Farming plant cooperation in crops

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

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

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

At the same time, the evolutionary biologist William Hamilton formalized the kin selection theory which aimed at understanding the evolution of social interactions, notably altruism where individuals act to increase the fitness of their social partners at the expense of their own reproduction [11,12]. Hamilton proposed a very simple rule which states that altruistic phenotypes can be selected if the fitness cost for the actor, $c$, is outweighed by the benefit received by the partners, $b$, weighted by the relatedness between the actor and the partners, $R$, i.e. when $c < Rb$. With this rule, Hamilton
explicitly incorporated the contribution of relatives in transmitting genes that are shared with the actor
to the next generations. Later works have emphasized that \(-c+Rb\) provides a representation of the
average effect of an allelic substitution on individual fitness (e.g. [13]) rather than an alternative to
individual fitness: \(-c+Rb\) gives the expected effects of copies of an allele in different individuals on
the expected fitness of individuals who bear the allele. Kin selection has been extremely successful in
explaining a wide range of altruistic phenotypes such as sterility in eusocial insects [12] or helping
behaviours in birds [14], and it has received increasing attention in plants in recent decades (reviewed in [15]).

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

Current crop improvement programs do not explicitly take into account social interactions
among plants [18,21]. Conversely, significant work has been achieved to integrate the effects of social
interactions into farm animals breeding programs [23]. Indeed, reducing competitiveness among
group-housed animals is critical for both productivity and animal welfare [24]. Based on the early
work of Griffing [25], quantitative genetic models have been developed to account for the effect of the
genes of the focal individual on its own phenotypic traits, known as the direct genetic effect (DGE),
and the effects of the genes of individuals interacting with the focal individual, known as the indirect
genetic effect (IGE) [26–28]. Experiments have shown that IGEs can represent a significant proportion
of the heritable variation on traits such as growth rate in pigs [29] or survival rate in laying hens [30].
Therefore, the genetic response to selection can significantly be improved by accounting for IGEs
Theoretical studies have shown how the IGEs frameworks connects with kin selection theory and how relatedness affects the genetic response to selection in presence of IGEs [31,32]. To a lesser extent, this framework has also been applied in tree breeding [33,34]. Yet we still poorly understand how social interactions affect the evolution of plant phenotypes, and the extent to which crop breeding schemes can improve yield depending on the intensity of social interactions.

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

**Methods**

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

Crop populations are spatially structured, either in fields when grown by a farmer, or in experimental plots when evaluated by a plant breeder. In our model we assume that the crop population is made of $n_F$ fields, with $n_P$ plants per field. In agreement with experimental evidence on several crop species [39,41], we assume that there is an optimal height $\hat{x}$ that maximizes plant fecundity, *i.e.* individual seed production, in the absence of competition for light (Fig. 1B). We model competition for light with the drop shadows of neighbouring plants (Fig. 1A). Plant fecundity is assumed to decrease proportionally to the size of the overlapping area between drop shadows and thus
with the height of the neighbours, as observed in experimental studies [35,38,40] (Fig. 1C). One of the
main parameters that drives intraspecific competition in crops is plant density [5,40]. In the model,
plant density is governed by the parameter $d$, the distance between plants. The intensity of competition
for light also depends on the angle $\alpha$ at the apex of the triangle used to represent drop shadows (Fig. 1A). We computed crop yield as the total number of seeds produced in a field divided by the field area (see Supplementary Information section 1.1). As expected, the plant height that maximises crop yield decreases with the distance between plants (Fig. 3 and Fig. S2), and crop yield is maximized by growing short plants at high density [5,40]. To fit as closely as possible to the specifics of real crops such as wheat, we set the optimal plant height $x$ to 100 cm and the angle $\alpha$ to $\pi/50$ rad. Such a small angle allowed us to generate a moderate and realistic intensity of competition at low plant-plant distances such as those classically encountered in cereals. Note that the choice of parameter values did not affect our results qualitatively.

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

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

We developed an analytical model from which we derived approximations for the Evolutionary Stable Strategy (ESS) for plant height, that is the strategy that cannot be invaded by any alternative strategy [45] (Supplementary Information section 1.2). The ESS approach is widely used in
evolutionary biology to predict the outcome of long-term evolutionary processes where fitness depends on the frequencies of the different phenotypes present in the population. In our study, we adopt the kin selection approach to account for the spatial structure of crops [46]: as mentioned above, the crop population is distributed into different fields, or different groups, that can be connected by migration. These groups delineate social interactions: individuals only interact within groups. The evolution of social traits is driven by the genetic similarity between actors and recipients and thus by genetic similarity between group members at the loci involved in social traits [12]. Relatedness ($R$) quantifies this similarity and measures the extent to which an actor is more likely to share an allele (and thus share a common phenotype) with an individual sampled in its own group than with an individual sampled in another group [47,48] (Supplementary Information section 1.3). Compared to traditional definitions of relatedness from pedigrees, the definition of relatedness used here averages pedigree relatedness over the distribution of pedigrees of gene copies within groups [49]. As this distribution depends on other features of the life cycle such as migration rates, relatedness depends on the life cycle (Fig. S3).

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

**Results**

Overall, ESS predictions agreed very well with simulation results and equilibriums were always monomorphic, meaning that a single phenotype was present in the population at the end of the simulations (Fig. 3, black dots). When plants were grown at low densities ($d > 12$), they did not compete for light and thus the mean phenotype at equilibrium was the optimal phenotype for individual fecundity, i.e. $\hat{x}$ (competition intensity 0 in Fig. 1A). At intermediate densities ($7 < d < 12$),
plants evolved smaller than their optimal phenotype in all scenarios. Indeed, when competition is low (competition intensity 1 in Fig. 1A), shorter phenotypes result in greater plant fecundity because the fecundity loss incurred by moving away from the optimum is overcompensated by the fecundity gain obtained by avoiding the shadow of the neighbours. At high densities ($d < 7$), where competition is more intense (competition intensity 2 in Fig. 1A), evolutionary outcomes differed greatly among scenarios. With the WF strategy, the higher the density (the lower $d$), the taller the plant evolved. At equilibrium, plant were well above the optimal height $\hat{x}$, leading to very low yields whatever the number of founding seeds (Fig. 3A, D, and G). In contrast, both AF and TF strategies resulted in the evolution of short high-yielding phenotypes when the number of founding seeds was low (Fig. 3B, C, and F). Increasing the number of founding seeds reduced relatedness (Fig. S3), drove the evolution of taller plants, and lowered crop yield (Fig. 3E, H, and I). Shorter phenotypes evolved under the TF strategy compared to the AF strategy, as a result of stronger selection among fields in the TF strategy (Fig. 3E and F). Interestingly, with both AF and TF strategies, two alternative evolutionary outcomes were possible for certain ranges of $d$ (e.g. Fig. 3E when $2 < d < 3.5$ cm). When such evolutionary bistability occurred, which evolutionary outcome was reached depended on the initial phenotypic value of the population (Fig. S4).

The ESS analysis captures the long-term evolutionary outcome of the model but does not predict the speed of phenotypic evolution towards the ESS. To explore the short-term evolutionary dynamics of plant height under realistic agricultural practices, we carried out individual-based 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 strategy (Fig. 4A). Consequently, the relative efficiency in increasing yield differed markedly among selection strategies: after 20 generations, yield had decreased by 5% with the WF strategy whereas it has increased by 15% with the AF strategy and by 110 % with the TF strategy (Fig. 4B).
Discussion

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

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

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

Controlled or uncontrolled crosses could be used to generate new allelic combinations and new
phenotypes over generations.

Our results shed new light on the evolution of plant height during the evolutionary history of
crops. For most cereals, plant height has increased between their wild ancestor and their earliest
domesticated form [42,43]. Moreover, most of these primitive domesticated forms remained tall, or
even evolved taller until the end of the 19th century [4]. The practices associated with the transition
from gathering to cultivation [1], as well as the most common selection method over this period,
namely mass selection, could be regarded in light of the kin selection: grains were collected from
isolated plants (or low-density grown plants), these plants being selected for their individual features,
and grains (or spikes) from different plants being mixed before sowing [52]. Such practices leading to
low among-field selection and low relatedness inevitably select for selfish phenotypes. Even if tallness
might have deliberately been selected for other needs such as chaff production or weed control [4], our
model suggests that mass selection might have reinforced selection for increased plant height.
Initiating breeding programs with plants that are too tall can hamper the evolution of short high-yielding phenotypes. This might have happened at least twice in the evolutionary history of crops. First, there is evidence that farmers chose relatively tall plants in the wild to start cultivation [53]. Second, for most cereals the main reduction in plant height was achieved in the 1960’s by introgressing dwarf genes from Asian varieties [54]. At that time, most wheat varieties were very tall in U.S.A [55] and Europe [41], and we could wonder whether plant breeding would have achieved such shortening by crossing and selecting among the local pool varieties.

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

We explored particular combinations of parameters that we thought relevant for a typical cereal crop. Yet, additional selection scenarios could be evaluated for applications in a broader set of crops including non-grain crops. Moreover, traits other than plant height can be important in driving competitive interactions. For example, root morphological traits can play a key role in the competition for soil resources in perennial species [57]. Flower size might also be important for cross-pollinated species [58]. More generally, many traits have been reported to be involved in plant-plant interactions, which offer as many opportunities to increase cooperation in crops [9]. Because of recurrent bottlenecks during the evolutionary history of crops [59] and historical practices of cultivation and breeding (see above for an illustration for plant height), altruistic phenotypes might have been lost in the pool of modern varieties. As illustrated with dwarf genes introduced from Japan, it might thus be
useful to further enlarge phenotypic variation available at the start of breeding programs by exploring gene pools such as landraces or wild relatives. Moreover, studying the genetic determinism of these traits could help to select for optimized mixtures of genotypes instead of mono-genotypic varieties. Indeed, not all genes need to be shared in the population for cooperation to evolve, only those involved in competitive interactions. In practice, the identification of specific genes (or linked molecular markers) encoding for competitive traits would allow to sample individuals which are highly related only at these specific loci instead of sampling individuals which are highly related on the whole genome, as illustrated in this study. These practices could select for mixtures of varieties that combine low variability on traits related to competitive ability and high variability on traits linked to other functions such as pathogen resistance, resource-use or stress tolerance. Such mixtures of varieties combining the positive effects of cooperation and biodiversity could help farmers facing the need for more sustainable agriculture [60].
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Figure 1 | Geometrical representation of plant competition for light. (A) We used triangles to represent drop shadows around the plants (grey triangles). The focal individual is represented in black, neighbours are represented in green. Neighbours are positioned at equal distance, $d$, from the focal individual. For simplicity, we here represented the left and right neighbours with the same plant height, $y$. Competition for light happens when triangles overlap. Competition intensity increases with increasing overlap (from yellow to red), with no competition (competition intensity 0), low competition (competition intensity 1), intermediate competition (competition intensity 2) and intense competition (competition intensity 3). (B) Relationship between focal plant fecundity, $f$, and focal plant height, $x$. We assumed that, for an isolated plant, there is an optimal plant height $\hat{x}$ which maximizes individual fecundity. The relationship is shown for three optimal plant height values $\hat{x} = 80$ cm (dotted line), $\hat{x} = 90$ cm (dashed line), and $\hat{x} = 100$ cm (solid line). (C) Relationship between focal plant fecundity and neighbours’ plant height. We computed the cost of competition as the proportion of shaded area of the focal triangle. The relationship is shown for a focal plant height equal to the optimal plant height so that $x = \hat{x} = 100$ cm, an angle $\alpha = \pi/50$, and three plant-plant distances $d = 10$ cm (dotted line), $d = 5$ cm (dashed line), and $d = 1$ cm (solid line). Competition intensity increases from yellow to red. Symbol: “Wheat” by efi kaperoni from the Noun Project.
Figure 2 | Strategies of selection. The crop is grown in a farm composed of $n_F$ fields. Here, $n_F = 3$, with fields respectively coloured in blue, yellow and green. In the Within-Fields (WF) selection strategy, fields are sown with seeds exclusively sampled in their own harvest. Consequently, the crop evolves separately in the different fields. In the Among-field (AF) selection strategy, seeds from the different fields are pooled together at harvest. Then, each field is sown with seeds sampled in that pool. In the Top-Field (TF) selection strategy, only the most productive field is retained for the next generation. Then, each field is sown with seeds exclusively sampled in the harvest of that top field. For all strategies, a multiplication stage precedes sowing when there are not enough founding seeds to re-populate the $n_F$ fields. Symbols: “Wheat” by lastspark from the Noun Project, “seed” by corpus delicti from the Noun Project, and “sow” by Symbolon from the Noun Project.
Figure 3 | Relationship between the mean plant height in the meta-population at equilibrium, $z$, and the physical distance between plants, $d$. Evolutionary Stable Strategies (ESS) predicted from the analytical model are reported as a red solid line. Results from individual based simulation are reported in black, with dots (error bars) representing the mean (standard deviation) plant height in the meta-population after 5000 generations. Grain yield is represented in the background of the graphs and increases with lighter grey shade (see Fig. S2). We tested the three seed selection strategies (WF, AF 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, I). Simulations were performed with $n_F = 20$ fields and $n_P = 200$ plants per field. In the first generation, the population was monomorphic, i.e. all plants had the same height $z$, with $z = \hat{z} = 100$ cm. Phenotypic variability was then generated by mutations. Mutation rate equalled 10% meaning that on average 1 individual out of 10 differed in height from its parent. Mutation effect was set to $\pm 5$ cm. We varied the plant-plant physical distance from 1 cm to 15 cm with steps of 2 cm. After 5000 generations, the selection-mutation-drift equilibrium was reached in all simulations. Orange solid lines represent unstable equilibriums, i.e. equilibriums at which any mutation makes the mean phenotype deviate further from its original value, either in the upward or the downward direction.
Figure 4 | Selection efficiency. We modeled the evolution of plant height (A) and we measured the yield gains (B) realized after 20 generations with the three selection strategies (WF in red, AF in green and TF in blue). We performed simulations with \( n_F = 5 \) fields, \( n_P = 200 \) plants per field, and a 5 cm plant-plant distance. At generation 1 (G1), each field was initiated by sampling two founding seeds in a normally distributed plant population with mean and standard deviation on plant height respectively equal to 100 cm and 20 cm. For all subsequent generations, we draw two founding seeds in the harvest to repopulate each field. Funding seeds were multiplied in equal proportion (x 100 each) to obtain 200 seeds per field. Mutation rate was equal to 10% with a \( \pm 5 \) cm mutation effect. Reported values are averaged over 20 simulation runs.