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DARWINIAN AGRICULTURE: WHEN CAN HUMANS FIND
SOLUTIONS BEYOND THE REACH OF NATURAL SELECTION?

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*We have seen that man by selection can certainly produce great results, and can adapt
organic beings to his own uses, through the accumulation of slight but useful variations,
given to him by the hand of Nature. But Natural Selection, we shall hereafter see, is a
power incessantly ready for action, and is as immeasurably superior to man's feeble
efforts, as the works of Nature are to those of Art (Darwin 1859:76).*

abstract

Progress in genetic improvement of crop yield potential has slowed since 1985. Simultaneously, more sustainable management of agricultural ecosystems is needed. A better understanding of natural selection can help solve both problems. We illustrate this point with two specific examples. First, the genetic legacy of crop plants has been refined by millions of years of natural selection, often driven by competition among plants. We therefore suggest that most simple, tradeoff-free options to increase competitiveness (e.g., increased gene expression, or minor modifications of existing plant genes) have already been tested by natural selection. Further genetic improvement of crop yield potential over the next decade will mainly involve tradeoffs, either between fitness in past versus present environments, or between individual competitiveness and the collective performance of plant communities. Eventually, we may develop the ability to predict the consequences of genetic alterations so radical that they have not yet been tested by natural selection. Second, natural selection acts mainly at the level of genes, individuals, and family groups, rather than ecosystems as a whole. Consequently, there is no reason to expect the structure of natural ecosystems (diversity, spatial, or temporal patterns) to be a reliable blueprint for agricultural ecosystems. Natural ecosystems are nonetheless an important source of information that could be used to improve agriculture.

A DECADE AGO, Williams and Nesse (1991) proclaimed "The Dawn of Darwinian Medicine" and applied modern evolutionary theory to problems ranging from human aging to the evolution of virulence in pathogens. Here we discuss ways in which agriculture might also benefit from a greater understanding of natural selection. Darwin (1859) used examples from plant and animal breeding in developing his theory of natural selection, and there have been some worthy analyses of agricultural problems from a Darwinian perspective. Natural selection is often ignored or misunderstood in agricultural research, however. This is unfortunate because in agriculture, as in medicine (Williams and Nesse 1991) and biology generally (Dobzhansky 1973), there is much that makes sense only in the light of evolution.

The evolution, in agricultural pests, of resistance to pesticides and nonchemical control methods has already received much attention (Barrett 1983; Alstad and Andow 1995; Heap 1997) and is not the focus of this review. Instead, we consider the implications of past natural selection for crop genetic improvement and for the overall design of agricultural ecosystems.

We present two main hypotheses. Our first hypothesis is that natural selection had ample opportunity, before the wild ancestors of our crops were domesticated, to test alternative solutions to problems that limited individual fitness under preagricultural conditions. Plant traits such as efficient enzymes, competitiveness, stress tolerance, and any broad-spectrum defenses against pests would have consistently conferred individual fitness (survival and reproduction relative to alternative genotypes) in preagricultural environments, so further improvement of these traits is likely to be difficult. Instead, opportunities for further genetic improvement of crop yield will mainly involve tradeoffs between plant adaptation to agricultural versus natural conditions, or between the competitiveness of individual plants and the collective performance of plant communities. Breeding crops resistant to evolving pests will continue to be an important ongoing activity, as will breeding to accommodate changing consumer preferences.

Our second main hypothesis is that natural selection is the only reliable source of improvement (by any definition relevant to agriculture) in natural ecosystems that operates on a time scale longer than the lifetime of individual plants. Natural selection acts at the level of genes, individuals, and family groups, not communities and ecosystems. Therefore, our second main hypothesis is inconsistent with the suggestion (Soule and Piper 1992; Lefroy et al. 1999) that agricultural ecosystems whose structure (species composition, spatial and temporal patterns) is based on natural ecosystems will be consistently more efficient, sustainable, and productive. Although this hypothesis rejects mindless mimicry, natural ecosystems, properly understood, are nonetheless a valuable source of ideas for agriculture.

Implicit in these hypotheses is the need to determine when natural selection has acted in ways congruent with human goals, and when it has not. If a plant trait has already been improved (by human criteria) through millions of years of natural selection, there may be little opportunity for further improvement of that trait through either traditional or molecular plant breeding. But when past natural selection and present human goals conflict, it may be possible to improve on nature. For example, crops may be improved by deliberately reversing the negative effects of past natural selection on the collective performance of plant communities. Similarly, we may be able to design agricultural ecosystems that maximize resource-use efficiency or control pests in ways not seen in natural ecosystems. A consideration of natural selection can explain past successes and predict which approaches are most likely to succeed in the future.

Hypothesis 1 and Crop Improvement

Over the last 10,000 years, humans have made substantial genetic improvements in crops, by human criteria. Modern cucumbers (*Cucumis sativus*), for example, are less bitter and therefore more palatable to humans (and to some pests), but our emphasis here is on crop yield. Yield potential—i.e., production of the harvested product per unit area, with adequate water and nutrients and in the absence of pests or disease (Evans and Fischer 1999)—has increased roughly twofold for wheat (*Triticum aestivum*), rice (*Oryza sativa*), and maize (*Zea mays*) since 1930 (Jennings and de Jesus 1968; Ortiz-Monasterio et al. 1997; Duvick and Cassman 1999). We suggest that virtually all of this progress in yield potential has, often unknowingly, exploited tradeoffs between individual plant competitiveness versus plant community (i.e., crop) performance, or between fitness in past (including preagricultural) versus present environments.

Our first main hypothesis implies that crop geneticists are unlikely to improve on natural selection anytime soon in solving those problems that have limited the fitness of individual plants for millions of years. More recent problems, or cases in which yield or other factors of value to humans lack a positive correlation with individual fitness, offer more opportunities for improvements. Leading crop physiologists have made various statements consistent with this hypothesis. Loomis (1993) suggested that "natural selection has already found efficient solutions to traits such as photosynthesis that lend *individuals* success in competition with their usual neighbors" (p 584). Similarly, Evans (1993) wrote that photosynthesis "has been subject to intense and prolonged natural selection and plant breeders have yet to improve upon it" (p 186).

Although our first hypothesis does not exclude the possibility of substantial increases in yield potential, we tend to agree with the prediction attributed to Donald Duvick, a senior statesman of plant breeding, that new molecular methods alone "will not produce sharp upward swings in yield potential except for isolated crops in certain situations" (Brown and Kane 1994:25), at least for the next decade or two. This contrasts with optimistic statements from some biochemists (Zelitch 1992), molecular biologists (Ku et al. 2000), and biotechnology enthusiasts (Conway 1998).

Before discussing the evidence for our first hypothesis, and its implications for crop genetic improvement in the future, we will consider recent progress in genetic improvement of crop yield potential. We emphasize the grain crops upon which most humans rely, directly or indirectly, for most of their dietary protein and energy, although our broader hypotheses also apply to horticultural crops and domesticated animals.

yield potential of major crops since 1985

World grain yields per unit area increased 26% between 1965 and 1975, and 31% between 1975 and 1985, but only 9% between 1985 and 1995 (Brown et al. 1998). Changes in global markets can affect total production, but do not explain the slower growth in yield per unit area. As a result of continuing population growth, grain production per person fell more than 10% between 1985 and 1995. Some combination of decreased population growth, more equitable distribution, and increased crop yields will be needed to

improve food security without additional expansion of the land under agricultural production. Most ecologists are opposed to major expansion of agricultural land area, which would likely involve draining wetlands or clearing tropical forests. What then are the prospects for further yield increases?

Even the slow yield increase since 1985 largely reflects more widespread adoption of the best available cultivars and other technologies (such as fertilizer) developed prior to 1980. Countries such as Korea, which had already adopted these technologies by 1980, have achieved little or no increase in yields since then (Cassman 1999). Any substantial increase in world food production will therefore require increases in crop yield potential, which sets an upper limit on the yields that even the best farmers can obtain.

Measuring progress in genetic improvement of yield potential is not simple. In a direct comparison of crop cultivars developed over a period of decades, IR8, an early Green Revolution rice cultivar released in 1966, yielded about 7,000 kg/ha, whereas the highest-yielding cultivar tested, released 30 years later, yielded almost 10,000 kg/ha (Peng et al. 1999). Peng et al. noted, however, that yields of 9,000 to 10,000 kg/ha were reported for IR8 in the 1970s. Yield declines for IR8 over the last 30 years presumably reflect evolution of pest and pathogen populations. These data therefore provide little evidence for real improvement in yield potential. Hybrid rice may offer some yield advantages, but it is unlikely to repeat the yield advances of the Green Revolution. On average, hybrid rice cultivars may outyield inbred (i.e., non-hybrid) cultivars by 9% or so (Peng et al. 1999), but in one two-site comparison, the hybrid cultivar that yielded best in China had yields identical to a good inbred, when tested in the Phillipines (Ying et al. 1998).

Reviewing similar data and results from yield contests, Cassman (1999) concluded that for "tropical rice and temperate maize . . . there has been no detectable increase in yield potential" in recent years. Similarly, an analysis of yield trends for wheat in Mexico found an increase of "0.9% y^{-1} . . . for cultivars released from 1960–1981 [still less than population growth], and zero for the period

1981–1988" (Bell et al. 1995:60). Although not all assessments are this pessimistic, it is clear that progress in yield potential during the past 20 years was much slower than in the previous 20. For example, a yield increase of 9% from hybrid rice would be less than one-third of the 31% increase achieved with inbred rice during the decade from 1975 and 1985 (Brown et al. 1998).

Why has yield potential stagnated? What was the basis of past progress? What approaches offer the greatest hope for further progress? To answer these questions, we need to consider the relative merits of human ingenuity and natural selection.

THE POWER AND LIMITATIONS OF NATURAL SELECTION

Natural Selection Vs. Human Ingenuity

The superiority of natural selection to human ingenuity can be illustrated by a brief excursion into engineering. A recent example is the successful development of enzymes made from DNA, which may be valuable in medicine (Santiago et al. 1999). Most enzymes in nature are made from protein and a few from RNA, but no one knew how to design an enzyme made from DNA. Instead, Breaker and Joyce (1995) generated $>10^{13}$ randomly varying DNA molecules and devised an automatic selection regime (not involving evaluation by humans) whereby only those DNA sequences with the greatest ability to catalyze the target reaction were retained from one "generation" to the next. Significant enzyme activity was obtained in six rounds of selection, and a useful enzyme was produced after adjustment of the selection process and an additional seven cycles of automated selection. An analogous process was recently used to simulate the evolution of crawling robots (Lipson and Pollack 2000). The resulting designs were built, and performed as predicted.

The growth of biomimetics (Ball 2001) and evolutionary computation (Harik et al. 1999) reflect increasing recognition by engineers of the limitations of human imagination, relative to natural selection and analogous processes. An optical computer mouse based on visual information processing in honeybees

(Giles 2001), drag-reducing coatings that mimic the tiny ribs on shark skin (Ball 1999), fracture-resistant composite materials based on conch shells (Kamat et al. 2000), and polarized image systems that work in muddy water (Rowe et al. 1995) are a few recent examples of reverse-engineering by humans of natural selection's inventions.

Agricultural Examples of Natural Selection

The rapid evolution of weedy grasses illustrates the power and rapidity of natural selection in improving the adaptation of plants that, like crops, are adapted to agricultural environments. Evolution of herbicide resistance, sometimes in as little as four years (Hill et al. 1994), may involve relatively simple genetic changes, comparable to those being introduced into transgenic crops. But other adaptations are more sophisticated than those typically attempted by molecular biologists today.

A prostrate foxtail (*Setaria lutescens*) ecotype survives in frequently harvested alfalfa fields by keeping much of its leaf area below the cutting height (Schoner et al. 1978). Barnyardgrass (*Echinochloa crus-galli)* has adapted to temperature conditions from Quebec to Mississippi in less than 300 years (Potvin and Simon 1989). Flooding-tolerant watergrass (*Echinochloa* sp.) and flooding-intolerant barnyardgrass are believed to have a recent common ancestor. Hand weeding by humans over hundreds of years imposed strong selection on watergrass—seedlings that can be confused with rice are less likely to be killed—but it is still remarkable that watergrass evolved to resemble traditional rice cultivars in physical appearance (based on a multivariate analysis of 15 quantitative characters) more than it does barnyardgrass (Barrett 1983). Would crop molecular geneticists have known, in advance, what genes to transfer to achieve these phenotypes? If we are unable to duplicate what natural selection has done over decades or centuries, it may be overoptimistic to assume that we will soon solve problems that natural selection has been working on for millions of years. Of course, evolution of weeds also illustrates the important point that utility to humans is not a criterion for natural selection.

Natural Selection Does Not Share Our Goals

Given the power of natural selection, it might seem that we could rely on natural selection to further improve crop yield potential. This approach would be effective only to the extent that traits conferring individual fitness also increase crop yields.

We suggest that the wild ancestors of crops were already well adapted, perhaps nearly optimal (Williams 1992), with respect to any traits whose effects on individual fitness were fairly consistent across the range of environments to which they were exposed. We do not necessarily expect optimality (even in terms of individual fitness) in new or variable environments, but we do assume "convergence to an optimum or an evolutionarily stable strategy" when "the regime of selection acting on the trait . . . remains invariant" (Eshel and Feldman 2001:186). For example, we assume that natural selection has always favored more efficient enzymes, because they would consistently have enhanced competitiveness, but that rooting patterns of some crops may not yet have adapted fully to the higher soil nitrogen typical of modern agriculture.

Simply allowing natural selection to operate under agricultural conditions (by sowing a random subset of seed harvested the previous year) can improve adaptation to local biotic, and especially abiotic, conditions. If local adaptation is initially poor, as may be the case when a cultivar is grown in a new environment, then natural selection, operating on a genetically diverse population, can increase yields significantly over a few generations (Suneson 1956).

But Suneson's (1956) "evolutionary plant breeding method," also popularized by Allard (1988), has never resulted in cultivars that outyield the best modern cultivars developed through human selection. For example, a mixture of barley lines, subject to 45 generations of natural selection under agricultural conditions, had only 85% the yield of a commercial cultivar (Soliman and Allard 1991), even when grown in narrow (four-row) plots. Due to interactions with neighbors, narrow plots tend to overestimate the relative yield of the more competitive genotypes favored by natural selection (Fischer 1978). Gustafsson (1951) summarized studies dating back to

1912 that showed that the genotypes that increase in frequency under natural selection imposed by intraspecific competition are not necessarily those that maximize yield per unit area. Earlier, Suneson and Wiebe (1942) suggested that natural selection can be useful in improving adaptation to cold and disease, but pointed out that "in the absence of such factors valuable material is likely to be lost as a result of competition" (p 1052). Similarly, Jennings and Aquino (1968) identified selection for competitive ability as "a basic cause of limited breeding advance in most tropical improvement programs" (p 541). Natural selection is powerful, but it will not select for community performance (e.g., higher seed or biomass yield per unit land area) when this conflicts with individual competitiveness. Only humans can do that.

If our first major hypothesis is true, then opportunities for improving crop yield potential may lie mainly in exploiting tradeoffs rather than simply the "continuation of crop evolution by other means" suggested by Simmonds (1979:v), at least if the latter implies continuation in the same direction. Simmonds probably did not intend to imply that plant breeding continues evolution in the same direction as natural selection, however, as most of his examples of changes that occurred during crop domestication, including reduced height, less branching, elimination of toxins and spines, nonshattering (reduced seed dispersal), and reduced seed dormancy, would have been opposed by natural selection in preagricultural environments.

If natural selection had ample opportunity, before the wild ancestors of our crops were domesticated, to test alternative solutions to problems that limited individual fitness under preagricultural conditions, then crop geneticists will be unable to beat natural selection at its own game anytime soon. The problem is not a lack of genetic variability; any large population will vary. The problem, for traits that would enhance both crop yield and individual plant fitness, is that rare variants remain rare precisely because they are less fit. Natural selection has never had maximizing the oil or protein content of seed as a goal, so it is not surprising that there has

been prolonged response to directional selection by humans for these traits (Dudley and Lambert 1969). Similarly, selection by humans can alter the balance between vegetative and reproductive growth away from that favored by natural selection, in order to favor seed production in grain crops or biomass production in forage crops or trees grown for biomass. However, as discussed below, many of the improvements suggested by molecular biologists involve traits that have already been subject to long-term improvement by natural selection and are currently under stabilizing selection.

Even with molecular tools, "magic is unlikely" (Simmonds 1998:139). However, that still leaves the following nonmagical avenues for genetic improvement of crop yield:

1) Red Queen breeding (keeping ahead in evolutionary arms races with pests).

2) Accelerating adaptation to new physical or chemical conditions (e.g., different climates or greater soil fertility).

3) Reversing the effects of past natural selection for traits that enhance individual competitiveness but limit community-level performance, either through deliberate selection of less competitive plants with specific traits or through human-mediated group selection.

4) Eventually, perhaps, designing truly novel phenotypes not previously tested by natural selection.

These approaches will be discussed, in order. But first, we explain why, even with new molecular tools, the problems that natural selection has been unable to solve over millennia will not easily be solved by humans.

"MAGIC IS UNLIKELY"

With molecular methods, it is now feasible to make minor genetic changes in specific genes of many crop plants. However, any new phenotype that could be achieved through minor genetic changes—usually there will be many routes to the same phenotype—is likely to have been tested by natural selection repeatedly in the past. Therefore, any minor changes that would consistently have improved individual competitiveness in pre-

agricultural environments (e.g., tradeoff-free improvements in photosynthesis) will already have been incorporated by natural selection. Minor changes will therefore contribute to yield potential only in cases involving tradeoffs between past natural selection and present human goals, as discussed below.

Major genetic changes may not have been tested by natural selection (at least in ancestors of a particular crop), so we cannot exclude the possibility that some major changes would increase yield potential. Making major changes at random will almost always decrease yield potential, however. Predicting the effects of any specific major genetic change is far beyond our current abilities, so we do not expect major genetic changes to contribute to crop yield potential anytime soon. A standard for distinguishing between minor and major changes is proposed below.

Minor Changes

So long as we are limited to minor variations on existing genes, we are tinkering, not engineering. By "tinkering" we mean such minor changes as: 1) modifications of the active site of key enzymes, hoping to improve efficiency; 2) overexpressing one or more enzymes believed to limit crop yield potential; or 3) converting an existing inducible gene to constituitive expression.

Trial-and-error tinkering is also the mainstay of natural selection (Jacob 1977), but natural selection has already tested incomparably more variants than any conceivable research program. "How fleeting are the wishes and efforts of man!" wrote Darwin (1859), "[H]ow short his time! and consequently how poor will be his results, compared with those accumulated by Nature during whole geological periods!" (p 94).

Major Changes

It is at least conceivable that there could be a radically different genotype, produced through major genetic modification, that would outperform any genotype that exists today. If every evolutionary path to this hypothetical genotype would require many successive mutations, some of which would significantly reduce fitness, then the improved genotype might never evolve through natural selection, despite its ultimate superiority.

How novel does a genotype need to be before we can reasonably entertain the possibility that it, or other genotypes giving similar phenotypes, have not already been tested by natural selection? The evolution of C4 photosynthesis from conventional C3 photosynthesis may be a useful standard against which the complexity of other genetic changes may be compared.

C4 photosynthesis is a complex adaptation. C4 plants have evolved sophisticated CO_2-concentrating mechanisms that can increase photosynthesis and essentially eliminate losses to photorespiration, which significantly reduces net photosynthesis in C3 plants. In C4 plants, the initial uptake of CO_2 is by phosphoenolpyruvate carboxylase rather than rubisco, the usual CO_2-fixing enzyme. The initial product is a four-carbon molecule (hence the name "C4") such as malate. Malate is transported to the interior of specialized structures known as bundle sheaths, where it is decarboxylated to release CO_2. Suberin layers prevent the CO_2 from leaking out again. Rubisco is concentrated inside the bundle sheaths, where elevated CO_2 concentrations increase its efficiency.

If C4 photosynthesis had only evolved once or twice, then we could speculate that it was but one of a large number of possible improvements on conventional C3 photosynthesis. In that case, it could be reasonable to look for an even better solution. But C4 photosynthesis, with minor variations, has evolved (and persisted) at least 31 separate times (Kellogg 1999). This is a conservative estimate, since it is not known how many times a C4 variant arose, only to die out in competition with C3 conspecifics. For example, C4 photosynthesis may be less beneficial under flooded conditions (Sage 2000). The fact that natural selection keeps finding variations on this same solution suggests that any better solution is even more different from C3 and C4 photosynthesis than they are from each other. If so, then any change in a plant's photosynthetic system less radical than C4 photosynthesis is unlikely to improve yield potential.

The repeated evolution of C4 photosynthe-

sis "provides very strong support for the argument that evolution of Rubisco has reached a barrier" (Long 1998). Long went on to argue, however, that the rubisco found in Rhodophyta is significantly less prone to photorespiration than that found in angiosperms. Given that the homology between these two rubiscos is only about 50%, it is conceivable that Rhodophyta rubisco is a solution that was never tested by natural selection in the immediate ancestors of crops. We suggest, however, that even such a major change to rubisco would evolve more easily (in terms of the number of intermediate genotypes and their relative fitness) than would the entire C4 system. Furthermore, there appear to be significant tradeoffs between the specificity of rubisco for CO_2 (reducing losses to photorespiration) and its specific activity (see Table 1 of Uemura et al. 1997). We therefore doubt that Rhodophyta rubisco represents a real opportunity to increase crop photosynthesis, but agree that it might be worth trying. On the other hand, we think it is safe to assume that any proposed change much less radical than C4 photosynthesis or Rhodophyta rubisco is likely already to have been tested and rejected by natural selection.

Designing Truly Novel Genotypes

Designing truly novel genotypes is beyond our current abilities. Berry (1975:649) noted that the repeated evolution of C4 photosynthesis and the difficulty of breeding new C4 plants in the lab "illustrates the massive difference in scale between the processes of nature and laboratory efforts at genetic manipulation" (p 649). Given the biochemical and anatomical complexity of this adaptation, converting a C3 crop to a C4 would be difficult or impossible with current molecular technology. Similarly, actually designing an improved rubisco (as opposed to just tinkering with it) would be impossible today.

So far, we cannot even predict the tertiary structure of an enzyme, much less its activity, from its sequence, except by comparison with similar enzymes. Most of the antibiotics we use are just copies, often with modifications, of those fungi and bacteria use to kill each other. Designing a new photosynthetic enzyme that would outperform those in existing plants

would be much more difficult than designing a new chemical to interfere with bacterial cell wall synthesis.

True genetic engineering will also require an ability to predict the overall phenotypes of genotypes substantially different from any that have previously existed. Random genetic changes, whether the result of mutation or genetic manipulation by humans, will rarely be beneficial. Predicting which major genetic changes will increase crop yield potential is well beyond our current capabilities. Although there have been post hoc attempts to explain the near-normal phenotype of genetically modified mice without myoglobin (Garry et al. 1998; Gödecke et al. 1999), nobody would have predicted this result in advance. Predicting the effects of genetic modification on crop yield potential will be equally difficult.

We doubt whether today's molecular biologists could even duplicate, by gene transfer, what has already been achieved, through selection, by traditional plant breeders. Could they, for example, convert wild kale (*Brassica* sp.) into cauliflower without using genes from cauliflower?

Can Rice Photosynthesis Be Improved?

As an example of the limitations of human tinkering, consider current attempts to develop rice with the photosynthetic potential of C4 crops. Ku et al. (2000) transferred the gene for phosphoenol pyruvate carboxylase (PEPC) from maize to rice, hoping to achieve some of the ability, in C4 maize, to concentrate carbon dioxide and thereby increase photosynthesis. Tests found, however, that "photosynthetic CO_2 assimilation of transgenic rice decreased with increasing PEPC activity" (Matsuoka et al. 2000:173), consistent with our hypothesis that photosynthetic traits are under stabilizing selection. Ku et al. nonetheless claimed a significant increase in rice yield, which they attributed, post hoc, to greater stomatal conductance.

Increasing stomatal conductance has in fact been an important contributor to increased yield potential in irrigated wheat (Amani et al. 1996) and cotton (Cornish et al. 1991). Greater stomatal conductance increases photosynthesis, but also transpira-

tional water loss from leaves, a tradeoff which may be beneficial in irrigated agriculture but not in dry, unpredictable environments. Rice has been grown under irrigation for thousands of years, however. Greater stomatal conductance is a trait that could presumably be achieved through many different simple genetic changes that would increase either stomatal opening or number. It therefore seems safe to assume that mutants with greater stomatal conductance have occurred repeatedly among the ancestors of present-day rice cultivars. Presumably, natural selection has already tested a wide range of stomatal strategies, i.e., genetically determined rules that adjust stomatal number and opening appropriately for the range of conditions to which rice was exposed. We consider it unlikely that a single gene that causes a constituitive increase in stomatal conductance would improve on these strategies.

We are therefore skeptical of claims that rice that contains a single maize gene has 30–35% higher yield (Ku et al. 2000). We predict that independent tests in several countries, in plots large enough to avoid edge effects, would fail to confirm that this transgenic rice significantly outyields the best locally adapted cultivars.

Eventually, it might be possible to transfer the entire C4 system to rice, as proposed by Sheehy (2000) and others. By the standard of the previous section, this might meet the minimum requirements for a novel phenotype not previously tested by natural selection. Given the frequency with which C4 photosynthesis has evolved, it is not clear whether C4 rice is an untested variant, or one that has already been tested and rejected by natural selection. Even assuming that C4 rice would have higher yield, developing it would be a long-term enterprise, beyond our current scientific and technological abilities. Meanwhile, further increases in atmospheric CO_2 during the course of this project would tend to reduce the photosynthetic advantage of C4 rice relative to C3 rice (Sage 2000).

WHAT HAS WORKED

If natural selection had millions of years, prior to crop domestication, to improve plant traits that enhance individual fitness, how can we explain the dramatic progress made by plant breeders? What additional opportunities remain?

Past progress in genetic improvement of crops has usually either sacrificed individual plant fitness in the pursuit of human goals (e.g., better flavor or higher yield per unit area), or dealt with traits whose fitness consequences under present agricultural conditions are different from those in the past. For example, natural selection will have improved some aspects of pest resistance, but will not have generated defenses specifically targeted against pests to which the ancestors of a crop have not been exposed.

Red Queen Breeding

The arms race (Dawkins and Krebs 1979) between plants and pests predates agriculture. Effective pest control is not a substitute for increases in yield potential, but it is essential to achieving that yield potential. Plant breeders make major contributions to yield by developing crops resistant to current pests. As pests continue to evolve and new pests arrive from other parts of the world, breeders race to develop cultivars resistant to the new pests. Lewis Carroll's Red Queen described the dilemma perfectly: we must run as fast as we can to stay in one place.

Because the pests that attack today's crops may be different from those that attacked their ancestors, genetic tinkering may sometimes provide short-term protection against recently arrived or rapidly evolving pests. For example, constituitive expression of existing defenses (Broglie et al. 1991; Cao et al. 1998) or gene overexpression (Liu et al. 1994; Cao et al. 1998) can sometimes increase disease or pest resistance.

But if constituitive expression of defenses sometimes increases pest resistance, then why are inducible defenses so common in nature? Many different simple mutations could convert a plant defense gene from inducible to constituitive expression. Mutant plants with constituitive defenses must have arisen frequently and competed against those with inducible defenses. Therefore, the prevalence of inducible genes suggests that they were valuable in the past, at least in terms of individual fitness. In addition to any meta-

bolic costs of producing defensive chemicals, the benefits of inducible defenses may include reduced chemical attraction of specialist herbivores, spatial variability that reduces herbivore performance or increases their rate of movement (thereby attracting predators), slower evolution of adaptation by herbivores, and decreased autotoxicity (Agrawal and Karban 1999). The question is whether these benefits are as important to agricultural productivity today as they were to individual fitness in the past. If pests are predictably more common now, then maybe constituitive defenses will be useful. But then we should at least ask why these pests have become more common.

In a narrow sense, transgenic crops that produce insecticidal toxins of bacterial origin could be considered an innovation not previously tested by natural selection. However, insects have a long evolutionary history of exposure to a wide variety of plant toxins, and minor evolutionary changes in pests may be sufficient to confer resistance to these "new" toxins. Even limited use of bacterial toxins as sprayed insecticides has led to the evolution of resistance in some insects (Tabashnik et al. 1997). There is no reason to expect transgenic solutions to be any more durable, as a class, than those generated by traditional plant breeding, although resistance-management strategies may delay the inevitable (Alstad and Andow 1995). Some transgenes may lack valuable control sequences (introduced by traditional breeding) that trigger defenses only when their benefit to the plant exceeds their cost. Traditional plant breeding may also transfer several defense genes that function synergistically, which could extend the useful lifetime of the defense genes.

Most of the transgenic crops approved by the U.S. Department of Agriculture through August 2002 fall under the general category of Red Queen breeding. Of 61 cases, 45 involved crop tolerance to herbicides, or resistance to insects or viruses (Table 1). The remaining cases involved fruit ripening, seed composition, or male sterility—traits which may be useful to humans and which would not have been favored by natural selection. None of the traits would increase yield potential or tolerance of abiotic stress.

TABLE 1
Transgenic crop petitions approved by USDA or withdrawn by applicant, as of 30 August 2002

Trait	Approved	Withdrawn
Herbicide tolerance	24	6
Insect or virus resistance	21	12
Fruit ripening or seed composition	11	3
Male sterility	5	1

Some applications withdrawn may subsequently have been resubmitted and approved. No applications were denied. Data from http://www.aphis.usda.gov/ppq/biotech/petday.html.

We may not be as good at evaluating long-term risks of biotechnology as we are at seeing short-term benefits (Snow and Palma 1997). If widespread use of transgenic crops leads to more consistent selection for resistant pests, or if pollen from crops transfers fitness-enhancing genes to weedy relatives, they may worsen pest problems in the long run. Molecular biology may speed the search for new pest control solutions each time an old one fails, but it is important not to confuse this short-term benefit with either permanent pest-control solutions (possibly an insurmountable challenge) or long-term improvements in yield potential. Thousands of years from now, dwarf wheat will still have higher yield potential than taller cultivars, whereas ongoing evolution of weeds and insect pests is likely to diminish the value of today's herbicide-tolerant and insect-resistant crops within a decade.

Changing Conditions Change Tradeoffs

During the millions of years prior to domestication, the ancestors of our crop plants were exposed, frequently or occasionally, to drought and nutrient-poor soils. They evolved numerous sophisticated adaptations that conferred resistance or tolerance to those stresses. As a result, it may be difficult to improve on natural selection with respect to the ability to survive and reproduce when soil water and nutrients are limiting. Opportunities may lie in the opposite direction, namely in developing crops that take advantage of agricultural improvements in water and nutrient supply. Accelerating adaptation to increasing atmospheric CO_2 might offer similar opportunities.

Prior to modern agriculture, uptake of soil nitrogen by the plant community often left little nitrogen in the soil by the time it was needed to make protein in seeds. Rubisco and other proteins in extra leaves (i.e., more leaves than needed to intercept the available solar radiation) may serve as reservoirs for nitrogen, allowing plants to take up nitrogen when it is available and then transfer it to seeds after soil nitrogen becomes scarce. It may make sense to breed cultivars with fewer leaves, but only if they also have sufficient nitrogen uptake capacity late in the season. A reliable and economic way to supply nitrogen during grainfill (e.g., from aircraft, or in irrigation water) would also be needed. Although crops that can use additional soil nitrogen, phosphorus, or water when available may be a key to increasing yield potential, crops that perform poorly without additional inputs could increase dependency on resources whose future on-farm availability (at reasonable cost) may be uncertain in some regions.

Reversing Past Selection for Competitiveness

So far, the most successful approach to increasing crop yield potential has been to do something that natural selection never does, namely, to select for characteristics that benefit a plant community at the expense of individual competitiveness. This may also be true of other measures of community performance, such as resource-use efficiency and interannual stability. When community performance and individual competitiveness conflict, natural selection favors competitiveness (Harper 1977). To a give a specific example relevant to agriculture, Zhang et al. (1999) have considered the conflict between individual plant and the plant community with respect to resource allocation to roots under water-limited conditions. The productivity of a community of identical plants was shown to be greatest with a moderate investment in root biomass: just enough root to capture the available water. But a population with this optimum root allocation pattern could be invaded by a genotype that allocated more resources to roots, thereby capturing a larger share of the limited water supply. They concluded that "optimal resource partition maximizing a crop's yield is never evolutionarily stable" (Zhang et al. 1999). Similarly, Schieving and Poorter (1999) showed that the leaf morphology that maximizes total photosynthesis by a plant community does not maximize individual competitiveness.

Modern wheat and rice cultivars owe their high yield potential largely to their short stature, relative to traditional cultivars. Short stature reduces lodging (falling over) and increases growth of grain at the expense of stems, but selection for these traits has resulted in decreased individual competitiveness. Forced to compete with traditional, low-yielding cultivars, modern high-yield rice cultivars completely disappear within as few as three generations (Jennings and de Jesus 1968).

How can we reverse past natural selection for individual competitiveness and select for the collective performance of the crop community instead? Donald (1968) proposed selection based on an "ideotype": a phenotype designed to maximize community performance, often at the expense of individual competitiveness. His specific suggestions, when soil nutrients and water are not limiting, included short stature, less branching, erect leaves, earlier flowering, and fewer leaves. Less branching and more erect leaves both require greater densities (plants/hectare) to produce increased yields. A high density of nonbranching plants will achieve a closed canopy (i.e., one that intercepts 95% of the available sunlight) earlier than a low density of branching plants, thereby increasing seasonal photosynthesis. Nonbranching plants waste less energy contesting space with their neighbors. Crop plants with more erect leaves use the light they intercept more efficiently, due to the nonlinear response of photosynthesis to light. Earlier flowering and fewer leaves are both associated with an earlier switch from vegetative to reproductive growth. Once a crop has enough leaves to intercept the available sunlight, any further leaf growth contributes little to canopy photosynthesis (but may store nitrogen), and comes at the expense of grain growth.

Donald's specific suggestions regarding traits to enhance community performance are generally consistent with the available

data. For example, Austin et al. (1980) compared wheat cultivars released between 1900 and 1980, and found a negative correlation between yield and both height and branching. Experimental manipulations of leaf angle and branching in soybean (*Glycine max*) also gave results consistent with Donald's hypotheses (Kokubun 1988). Higher-yielding cotton (*Gossypium barbadense*) cultivars have less leaf area per plant (Lu et al. 1994). Increases in crop yield potential have involved, and will continue to involve, tradeoffs between individual fitness and community performance, and selection (deliberate or incidental) favoring the latter.

It is possible, though far from certain, that there will be synergistic interactions among the approaches discussed. If the biotechnology and chemical industries could keep finding new combinations of herbicides and herbicide-tolerance genes fast enough to stay ahead of evolving weed populations, that might allow crop geneticists to exploit tradeoffs between crop competitiveness and yield to a greater extent than would otherwise be possible. This approach would entail some risks, as the consequences of faster-than-expected evolution of herbicide resistance or unexpected loss of herbicides (e.g., due to increasing regulation or due to disruption of transportation infrastructure by natural disaster or war) would be more serious. These risks might be considered acceptable in some countries, if major increases in yield potential could be achieved through moderate reductions in competitiveness, but not if increases in yield potential are relatively small.

what else might work
Practical Group Selection

There are two general approaches to further exploitation of the tradeoffs between individual competitiveness and the performance of the crop community. We could extend Donald's (1968) ideotype approach, applying human intelligence (perhaps aided by computers), to the design of high-yielding ideotypes. It may also be possible to develop mechanized field protocols that select for community performance. These two approaches are not necessarily mutually exclusive.

As an example of the first approach, consider the optimum timing of spring growth in perennial crops, which involves multiple tradeoffs. Growth earlier in the spring offers the potential reward of greater seasonal photosynthesis, but increased risk of losing leaves to late frost. Natural selection may have overweighted an additional risk, however, namely the risk of being shaded by a neighbor that started growing earlier. In a given environment, therefore, the optimum starting time for spring growth of the crop community may be somewhat later than that favored by individual selection. Computer models with enough physiological realism and detail to simulate tradeoffs mechanistically (Cock et al. 1979) might be useful in identifying additional tradeoffs that could form the basis of ideotypes (Loomis 1979).

The second approach would impose selection for community performance, without advance knowledge of the plant traits involved. Harper (1977) suggested that "group selection which is believed to be extremely rare or absent in nature . . . may be the most proper type of selection for improving the productivity of crop and forest plants" (p 892). The conditions under which natural selection can favor traits that enhance group performance, when it conflicts with individual competitiveness, are quite restrictive, as discussed below. But humans can, and have, selected for crop yield and other group-level traits. For example, six generations of selection among groups of hens (*Gallus domesticus*) based on collective egg production led to decreased aggression among hens, decreased mortality, and increased production of eggs (Muir 1996).

It is possible that large-scale screening for crop yield would identify genotypes whose yield advantage comes from traits not yet understood. Machines that measure yield at each location in a field during harvest are now commercially available for several crops. Such a harvester could be modified to segregate harvested seed from the highest-yielding locations within a field into a container separate from the bulk of the harvested grain. If only seeds from high-yielding locations were replanted in successive years, that could select for higher yields, even at the expense of indi-

vidual competitiveness. Several problems would need to be solved before this approach would be ready for testing, however. Yield differences across a field could result from differences in soil properties unrelated to crop genotype. Uniform fields would help, but it might also be helpful to compare yields to a computerized yield map from a previous year, when a genetically uniform crop had been grown. The field would also need to be planted in such a way that genotype varied with location in the field; simply planting a well-mixed batch of genotypes would not work well. Ideally, the field would be a mosaic, with each patch containing progeny of a single plant. The scale of yield measurement of commercial harvesting equipment is too coarse to detect such small patches, but similar capability could be added to small-plot harvesters.

Given these challenges (and others not identified), automating group selection for yield would be an expensive project, but not compared to major DNA sequencing projects now underway. A few such tests might suffice, either to identify valuable new ideotypic traits (by looking for consistencies among the highest yielding lines), or to show that we have already identified the most important yield-enhancing traits among available plant materials. Automated screening for other group-level traits, such as more efficient water use, might be more difficult. Methods based on remote sensing of leaf temperature as an indication of water use can be automated to some extent, however (Amani et al. 1996).

THE FUTURE OF NOVEL GENOTYPES

We are defining truly novel genotypes as those that are so different from any previously tested by natural selection that we cannot predict their performance. In particular, we cannot exclude the possibility that they would outperform existing genotypes in ways that might contribute to crop yield potential. We suggest, however, that novel genotypes such as those discussed in the following paragraphs are unlikely to be achieved within the next two decades. It is nevertheless interesting to consider some future possibilities.

Because there has never been a plant that could assimilate N_2 directly from the atmo-sphere (without microbial symbionts), we cannot conclude that this phenotype was tested and rejected by natural selection. It is therefore at least plausible that nitrogen-fixing rice or wheat would have significantly higher yield, at least under some conditions. The evolutionary persistence of symbiotic cooperation in legumes and some other plants suggests that the photosynthate cost of supporting symbiotic rhizobia was often a good investment for plants, at least under preagricultural conditions, when soil fertility was usually low. Nonsymbiotic nitrogen fixation by a plant without microbial symbionts might be an even better investment, because conflicts of interest among unrelated rhizobia infecting the same plant may limit the efficiency of nitrogen fixation (Denison 2000). The development of crops that fix N_2 without a symbiotic partner would not be easy, however. It is not just a matter of transferring the key bacterial enzyme, nitrogenase, to a crop plant. Nitrogenase is quite sensitive to O_2, but the ATP and reductant needed to drive N_2 fixation come from respiration, which requires O_2. Legumes have sophisticated mechanisms, including a variable-permeability gas diffusion barrier (Denison 1998) and leghemoglobin-facilitated diffusion of O_2 within infected cells, that regulate O_2 supply in their nodules. Duplicating this system in nonlegumes is beyond our current abilities. Recently, however, an oxygen-insensitive nitrogenase has been reported (Ribbe et al. 1997). If confirmed, this would solve some of the technical problems that limit the expansion of N_2 fixation to new crops. Even so, there will be other technical challenges, and we consider it unlikely that agronomically useful nitrogen-fixing rice or wheat could be developed within the next decade or two.

Other examples of truly novel genotypes would include crops that, like fungi, can extract energy and nutrients directly from soil organic matter. Or perhaps new crops could be developed that, like some *Acacias,* house and feed ants in exchange for protection from herbivorous insects and other pests. Transgenic crops that produce drugs, including illegal ones, could be highly profitable. All of these examples would presumably involve new tradeoffs that might limit yield

potential, or could create serious social or environmental problems beyond the scope of this paper. We mention them only as examples of phenotypes novel enough that they may never have been tested by natural selection.

Hypothesis 2 and Agroecosystem Design

The idea that agricultural ecosystems would be more productive or sustainable if they were more similar to natural ecosystems is widespread. One influential paper (Jackson and Piper 1989) suggested we should "model agroecosystems on nature's standards," basing agriculture on natural communities "beyond complete human comprehension" (pp 1591–1592). Similarly, it has been suggested that agricultural pest management strategies should be modeled on natural ecosystems (Altieri 1987). These ideas still persist today, as evidenced by a recent book titled, *Agriculture as a Mimic of Natural Ecosystems* (Lefroy et al. 1999).

should agriculture mimic nature?

The argument for mimicking natural ecosystems is unclear. Natural ecosystems may have "withstood the test of evolutionary time" (Ewel 1999), but the test criteria were not stated explicitly. No natural terrestrial ecosystem has exported as much human food per hectare, over millennia, as rice fields in Asia. Some agricultural ecologists appear to assume that natural ecosystems somehow have been optimized, perhaps by natural selection. Natural ecosystems have been described as "stable, self-sustaining . . ." perhaps due to "[s]election through time . . . of the most complex structure biologically possible within the limits set by the environment" (Gliessman 1990:5,7). Others apparently assume that natural selection operates, if not for the benefit of an entire ecosystem, at least for the benefit of a species as a whole. The only reference to natural selection in the index of a recent book on *Ecology in Agriculture* states that while natural selection may conflict with the goals of plant breeders, it "operates to continue the survival of species" (Jackson and Koch 1997:3). Similarly, it has been sug-

gested that the apparent stability of many natural ecosystems is due to each species having "evolved so that it does not overexploit its resources" (Gutierrez and Daxl 1984:200). Some of these statements may not fully reflect their authors' current views, but they are representative of the implicit assumptions made by many who have attempted to apply ecological principles to agriculture. Most evolutionary biologists, however, would reject these assumptions as inconsistent with modern evolutionary theory.

Our second major hypothesis is that natural selection is the only process that consistently improves the performance of anything in nature. If this hypothesis is true, then "nature's wisdom" should be manifest only in those entities that have been subject to natural selection. Individual plants and animals contain genes that have repeatedly passed through the screen of natural selection, but has anything analogous to natural selection also improved the structure and function of the ecosystems where those species live?

NATURAL SELECTION AND ECOSYSTEM STRUCTURE

Natural selection acts to maximize transmission of some alleles relative to alternative alleles (Dawkins 1976), usually by maximizing the reproductive success of individuals carrying those alleles. Some plant genes, such as maternally inherited genes that increase seed production at the expense of pollen production, enhance their own transmission at the expense of the plant's overall fitness (Dominguez 1995).

Classic group selection, the expectation that individuals would often sacrifice their own reproduction in the interests of the species as a whole (Wynne-Edwards 1962), was discredited in the 1960s (Hamilton 1964; Maynard Smith 1964; Williams 1966). But, as Goodman (1975:261) predicted of the diversity-stability hypothesis, this form of group selectionism has persisted "as an element of folk-science," among some agricultural ecologists. Kin selection in animals can favor cooperation or even self-sacrifice to help close relatives. Sterile worker bees are a dramatic example, although egg-laying worker bees can sometimes exploit this system (Mar-

TABLE 2

Conclusions of key papers that examined the conditions under which natural selection will favor the interests of a group over those of those of the individuals that compose that group

Author	Conditions For Group Selection to Work
Levin and Kilmer 1974	Groups consist of fewer than 25 individuals, and usually closer to 10. Rate of gene flow by migration is lower than 5% per generation (i.e., one individual).
Maynard Smith 1976	The number of successful migrants produced per group is one or less. Successful migrants are individuals who leave a group and leave descendents in another.
Leigh 1983	Assuming N groups which each contain n individuals and last for L generations: (a) each group is founded by a single individual; (b) the groups never exchange migrants; (c) $N > n$.

All results assume unrelated individuals within groups (i.e., kin selection is not at work).

tin et al. 2002). There is no clear evidence for kin selection in plants (Cheplick 1992) and its importance in general has been overestimated (Griffin and West 2002).

The conditions under which natural selection will favor an individually costly trait (e.g., restraint in exploiting resources) that benefits a group of unrelated individuals are quite restrictive (Dawkins 1976). Individually costly traits that increase the ability of a group to "reproduce" (generate another group) may be favored by differences in the survival of groups, but only if each group contains fewer than about 25 individuals, and only if an average of fewer than one individual changes groups during the time it takes a group to spawn another group (Table 2). These extremely restrictive conditions can be met for group selection imposed by humans. For example, Muir (1996) used groups of four hens, and prevented movement among groups. But these conditions are rarely met in nature.

The agricultural ecologist de Wit (1978) pointed out that "there is nothing in the process of evolution that has any aspect of community behaviour as a goal" (p 405). Even the few evolutionary biologists who think natural selection may operate on groups of plants generally agree that natural selection is unlikely to consistently improve ecosystem function, when the collective interests of species in the ecosystem are in conflict with individual competitiveness (Goodnight 1990).

Conflicts between individual competitiveness and collective benefits are also apparent in the evolution of pathogenicity in parasites.

It may be true that an obligate fungal parasite that produces very large numbers of spores at the expense of a host plant is likely to go extinct because "in the long run, this would tend to destroy the host" (Browning 1981:166). However, the claim that therefore "pathogens have responded by evolving rates of sporulation" low enough to eliminate the "risk of domination" contains two serious fallacies. First, natural selection is blind to long-term consequences. Like a river, which rarely follows the most direct route to the nearest ocean, natural selection responds only to current conditions. Second, natural selection is driven mainly by competition (often indirect) within a species. If two fungal genotypes differ only in the number of spores they produce, a consistently more prolific strain will almost always outcompete and displace the other strain, whatever the long-term consequences for the species as a whole. If each host plant is infected by a single clone of parasitic fungi, there may be selection for keeping individual hosts alive longer, but this is simply within-host kin selection, unrelated to the long-term interests of either species. There is clear empirical evidence that parasites maximize their own transmission and not the survival of their hosts (Herre 1993). Selection among individual plants may indirectly improve some aspects of ecosystem function—a forest mainly containing insect-resistant trees will be less subject to massive defoliation—but there is no reason to expect the overall structure of even ancient natural ecosystems to be optimal unless they have been improved by some process other than natural selection.

have other processes improved ecosystems?

Are there processes other than natural selection that consistently improve natural ecosystems in ways that would make them appropriate models for agriculture? We think not, but this question may merit additional research.

Succession

Succession may improve some aspects of ecosystem function but make others worse, by human criteria. Like most modern ecologists, we reject old analogies (Odum 1969) between ecological succession and individual development. Communities and ecosystems are not superorganisms (McIntosh 1998). Developmental changes of individual organisms are part of the organism's phenotype, controlled by genes subject to natural selection. There is nothing analogous in nature that operates over millennia to improve the process of ecological succession.

Successional changes in species composition of plant communities may improve some aspects of ecosystem function, by human criteria, but other aspects typically deteriorate. For example, productivity, nutrient retention (as opposed to loss to rivers), and greenhouse gas absorption by forests decline as succession proceeds (Gorham et al. 1979; Robertson et al. 2000). A comparison among islands differing mainly in successional stage found that microbial biomass and microbial activity, two parameters well-loved by some ecologists, were both lower later in succession (Wardle et al. 1997).

Some ecologists might find changes during succession counterintuitive. Succession often leads to increased dominance by a small number of species (Paine 1966)—the *Sequoia*-dominated oldgrowth forests of the northern California coast are a dramatic example—but we would hesitate to conclude from this that agriculture would always benefit from a reduction in crop diversity.

The longer an ecosystem has been in existence, the greater the opportunity for coevolution. Mutualisms requiring complex coordinated adaptations might therefore be more common in ancient natural ecosystems than in agroecosystems of more recent origin. But greater ecosystem duration also provides enough time for more sophisticated negative interactions to evolve, such as parasitism or "cheating" by symbiotic partners (Letourneau 1990).

Complexity

We have seen no convincing theoretical or empirical evidence that complex entities not subject to natural selection spontaneously organize themselves in ways that are optimum in any reasonable sense of the word. Our experience with human organizations and with computer operating systems suggests that complexity does not necessarily enhance performance.

Ecosystems, like individual organisms, may have homeostatic mechanisms (Lewis et al. 1997). However, organism-level homeostatic mechanisms have been fine-tuned by selection among organisms, whereas ecosystem-level homeostatic mechanisms have not been fine-tuned by natural selection among ecosystems. Certain kinds of trophic interactions may promote stability (McCann et al. 1998), but it is not clear why natural ecosystems would be especially likely to have just those sorts of interactions. Assuming that some optimum number of species will maximize community productivity or stability in a given environment, is there some mechanism that adjusts the actual number of species in a natural ecosystem upwards or downwards towards that optimum? We know of no data or convincing (i.e., not group selectionist) theoretical argument showing that this is, or should be, generally the case.

Comparing Natural and Agricultural Systems

"[W]e have no idea how evolution adapts ecosystems," wrote Leigh (2001), since they are "not units of selection." Leigh argued, however, that the productivity of natural ecosystems is usually affected adversely by human disturbance, and therefore that undisturbed ecosystems must somehow be structured in ways that enhance productivity. In principle, we accept the argument that if human-induced changes in ecosystem structure usually have an adverse effect on specific ecosystem functions, that would provide strong

evidence that the structure of undisturbed natural ecosystems is well-suited to those functions. But do undisturbed natural ecosystems actually excel in those functions relevant to agriculture, such as the ability to export food sustainably? The greater year-to-year stability of nut production by almond orchards (7,500 to 12,800 kg/ha) relative to oak forests (0.4 to 55 kg/ha) seems inconsistent with this hypothesis (Feldhamer et al. 1989; Hutmacher et al. 1994). In one study, total seed yield of native prairie ranged from 7 to 525 kg/ha over three years (Brown 1943), a small fraction of the 1988 average world grain yield of 2480 kg/ha (Loomis and Connor 1992). Improved pastures typically have greater productivity or carrying capacity for livestock, relative to native vegetation (Phillips and Coleman 1995; Rosiere and Torell 1996). Few, if any, comparisons between natural and agricultural ecosystems have thoroughly controlled for the effects of soil, climate, or external inputs, but we consider it unlikely that natural ecosystems will consistently outperform agricultural systems, by most agricultural criteria.

We conclude that "Nature's wisdom" resides mainly in the sophisticated adaptations of individual plants and animals, not in ecosystem structure. Any given feature of a natural ecosystem may be there "for a reason," in the same sense that earthquakes happen for a reason, but that does not mean they are there for a purpose. Mindless mimicry of natural ecosystems reveals ignorance of, not respect for, ecological principles.

THE TRUE VALUE OF NATURAL ECOSYSTEMS

There are many reasons to preserve natural ecosystems unrelated to their potential as models for agriculture, including recreational value, beneficial effects on air and water quality, and the "ecosystem services" such as pollination or biological control of pests they provide to nearby agricultural areas (Constanza et al. 1997). Furthermore, despite the limitations discussed above, natural ecosystems may be a rich source of ideas for agriculture.

Natural Ecosystems As Case Studies

If we were trying to improve our educational system, we would be wise to study the educational systems of a variety of countries.

Some might serve as models to imitate, while others might be equally valuable as examples of mistakes to avoid. We should take a similar approach when looking at natural ecosystems as a source of ideas for agriculture. Although there is no reason to expect all natural ecosystems to be optimal, some are likely to be more stable or efficient than others. Differences among natural ecosystems may be as informative as differences between natural and agricultural ecosystems. Comparative studies, preferably based on long-term data sets, may well provide information useful in designing agricultural ecosystems. But blindly copying a natural ecosystem would be as illogical as advocating ethnic cleansing because "they're doing it in Europe."

Copying Time-Tested Individual Strategies

A second major way in which the study of natural ecosystems may contribute to improving agriculture is more directly linked to our gene-centered view of natural selection. Natural selection optimizes genes, if anything (Dawkins 1976, 1982). But plant genes that persist and spread usually code for functions that benefit the plant. Seed collections and other gene banks can preserve valuable genes, but to understand their function we will often need to preserve, and refer to, the ecosystems in which they evolved.

Consider, for example, plant defensive strategies. Wild potatoes repel aphids by releasing a volatile chemical functionally equivalent to aphid alarm pheromone (Gibson and Pickett 1983). Volatile chemicals released by other plants, when attacked by herbivorous insects, attract predators and parasitoids (Stowe et al. 1995; Turlings et al. 1995) Other plants recruit defenders by providing shelter or other resources to predatory arthropods (Agrawal and Karban 1997) or ants (Brouat et al. 2001). We suggest that it would be nearly impossible to decipher the phenotypic effects of the plant genes responsible for these types of indirect defenses, in the absence of the other species (herbivores, predators, or parasitoids) involved.

Understanding the strategy may be more important than understanding the gene. Transferring genes from wild to cultivated plants has often been useful, but this may not

always be the best way to implement the wild plant's strategy. Understanding costs and benefits of defenses against aphids based on chemical alarm signal mimicry could be useful when considering analogous defenses against other pest species, even if the specific chemicals were different. Understanding how plants maximize benefits from one root-associated microbial species may have application to other rhizosphere mutualisms (Denison et al. 2003). Some plants produce clusters of ephemeral roots that solubilize and take up soil phosphorus that would normally be unavailable (Dinkelaker et al. 1995). Transferring this trait to new species might be difficult, but understanding the spatial and temporal distribution of these "proteoid roots" might suggest new approaches to fertilizer placement that would differentially benefit crops relative to weeds.

DEPLOYING CROP DIVERSITY

As an example of how a Darwinian perspective might contribute to the design of agricultural ecosystems, consider the use of crop diversity in the control of specialist agricultural pests. Many natural ecosystems contain intimate mixtures of plant species. Naïve ecologists might see this as sufficient evidence for the benefits of such mixtures (i.e., intercropping) in agriculture. There may sometimes be advantages to growing mixtures of crops. Some pests may be less common with intercropping, although a yield benefit linked to reduced pest populations with intercropping has rarely been demonstrated (Risch et al. 1983). A mixture of two or more species may sometimes use resources more thoroughly than one (Loreau and Hector 2001), although agricultural studies that claim this result have often failed to show that the single-species reference crop was grown at optimum density (Fukai 1993). One recent study showed that a serious disease affecting a high-value rice cultivar could be controlled by growing it in single rows surrounded by 4 to 6 rows of a resistant cultivar (Zhu et al. 2000). This study also reported 18% higher total yield with intercropping, but it appears from their Figure 1 that this may have been an artifact due to suboptimal density of their monoculture control.

Attempts to mimic natural ecosystems can blind us to strategies for deploying the available crop diversity that would have even greater benefits. For example, assume that there are three crop species adapted to a given region and in sufficient demand that they could profitably be grown in quantity. We could grow a mixture of all three species each year (Figure 1A), hoping that by mimicking diverse natural ecosystems we would confuse herbivorous insects enough to prevent serious crop losses. A Darwinian perspective might lead to the opposite conclusion. Herbivorous insects that evolved in the midst of diverse vegetation are presumably adept at finding their preferred food plants in a mixture of many other species; a mixture of three species is unlikely to be a formidable challenge.

One problem with growing an intercropped mixture of all available species is that it exhausts the available crop diversity. Maximizing small-scale spatial diversity leaves no remaining crop diversity to be deployed at the landscape scale. For pests with effective dispersal differences on the order of 10 to 100 m, a patchwork of fields, each containing a single crop species, might be more effective in limiting pest dispersal than an intimate mixture of species.

Deploying crop diversity on the landscape scale is also more compatible with crop rotation (Figure 1B), which deploys diversity over time. Darwin (1859:119) used the metaphor of a "simultaneous rotation" in discussing species mixtures in nature, but the effects on pests of diversity in time may be different from those of diversity in space. Pests adapted to considerable spatial diversity (as found in natural ecosystems) may be poorly adapted to dramatic changes in vegetation from one year to the next, because this sort of change is relatively uncommon in many natural ecosystems. A three-year rotation, growing each crop in sequence, might therefore provide more effective pest control than growing the same three-crop mixture each year.

Pest evolution can overcome relatively simple crop rotations. A two-year rotation of maize with a nonhost was once effective against northern corn rootworm (*Diabrotica barberi*), but a mutant with two-year diapause
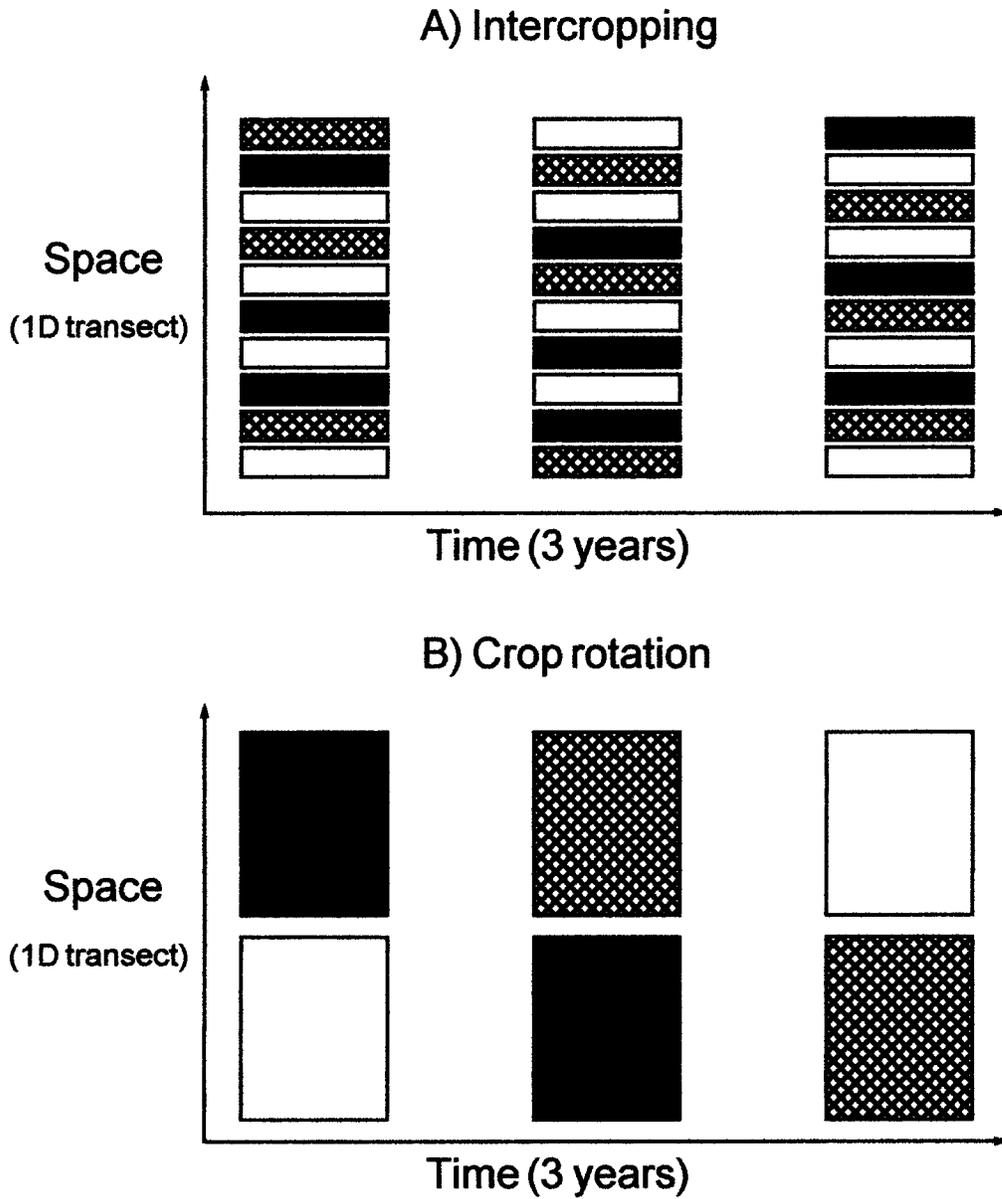
A) Intercropping

B) Crop rotation

FIGURE 1.   TWO ALTERNATIVE WAYS OF DEPLOYING CROP DIVERSITY IN SPACE AND TIME

Time from planting to harvest is shown on the horizontal axes for three successive years, with intervening periods when nothing is grown (e.g., severe winters). The vertical scale may differ between A (Intercropping) and B (Crop rotation). The vertical extent of each species shown in A could correspond to a single plant or a transect across one or a few rows of the same species, as opposed to whole fields in B. Numerous variations are possible, including use of perennials and multiple crops per year as well as systems that incorporate features of both intercropping and crop rotation. The main point is that, in evaluating alternative spatial and temporal patterns, we should not limit ourselves to patterns that resemble the nearest natural ecosystem.

survives until maize is again available (Krysan et al. 1986). A maize-soybean rotation was once effective against western corn rootworm (*D. virgiferea*), but some rootworms now leave the maize field where they matured and lay their eggs in adjacent soybean fields in fall, emerging the next spring when maize is sown (Onstad et al. 1999). These pest strategies could perhaps be defeated by a synchronous, three-year crop rotation over an area larger than the effective dispersal distance of the pests. If no maize were grown in a large area for two years, any maize-dependent pest with limited mobility could become locally extinct. This approach would be less effective with highly mobile pests and would require control of any weeds or wild plants that would serve as alternate hosts. Such an approach would present logistic problems that may not be immediately evident to ecologists but which would be obvious to farmers. Whether or not this particular strategy could prove successful is unclear, but it illustrates the point that, in designing agricultural ecosystems, we should consider the full range of possibilities, not just those that resemble natural ecosystems.

Conclusions

We conclude that human ingenuity is no match for natural selection, when the latter has been working on a problem, worldwide, for millennia. Prospects for tradeoff-free improvements in traits like photosynthetic efficiency or drought tolerance are therefore poor, because these traits would have increased individual fitness in most environments. On the other hand, natural selection has little or no power to optimize the performance of plant communities or ecosystems, when collective performance conflicts with individual fitness. In designing crop plants and agricultural ecosystems that maximize community performance in ways that are beyond the scope of natural selection, there is still ample room for human ingenuity.

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