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Farming plant cooperation in crops

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26 **Abstract**

27 Selection of the fittest can promote individual competitiveness but often results in the erosion
28 of group performance. Recently, several authors revisited this idea in crop production and proposed
29 new practices based on selection for cooperative phenotypes, *i.e.* phenotypes that increase crop yield
30 through decreased competitiveness. These recommendations, however, remain difficult to evaluate
31 without a formal description of crop evolutionary dynamics under different selection strategies. Here,
32 we develop a theoretical framework to investigate the evolution of cooperation-related traits in crops,
33 using plant height as a case study. Our model is tailored to realistic agricultural practices and shows
34 that combining high plant density, high relatedness and selection among groups favours the evolution
35 of shorter plants that maximize grain yield. Our model allows us to revisit past and current breeding
36 practices in light of kin selection theory, and yields practical recommendations to increase cooperation
37 among crops and promote sustainable agriculture.

38 Introduction

39 Ever since the dawn of Agriculture, humans have imposed artificial selection on plants to
40 increase the quality and the quantity of crop production [1,2]. The domestication of wild species led to
41 the selection of phenotypes that would never have been favoured by natural selection under
42 unmanaged conditions, such as the loss of seed dispersal or the decrease in defence compounds
43 production [3,4]. This was further amplified in the 20th century with the progressive mechanization of
44 field work and the increasing use of herbicides and fertilizers. Agronomists indeed observed that
45 varieties with weak competitive abilities performed better than competitive ones under such conditions
46 [5–7]. This led Donald to define a cereal ideotype designed to perform “as a community” by having a
47 set of phenotypic characteristics such as a short stem, few tillers and few erected leaves [5]. As such,
48 Donald disseminated the idea that phenotypes which maximize group productivity, or crop yield, also
49 decrease individual competitiveness.

50 This idea was further generalized as the “Tragedy of the commons” (TOC): phenotypes that
51 maximize group performance are necessarily sub-optimal for individual performance, making them
52 susceptible to invasion by selfish phenotypes [8]. TOCs were widely investigated in crops using
53 Evolutionary Game Theory (EGT) approaches (reviewed in [9]), most studies concluding that humans
54 have to work against natural selection to prevent invasions of the best performing groups by
55 competitive phenotypes. This was early observed by plant breeders in bulk breeding programs, where
56 the most favourable phenotypes for yield, such as short plants, were lost over few generations due to
57 intraspecific competition [6,7,10].

58 At the same time, the evolutionary biologist William Hamilton formalized the kin selection
59 theory which aimed at understanding the evolution of social interactions, notably altruism where
60 individuals act to increase the fitness of their social partners at the expense of their own reproduction
61 [11,12]. Hamilton proposed a very simple rule which states that altruistic phenotypes can be selected if
62 the fitness cost for the actor, c , is outweighed by the benefit received by the partners, b , weighted by
63 the relatedness between the actor and the partners, R , *i.e.* when $c < Rb$. With this rule, Hamilton

64 explicitly incorporated the contribution of relatives in transmitting genes that are shared with the actor
65 to the next generations. Later works have emphasized that $-c+Rb$ provides a representation of the
66 average effect of an allelic substitution on individual fitness (e.g. [13]) rather than an alternative to
67 individual fitness: $-c+Rb$ gives the expected effects of copies of an allele in different individuals on
68 the expected fitness of individuals who bear the allele. Kin selection has been extremely successful in
69 explaining a wide range of altruistic phenotypes such as sterility in eusocial insects [12] or helping
70 behaviours in birds [14], and it has received increasing attention in plants in recent decades (reviewed
71 in [15]).

72 Since farmers are more interested in productivity per unit area than in individual plant
73 productivity, it was early advanced that plant breeding should take advantage of the mechanisms that
74 maximize group productivity to increase crop yield [16]. More recently, several authors argued that
75 plant breeding had not fully explored the trade-off between group productivity and individual
76 performance and that significant yield gain could be achieved by reversing past natural selection for
77 competitiveness [17–20]. To do so, recommendations drawn from the general principles of kin
78 selection or group selection have been proposed [17,18,20–22]. Yet, it remains difficult to assess the
79 extent to which plant breeding could benefit from these principles as long as they are not formally
80 applied to crops.

81 Current crop improvement programs do not explicitly take into account social interactions
82 among plants [18,21]. Conversely, significant work has been achieved to integrate the effects of social
83 interactions into farm animals breeding programs [23]. Indeed, reducing competitiveness among
84 group-housed animals is critical for both productivity and animal welfare [24]. Based on the early
85 work of Griffing [25], quantitative genetic models have been developed to account for the effect of the
86 genes of the focal individual on its own phenotypic traits, known as the direct genetic effect (DGE),
87 and the effects of the genes of individuals interacting with the focal individual, known as the indirect
88 genetic effect (IGE) [26–28]. Experiments have shown that IGEs can represent a significant proportion
89 of the heritable variation on traits such as growth rate in pigs [29] or survival rate in laying hens [30].
90 Therefore, the genetic response to selection can significantly be improved by accounting for IGEs

91 [26]. Theoretical studies have shown how the IGEs frameworks connects with kin selection theory and
92 how relatedness affects the genetic response to selection in presence of IGEs [31,32]. To a lesser
93 extent, this framework has also been applied in tree breeding [33,34]. Yet we still poorly understand
94 how social interactions affect the evolution of plant phenotypes, and the extent to which crop breeding
95 schemes can improve yield depending on the intensity of social interactions.

96 To fill these gaps, we develop a kin selection model to investigate the evolution of cooperation
97 in crops. The model allows us to identify the most important parameters that promote cooperation and
98 increase crop yield, and to revisit crop evolutionary history in light of the kin selection theory.

99 **Methods**

100 We define cooperation as the evolution of a phenotype that decreases the intensity of
101 intraspecific competition. We focus on competition for light, using plant height as the competitive trait
102 for three main reasons. Over the different axes of phenotypic variation in plants, height is classically
103 reported as the main driver of competitive ability [35,36]. Second, the impact of competition for light
104 on plant fitness has been widely documented [35,37,38] including in crops [39,40], enabling us to
105 have a reasonably realistic mathematical formalism. Finally, plant height is one of the traits for which
106 we have important historical data in crops [41–44], making it possible to interpret our results in light
107 of human selection practices. It must be stressed that we deliberately kept the mechanistic and genetic
108 aspects of the model simple to focus on processes of interest in this study, which are evolutionary
109 dynamics and their interaction with human practices.

110 Crop populations are spatially structured, either in fields when grown by a farmer, or in
111 experimental plots when evaluated by a plant breeder. In our model we assume that the crop
112 population is made of n_F fields, with n_P plants per field. In agreement with experimental evidence on
113 several crop species [39,41], we assume that there is an optimal height \hat{x} that maximizes plant
114 fecundity, *i.e.* individual seed production, in the absence of competition for light (Fig. 1B). We model
115 competition for light with the drop shadows of neighbouring plants (Fig. 1A). Plant fecundity is
116 assumed to decrease proportionally to the size of the overlapping area between drop shadows and thus

117 with the height of the neighbours, as observed in experimental studies [35,38,40] (Fig. 1C). One of the
118 main parameters that drives intraspecific competition in crops is plant density [5,40]. In the model,
119 plant density is governed by the parameter d , the distance between plants. The intensity of competition
120 for light also depends on the angle a at the apex of the triangle used to represent drop shadows (Fig.
121 1A). We computed crop yield as the total number of seeds produced in a field divided by the field area
122 (see Supplementary Information section 1.1). As expected, the plant height that maximises crop yield
123 decreases with the distance between plants (Fig. 3 and Fig. S2), and crop yield is maximized by
124 growing short plants at high density [5,40]. To fit as closely as possible to the specifics of real crops
125 such as wheat, we set the optimal plant height \hat{x} to 100 cm and the angle a to $\pi/50$ rad. Such a small
126 angle allowed us to generate a moderate and realistic intensity of competition at low plant-plant
127 distances such as those classically encountered in cereals. Note that the choice of parameter values did
128 not affect our results qualitatively.

129 We compared the efficiency of three selection strategies. In the Within-Field (WF) strategy,
130 seeds sown in a given field are exclusively sampled in the harvest of this same field; in the Among-
131 Field (AF) strategy, fields are sown with seeds sampled after pooling the harvest of all fields; in the
132 Top-Field (TF) strategy, fields are sown with seeds exclusively sampled in the harvest of the most
133 productive field. In the WF strategy, the best performing plants within their fields contribute more to
134 the next generation, whereas in the AF strategy, the best performing fields within the crop population
135 contribute more to the next generation, this phenomenon being magnified in the TF strategy.

136 Relatedness, a key parameter of kin selection theory, is modulated by the parameter n_s , the number of
137 founding seeds (Supplementary Information section 1.3 and Fig. S3). For cases where $n_s < n_p$, we
138 multiply each founding seed in equal proportion, *i.e.* no selection during this step, until we obtain
139 enough seeds to have n_p plants in each field.

140 We developed an analytical model from which we derived approximations for the
141 Evolutionary Stable Strategy (ESS) for plant height, that is the strategy that cannot be invaded by any
142 alternative strategy [45] (Supplementary Information section 1.2). The ESS approach is widely used in

143 evolutionary biology to predict the outcome of long-term evolutionary processes where fitness
144 depends on the frequencies of the different phenotypes present in the population. In our study, we
145 adopt the kin selection approach to account for the spatial structure of crops [46]: as mentioned above,
146 the crop population is distributed into different fields, or different groups, that can be connected by
147 migration. These groups delineate social interactions: individuals only interact within groups. The
148 evolution of social traits is driven by the genetic similarity between actors and recipients and thus by
149 genetic similarity between group members at the loci involved in social traits [12]. Relatedness (R)
150 quantifies this similarity and measures the extent to which an actor is more likely to share an allele
151 (and thus share a common phenotype) with an individual sampled in its own group than with an
152 individual sampled in another group [47,48] (Supplementary Information section 1.3). Compared to
153 traditional definitions of relatedness from pedigrees, the definition of relatedness used here averages
154 pedigree relatedness over the distribution of pedigrees of gene copies within groups [49]. As this
155 distribution depends on other features of the life cycle such as migration rates, relatedness depends on
156 the life cycle (Fig. S3).

157 In addition to the ESS approach, we ran individual-based simulations to track the evolution of
158 plant height across generations (Supplementary Information section 1.4): we simulated the life cycle
159 of all plants from sowing to harvest over thousands of generations until the selection-drift-mutation
160 equilibrium was reached. Finally, we compared the mean plant height at equilibrium with ESS
161 approximations. We hereafter present ESS and simulation results for the three selection strategies
162 (WF, AF, and TF) with varying planting density and relatedness.

163 **Results**

164 Overall, ESS predictions agreed very well with simulation results and equilibriums were
165 always monomorphic, meaning that a single phenotype was present in the population at the end of the
166 simulations (Fig. 3, black dots). When plants were grown at low densities ($d > 12$), they did not
167 compete for light and thus the mean phenotype at equilibrium was the optimal phenotype for
168 individual fecundity, *i.e.* \hat{x} (competition intensity 0 in Fig. 1A). At intermediate densities ($7 < d < 12$),

169 plants evolved smaller than their optimal phenotype in all scenarios. Indeed, when competition is low
170 (competition intensity 1 in Fig. 1A), shorter phenotypes result in greater plant fecundity because the
171 fecundity loss incurred by moving away from the optimum is overcompensated by the fecundity gain
172 obtained by avoiding the shadow of the neighbours. At high densities ($d < 7$), where competition is
173 more intense (competition intensity 2 in Fig. 1A), evolutionary outcomes differed greatly among
174 scenarios. With the WF strategy, the higher the density (the lower d), the taller the plant evolved. At
175 equilibrium, plants were well above the optimal height \hat{x} , leading to very low yields whatever the
176 number of founding seeds (Fig. 3A, D, and G). In contrast, both AF and TF strategies resulted in the
177 evolution of short high-yielding phenotypes when the number of founding seeds was low (Fig. 3B, C,
178 and F). Increasing the number of founding seeds reduced relatedness (Fig. S3), drove the evolution of
179 taller plants, and lowered crop yield (Fig. 3E, H, and I). Shorter phenotypes evolved under the TF
180 strategy compared to the AF strategy, as a result of stronger selection among fields in the TF strategy
181 (Fig. 3E and F). Interestingly, with both AF and TF strategies, two alternative evolutionary outcomes
182 were possible for certain ranges of d (e.g. Fig. 3E when $2 < d < 3.5$ cm). When such evolutionary
183 bistability occurred, which evolutionary outcome was reached depended on the initial phenotypic
184 value of the population (Fig. S4).

185 The ESS analysis captures the long-term evolutionary outcome of the model but does not
186 predict the speed of phenotypic evolution towards the ESS. To explore the short-term evolutionary
187 dynamics of plant height under realistic agricultural practices, we carried out individual-based
188 simulations under the three selection strategies for 20 generations with a small number of fields ($n_F=5$, Fig. 4). The WF strategy and the AF strategy generated slow evolution compared to the TF
189 strategy (Fig. 4A). Consequently, the relative efficiency in increasing yield differed markedly among
190 selection strategies: after 20 generations, yield had decreased by 5% with the WF strategy whereas it
191 has increased by 15% with the AF strategy and by 110 % with the TF strategy (Fig. 4B).

193 **Discussion**

194 While most studies concluded that phenotypes which maximize group productivity are not
195 evolutionary stable [9,50], our model demonstrates that evolutionary principles can be used to select
196 for cooperation and increase crop yield. Our results thus provide new insights into the relative
197 importance of parameters that could be used to select for cooperation in breeding programs. First, as
198 widely acknowledged in agronomy, plant density has a critical role in controlling the balance between
199 individual competitiveness and group performance [17]. The closer the plants, the stronger the direct
200 and indirect fitness effects, resulting in stronger selection for either selfish tall phenotype or altruistic
201 short phenotype depending on relatedness. Yet, the effect of density is not monotonic. Therefore, the
202 phenotypic value of the crop population at the beginning of the breeding program can constrain
203 selection even if all conditions are met for cooperation to evolve. For example, starting with tall plants
204 might hamper the evolution of short phenotypes. Second, although selection at the group level is
205 indeed mandatory to select altruistic phenotypes [17,18,21], our results demonstrate that group-level
206 selection is not sufficient: when relatedness becomes too low, the AF and TF strategies fail to select
207 for short phenotypes. More precisely, as the number of founding seeds increases, the within-field
208 variability increases and the between-field variability decreases. This reduces relatedness and limits
209 the ability to discriminate the different fields based on their productivity, thus reducing the strength of
210 among-field selection. Such an important role of relatedness in interaction with group level selection
211 has been missed in the literature on cultivated plants.

212 The potential of group selection in agriculture was early demonstrated in poultry. In a seminal
213 experiment, Muir demonstrated that selection at the family level (half sib families) was very efficient
214 to increase egg production and to reduce mortality in laying hens [51]. Moreover, such practices have
215 been shown experimentally to be more efficient when groups are composed of relatives [26]. These
216 results are in line with our study and previous theoretical works in quantitative genetics showing that
217 relatedness and the degree of group selection jointly affect genetic response to selection [31,32]. More
218 generally, the convergence between our results and the findings obtained in quantitative genetics and
219 animal breeding literature suggest that the principles and the tools (*e.g.* mixed model [26,34])

220 developed in these areas could be applied in crops whenever breeding programs can rely on strong
221 phenotyping efforts.

222 In crops, the very common pedigree selection is quite similar to the TF strategy, at least in the
223 last generations of selection where plots are planted with single genotypes, and only the most
224 productive plots are retained from one generation to another, which generates both among-field
225 selection and high relatedness. Yet, as mentioned in previous studies, such programs could be even
226 more efficient in improving yield by increasing plant density [17] and by selecting at the group level
227 from the very beginning [21]. In practice, the TF strategy could be implemented with a number of
228 experimental plots as limited as 5, with 200 or 300 plants per plot (Figure 4). Increasing the number of
229 plots would increase the effective population size and thus increase the evolutionary speed. To take
230 into account the effect of environmental variability on the evaluation of crop yield and on the selection
231 procedure, it could be useful to replicate the plots or to sample founding seeds in a handful of the most
232 productive fields (Figure S5). Then, founding seeds could be multiplied in a greenhouse between two
233 growing seasons by growing plants at low densities to maximize the seed multiplication rate.
234 Controlled or uncontrolled crosses could be used to generate new allelic combinations and new
235 phenotypes over generations.

236 Our results shed new light on the evolution of plant height during the evolutionary history of
237 crops. For most cereals, plant height has increased between their wild ancestor and their earliest
238 domesticated form [42,43]. Moreover, most of these primitive domesticated forms remained tall, or
239 even evolved taller until the end of the 19th century [4]. The practices associated with the transition
240 from gathering to cultivation [1], as well as the most common selection method over this period,
241 namely mass selection, could be regarded in light of the kin selection: grains were collected from
242 isolated plants (or low-density grown plants), these plants being selected for their individual features,
243 and grains (or spikes) from different plants being mixed before sowing [52]. Such practices leading to
244 low among-field selection and low relatedness inevitably select for selfish phenotypes. Even if tallness
245 might have deliberately been selected for other needs such as chaff production or weed control [4], our
246 model suggests that mass selection might have reinforced selection for increased plant height.

247 Initiating breeding programs with plants that are too tall can hamper the evolution of short
248 high-yielding phenotypes. This might have happened at least twice in the evolutionary history of
249 crops. First, there is evidence that farmers chose relatively tall plants in the wild to start cultivation
250 [53]. Second, for most cereals the main reduction in plant height was achieved in the 1960's by
251 introgressing dwarf genes from Asian varieties [54]. At that time, most wheat varieties were very tall
252 in U.S.A [55] and Europe [41], and we could wonder whether plant breeding would have achieved
253 such shortening by crossing and selecting among the local pool varieties.

254 Reducing plant height in crops was motivated by the need for varieties that better respond to
255 intensive cultivation practices, notably through increased allocation to grains and decreased sensitivity
256 to lodging [56]. Although such varieties achieved significant yield gain, yield improvement was
257 perceived more as an improvement in individual plant properties, *i.e.* grain allocation and lodging
258 resistance, than as an improvement in community properties, *i.e.* lower intraspecific competition [41].
259 As a consequence, plant height is still mainly selected at the single-plant level by eliminating tall
260 plants in the early steps of breeding programs than through indirect selection for group performance,
261 as described in this study. Such direct selection on a plant trait can indeed prove very efficient when
262 the trait measurement is cheap and heritable, which might not be the case of all traits involved in
263 plant-plant interactions.

264 We explored particular combinations of parameters that we thought relevant for a typical
265 cereal crop. Yet, additional selection scenarios could be evaluated for applications in a broader set of
266 crops including non-grain crops. Moreover, traits other than plant height can be important in driving
267 competitive interactions. For example, root morphological traits can play a key role in the competition
268 for soil resources in perennial species [57]. Flower size might also be important for cross-pollinated
269 species [58]. More generally, many traits have been reported to be involved in plant-plant interactions,
270 which offer as many opportunities to increase cooperation in crops [9]. Because of recurrent
271 bottlenecks during the evolutionary history of crops [59] and historical practices of cultivation and
272 breeding (see above for an illustration for plant height), altruistic phenotypes might have been lost in
273 the pool of modern varieties. As illustrated with dwarf genes introduced from Japan, it might thus be

274 useful to further enlarge phenotypic variation available at the start of breeding programs by exploring
275 gene pools such as landraces or wild relatives. Moreover, studying the genetic determinism of these
276 traits could help to select for optimized mixtures of genotypes instead of mono-genotypic varieties.
277 Indeed, not all genes need to be shared in the population for cooperation to evolve, only those
278 involved in competitive interactions. In practice, the identification of specific genes (or linked
279 molecular markers) encoding for competitive traits would allow to sample individuals which are
280 highly related only at these specific loci instead of sampling individuals which are highly related on
281 the whole genome, as illustrated in this study. These practices could select for mixtures of varieties
282 that combine low variability on traits related to competitive ability and high variability on traits linked
283 to other functions such as pathogen resistance, resource-use or stress tolerance. Such mixtures of
284 varieties combining the positive effects of cooperation and biodiversity could help farmers facing the
285 need for more sustainable agriculture [60].

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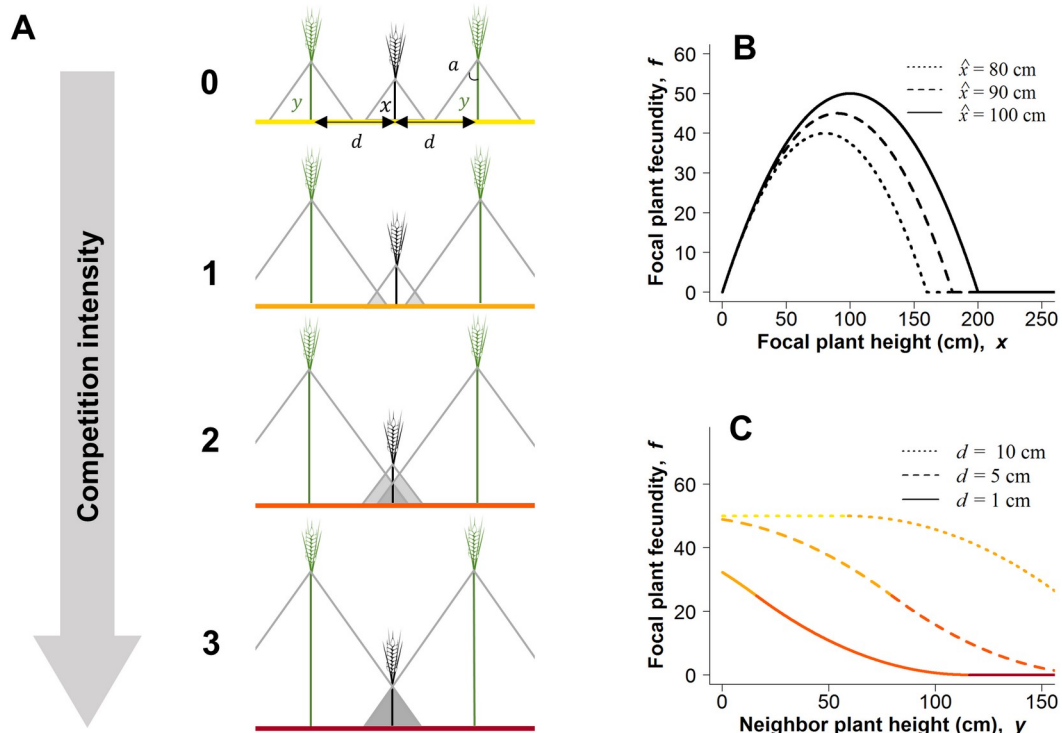
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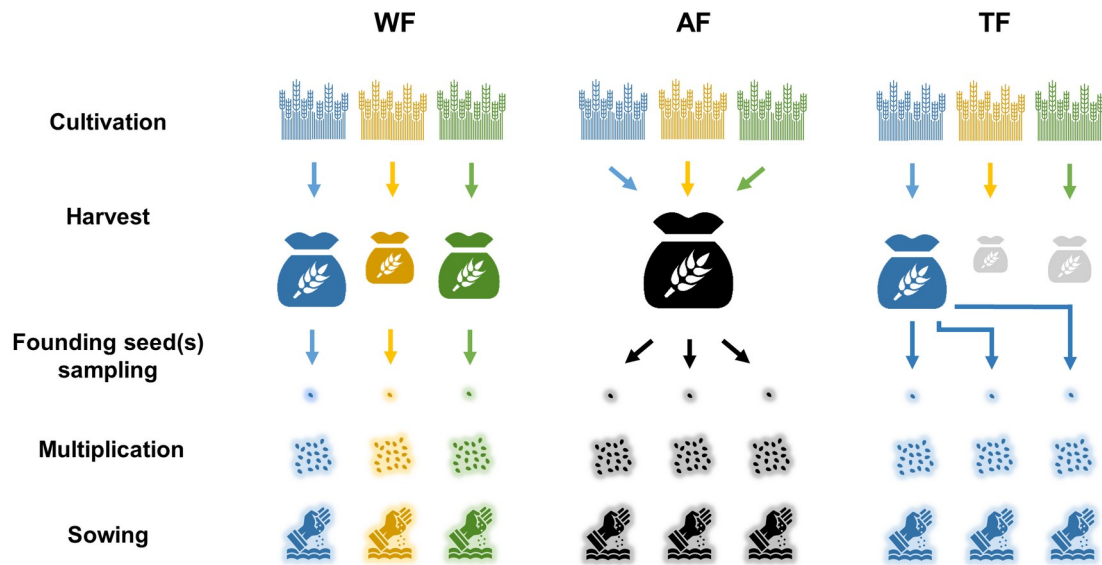
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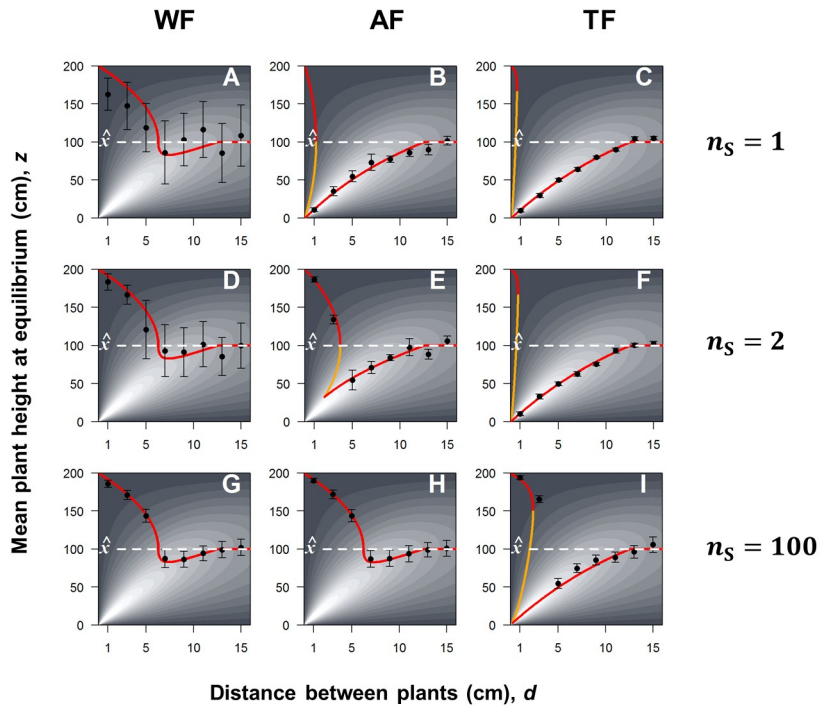
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435 **Figure 1 | Geometrical representation of plant competition for light.** (A) We used triangles to
 436 represent drop shadows around the plants (grey triangles). The focal individual is represented in black,
 437 neighbours are represented in green. Neighbours are positioned at equal distance, d , from the focal
 438 individual. For simplicity, we here represented the left and right neighbours with the same plant
 439 height, y . Competition for light happens when triangles overlap. Competition intensity increases with
 440 increasing overlap (from yellow to red), with no competition (competition intensity 0), low
 441 competition (competition intensity 1), intermediate competition (competition intensity 2) and intense
 442 competition (competition intensity 3). (B) Relationship between focal plant fecundity, f , and focal
 443 plant height, x . We assumed that, for an isolated plant, there is an optimal plant height \hat{x} which
 444 maximizes individual fecundity. The relationship is shown for three optimal plant height values $\hat{x} = 80$
 445 cm (dotted line), $\hat{x} = 90$ cm (dashed line), and $\hat{x} = 100$ cm (solid line). (C) Relationship between focal
 446 plant fecundity and neighbours' plant height. We computed the cost of competition as the proportion
 447 of shaded area of the focal triangle. The relationship is shown for a focal plant height equal to the
 448 optimal plant height so that $x = \hat{x} = 100$ cm, an angle $a = \pi/50$, and three plant-plant distances $d = 10$
 449 cm (dotted line), $d = 5$ cm (dashed line), and $d = 1$ cm (solid line). Competition intensity increases
 450 from yellow to red. Symbol: "Wheat" by efi kaperoni from the Noun Project.

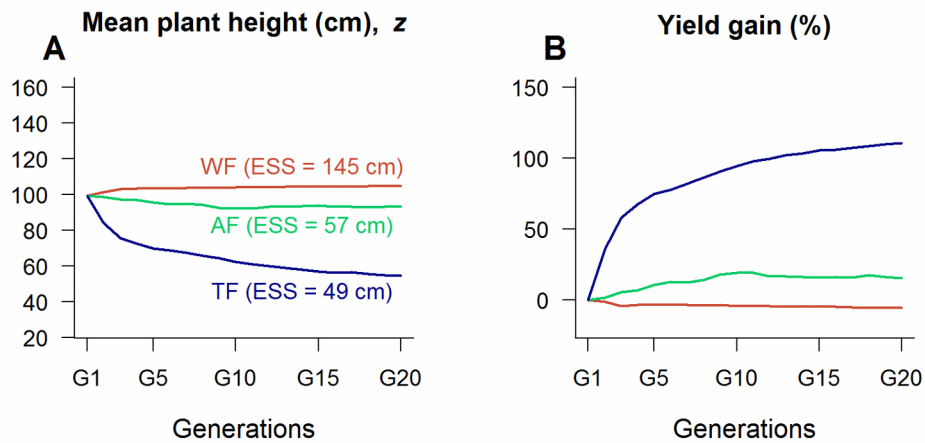


451 **Figure 2 | Strategies of selection.** The crop is grown in a farm composed of n_F fields. Here, $n_F=3$,
452 with fields respectively coloured in blue, yellow and green. In the Within-Fields (WF) selection
453 strategy, fields are sown with seeds exclusively sampled in their own harvest. Consequently, the crop
454 evolves separately in the different fields. In the Among-field (AF) selection strategy, seeds from the
455 different fields are pooled together at harvest. Then, each field is sown with seeds sampled in that
456 pool. In the Top-Field (TF) selection strategy, only the most productive field is retained for the next
457 generation. Then, each field is sown with seeds exclusively sampled in the harvest of that top field.
458 For all strategies, a multiplication stage precedes sowing when there are not enough founding seeds to
459 re-populate the n_F fields. Symbols: “Wheat” by lastspark from the Noun Project, “seed” by corpus
460 delicti from the Noun Project, and “sow” by Symbolon from the Noun Project.
461



462 **Figure 3 | Relationship between the mean plant height in the meta-population at equilibrium, z ,**
 463 **and the physical distance between plants, d .** Evolutionary Stable Strategies (ESS) predicted from
 464 the analytical model are reported as a red solid line. Results from individual based simulation are
 465 reported in black, with dots (error bars) representing the mean (standard deviation) plant height in the
 466 meta-population after 5000 generations. Grain yield is represented in the background of the graphs and
 467 increases with lighter grey shade (see Fig. S2). We tested the three seed selection strategies (WF, AF
 468 and TF) with three numbers of founding seeds $n_S = 1$ (A, B, C), $n_S = 2$ (D, E, F), and $n_S = 100$ (G, H,
 469 I). Simulations were performed with $n_F = 20$ fields and $n_P = 200$ plants per field. In the first
 470 generation, the population was monomorphic, *i.e.* all plants had the same height z , with $z = \hat{x} = 100$
 471 cm. Phenotypic variability was then generated by mutations. Mutation rate equalled 10% meaning that
 472 on average 1 individual out of 10 differed in height from its parent. Mutation effect was set to ± 5 cm.
 473 We varied the plant-plant physical distance from 1 cm to 15 cm with steps of 2 cm. After 5000
 474 generations, the selection-mutation-drift equilibrium was reached in all simulations. Orange solid lines
 475 represent unstable equilibria, *i.e.* equilibria at which any mutation makes the mean phenotype
 476 deviate further from its original value, either in the upward or in the downward direction.

477



478 **Figure 4 | Selection efficiency.** We modeled the evolution of plant height (A) and we measured the
 479 yield gains (B) realized after 20 generations with the three selection strategies (WF in red, AF in green
 480 and TF in blue). We performed simulations with $n_F = 5$ fields, $n_p = 200$ plants per field, and a 5 cm
 481 plant-plant distance. At generation 1 (G1), each field was initiated by sampling two founding seeds in
 482 a normally distributed plant population with mean and standard deviation on plant height respectively
 483 equal to 100 cm and 20 cm. For all subsequent generations, we draw two founding seeds in the harvest
 484 to repopulate each field. Funding seeds were multiplied in equal proportion (x 100 each) to obtain 200
 485 seeds per field. Mutation rate was equal to 10% with a ± 5 cm mutation effect. Reported values are
 486 averaged over 20 simulation runs.