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Evolutionary Agroecology: the potential for cooperative, high density, weed-suppressing cereals

Jacob Weiner, Sven B. Andersen, Wibke K.-M. Wille, Hans W. Griepentrog and Jannie M. Olsen

Department of Agriculture and Ecology, University of Copenhagen, Frederiksberg, Denmark

Abstract

Evolutionary theory can be applied to improve agricultural yields and/or sustainability, an approach we call Evolutionary Agroecology. The basic idea is that plant breeding is unlikely to improve attributes already favored by millions of years of natural selection, whereas there may be unutilized potential in selecting for attributes that increase total crop yield but reduce plants' individual fitness. In other words, plant breeding should be based on group selection. We explore this approach in relation to crop-weed competition, and argue that it should be possible to develop high density cereals that can utilize their initial size advantage over weeds to suppress them much better than under current practices, thus reducing or eliminating the need for chemical or mechanical weed control. We emphasize the role of density in applying group selection to crops: it is competition among individuals that generates the 'Tragedy of the Commons', providing opportunities to improve plant production by selecting for attributes that natural selection would not favor. When there is competition for light, natural selection of individuals favors a defensive strategy of 'shade avoidance', but a collective, offensive 'shading' strategy could increase weed suppression and yield in the high density, high uniformity cropping systems we envision.

Introduction

Recent advances in plant ecology, agroecology and evolutionary biology lead to exciting new hypotheses for increasing agricultural sustainability while maintaining or even increasing current yields. A new and deeper understanding of the potential contribution of evolutionary theory to agriculture (Denison et al. 2003; Weiner 2003; Denison 2007) can help us to predict when breeding can and when it cannot improve on what nature has achieved via natural selection, and help set new goals and approaches to crop improvement. Here we pursue some of these arguments in the context of a pressing problem in plant production: weed management.

Evolutionary agroecology ('Darwinian Agriculture')

Group versus individual selection in nature

Altruistic behavior (i.e. behavior that decreases individual fitness but is beneficial to the group or populations) is a problem for Darwinian theory. In the 1960s, Wynne-Edwards hypothesized that selection among groups, not among individuals, could explain altruistic behavior in birds (Wynne-Edwards 1986). Simply put, if a population of birds consists of sub-populations, some of which show 'selfish' behaviors and some of which show 'altruistic' behaviors, the former groups will be more likely to go extinct than the latter, and the whole population will evolve to be altruistic. There was a vigorous reaction against his ideas from evolutionary theorists, most notably G.C. Williams (1966). The primary problem with Wynne-Edwards's argument is that the mathematical conditions necessary for group selection to overwhelm individual selection when they are in conflict seem to be unrealistic. Every time a 'selfish' gene appears in an 'altruistic' group, the group must go extinct, or the selfish gene will spread through the population. Since the number of individuals is much greater than the number of groups among which group selection can act, the mathematical conditions needed for group selection to dominate individual selection are extreme.

While the mathematical requirements for group selection were being explored, Hamilton (1964) described the concepts of kin selection and inclusive fitness, which was

further developed by other researchers (Maynard Smith 1964; Michod 1982). Kin selection provided an explanation of altruistic behavior (among related individuals) that did not require group selection, and revolutionized our understanding of behavior in social animals as well as many other phenomena. Although there has been renewed interest in group selection's potential role in evolution in the context of multilevel selection theory (Goodnight 2005; Wilson and Wilson 2007), and the distinction between kin and group selection has even been questioned, most evolutionary biologists still think that group selection will rarely be stronger than individual selection.

The point is simply that Darwinian evolution by natural selection is driven primarily if not solely by differential survival and reproduction among individuals within a population. It is a common popular scientific misunderstanding that natural selection inevitably works to increase the survival or performance of the population or species: over the past 30 years evolutionary biologists, using data from molecular biology to social behavior, have shown clearly that evolutionary interest of the individual is often in conflict with the interests and even the survival of the population or species. When this occurs, genes that increase individual fitness at the cost of population performance will increase in frequency. Individual selection will overwhelm group selection in the vast majority of cases when they are in conflict. This has been referred to as a 'Tragedy of the Commons' (e.g. Hardin 1968; Gersani et al. 2001).

Group versus individual selection in agriculture

Even if group selection is not important in nature, that does not mean it cannot play a role in agriculture, where nature is manipulated to meet human needs (Denison et al. 2003; Weiner 2003). The idea that group selection should be a goal for plant breeding goes back several decades. J.L. Harper, the founder of modern plant population ecology, mentions it briefly in his book: '...group selection, which is believed to be extremely rare in or absent in nature...may be the most proper type of selection for improving the productivity of crop and forest plants' (Harper 1977, p. 892). Working independently, the Australian agronomist C.M. Donald developed the concept of the 'ideotype' to refer to all 'model' phenotypic characteristics that are predicted to enhance yield potential (Donald 1968; Rasmusson 1987), but he also alluded to group selection: '...a successful crop ideotype will be a weak competitor ... [so] ... plants in the crop community will compete with each other to a minimum degree'. Later, Donald took the idea of group versus individual performance farther and referred to 'communal plants': 'A "communal plant" has features in accord with

the success of the crop community rather than the plant itself' (Donald 1981).

Donald's ideas contributed to the development of shorter, less competitive varieties with a higher reproductive allocation (Harvest Index) for the 'Green Revolution'. These varieties could produce higher yields under high nutrient levels without lodging. We argue here that the full potential of Donald's ideas has not been appreciated. To most agronomists, the word 'ideotype' means the short, nitrogen hungry, pesticide requiring, high yielding cereals of the Green Revolution. Evolutionary Agroecology extends the concept of the 'communal plant' to group selection under any agricultural conditions. In some agricultural contexts the difference between individual- and group-selected genotypes may be very small or nonexistent, in other cases, it will be considerable.

We are just beginning to understand the implications of evolutionary conflicts among individuals for agricultural production. Yield, the most fundamental agronomic variable, is a characteristic of the population, not the individual. The farmer is not interested in the yield of the individual plant but the yield per hectare. Plant breeding can improve crops most effectively when it is directed towards goals that are *different* from natural selection, e.g., characteristics that maximize population, not necessarily individual, performance. In the majority of cases, individual and group performance are not in conflict, and in such cases it seems unlikely that plant breeding can improve on millions of years of evolution via natural selection. For example, genes and gene combinations improving the efficiency of photosynthesis enhance the fitness of individuals which posses them, and they also increase the performance of the population as they spread within it – there is no conflict between individual and group selection. Thus, from an evolutionary perspective, efforts to improve basic plant physiological processes such as photosynthesis or respiration through plant breeding or genetic engineering are not likely to be successful, because natural selection has been optimizing these processes for millions of years (Evans 1993; Loomis 1993). On the other hand, those characteristics that increase yield or sustainability but are not advantageous to the individuals which posses them, would be good candidates as goals for breeding programs (Donald 1981).

Plant breeders have become aware of the difference between individual and group performance, so they are careful to not inadvertently select individuals at the expense of population yield. They do this by selecting among small groups of related plants, rather than individuals, or by selecting among highly inbred lines or uniform hybrid offspring, thus reducing or removing the genetic variation within the crop population that can lead to individual selection. But using group selection as a source

of hypotheses for desirable traits and goals for breeding is an approach that has not yet been explored. Below we advance general and specific hypotheses.

Plant breeding has selected for attributes different than those selected in nature in large part because the environment in the agricultural field is different than that in nature. Agronomy is largely about improving the conditions for plant growth and production through fertilization, irrigation, pest control, etc. Breeding has been very successful in developing genotypes that can utilize these increased resources and improved conditions to produce high yields, but evolutionary theory suggests that we have not yet optimized population performance.

The importance of density

One aspect of the argument that has not been fully appreciated in discussions about the potential for group selection in agriculture is the role of density. The difference between optimal individual and optimal population performance increases with density, because it is competition among individuals that creates and exacerbates the difference between individual and group selection. If the plants in an agricultural field (without weeds) are so far apart that there is no competition among them, then there is no difference between optimal individual and optimal population behavior: the genotype that gives the highest individual yield gives also the highest population yield. A 'Tragedy of the Commons' can only exist when there is a common resource for which there is competition. While high density results in strong competition, it also increases potential for cooperation, creating the difference between individual and group performance that we want to utilize. We argue below that there are additional advantages of higher density crops.

Agroecological context: controlling weeds and increasing sustainability – 'high density cropping systems'

The agricultural system, as well as the climate and soil, provide the ecological 'stage' on which our evolutionary 'play' takes place (Hutchinson 1965). Just as evolution often occurs more quickly when the environment changes, changes in agricultural practices offer new possibilities for plant breeding.

As argued above, higher crop density leads to greater competition among plants, and this creates the opportunity to manipulate plants' competitive interactions and increase greatly the suppression of weeds by the crop. Competition from weeds is the largest source of yield loss globally (Liebman et al. 2001). This can be seen in the time farmers in developing countries spend on weed con-

trol, and in the extensive use of herbicides in modern industrial agriculture or mechanical weed control in organic farming.

Model of weed suppression based on high crop density and spatial uniformity

We have developed a model of weed suppression, based on the concept of 'size-asymmetric competition' (Weiner et al. 2001). According to the model, effective suppression of weeds by the crop should be possible when several assumptions are met:

1. The crop must have reasonably good competitive ability. Our ideas have been developed in the context of cereal crops, which meet this criterion. Crops that have very limited competitive abilities, e.g. onions and other biennials, will never be able to suppress weeds. Their evolved strategy does not involve competitive strength and they do not have the ability to suppress weeds under any circumstances.

2. Weed seeds are smaller than crop seeds, and therefore weed seedlings are smaller than crop seedlings, so the crop has an initial size advantage. This condition is met in the vast majority of cases, where most weeds are annuals with high dispersibility.

3. The advantage of larger initial size in competition among plants increases with density. There is much evidence that this is the case (Weiner and Thomas 1986; Schwinning and Weiner 1998).

4. The yield versus density curve for the crop is flat for a range of densities. Total biomass production does not decrease at high densities, a phenomenon called 'Constant Final (Biomass) Yield' (Farazdaghi and Harris 1968; Weiner and Freckleton 2010), although 'harvestable yield' often does. In many crops, such as cereals, this decline occurs at much higher densities than the lowest density that gives maximum yield (i.e. the optimum density without weeds). Thus the total harvestable yield increases with density at low densities and then levels off, before declining at very high densities (Fig. 1).

Under these assumptions, the crop fraction of the total (crop + weed) biomass should increase with increasing density, resulting in almost complete weed suppression at very high crop densities (Fig. 1A). But ever-increasing weed suppression at ever-higher crop densities has not been observed in most studies on crop density and weeds (Mohler 2001). Rather, the effect of crop density on weeds levels off at high densities, resulting in only limited weed suppression and therefore major yield loss (Fig. 1B). The discrepancy between the model and the field data appears to be due to the spatial pattern of the individual crop plants. Crop rows are long, thin clumps, in which
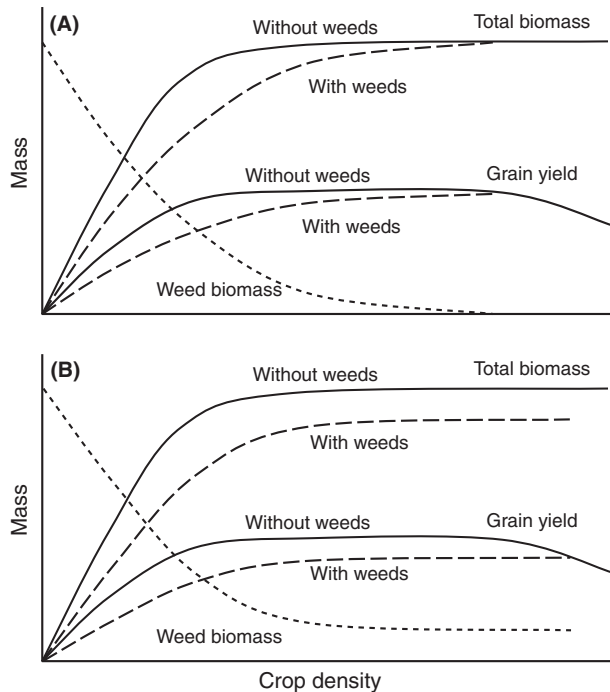
Figure 1 Theoretical (A) and observed (B) relationship between crop density and weed biomass and losses under very high weed pressure. Relationship (B) is observed when the crop is sown in a standard row pattern. When the crop is sown in a uniform pattern, the results are similar to (A).
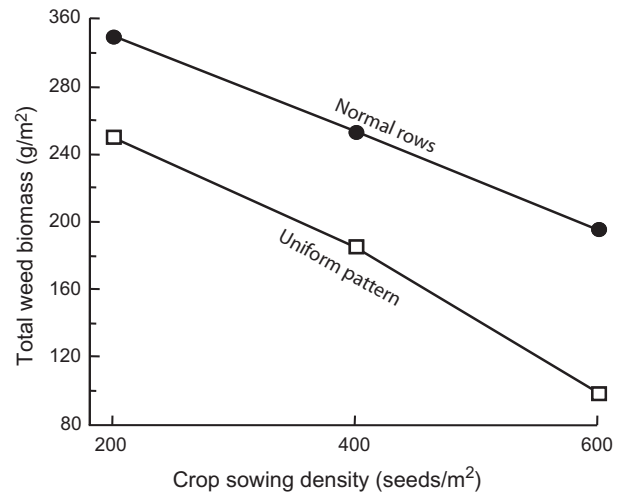

Figure 2 Total weed biomass versus sowing density of weed-infested spring wheat (*Triticum aestivum* L.) sown in standard rows (13 cm) and in a highly uniform, grid-like pattern (after Weiner et al. 2001a). Thus, there was 65% less weed biomass in the high density, uniform sowing pattern than in the standard sowing pattern (300–350 seeds/m² in rows), and this resulted in 60% greater yield.

individuals are very crowded in one horizontal direction (within the row), but very far apart in the other (between the rows). Increasing sowing density in a standard row-sowing pattern increases competition within the crop population (intraspecific competition) more than it increases crop-weed (interspecific) competition. Tests of our model over the past 9 years have demonstrated convincingly that the suppression of weeds by cereal crops can be increased greatly without reducing yield through a combination of (1) increased crop density and (2) increased crop spatial uniformity (Fig. 2; Weiner et al. 2001; Olsen et al. 2005a,b, 2006; Kristensen et al. 2008). If effective weed suppression occurs at densities lower than those resulting in substantial yield loss due to intraspecific competition, as is the case for cereals (point 4 above), increased crop density and spatial uniformity can play an important role in future weed management.

High biomass as the key to increased sustainability

Agricultural research in the 21st century must address sustainability as well as short-term yield. The behavior of natural and agricultural plant communities suggests that increased plant biomass density in the field is one of the keys to increased agricultural sustainability while main-

taining high yields. Biological sustainability at the farm level is basically about maintaining soil fertility. This can be achieved in practice by maintaining or increasing semi-decomposed organic matter in the soil (humus). There are two types of evidence for this: (1) Natural plant communities that are best at retaining resources and making them available to growing plants are those with high standing and/or dead biomass (Archibold 1995); (2) Soil fertility and therefore biological sustainability remains highest in farming systems in which soil organic matter input is high, as we observe in some organic and alternative approaches to plant production, such as biodynamic farming or permaculture (Mäder et al. 2002).

Many of the negative environmental impacts of modern conventional agricultural practices are the results of low quantities of living and dead biomass in the field, e.g. bare soil leading to increased nutrient loss and erosion, reduced soil quality due to reduced input of organic matter, etc. Low standing biomass (and therefore low soil organic matter input) is often assumed to be necessary conditions for high yields, but there is no theoretical or empirical basis for this assumption: the most productive natural ecosystems are not those with very low standing biomass. The problem is that these highly productive natural plant communities produce large quantities of biomass, not seeds or fruit. Agricultural research and technology can change this, and we can develop high yielding cropping systems with higher standing biomass: 'High Density (or High Biomass) Cropping Systems' (Weiner et al. 2001). This represents the next stage in the

engineering of agricultural ecosystems to achieve both the high productivity and the increased sustainability that world agriculture needs. Increasing crop density is a small but important step in this direction.

While sowing cereals at a higher density in a uniform pattern would require some increased expenditures for new machinery and more seed for sowing, there would be corresponding reduction in expenses for weed control (chemicals, fuel, machinery, and manpower). We hypothesize that positive environmental impacts of such 'High Density Weed-Suppressing Cropping Systems' would be significant: much reduced or no herbicide application, less traffic on the fields and therefore less soil compaction, less fuel consumption and CO_2 production, reduced erosion, increased plant diversity in the field (because weeds are not killed but suppressed), providing increased resources to invertebrates, birds, etc. There may well be costs or tradeoffs associated with growing cereals at higher densities. For example, increased crop density may result in increased levels of some crop diseases, but increased crop spatial uniformity may reduce spread of other diseases. In our 10 years of research on increased wheat density and spatial uniformity we have not observed increased levels of disease, but this has yet to be rigorously tested. There may also be unforeseen advantages. The increased biodiversity from the presence of many small, suppressed weeds can increase the control of pests by harboring their natural enemies, but it could also attract undesirable pests. Research on these questions is needed, but what is most needed at this point is to investigate the potential of such an approach to cereal production is the breeding of crop varieties for this altered biotic environment.

Spatial uniformity and cooperative behavior

Spatial uniformity creates improved possibilities for cooperative behavior among crop plants. In a highly uniform spatial pattern, all plants have approximately the same 'available area' (Fischer and Miles 1973; Mithen et al. 1984; Regnier and Bakelana 1995), and therefore approximately the same resource base. This increases the possibility for cooperative behavior among crop plants. We can design plants that improve the utilization of resources and suppress weeds within their 'territories', without interfering much with each other. If crop plants are very crowded in one dimension, as they are in the standard row-sowing pattern, they cannot avoid competing with one another immediately after germinating, while leaving space and resources between rows for weed development. In a uniform pattern, intraspecific competition within the crop population is *delayed* while competition with weeds begins *sooner*, while the crop still has its size advantage,

allowing the crop population to shade and suppress the weeds.

Thus, a high density, uniform sowing distribution of crop plants provides the agroecological background for the hypothesis that cooperative weed suppression is possible. Our hypothesis involves both a changed environment and new genotypes for this environment. Major advances in agricultural production have occurred when both agronomic practices and crop genotypes have changed.

We have some evidence suggesting that there is potential for the development of varieties which will be highly effective in suppressing weeds under high density, high spatial uniformity conditions. In our first study on the effects of crop density and spatial uniformity on weed suppression in spring wheat (Weiner et al. 2001), four varieties of wheat were investigated. There was a large and highly significant variety × density interaction (Table 1) on yield, such that the variety with the highest yield at low crop density had the lowest yield at high crop density (Fig. 3). This suggests a tradeoff in performance at low versus high crop density under high weed pressure.

The results suggest that the concept of a general 'competitive ability' of a variety (Christensen 1995) may be too simplistic for further progress on weed suppression by crops, because the relative competitive abilities of varieties changes with crop density. Effective weed suppression is only possible at high density, but the plant attributes that give the best competitive performance at low density, where most research has been performed, are not likely to give optimal performance at high density.

The attributes determining effectiveness of weed suppression at high crop density are not yet clearly identified, but there are some hypotheses, one of which we present below.

Table 1. Mixed linear model analysis of an experiment on the effects on yield of spring wheat (*Triticum aestivum*) density (200, 400, 600 seeds/m²), sowing pattern (rows versus uniform) and variety ('Harlekin', 'Jack', 'Dragon', 'Baldus') under very high weed pressure. Nonsignificant interactions are removed from the analysis. The variety × density interaction is strong and highly significant, but the main effect of variety is nonsignificant, indicating a 'crossover' genotype × environment interaction.

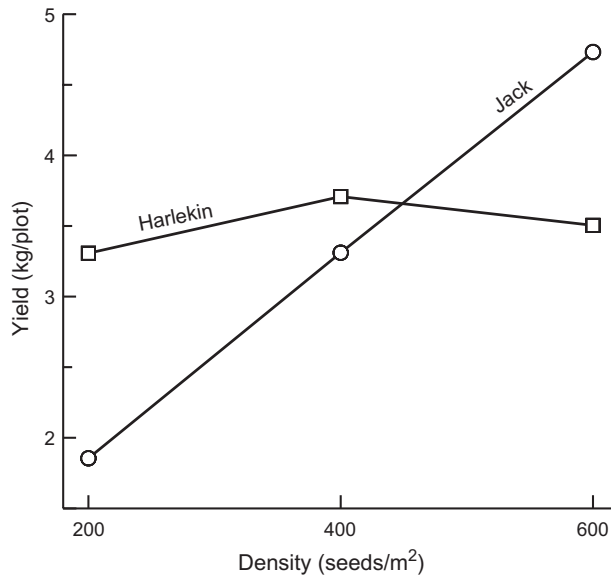| Source	df	SS	F	P
Block	3	3.54	2.75	0.048
Density	1	28.10	68.35	<0.0001
Variety	3	1.17	0.91	0.442
Pattern	1	13.81	32.13	<0.0001
Variety × density	3	9.07	7.03	0.0003
Pattern × variety	3	4.46	3.46	0.020

Figure 3 The effects of variety and density on yield for two of the four varieties of spring wheat (*Triticum aestivum*) grown under very high weed pressure (Weiner et al. 2001). Harlekin was the best performer at low density and the worst at high density whereas Jack was worst at low density and best at high density.

Hypothesis: reduced phenotypic plasticity in some traits can increase weed suppression and give higher yields

One hypothesis we have advanced is that certain forms of phenotypic plasticity, which arise through natural selection because they increase individual fitness, can be disadvantageous in controlled plant production systems where it is population and community performance we want to optimize (Weiner 2004). Plants respond to changes in the light spectrum due to shading and even to light reflected by their neighbors before they are shaded (Smith 1982; Ballaré et al. 1994; Ballaré 1999), by changing their growth form (Schmitt et al. 1999) – the well documented 'shade avoidance' response. Cereals, for example, reduce tillering in response to crowding (Evers et al. 2006). A specific hypothesis is that the phytochrome-mediated 'shade-avoidance' response of plants to competition from neighbors, in which plants show increased extension growth at the expense of yield and increased risk of lodging (Sawers et al. 2005), is detrimental to population production (Boccalandro et al. 2003) and weed suppression in cereal crops. Our research on the potential role of increased crop density and spatial uniformity for increasing weed suppression in cereal crops (Weiner et al. 2001; Olsen et al. 2005a,b, 2006; Kristensen et al. 2008), leads to the hypothesis that an offensive, cooperative 'shading' strategy can be much more effective in competition with weeds than the defensive, individualistic 'shade-avoidance'

strategy if cereals are grown in a uniform pattern at high density.

Researchers who investigate plant competition distinguish between two aspects of competition: the competitive effect and the competitive response (Miller and Werner 1987; Goldberg 1990). The competitive effect of a plant on a neighbor is the reduction in resources available to the neighbor due to the plant in question. The competitive response of a plant to its neighbors is its ability to grow, develop and reproduce despite the reduction in resources due to neighbors. In theory, a plant can be a good competitor either by reducing resources available to neighbors greatly, or by thriving despite the low resource levels caused by its neighbors. These abilities do not seem to be positively correlated (Cahill et al. 2005). The goal in our approach is to *suppress* weeds, i.e. maximize the competitive effect of the crop on the weeds. Such an offensive 'shading' strategy would never evolve in nature, because (1) it requires cooperation rather than competition among individuals, (2) 'cheaters' might be favored by natural selection at the individual level, and (3) it requires a high density and a predictably uniform (hyperdispersed) distribution of individuals in space. Viewed this way, weed suppression by a crop population is a 'communal' activity. A single plant cannot suppress its neighbors. This is, in part, why individual selection favors a 'shade avoidance' strategy.

Perspective: Crossing genetic and ecological valleys to reach higher peaks

Agricultural research and evolution are both confronted by the problem that incremental improvements do not always lead towards breakthroughs. To borrow the evolutionary metaphor of the 'adaptive landscape' from one of the 20th century's great evolutionary biologists, Sewall Wright (1932): The different possibilities for production of any specific crop are like a landscape with peaks and valleys (Weiner 2003). Current agricultural production is at or close to a local optimum. Most agricultural research is directed towards approaching ('climbing') this peak. There may be other, even higher peaks, but agricultural research as usually practiced will never discover them, because it does not explore areas far away from the current local optimum. If agricultural researchers are to discover these other possible peaks, we must jump over the 'valleys' in between. This can only be done by investigating radical new ideas, by varying factors and their combinations much more than is usual in current agricultural research. Our hypotheses involve several major, simultaneous changes in crop populations and communities:

1. A major increase in crop density
2. A change in crop spatial pattern from rows to a uniform pattern

3. Highly reduced or no additional weed control measures

In summary, we hypothesize the existence of an unexplored peak in the adaptive agricultural landscape, built around increased crop density, spatial uniformity and tolerance for small, suppressed weeds, which have only minor effects on yield, while increasing sustainability and biodiversity in the field.

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