachment (the former) or
169 destroyed before parasite maturity (the latter).

170 Each system was simulated over 30 years with the typical soil, weather and a typical weed flora from
171 Poitou-Charentes (south-western France) given as inputs in FLORSYS. Simulations were repeated ten
172 times with ten weather repetitions, each repetition consisting of a series of 30 years randomly chosen in
173 the regional weather database. A moderate broomrape seed density was included in the initial weed seed

174 bank, corresponding to 2000 seeds/m² per centimetre of soil layer (Jestin *et al.*, 2014) in the top 10 cm
175 of soil (Prider *et al.*, 2013).

176 Four sets of simulations were run: (a) with weeds but no broomrape, (b) without weeds but with
177 broomrape, (c) with weeds and broomrape and (d) without weeds nor broomrape. They allowed to
178 deduce the yield losses due to weeds only, due to broomrape only and due to both weeds and broomrape
179 by comparing (a), (b) and (c) to (d) respectively. In each simulation set, the starting point in terms of
180 weed and broomrape seed-bank densities was the same for all five cropping systems and 10 weather
181 repetitions, i.e., an average of 171 seeds/m² per weed species (varying from 0.02 to 598 seeds/m²
182 depending on the species) and zero broomrape seeds in (a), 20000 broomrape seeds/m² and zero weed
183 seeds in (b), 171 weed seeds/m² and 20000 broomrape seeds/m² in (c) and zero weed and broomrape
184 seeds in (d). Further details can be found in section S.3 online.

185 2.3 Statistical analysis

186 The effects of the type of infestation (i.e. with weeds and/or broomrape) and of cropping systems on
187 annual crop yield losses due to pests (i.e. weeds and/or broomrape) were analysed with a linear model
188 with the function “lm” of R (R Core Team, 2019):

$$189 L_{iscyr} = cte + I_i + S_s + C_c + Y_y + R_r + (I \times S)_{is} + (I \times C)_{ic} + e_{iscyr}$$

190 L_{iscyr} is the yield loss due to pests in crop c of year y in cropping system s and weather repetition r ,
191 starting with infestation i . I_i is the effect of type of infestation i on yield loss, with $i \in \{\text{only weeds, only}$
192 $\text{broomrape, both, none}\}$. Similarly, S_s , C_c , Y_y and R_r are the effects of, respectively cropping system
193 $s \in \{\text{reference, ...}\}$, crop $c \in \{\text{oilseed rape, ...}\}$, year $y \in \{1, \dots\}$ and weather repetition $r \in \{1, \dots\}$ on yield
194 loss. $(I \times S)_{is}$ is the interactive effect of infestation i and system s on yield, and $(I \times C)_{ic}$ the effect of system
195 i in interaction with crop c . Finally, cte is a constant and e_{iscyr} the residual.

196 Yield loss (%), i.e. the difference in yield (MJ/ha) in simulations with and without pests, was calculated
197 relatively to yield obtained in simulations without pests. When analysing broomrape-caused yield loss,
198 only host crop species were included in the analysis. Data were squared-root-transformed before analysis
199 to achieve normality of residuals. Least significant difference tests were performed to compare yield
200 losses due to broomrape between cropping systems for each crop species with the function `LSD.test`
201 from the package `agricolae` of R.

202 Finally, we analysed which weed species and parameters drive broomrape infection. RLQ analyses were
203 used to identify significant relationships between broomrape-infection indicators and weed species
204 parameters, using the library `ade4` (Chessel *et al.*, 2004) of R (R Core Team, 2016). The RLQ analysis
205 was initially developed to analyse correlations between cultural techniques (R matrix) and species traits
206 (Q matrix) via weed species densities (L matrix). Here, we used annual indicator values of broomrape
207 shoot density, biomass, seed production and soil seed bank from the 30 simulated years and 10 weather

208 repetitions for the R matrix. The Q matrix consisted of the 142 parameters driving the annual life-cycle
209 of the 26 weed species in FLORSYS, two parameters determining the species ability to trigger broomrape
210 germination and allow broomrape attachment. The L matrix comprised the plant density of each weed
211 species for each of the 30 years and the 10 repetitions, using the maximums of the daily weed species
212 densities between crop sowing and harvest. In all three matrixes, we distinguished summer fallow from
213 in-crop variables (e.g., broomrape shoots during summer fallow vs broomrape shoots during cash crop).
214 Only parameter-indicator relationships significant at $p < 0.05$ after a 4th corner analysis were considered,
215 using the `fourthcorner()` function of R. This analysis tests whether species are distributed independently
216 of their effect on indicators and of their traits, retaining for each indicator \times trait combination the highest
217 p values of models permuting either indicators or traits. To check whether weed species could be
218 aggregated into functional groups in terms of impact on crop production related to plant morphology
219 and shading response, species were grouped based on a Ward ascendant hierarchy classification using
220 the `hclust()` function of R according to the Euclidian distances separating coordinates of species in the
221 RLQ multidimensional space.

222 3 Results

223 3.1 Broomrape dynamics

224 In simulations with broomrape only, all cropping systems led to a continuous increase of the broomrape
225 seed bank over 30 years, with regular sharp increases of the seed bank after host crops and slow
226 decreases in-between (Figure 2). This dynamic was slower in cropping systems with delayed sowing
227 and diversified crop rotation (scenarios 3 and 2 in Figure 2), where the seed bank was multiplied by only
228 4.3 and 7.3 respectively over 30 years, compared to 18-20 in the other three systems (Table 2).

229 Seed bank increased mostly after oilseed rape (Figure 2). Broomrape is highly reproductive on this crop
230 (Figure 3.A and C), except in the cropping system with delayed sowing where broomrape did not have
231 time to reproduce on oilseed rape (Figure 3.B). Indeed, the more oilseed rape sowing was delayed (i.e.
232 from system 1 to 2 to 3), the later broomrapes matured (from mid-April, mid-June and the end of June
233 respectively, Figure 3.A-B). Sunflower (which stimulates broomrape germination less than oilseed rape,
234 Figure 4.A) increased the broomrape seed bank in cropping systems with delayed sowing and diversified
235 rotation (systems 3 and 2 in Figure 2), but depleted it in other systems. There, the number of germinated
236 seeds exceeded broomrape seed production, resulting in a net decrease of the broomrape seed bank (e.g.,
237 system 1 in Figure 2). Flax and mustard achieved their goal as trap and catch crops: they induced
238 broomrape germination (Figure 4.B-C) but did not allow its reproduction (Figure 3.A-C). However, the
239 mustard benefits were largely cancelled out by broomrape seed production on the following sunflower
240 (Figure 2).

241 Overall, most broomrape germination occurred in spring, after a smaller germination peak in autumn in
242 winter crops (Figure 4.A-C). Broomrapes started to reach maturity in June in oilseed rape crops sown at
243 the end of August (Figure 3.A-C).

244 3.2 How weeds change broomrape dynamics

245 Generally, broomrape dynamics followed the same interannual pattern (i.e. succession of increases and
246 decreases) in weed-infested (broken lines in Figure 2) vs weed-free simulations (continuous lines). The
247 final broomrape seed bank was always lower than in the weed-free simulations (Table 2). The reduction
248 was strongest in the delayed sowing and no-till systems; it was the weakest in the reference and the no-
249 plough systems whereas there was no difference in the diversified rotation.

250 Indeed, weeds stimulated broomrape germination over all seasons, regardless of the crops in place (Figure
251 4.D-F) but did not allow more broomrape reproduction (Figure 3.D-F vs A-C). As a consequence, the
252 broomrape seed bank decreased even in crops such as wheat, which is neither a catch nor a trap crop.

253

254 3.3 The main drivers of crop yield loss

255 All factors tested in the analysis of variance (type of infestation, cropping system, crop species, weather
256 repetition, simulation year, section 2.3) had a significant effect on annual yield losses due to broomrape
257 and/or weeds predicted by PHERASYS ($p < 0.05$, section S4.4 online). Crop yield losses were 38%
258 averaged over all crop species and situations (type of infestation, cropping system, weather repetitions,
259 simulation year). They depended mostly on the crop species (partial $R^2 = 0.28+0.03$ for primary effect
260 and interactions), on the cropping system (partial $R^2 = 0.15+0.05$), and to a lesser extent on the type
261 infestation (i.e. with weeds, broomrape, or both, partial $R^2 = 0.00+0.09$). In other words, cropping
262 techniques, including crop choice, were more important than the pest community composition (i.e.,
263 including weeds and/or broomrape). Although weeds contributed to deplete the broomrape seedbank
264 (section 3.1), this did affect yield loss only in some crops and cropping systems (as shown by the
265 negligible primary-effect R^2) and this effect was small on average compared to effects of cropping
266 techniques.

267 3.4 Which management techniques drive broomrape-caused yield loss?

268 Broomrape caused on average 16 % yield losses in oilseed rape and 45% yield losses in sunflower in
269 the reference cropping system (system 1 in Figure 5.C and D), with a high variability in oilseed rape
270 depending on the year and weather repetition (size of boxes in Figure 5). Only the cropping system with
271 delayed oilseed rape sowing and mustard catch crop significantly reduced yield losses due to broomrape
272 to almost zero in oilseed rape (system 3 in Figure 5.C). Diversified rotation and no plough (systems 2
273 and 4) also tended to reduce yield loss compared to the reference system, particularly its variability, but
274 this was not significant.

275 In sunflower, whose management differed little between cropping systems, broomrape-caused yield loss
276 was similar in all systems, though it was lower in system 3 where sunflower was sown after a mustard
277 catch crop (Figure 5.D). The variations in yield loss (which is the relative difference of simulations
278 running with and without broomrape) observed in wheat (Figure 5.B) were entirely due to stochasticity
279 in the simulations as this crop cannot be infected by broomrape.

280 3.5 In which conditions do weeds increase broomrape impacts?

281 Overall, the combination of weeds and broomrape caused more yield losses than weeds alone (i.e.
282 symbols are significantly above the $y=x$ line in Figure 6.A). Adding broomrape did not change the
283 ranking of the cropping systems in terms of yield loss (i.e. the symbols are placed along a straight line
284 in Figure 6.A). The increase in yield loss caused by adding broomrape was the most important (i.e.
285 symbols were increasingly above $y=x$ when moving to the right of Figure 6.A) in those cropping systems
286 where weeds already caused large yield losses, i.e. the systems with little or no tillage.

287 When doing the opposite, i.e. when adding weeds to broomrape, the cropping system ranking did not
288 change either (i.e. the symbols were again on an approximate straight line in Figure 6.B). However,
289 adding weeds in the delayed-sowing system (system 3) decreased yield loss compared to a field infested
290 with broomrape only (i.e. blue diamond below the $y=x$ line in Figure 6.B). This was due to weeds
291 inducing broomrape germination year-round (Figure 4.F) which reduced the final broomrape seed bank
292 by 93% compared to the final seed bank in weed-free simulations (Figure 2). Conversely, in simplified
293 (system 4) or no till (system 5), adding weeds increased yield loss tremendously (i.e. triangles above the
294 $y=x$ line), because yield losses due to weeds cancelled out the benefits of broomrape seedbank depletion
295 by weeds (-30% and -89% for systems 4 and 5, respectively).

296 3.6 Which weed traits drive broomrape infection

297 The same simulated situations favoured broomrape seed bank densities at the end of summer fallow and
298 at crop harvest as the arrows for SeedBank0 and SeedBank1 were very close in the lower right quadrant
299 on Figure 7.A and the Pearson correlation coefficient was high (0.86 in section S4.6 online). There was
300 little correlation between broomrape seedbank densities with broomrape shoots, biomass or seed
301 production during summer fallow ("0" suffix) as the corresponding arrows were approximately
302 perpendicular to the seedbank arrows (non-significant Pearson correlations). Correlations were higher
303 during the cash-crop period (correlations between 0.13 and 0.43) but difficult to see on Figure 7.A (suffix
304 "1") as these variables were less linked to the first two axes of the correlation circle. Seed bank was only
305 linked to the seed rain during cash crop (correlation = 0.50) which was linked more to shoots on crop
306 plants (correlation = 0.40) than to total shoots (correlation 0.26), indicating that seed bank densities
307 resulted mostly from seed production from infected crop plants, and this cumulated over several years
308 rather than only from the most recent seed rain (i.e., the correlation was not that high).

309 The shoot/biomass/seed rain arrows during cash crops were shorter than the corresponding summer-
310 fallow arrows, indicating that the latter were more linked to weed species than the former. During cash
311 crops, most broomrape shoots were attached to crop plants (ShootsonCrop1 close to Shoots1 on Figure
312 7.A, correlation = 0.75) whereas any configuration was possible during summer fallow (the
313 corresponding arrows were far away from each other), depending on whether a cover crop was grown
314 during this period as in cropping system 3.

315 The simulated weed community was not structured according to its interactions with broomrape (Figure
316 7.B). The 26 simulated species were clustered into five groups which, except for group B, comprised
317 both germination-stimulating and/or broomrape-attaching species (red, blue and grey labels) as well as
318 species that neither attached nor triggered broomrape (white labels). Broomrape seed bank densities
319 were actually the highest in the situations with group-B weeds (both were located in the right lower
320 quadrant in Figure 7.A and B), which consisted exclusively of winter grass weeds (which neither trigger
321 nor attach broomrape). For each weed species, labels with "0" and "1" suffixes were located closely,
322 indicating that the same simulated situations favoured densities during summer fallow and during cash
323 crops.

324 Generally, the correlation between the weed parameters and broomrape indicators were very low (< 0.10
325 in absolute values, Table 3), again indicating that broomrape infection was not linked to individual weed
326 species or parameters, but rather to an interacting weed community. The two infection-specific weed
327 parameters, the ability to let broomrape attach ("attachingAbility") and the ability to trigger broomrape
328 germination ("alpha_h_GR24") were not among the 10 weed parameters that were the most correlated
329 to broomrape indicators (Figure 7.C, Table 3). Weed species able to trigger broomrape germinations
330 increased broomrape shoots, biomass and seed production, but mostly during summer fallow (negative
331 correlations in Table 3, arrows in the same quadrant in Figure 7.A and C). But these species were
332 associated to a decrease in broomrape seed bank indicating that they triggered more suicide broomrape
333 germinations and successful host infections.

334 Unexpectedly, broomrape shoots, biomass and seed rain during cash crop as well as broomrape seed
335 bank were negatively correlated to the weed ability to let broomrape attach (Table 3). But general weed
336 parameters were more correlated to broomrape infection than the two infection-specific parameters.
337 Broomrape infection during summer fallow (which was mostly on weed species) was increased in the
338 presence of weeds whose emergence period includes May and June, with a high base temperature and a
339 high frost sensitivity, which are all characteristics of spring and summer weed annuals. In addition, these
340 weed species presented a rather uniform leaf area distribution (low "RLH" values), usually not needing
341 to avoid shadowing by crops. However, these are the opposite characteristics of the weed species linked
342 with a high broomrape seed bank density, indicating that broomrape seedbank replenishment was not
343 linked to weeds but resulted mostly from infected crops co-occurring with autumn/winter weeds,

344 particularly those with the ability to let broomrape attach such as the winter grass weeds of group B in
345 Figure 7.B.

346 4 Discussion

347 4.1 Novelty

348 PHERASYS is the first model of broomrape dynamics in agroecosystems specifically designed and
349 parameterized for branched broomrape (Pointurier *et al.*, 2021a). Compared to other broomrape models
350 (Schnell *et al.*, 1996; López-Granados and García-Torres, 1997; Eizenberg *et al.*, 2005; Grenz *et al.*,
351 2005a; Ephrath and Eizenberg, 2010; Pérez-de-Luque *et al.*, 2016), it includes several major novelties:
352 (1) interactions between broomrape and several dozens of annual crop and weed species, (2) broomrape
353 impacts on crop growth and yield production, (3) a mechanistic description of the effects of all cropping
354 techniques on broomrape, crops and weeds, (4) a 3D individual-based representation of the crop-weed-
355 broomrape canopies allowing to investigate complex plant-plant interactions such as a biological
356 regulation of broomrape by non-parasitic weeds or crop diversification resulting from the introduction
357 of catch/trap crops into rotations and crop associations.

358 4.2 Consistency of PHERASYS with literature

359 During model design, we already checked that the various model formalisms were consistent with
360 literature reports (Pointurier *et al.*, 2021a) (Pointurier *et al.*, 2021a). Here, we could go one step further
361 and compare model output to field observations. The effects of the cropping techniques that we tested
362 by simulation were generally consistent with the literature (Table 4), demonstrating that despite the
363 many simplifications, the model produces realistic predictions.

364 The model produces many state variables that allow checking finer aspects of model consistency. For
365 instance, in the simulations, broomrapes started to reach maturity in June in oilseed rape crops sown at
366 the end of August (Figure 3.A-C), which is consistent with field observation (Gibot-Leclerc *et al.*, 2012).
367 Decomposing the effect of cropping techniques into a series of processes also allows to explain
368 contradictory effects reports in literature. For instance, deep vs superficial is reported to both decrease
369 broomrape infection because buried seeds germinate badly (Rubiales *et al.*, 2009b) and increase infection
370 because it places seeds closer to host roots (Fernández-Aparicio *et al.*, 2016b). Potentially, both effects
371 can cancel each other out, which is consistent with our simulations where tillage effects on broomrape
372 dynamics were not significant.

373 Another critical point is the prediction of the weeds' life-cycle duration. Weed flowering and maturity
374 dates simulated by FLORSYS were shown to be too early at some latitudes (Colbach *et al.*, 2016). So,
375 even though a corrective patch was used in the present simulations (section 2.1.2), the catch-crop effect
376 simulated here for weeds (section 4.3) could be overestimated. This could explain why, in contrast to
377 our simulations, recommendations usually advise to control host weed species as they might relay

378 broomrape infestation in the absence of crop (Gibot-Leclerc *et al.*, 2003; Jestin *et al.*, 2014). Moreover,
379 PHERASYS is still missing some common host species, such as *Aphanes arvensis* (Gibot-Leclerc *et al.*,
380 2003).

381 4.3 Agronomic implications

382 Our simulations showed that cropping techniques must be combined (e.g., trap and catch crops aiming
383 to deplete the soil seed bank, with delayed sowing or reduced host crops frequency in the rotation aiming
384 to limit broomrape reproduction) for an efficient control of broomrape in various weather scenarios.
385 These conclusions on which techniques or systems may not be valid in other pedoclimates, weed floras
386 contexts or cropping system types. This may also contribute to explaining why, contrary to the literature,
387 we did not observe any effect of soil tillage on broomrape dynamics (Table 4).

388 Our simulations also show that interactions between broomrape and weeds can be exploited to regulate
389 broomrape. Weeds helped to deplete the broomrape seed bank by inducing germination, particularly
390 during summer fallow. Although they sometimes allowed broomrape to reproduce, they mostly played
391 the role of catch plants, as they generally had a shorter life cycle than broomrape so they died before it
392 could reproduce. This effect is highly dependent on the type of weed species present and might also be
393 overestimated because of some deficiencies in the weed phenology predictions in FLORSYS (section
394 4.2).

395 Finally, the catch-crop effect of weeds was only beneficial in terms of crop yield loss when weeds did
396 not compete for light with the crop. Using biological regulation by weeds to control broomrape involves
397 finding the right balance between tolerating a residual weed flora to stimulate broomrape germination,
398 and controlling it to avoid competition with the crop. One way would be to let weeds grow unchecked
399 during summer fallow (where they do not hinder crop production) and destroy them before they and/or
400 broomrape reproduce (to avoid seed bank replenishment). Dealing with such complex questions shows
401 the need of simulation models such as PHERASYS.

402 4.4 Perspectives

403 The present simulation results are encouraging as they are mostly consistent with literature reports.
404 However, they must still be interpreted carefully since the model has not yet been evaluated with
405 independent field data. A sensitivity analysis will also be needed to identify which model parameters
406 need to be measured more precisely and which formalisms must be improved. The present simulation
407 study can be considered as a first step of a very basic sensitivity analysis insofar as it ranked the main
408 levers influencing broomrape dynamics, identified the main species traits interacting with broomrape
409 dynamics via the RLQ/4th corner analyses as well as key plant stages whose prediction quality must be
410 checked (e.g., host flowering dates, broomrape life-cycle duration). But the present study needs to be
411 completed by a large-scale simulation study investigating the huge range of combinations of models
412 inputs as well as model parameters.

413 Once the model has been evaluated, a larger set of cropping systems should be simulated in order to
414 track innovative broomrape-management strategies that benefit from biological regulation by weeds.
415 The model could even be used as a decision support system to help designing cropping systems by testing
416 prospective systems and improving them based on simulation results (Colbach *et al.*, 2017b; Colbach *et*
417 *al.*, 2021).

418 5 Conclusion

419 The PHERASYS model was developed in a companion paper to simulate branched-broomrape dynamics
420 in agroecosystems. It allowed here, for the first time, to simulate (1) interactions between broomrape
421 and heterogeneous multispecies stands of crops and weeds, (2) the effects of multiple cropping
422 techniques, including complex ones playing on the competition between broomrapes and hosts for host
423 resources. Although the model needs to be evaluated, simulation results are consistent with the literature.
424 Combining delayed sowing, which prevents broomrape from reproducing, to the use of trap and catch
425 crops, to deplete the broomrape seed bank, allows a long-term control of the parasitic plant. Tolerating
426 weed flora during summer fallow, could also help to accelerate the seed bank depletion by stimulating
427 broomrape germination.

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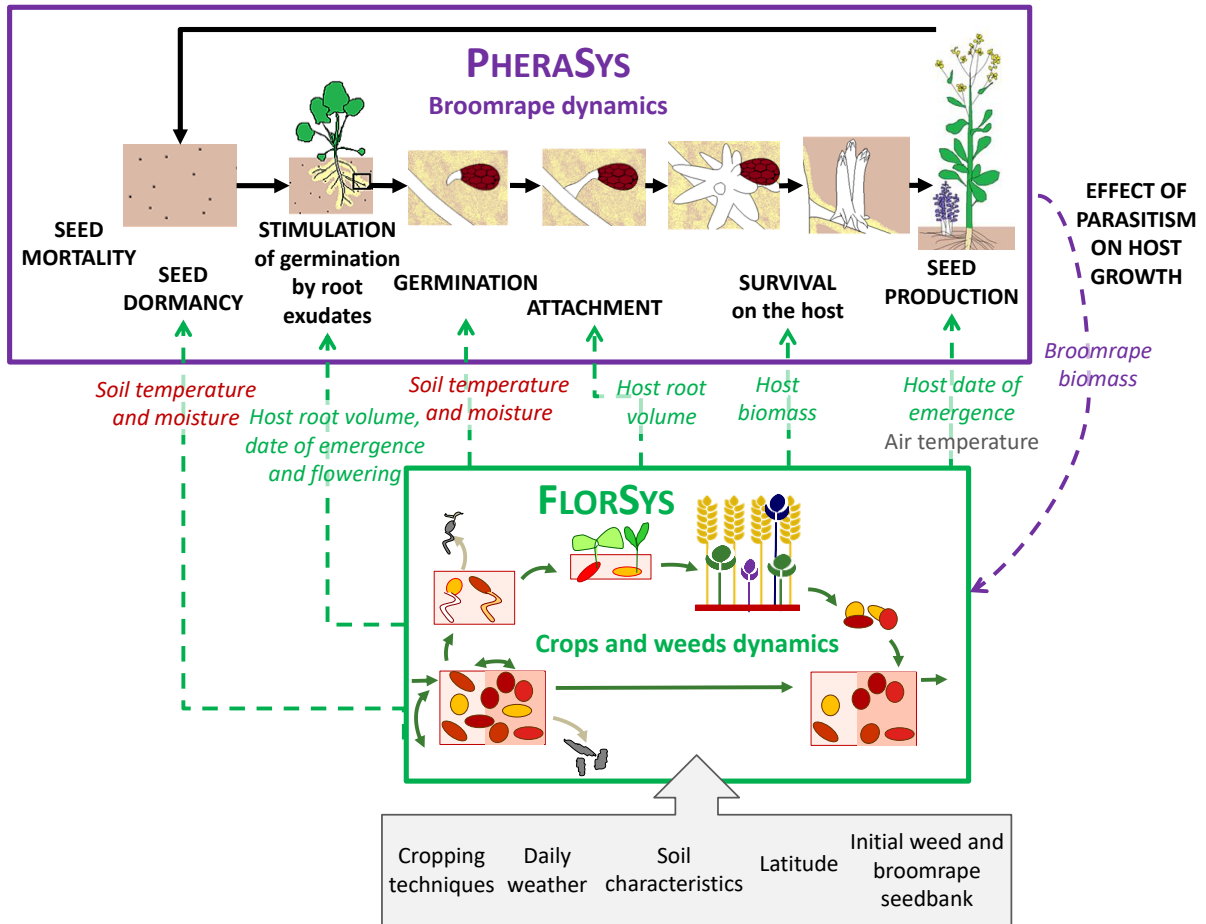
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615 Figure 1: Processes of branched-broomrape life cycle modelled in the PHERASYS submodel of FLORSYS.
 616 Inputs given by the user are in grey. Variables used to connect both models are in italics (green and
 617 purple: biotic variables from FLORSYS and PHERASYS respectively, brown: abiotic variables) (Olivia
 618 Pointurier 2019 )

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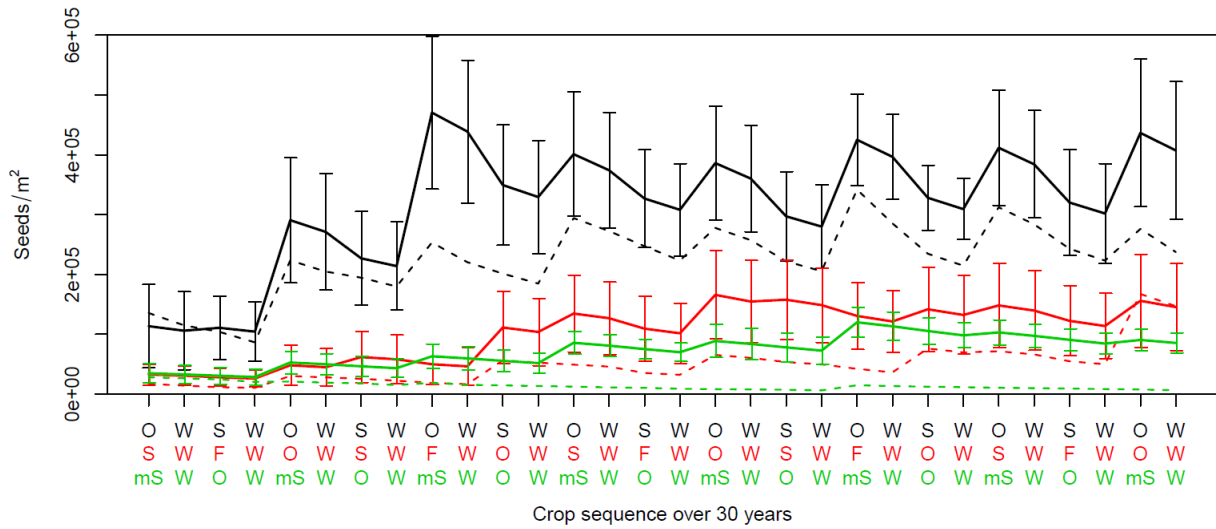
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622 Table 1: Characteristics of the simulated cropping systems

Cropping system	Rotation*	Oilseed rape sowing date	Tillage	Chemical/ mechanical weeding
1. Reference	O-W-S-W	July 19	25-cm-deep mouldboard ploughing once a year + superficial tillage (≤ 7 cm depth)	2-3 herbicide treatments per year** + mechanical weeding in sunflower
2. Diversified rotation	S-W-F-W-O-W	Aug. 19	25-cm-deep mouldboard ploughing 4 years out of 6 + other tillage operations (5-10 cm depth)	1-3 herbicide treatments per year** + mechanical weeding in sunflower
3. Delayed sowing	Same as reference, with mustard as cover crop before sunflower	Sept. 6	25-cm-deep mouldboard ploughing every 4 years + other tillage operations (5-12 cm depth)	1-2 herbicide treatments per year** + mechanical weeding in sunflower
4. No plough	Same as reference	Same as reference	No mouldboard ploughing Superficial tillage (≤ 7 cm depth)	Same as reference
5. No till	Same as reference	Same as reference	No tillage	Same as reference + glyphosate before sowing

623 *O = winter oilseed rape, W = winter wheat, S = sunflower, F = flax; ** herbicide treatments at sowing or on crop.



625

626 Figure 2: Dynamics of the branched-broomrape seed bank in three cropping systems predicted by
627 PHERASYS over 30 years. Each line shows the mean number of broomrape seeds in the soil after crop
628 harvest averaged over 10 weather repetitions in a given cropping system. Thick lines show data from
629 simulations of infestation with broomrape only, and dashed lines from simulations with both non-
630 parasitic weeds and broomrape. Bars represent standard deviations. Each colour shows a cropping
631 system (black: 1-reference; red: 2-diversified rotation; 3-green: delayed sowing, details in Table 1).
632 Letters indicate the harvested crop (O = winter oilseed rape, W = winter wheat, S = sunflower, mS =
633 sunflower was sown after a mustard cover crop, F = flax) (Olivia Pointurier 2019 )

634

635 Table 2. Effect of cropping system and non-parasitic weeds on broomrape seed bank left after 30 years
 636 of simulation as well as on seed-bank variation over time

Cropping system	Final seed bank		Variation relative to initial seed bank ^{&}	Variation relative to weed-free simulations [#]	
	Mean [§] (seeds/m ²)	Variation relative to reference [§]			
A. Simulations without weeds					
1	Reference	407305	100%	20.4	
2	Diversified rotation	145378	36%	7.3	
3	Delayed sowing	85373	21%	4.3	
4	No plough	362941	89%	18.1	
5	No till	391414	96%	19.6	
B. Simulations with weeds					
1	Reference	237399	100%	11.9	58%
2	Diversified rotation	146864	62%	7.3	101%
3	Delayed sowing	6223	3%	0.3	7%
4	No plough	254780	107%	12.7	70%
5	No till	44963	19%	2.2	11%

637 [§] Coloured from white (0) to red (maximum)

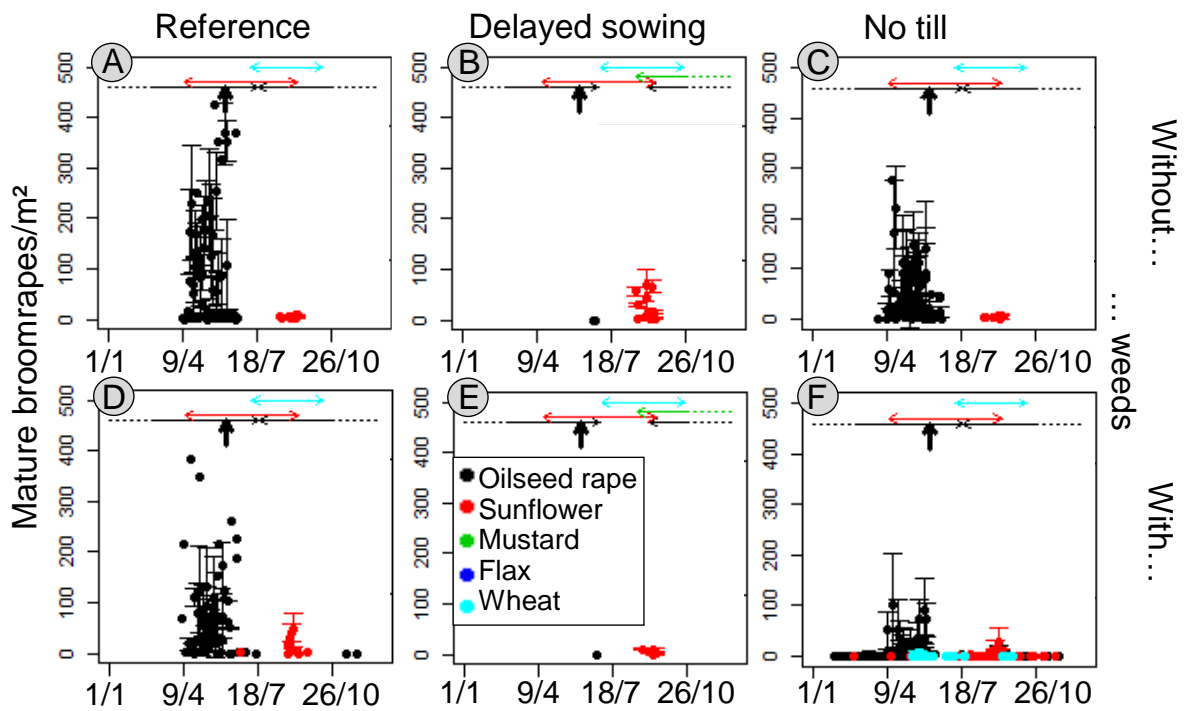
638 [§] Coloured from red (strongest increase) to white (no variation) to green (strongest decrease)

639 [&] Coloured from red (strongest increase) to white (no variation) to green (strongest decrease)

640 [#] Coloured from red (strongest increase) to white (no variation) to green (strongest decrease) (only for B)


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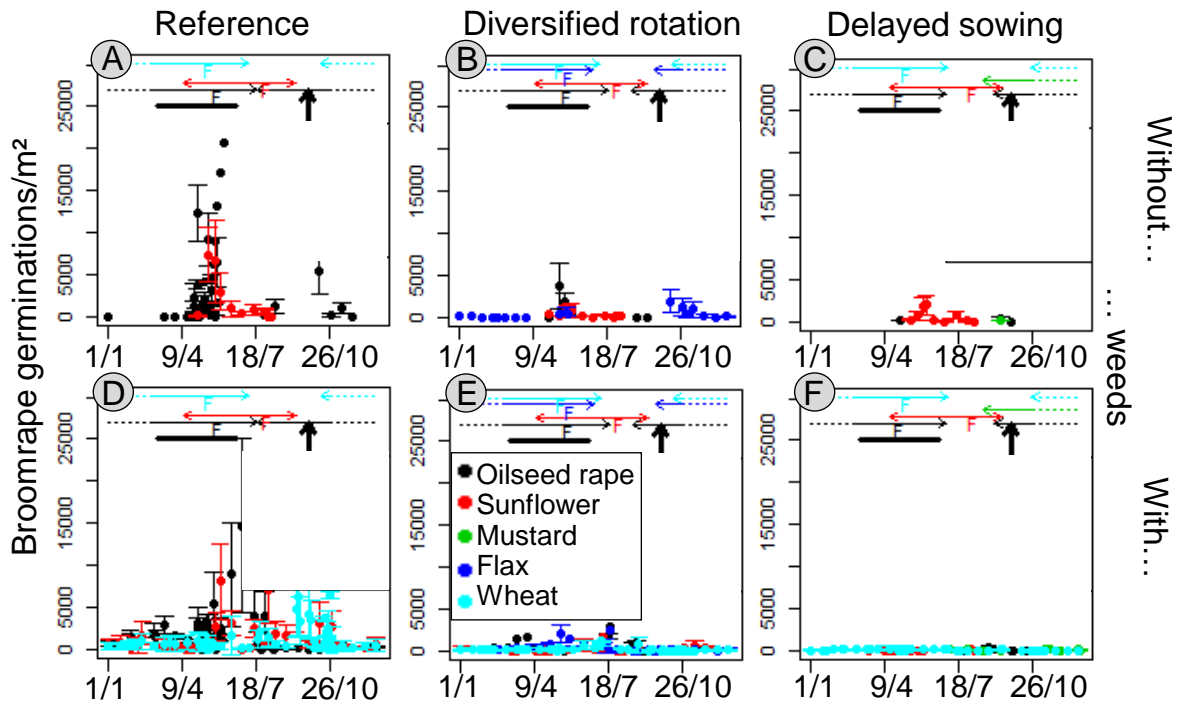


644


645 Figure 3. Number of broomrapes reaching maturity throughout the year in simulations without (A-C)
 646 and with weeds (D-F) in three cropping systems (reference: A and D, delayed sowing: B and E, no-till:
 647 C and F). Each dot represents the mean number of mature broomrape per day averaged over 30 years
 648 and 10 weather repetitions. Each colour represents the growing season of a crop (from harvest of the
 649 previous crop to harvest). Vertical bars represent standard deviations. Horizontal arrows show durations
 650 from sowing to harvest of each crop. The vertical thick arrow shows the estimated date when broomrapes
 651 start fructifying in an oilseed rape field sown in August 28th in the study by Gibot-Leclerc et al. (2012)

652 (Olivia Pointurier 2018 )

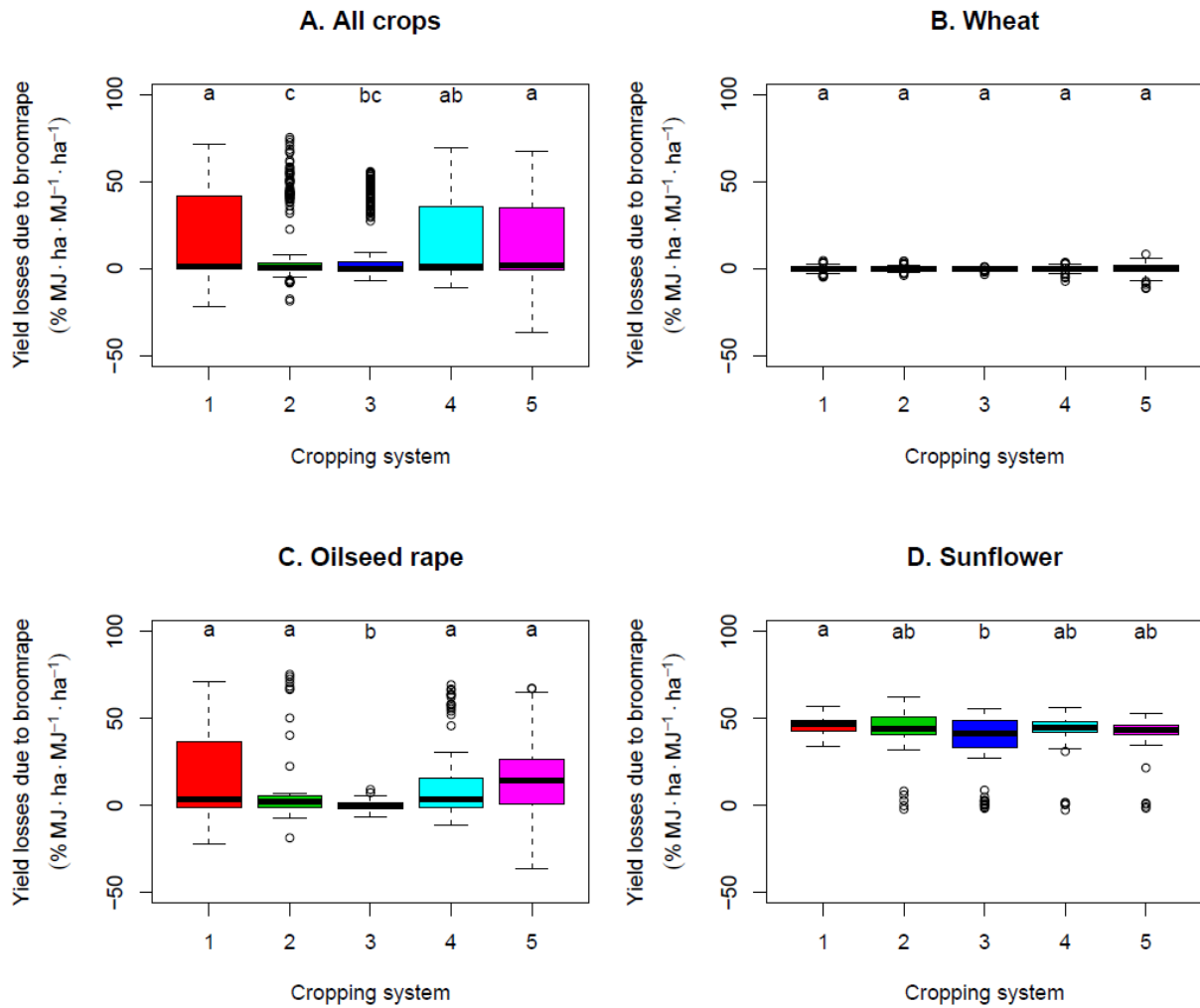
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654


655 Figure 4. Broomrape germinations throughout the year in simulations without (A-C) and with weeds
 656 (D-F) in three cropping systems (reference: A and D, delayed sowing: B and E, no-till: C and F). Each
 657 colour represents the growing season of a crop (from harvest of the previous crop to harvest). Vertical
 658 bars represent standard deviations. Horizontal arrows show durations from sowing to harvest of each
 659 crop. The horizontal thick line shows the period of high dormancy in broomrape seeds in PHERASYS. F
 660 indicate mean dates of crop flowering onset. The vertical thick arrow shows the estimated date when the
 661 maximum number of broomrape germinations were induced in an oilseed rape field sown in August 28th
 662 in the study of Gibot-Leclerc et al. (2012) (Olivia Pointurier 2018 )

663



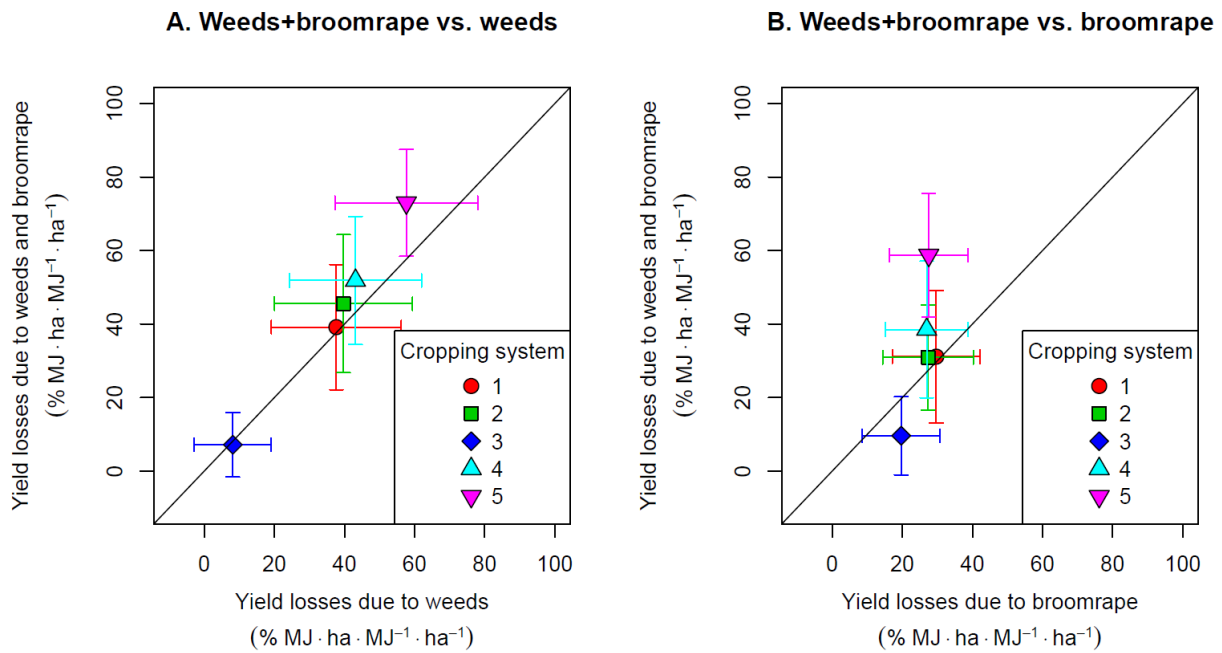
664

665 Figure 5: Annual yield losses due to branched broomrape predicted by PHERASYS in each cropping
 666 system and crop (simulations without weeds). Cropping systems are 1: reference system, 2: diversified
 667 rotation, 3: delayed sowing, 4: no plough and 5: no-till. For details on the cropping systems, see Table
 668 1. Different letters above bars show significant differences in yield losses between cropping systems

669 (Olivia Pointurier 2019 )


670

671



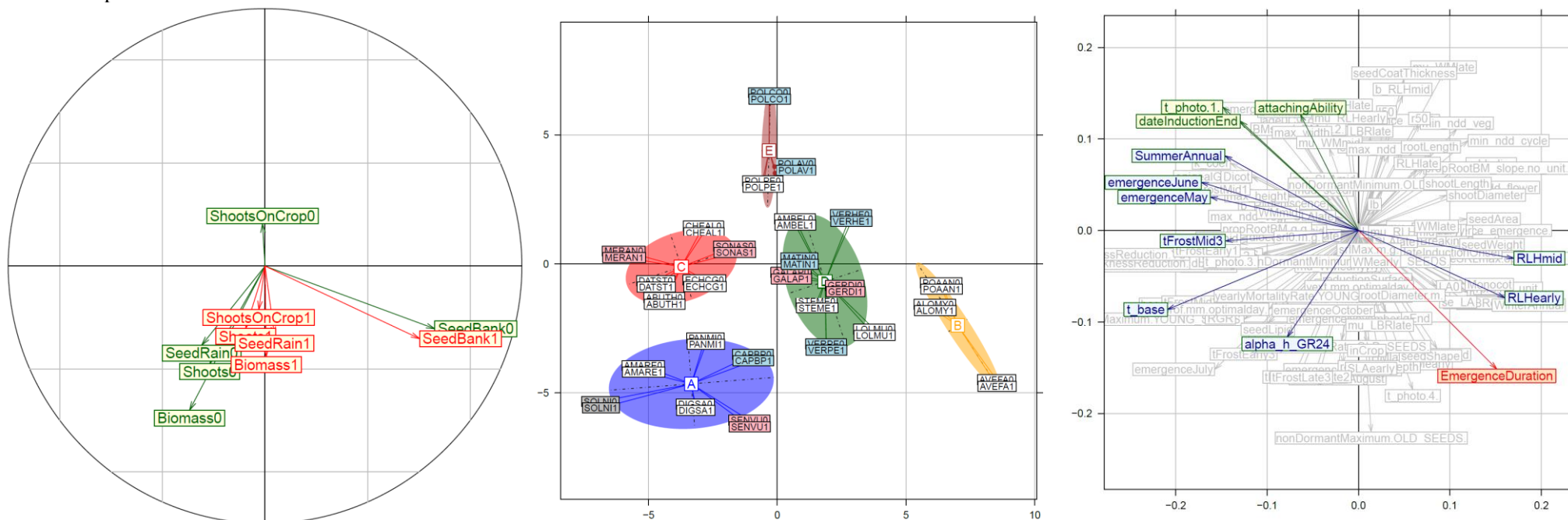
672


673 Figure 6: Yield losses due to weeds and branched broomrape compared to annual yield losses due to
 674 weeds only (A) and broomrape only (B) simulated with PHERASYS. Each dot represents the mean yield
 675 loss averaged over crops, years and weather repetitions for a given cropping system. Cropping systems
 676 1 to 5 refer to 1: reference system, 2: diversified rotation, 3: delayed sowing, 4: no plough and 5: no-till.
 677 For details on the cropping systems, see Table 1. Bars show standard deviation. Black line shows $y=x$

678 (Olivia Pointurier 2019 )

679

A. Correlation circle from Principal Component Analysis B. Correspondence Analysis on weed species densities on broomrape-infection indicators C. Principal Component Analysis on weed-species traits



680 Figure 7. The weed species (shown with EPPO codes) and species traits that explain broomrape infection, irrespective of crops and cropping systems. Synthetic representation
 681 of the RLQ results with broomrape-infection indicators and weed plant density in simulated fields as matrix R and L, respectively, and FLORSYS species parameters as matrix
 682 Q. A. Broomrape-infection indicators with correlation circle, discriminating during summer fallow (suffix 0) and during cash crop (suffix 1), B. Weed species, clustered into
 683 groups, following a Ward ascendant hierarchy classification, discriminating during summer fallow (suffix 0) and during cash crop (suffix 1) as well as broomrape-attaching
 684 species (blue), broomrape-triggering species (grey) and species that do both (red), C. Species parameters, with the 2 broomrape-specific parameters ("attachingAbility" and
 685 "alpha_h_GR24") and the 10 most correlated ones shown in red, green or blue (respectively, positively, negatively or both correlated to broomrape infection) based on fourth-
 686 corner analysis. For the meaning of species parameters, see Table 3. (Nathalie Colbach 2021 )

687 Table 3. The 10 most important and the 2 broomrape-specific (highlighted in yellow) weed species traits that drive broomrape infection during summer fallow
688 and during cash crop. Pearson correlation coefficients identified via RLQ and 4th-corner analyses. Cells were coloured from red (the strongest positive
689 correlation) to green (the strongest negative correlation)

Parameter			Broomrape during summer fallow					Broomrape during cash crop				
Abbreviation	Meaning	Unit	Shoots	Shoots on crop	Biomass	Seed rain	Seed bank	Shoots	Shoots on crop	Biomass	Seed rain	Seed bank
alpha_h_GR24	Ability to trigger broomrape germinations	1=as good as OSR, 0=none	0.02		0.03	0.02	-0.02			0.01		-0.02
attachingAbility	Ability to attach broomrape	1 vs 0					-0.03		-0.01	-0.02	-0.02	-0.03
dateInductionEnd	Date when induction of seed dormancy stops	Julian days					-0.06					-0.05
EmergenceDuration	Duration of emergence	Days					0.07					0.06
emergenceJune	Emergence period includes June	1 vs 0	0.02		0.02	0.02	-0.07					-0.06
emergenceMay	Emergence period includes May	1 vs 0	0.02		0.02	0.02	-0.06					-0.06
RLHearly	Relative leaf area height after emergence (relative plant below which 50% of leaf area are found)	cm/cm			-0.02	-0.02	0.06					0.06
RLHmid	Relative leaf area height during vegetative stage (relative plant below which 50% of leaf area are found)	cm/cm			-0.03	-0.02	0.06					0.06
SummerAnnual	Spring/summer emerging (1) vs autumn/winter (0)					0.01	-0.06					-0.05
t_base	base temperature for development	°C	0.03		0.05	0.04	-0.07					-0.06
t_photo.1.	Min temperature needed for photosynthesis	°C					-0.07			-0.01		-0.06
tFrostMid3	Max temperature where all plants are killed by frost during vegetative stage	°C	0.01		0.02	0.02	-0.06					-0.05

690

691

692 Table 4: Effects of cropping techniques on branched-broomrape dynamics and crop yield losses in simulations with PHERASYS and consistency with the literature
 693 (green cells indicate consistent results, yellow limited consistency)

Cropping technique	Effects on broomrape and crop yield losses in simulations	Consistency of the effects with the literature	Consistency of the mechanisms involved with the literature
Delayed sowing	Fewer broomrape attachments on host crops and less yield loss	Fewer attachments in obligate parasitic plants (Grenz <i>et al.</i> , 2005b; Díaz <i>et al.</i> , 2006; Gibot-Leclerc <i>et al.</i> , 2006a; Tippe <i>et al.</i> , 2017), but benefits in terms of yield loss can be cancelled out by reduced yield potential (Díaz <i>et al.</i> , 2006; Gibot-Leclerc <i>et al.</i> , 2006a).	Crops sown later grow faster so they are more competitive than broomrapes (Fernández-Aparicio <i>et al.</i> , 2016b). Fewer broomrape seeds germinate at crop sowing as they are more dormant later in the season (Tippe <i>et al.</i> , 2017).
Trap and catch crops	Seed bank depletion by flax, sunflower (if high infestation) and, to a lesser degree, mustard	Flax and mustard are trap and catch crops (Goldwasser and Rodenburg, 2013); sunflower depletes broomrape seed bank (Jestin <i>et al.</i> , 2014); summer crops and flax deplete more than autumn cover crops (Jestin <i>et al.</i> , 2014).	The ability of a plant to stimulate broomrape germination depends on the species emitting them (Fernández-Aparicio <i>et al.</i> , 2009; Gibot-Leclerc <i>et al.</i> , 2016; Perronne <i>et al.</i> , 2017). The longer the crops grow, the larger their root systems are, the more germination they induce (Grenz <i>et al.</i> , 2005a). The spring germination flush simulated here in oilseed rape is not systematically observed in the field (Gibot-Leclerc <i>et al.</i> , 2012; Gaudin, 2013). The quantity and quality of germination stimulants exudated by plants varies over season (López-Granados and García-Torres, 1996; Auger <i>et al.</i> , 2012), whereas it only depends on stage in PHERASYS.
	Sunflower slightly infected by broomrape	Sunflower only rarely allows broomrape to reproduce in the field (Jestin <i>et al.</i> , 2014).	Unknown mechanisms
Soil tillage	No effect	Deep tillage vs superficial or no tillage reduces the number of broomrape germinated seeds (Rubiales <i>et al.</i> , 2009b)	Lack of oxygen in deep soil layers prevents broomrape germination (Rubiales <i>et al.</i> , 2009b), not modelled.
		Reduced tillage vs deep tillage can reduce the number of broomrape germinated seeds and attachments (Fernández-Aparicio <i>et al.</i> , 2016b)	Prevents seeds from being buried close to host roots where they could be stimulated and attach (Fernández-Aparicio <i>et al.</i> , 2016b). Volume of host roots in superficial soil layers overestimated by our simplistic representation of root systems, which grow directly from the soil surface instead of from the seed.