Opinion

Looking in the Wrong Direction for Higher-Yielding Crop Genotypes

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A misunderstanding of evolution via natural selection has led many plant physiologists and genetic engineers to look in the wrong direction for higher-yielding crop genotypes. Large investments in attempts to make 'better' plants by improving basic physiological processes are not likely to succeed because natural selection has been optimizing these for millions of years. Increases in yield from plant breeding have usually resulted from decreases, not increases, in plant fitness. Examples include reduced plant height and more vertical root growth in cereals. Plant scientists and breeders should generate hypotheses based on what evolutionary biologists call 'group selection', looking for attributes that increase yield in ways that decrease fitness, rather than attempting to improve upon the achievements of natural selection.

Highlights

Increasing crop yields is the Holy Grail for plant breeders.

Evolutionary biology gives us reasons to expect that attempts to increase crop yields by 'improving' plants are not likely to succeed, but this is the objective of much plant research.

Evolution by Natural Selection and Plant Breeding

Much of Darwin's *Origin of the Species* deals with domestication, which in 1859 provided the best-documented examples of selection available at the time. Now, 160 years after the publication of Darwin's book, evolutionary biology is in a position to provide useful guidance for the further development of domesticated species [1,2], specifically higher-yielding crops. Agriculture can be best understood scientifically as a form of ecological engineering: the manipulation of populations, communities, and ecosystems to meet human needs [3–5]. Engineering is most successful when it is based on basic science, and evolutionary biology is the basic science that corresponds to the applied science of plant breeding: change in the heritable characteristics of populations over successive generations.

Evolutionary biology gives us compelling reasons to predict that many of the most ambitious objectives plant breeders and genetic engineers have proposed to increase crop yields are not likely to be successful. There is a fundamental misunderstanding of evolution among many biologists, including plant breeders and genetic researchers, and this misunderstanding has led many plant researchers to look in the wrong direction for higher-yielding genotypes. Many of the most ambitious efforts to increase crop yields have been directed towards making a 'better' (or, in the language of evolutionary biology, a more 'fit') plant. Indeed, many university departments of plant breeding are named 'Department of Plant Improvement'. In this opinion article I argue that, on the contrary, the impressive achievements of plant breeding in producing higher yields to date have not resulted from the development of improved plants, but have resulted from the development of worse (i.e., less 'fit') plants [6], that are better for the very narrow and specific needs of crop production. Although implicit awareness of this has increased in recent years, making this awareness explicit would accelerate progress towards the development of higher-yielding genotypes.

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Individual Fitness versus Group Performance

There are two basic, unappreciated lessons from evolutionary biology regarding plant breeding and/or genetic modification of crops to increase yield. First, natural selection is very powerful

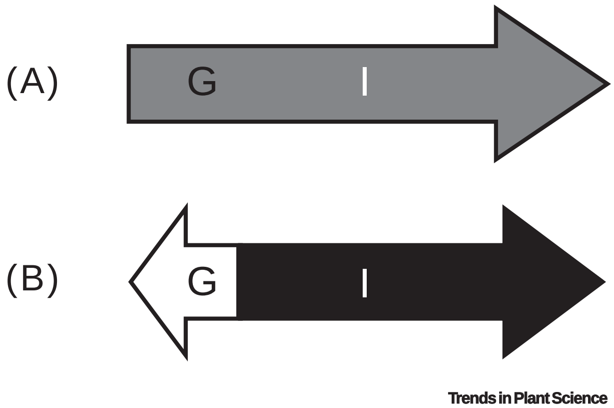

Figure 1. Two Evolutionary Scenarios for Selection at Two Levels. When group selection, G, and individual selection, I, are in the same direction (A), as they are in response to most abiotic factors, it is unlikely that plant breeding or genetic modification can improve upon what natural selection has achieved. When group and individual selection are in conflict (B) because of biotic interactions such as competition, individual selection is much stronger than group selection (arrow length). In this case it is possible for plant breeders and genetic engineers to find group solutions (e.g., increased population yield) that nature would not produce.

when given sufficient time to address problems. Millions of years of evolution have produced extraordinary innovations and brilliant solutions to very general, as well as highly specific, challenges facing organisms. It is highly unlikely that plant breeders or genetic engineers can improve on such evolutionary achievements [7]. We are only likely to do better than nature when we try to do something different from what nature does.

High-yielding crops are not ‘improved’ over their wild ancestors in any general sense. On the contrary, high-yielding crop plants are worsened (i.e., less ‘fit’, one could even say ‘impaired’) in most ways in comparison with wild plants. Most crop plants would die out in a few generations if left to fend for themselves and reproduce in the field in competition with weeds. However, under specific ‘luxury’ conditions created by farmers, some low-fitness genotypes can produce very high population yields, in large part as a result of their lower fitness. High yield comes, in large part, at the expense of fitness, and further yield increases are possible through further reductions in fitness [8,9]. High-yielding crops have reduced ability to compete, to tolerate low-resource or other extreme conditions, and to defend themselves against many herbivores. The farmer’s management ensures that these lost abilities are not needed in the agricultural field, and the resources that would have been used to maintain them can be used to increase the yield.

Second, natural selection promotes individual fitness (individual yield in a plant community), but agriculture is about group performance (i.e., population yield). This difference is profound and represents the most promising opportunity to produce higher-yielding genotypes. In nature, individuals that increase the proportion of their genes in coming generations (i.e., the most ‘fit’) are selected. This does not always improve the performance of the population, however, because ‘selfish’ genes, traits, and behaviors [10], which increase individual fitness by decreasing the performance of other individuals, are selected. The natural world is full of such traits and behaviors, from fighting among males for access to females within an animal population, to plants growing taller than their neighbors or proliferating their roots in the presence of the roots of other individuals [2].

This misunderstanding is summarized in the assumption, implicit in most of the literature on plant breeding and genetic modification, that what is good for the individual (individual selection) is also good for the population (group selection). Although this is true for many traits, there is abundant evidence from the behavior of animals to that of cells within an organism, that many of the attributes that increase individual fitness actually reduce population performance. Those attributes that increase both individual fitness and population performance have already been naturally selected (Figure 1A). Therefore, when the interests of the individual and the population are mutual, it is unlikely that researchers can improve on the achievements of natural selection. By contrast, when group and individual interests are different, it is possible to improve on nature (Figure 1B). This situation often arises in response to biotic selection pressures, especially competition among plants.

Attempting to Improve Plants

Many engineers, architects, and designers are trying to learn from nature, looking for solutions to human challenges by emulating nature's amazing and time-tested solutions, an approach called biomimicry [11]. By contrast, some molecular biologists and plant physiologists believe that they can teach nature some lessons. There are compelling reasons to think that the likelihood of success is very small.

Several years ago there were numerous articles in high-prestige journals claiming that, by increasing the attributes or levels of ribulose diphosphate in plants, we can increase plant growth [12–14]. But if this were the case, it would have evolved in nature. The amount of a specific compound produced by plants is highly evolutionarily labile. Similarly, there have been scores of papers in molecular plant journals showing that the introduction or inactivation of specific genes can increase the growth of cells in the laboratory, and predicting that this will result in a larger and higher-yielding plant. In every case there were unforeseen tradeoffs (often described as 'downregulation' of the process the researcher was trying to increase), such that the laboratory results do not 'scale up' to the whole plant, yet alone to the population level, under field conditions [15].

The clearest, although by no means the only, current example of an attempt to improve plants is the millions of dollars and Euros being invested in research to improve photosynthesis in crop plants through genetic manipulation. Photosynthesis in plants is very inefficient, converting only a small percent of the solar energy into chemical energy, and many plant molecular biologists and biochemists think it could be higher. The richest of all funding agencies, the Gates Foundation, has the improvement of crop photosynthesis as a goal, and US and EU granting agencies have also been funding such efforts. There are compelling reasons to think that these efforts are unlikely to succeed. The light-requiring reactions of photosynthesis have been under natural selection for over three billion years, and all photosynthetic organisms employ the same basic reactions, referred to as type I and II reaction centers [16]. Any organism that discovered a better method for capturing light energy to be used for fixing CO_2 would have had a huge fitness advantage.

It is possible that photosynthetic mechanisms have been evolutionarily/historically constrained, and that natural selection has never been offered an opportunity to overcome such constraints because the genes or gene combinations necessary were not available. This is conceivable, but seems unlikely given the power of evolution via natural selection to achieve the many wonders of the biological world. The most likely explanation for why the light-energy capturing reactions are basically the same in all photosynthetic organisms is convergence: it is the best possible solution for organisms.

It is also possible that the environment in an agricultural field is sufficiently different from that in nature, that even basic processes such as photosynthesis have not been optimized for this relatively new environment. It is certainly the case that a modern agricultural field represents a very different environment than that in which plants evolved, and that many traits inherited from nature will not be optimal in this new environment. Indeed, much plant breeding has been about adapting crop plants to agricultural environments [17], such as breeding crop plants that can use unnaturally high resource levels in agricultural fields to produce unnaturally high yields, or the breeding of maize to grow in cooler climates. However, if we look at the 'wild' plants growing in agricultural fields (i.e., weeds), we see no evidence of changes in basic plant processes from their origins in nonagricultural environments. The difference between a grassland and an agricultural field is in all likelihood not so great that it would lead to the evolution of different basic processes such as photosynthesis or respiration. Rising CO_2 levels have also been cited as a change in the environment which could result in a new optimum for basic physiological processes [18]. Again, this is not inconceivable, but unlikely. Predicted changes in atmospheric CO_2 in the coming decades are not so great that one would expect the evolution of changes in basic photosynthetic processes. CO_2 levels have been much higher in the geological past than they will be in the coming decades, and there are naturally occurring places on earth that have had very high CO_2 levels for thousands of years [19], but there is no evidence that photosynthetic pathways and reactions were different in these periods or places.

One of the most important sources of the inefficiency of photosynthesis in plants is photorespiration, a reaction in which much of the energy captured is lost immediately. Several plant physiologists have suggested that crop production can be increased by removing photorespiration [20]. Many plants have evolved a way to avoid photorespiration: the C4 carbon-fixation pathway. But C4 photosynthesis is not a general 'plant improvement', or all plants would be C4. It has disadvantages as well as advantages, and the majority of plants, including crop plants, are C3. C4 photosynthesis is advantageous in some environments and not in others. A recent study [21] introduced alternative pathways for C3 plants to avoid photorespiration, and showed increased early growth in one line, but, as the authors state, it remains to be shown whether this will result in higher crop yields. Nowhere in their report do the authors ask the question of why this innovation never evolved in nature, whereas the C4 pathway has evolved numerous times in different lineages.

It is likely that photosynthesis can be made more efficient if performed outside of plants. When photosynthesis researchers succeed in developing methods to harness light energy and build high-energy molecules in the laboratory, such technology will eventually produce much higher efficiency than can be achieved by plants, because industrial processes do not have the same constraints as organisms, which have many other needs to fulfill. Such efforts are well underway (e.g., [22]).

My argument applies to all efforts to increase total plant biomass production in the field. Because growth (i.e., biomass production) is so fundamental for plants, natural selection has resulted in plant communities that tend to maximize biomass production in their environment if plant density is sufficiently high [23]. We can breed individual species or cultivars to be larger or smaller, but if we look at plant communities in the field, immigration and natural selection together will tend to maximize biomass production for any given combination of resources and conditions. For example, without any control measures, locally adapted weed communities will reach very high densities and produce as much biomass as the crop, but this is not the biomass that farmers and consumers want. The belief that genetic engineering of plants can increase plant biomass production in deserts or high-salt environments is unwarranted. Any plant that could grow and produce high biomass in a desert would have been selected millions of years ago. Similarly, the idea that researchers can invent new mechanisms for drought or salt tolerance that natural selection has not discovered is highly unlikely. Genetic engineers can move the genes for salt or drought resistance from wild plants to crops, but the idea that plant researchers can develop new mechanisms that nature has not found seems unlikely.

One should never say 'never' in evolutionary biology, and there is a small, unknown probability that researchers can improve on millions of years of natural selection. I am simply arguing that much of the money, time, and brain power being invested to 'improve' plants would be better used looking in the opposite direction: plants that are impaired, but in ways that produce high yields under agricultural conditions.

There are conceivable scenarios in which researchers could improve basic plant processes. First, the utilization of novel resources that are not available in nature. For example, if researchers develop an improved photosynthetic pathway or a new mechanism for drought or salt tolerance in the laboratory, and this pathway requires a cofactor that is not available in the field but could be added in fertilizer, this would be something natural selection has never had an opportunity to try.

Second, a major change in the environment that makes current genetic material unadapted. This is the argument used by many 'plant improvers', and it is correct to point out that many of the differences between older and newer varieties are due to artificial selection for specific agricultural environments. Nevertheless, it is not likely that the high resource levels of agricultural production are sufficiently different from those found anywhere in nature that improvements in basic plant processes are possible.

Third, a major reorganization of plant structure or cells beyond microevolutionary genetic changes. There is evidence that the eukaryotic cell arose from a symbiosis between prokaryotes only once in evolutionary history [24,25]. This is a clear example of historical constraints on evolution. At some point in the future, such a major re-engineering of plant cellular organization by researchers may be possible, but this is very different from the adding or disabling of specific genes, as current research is attempting. It is also a very distant goal at this point.

An Alternative to 'Plant Improvement': Group Selection

If the Dean of an agricultural university were an evolutionary ecologist, she might be tempted to rename the plant breeding department the 'Department of Plant Tradeoffs'. Plant breeders and plant physiologists understand many tradeoffs. For example, breeders working on increasing a specific quality of yield (e.g., taste or nutritional value) understand that there will in all likelihood be a cost in yield quantity, or that drought resistance will involve a reduction in yield potential [26]. However, the tradeoff between individual performance ('fitness') and population performance (yield per unit area) is not yet widely recognized. I predict the appearance of exciting new hypotheses for breeding/genetic modification to increase crop yields as this becomes understood and appreciated (see Outstanding Questions).

Natural selection can, in principle, occur at different levels of organization [27]. Over the past 50 years there has been a lively debate among evolutionary biologists about whether natural selection occurs at the group or population level, as well as at the individual/kin level [28–31]. Can a trait that reduces individual fitness, such as altruistic behavior, evolve and be maintained because groups that have it tend to persist, whereas populations of 'selfish' individuals become extinct? Although a small minority of evolutionary biologists argue that such 'group selection' can overwhelm selection at the individual level when these are in conflict [30,31], most are convinced that individual selection will always or almost always overwhelm group selection (Figure 1) because of simple mathematics: there are many more individuals than groups [28,29]. When 'selfish' genes appear within an altruistic population, they will spread within the population, even if they increase the likelihood that the population will go extinct.

The difference between individual and group selection has been a practical problem for plant breeding because individual plants growing in competition are often screened and selected, especially at the early stages of screening. Such individuals are likely to have 'selfish' traits and

Outstanding Questions

What attributes and behaviors of plants are 'selfish' and increase individual fitness but reduce population performance?

Can we remove or reduce such attributes and behaviors without damaging plant performance in other ways?

What tradeoffs are necessary to achieve higher yields?

How much risk is acceptable to achieve higher yields in a given agricultural context?

How can plant breeders practice group selection without using thousands of plots?

behaviors that can reduce population yield. But the difference between individual and group selection also provides an opportunity to improve on nature. Evidence is accumulating that many of the successes in plant breeding for higher yields have been due to inadvertent group selection [32]. The best-documented example of this is the reduction in the height of cereals. C.M. Donald, one of the greatest agronomists of the 20th century, pointed out that the major innovation in cereal breeding, which was the basis of the 'Green Revolution' of the 1960s, was the development of shorter varieties [33]. A tall individual in a stand will have higher yield than shorter individuals if there is competition for light. But population yield will be higher if all individuals are short, because there is a cost to being a good competitor, in this case the structural cost of being tall. If all individuals are tall, the whole population pays this cost. If all individuals are short, all have more resources to invest in yield formation. Decreased competitiveness is a hallmark of high-yielding crop varieties [34–40]. Similarly, it has been argued [41] that some forms of phenotypic plasticity, such as the 'shade-avoidance response' [42,43] or root proliferation in response to neighboring roots [44], are 'selfish' and disadvantageous in crop production.

Unfortunately, Donald's concept of the 'communal plant ideotype' [33] was interpreted far too narrowly by plant breeders: only in terms of plant height. Metaphorically, one could say that crop plants can be too 'tall' in ways other than height. For example, land races of spring wheat grown in western China at the end of the 19th century through to the first decades of the 20th century show highly branched root systems with much lateral spread close to the soil surface [32]. Such a rooting pattern is advantageous for individuals in obtaining water from recent precipitation events or melting snow, and in competing with neighbors for this water. Newer, higher-yielding varieties have root systems that are more vertical, with fewer branches, thereby reducing competition for water near the surface while increasing access to previously unutilized water deeper in the soil. If maximizing individual performance is the goal, as in nature, the best strategy is to go after and compete for water near the surface. If maximizing population performance is the objective, as in agriculture, then the best strategy is to reduce competitive behaviors and increase access to un- or underutilized resources.

Some will say that my argument is simply a semantic point about the word 'improvement' (improved in nature vs improved for agriculture), but I think the word reveals the misunderstanding of evolutionary biology that underlies the approach I am criticizing. More progress is likely if plant physiologists and geneticists think in terms of 'tradeoffs' rather than 'improvements' [8]. Plant breeders have been doing this unconsciously, but they could do it better consciously. In any given situation, there will be an optimal individual strategy, which will be favored by natural selection, and an optimal collective strategy, which will be best for agriculture. These will not be the same unless there is no competition among crop plants [9].

In conclusion, when considering specific proposed breeding/genetic engineering objectives to increase yield in a highly domesticated crop, I suggest that plant breeders and genetic engineers ask the question – would this proposed breeding objective increase the performance (fitness) of an individual plant under field conditions? If the answer to this question is yes, evolutionary biology gives us reasons to think that it is unlikely to succeed. If the answer is no, the objectives may be much more promising.

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