GENETIC POTENTIALS FOR INCREASING YIELDS OF FOOD CROPS AND ANIMALS

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The title of my paper is concerned with genetic potentials, but since the genotype is never independent of the environment with which it constantly interacts, it is not always possible to separate the two. Especially is this true in agricultural production where the use of improved varieties is usually accompanied by improved cultural practices. Consequently, from the standpoint of the subject of this symposium, "Prospects of World Food Supply," we are concerned with the potentials for increasing food production by the use of improved genotypes performing their functions in the milieu of improved environments.

There are two obvious ways of estimating what such combinations of improved genotypes and improved environments can do. One is to compare present-day cultivated plants and domestic animals with their wild progenitors; the other is to compare average yields or production with maximum record yields or production for the same species. Examples of the two methods follow.

A spectacular example of genetic potential is that of the evolution of cultivated corn in Mexico. The prehistoric wild corn, recently uncovered in once-inhabited caves in the Valley of Techuacán and dated at *ca.* 5000 B.C., has cobs about two centimeters long—about the same length as a man's thumbnail—which once bore small kernels averaging about 55 in number. The first domesticated corn from the same sites dated at *ca.* 3500 B.C. is similar to the wild corn in its principal botanical characteristics but has cobs several times as long. The difference in size between the wild and early cultivated corn may have been in large part the result of the improved environment provided by man when he began to practice agriculture and to remove some of the competing vegetation. About 900 B.C., following hybridization with one of its relatives, *Tripsacum* or teosinte, corn began to evolve with explosive rapidity and by A.D. 200 one of the still-existing but ancient races of Mexico, Chapalote, was already well established. By A.D. 1500 several of the modern Mexican races of corn were being grown. Evolutionary progress with respect to size of the ear has continued and in the $4^1/_2$ centuries since the conquest of Mexico numerous highly productive races of corn have developed. One of these, a giant-eared corn from the Jala Valley, has ears up to 15 inches in length, bearing more than a thousand large kernels.

There is no reason to believe that the genetic potential of cultivated corn has been exhausted. Further improvement may be in the direction of more numerous rather than larger ears, but the capacity to produce large amounts of grain will undoubtedly continue to increase.

Another example of the difference in genetic potential between a cultivated plant and its wild progenitors is provided by the hexaploid bread wheat, *Triticum aestivum*, which has a haploid chromosome number of 21. The bread wheats are the product of hybridization of three different species, each with seven chromosomes, *T. monococcum*, *Aegilops speltoides*, and *Aegilops squarrosa*. Only one of these, *T. monococcum*, has ever been cultivated. It is grown on the poor soils of Greece and parts of the Near East where its yields of grain are said to be "insignificant."

The other two species, *A. speltoides* and *A. squarrosa*, have never been considered worth domesticating. Yet the allopolyploid hybrid, which combines the chromosomes of these three unpromising grasses, has become one of the most productive of the world's cereals, capable of producing a record yield (Table 1) of more than 200 bushels per acre. The interaction of the chromosomes of the three component species has created a high degree of hybrid vigor which in turn has greatly increased the genetic potential.

There are comparable examples among animals of the difference between the wild and domesticated forms. Milk cows, whose wild progenitors produced only enough milk to nourish one calf, have evolved into animals capable of producing more than 40,000 pounds of milk per year. A classic example is Bridge Birch, the British cow which produced more than 45,000 pounds of milk in 1 year, a record not officially recognized in the United States.

The wild jungle fowl, laying one clutch of 5–8 eggs a year, is the progenitor of modern hens capable of laying 365 eggs per year. A substantial part of the genetic potential for egg laying is inherent in the wild fowls, since it is characteristic of many species of birds to continue laying eggs daily if the eggs are removed from the nest as they are laid. A common flicker has in this way been induced to lay 72 eggs. Jungle fowls in captivity, when fed and treated as domesticated hens, have an average production of about 70 eggs per year. The genetic egg-laying potential of chickens has been further increased by largely eliminating, through selection, the brooding instinct. Modern hens in modern environments are virtually egg-laying machines.

The second way of estimating what combinations of improved genotypes and improved environments can do is illustrated by the data in Table 1.

Obviously, we cannot raise the average yield or production of our food plants and domestic animals to the maximum production shown in Table 1, but we can cause the average to *approach* the maximum. And even now we have the information and techniques to do this. We can breed superior genotypes for any part of the world; we can provide improved environments for such genotypes; but the problem is more than a scientific one—it is an economic and social one. As Dr. Schultz has pointed out in his book, *Changing Traditional Agriculture*, the rate at which the agriculture of underdeveloped countries can be improved is dependent in large part on the general level of literacy and education in the population and on the willingness of governments to provide generous support for agricultural education and research.

Since agricultural improvement in underdeveloped countries is in most cases necessarily slow, it now appears that the United States will be called upon to make up from its own abundance the impending food deficiencies in certain other coun-

TABLE 1

AVERAGE AND RECORD YIELDS OF FOODSTUFFS

Plant or animal	Average yield	Record yield
Corn, bu/acre	29 (World)	304 (U.S.)
Wheat, " / "	17 (World)	209 (U.S.)
Rice, " / "	24 (World)	266 (India)
Sugar cane, tons sugar/acre-year	2 (World)	5.5 (Hawaii)
Cow, lb milk per year	6,800 (U.S.)	43,000 (U.S.)
Chicken, eggs per year	205 (U.S.)	365 (Japan)

tries, of which India is at the moment a conspicuous example. One of the critical questions then becomes, "What is our capacity in the United States for increasing our production over its present high levels?" If we base our projections upon the performances of the past, we have reason to be optimistic because since 1940 our production has been increasing, despite declining acreages, at the rate of 2 per cent per year. However, there are certain factors in this favorable growth rate which may be nonrecurrent. In the case of our principal American food plant, corn, we have succeeded in the 30-year period from 1930 to 1969 in exactly doubling our average production from 26 to 52 bushels per acre. Can we double this figure again in the next 30 years or less? Unless we achieve some important "breakthroughs" which are not now in sight, I seriously doubt it.

What have been the principal factors in doubling average acre production of corn between 1930 and 1960? One of these, of course, has been the improved genetic potential in the form of hybrid corn. But hybrid corn has now replaced open-pollinated corn on more than 95 per cent of the corn acreage of the United States. There can be no substantial further improvement resulting from such replacement. This is a nonrecurrent improvement. But cannot we produce better hybrids than those now in use? Theoretically we can, but in practice we have so far not achieved spectacular success in this direction. Of the 12 inbred strains involved in the hybrids most commonly recommended by the state agricultural colleges and experiment stations, the majority were developed in the 1920's, 40 or more years ago. Corn breeders, it is true, have produced many new hybrids which are superior for certain purposes, better adapted for machine harvesting, for example, but corn breeders have not made great progress in increasing the genetic potential for increased yields beyond the initial increment resulting from replacing open-pollinated varieties with hybrids.

A second factor involved in doubling average yields of corn between 1930 and 1960 has been the increased use of fertilizer, an example of the improved cultural practices which accompany the use of improved varieties. In the decade between 1950 and 1960, the use of fertilizer in the United States has greatly increased. The consumption of nitrogen fertilizer, for example, has more than doubled, increasing from about 1,171,000 to 2,734,000 tons. Similar but slightly smaller increases have occurred in other fertilizer constituents. The use of nitrogen has been especially important in causing corn plants to develop deeper root systems, and this in turn has rendered them better able to take advantage of deep subsoil moisture. The effect of fertilization on improving corn yields has probably been greater than the effect of planting hybrid corn. But this improvement is also, to some extent, nonrecurrent because in the Corn Belt and Lake states which produce 73 per cent of U.S. corn, 87 per cent of the corn acreage is already being fertilized at an average rate of 145 lb per acre. Thus, almost two thirds of the corn produced in the United States already comes from fertilized fields. Applying still greater amounts of fertilizer, although usually increasing yields, gives farmers a smaller return on their investment. Furthermore, large applications can sometimes have a depressing effect on yield in seasons of below-average rainfall.

A third factor involved in doubling our average yields of corn has been the use of remarkably selective herbicides which kill weeds but do not injure corn plants. The amount of water gained by eliminating the losses from that transpired by weeds is equivalent to providing corn fields with an irrigation when it is most needed. However, it will be a matter of only a few more years until the use of herbicides is virtually universal, so this, too, may soon become a nonrecurrent improvement.

With more than 95 per cent of the corn acreage already planted to hybrid corn, with the genetic potentials of the hybrids having reached a plateau, with 87 per cent of the acreage in the Corn Belt and Lake states already using fertilizer, and with many farmers already employing herbicides, from where will come the future improvements that will allow us to continue our present rate of improvement?

I doubt that this question can be answered until we expand basic research in two important areas: (1) the nature of hybrid vigor, or heterosis, and (2) gaining an understanding of our principal food plants and animals as unique biological systems.

There are many different biological phenomena involved in agricultural production, of which three are of outstanding importance. (1) Replication of the hereditary material is the phenomenon which permits man to reap what he sows. (2) Photosynthesis is the phenomenon which permits man through the growing of plants to convert the energy of the sun, the carbon dioxide of the air, and the minerals and water of the soil into food. (3) Heterosis, or hybrid vigor, is the phenomenon which, more than any other, has made our cultivated plants superior to their wild progenitors; it is this phenomenon which we are exploiting when we produce hybrid corn and a host of other hybrid agricultural, horticultural, and ornamental plants, as well as hybrid chickens and pigs.

In crops which are vegetatively propagated, such as sugar cane, potatoes, sweet potatoes, and cassava and most of our fruit crops, hybrid vigor is perpetuated by asexual reproduction. In crops that are complex allopolyploids such as the bread wheats, the hybrid vigor results from the interaction of chromosomes from three different species. It is perpetuated through the diploidization of the polyploid chromosome complement. In other crops such as corn, hybrids must be produced anew in each generation, and this has now been greatly facilitated by the use of forms of male sterility transmitted through the cytoplasm which eliminate the need for costly hand emasculation. Cytoplasmic sterility is now used to produce hybrid corn, sugar beets, sorghum, and is being used experimentally in producing hybrid wheat.

The phenomenon of heterosis which is being exploited in so many ways in food production is not as well understood as the first two that I have mentioned. Spectacular progress has been made in recent years in research on the hereditary material, DNA, and on its transmission of coded genetic information. Similar progress has been made on elucidating the principal biochemical processes involved in photosynthesis. But heterosis still remains largely a mystery. Our present theories about heterosis are essentially the theories of 30, 40, and even 50 years ago. There has been extensive experimentation but little progress. One reason for lack of progress, I suspect, has been the methods employed—in the case of corn, for example, attempting to distinguish between different theories by statistical analysis of yields of different kinds of genetic combination without any clear understanding of the biological nature of the corn plant. To understand heterosis we need to know much more than we now do about the species of plants and animals in which we are attempting to exploit it. And this brings me to what I consider to be the second most pressing need in improving the genetic potentials for food production.

During his history, man has used at least 3000 species of plants for food and has cultivated at least 150 of these to the extent that they have entered into the world's commerce. The tendency through the centuries has been to use fewer and fewer species and to concentrate on the more efficient ones, those that give man the greatest return for his land and labor. Today the world's people are actually fed by about 15 species of plants. These include five cereals: rice, wheat, corn, sorghum, and barley; two sugar plants: sugar cane and sugar beet; three "root" crops: potato, sweet potato, and cassava; three legumes: the common bean, soybean, and peanut; and two so-called tree crops: the coconut and banana.

Since these plants quite literally stand between mankind and starvation, perhaps we should know as much about each of them as we know about some of the destructive agents of the world—as the medical profession, for example, knows about the world's principal human diseases, or as aeronautical engineers know about the world's principal bombers or guided missiles. Today we do not have that kind of information, though we are beginning to get it. Rice is an example. At least 50 per cent of the world's people get at least 60 per cent of their energy from rice. Thus, *more than 30 per cent of all the human energy on the globe now comes from one plant species, the rice plant.*

Realizing this fact, the Rockefeller and Ford Foundations some years ago combined forces to set up a rice research institute in Asia where geneticists, plant physiologists, mycologists, biochemists, engineers, and others are devoting themselves to understanding the rice plant and learning how to improve both the plant and its environment.

The need for similar research on the remaining principal food plants is only slightly less urgent. What are the characteristics that makes each of these plants an important contributor to the world's food supply? Again taking corn as an example, why is corn the most productive of the world's cereals? I once supposed that it might be so because it bears its grain not in a terminal head like wheat, rice, and barley, but on a short lateral branch rising from the middle region of the stalk. I supposed that there might be a physiological advantage of this middle position, the ear being in the center of the photosynthetic activity instead of at the periphery, as are the heads of other cereals. Some rather simple experiments have shown that there is indeed a physiological advantage in the middle position, but the nature of that advantage is not what I first supposed. The advantage stems from the fact that the movement of the food manufactured in the leaves is downward in corn plants as it is in trees. Consequently, corn with its extensive area of leaves above the ear has a decided advantage over cereals in which the major part of the leaf area is below the grain-bearing organ. In corn the leaves below the ear appear to be concerned primarily with nourishing the root system, while those above the ear are primarily responsible for grain production. These simple facts explain some things which we already know about the corn plant and also suggest possible ways of improving the plant. For example, we know that varieties of corn of the humid tropics tend to bear their ears in high positions on the stalk and the larger part of the leaf area is below the ear. The explanation is that in most tropical countries cultural methods are still crude and corn must compete with aggressive tropical weeds. To do this, it must have an active and well-nourished root system, and consequently the larger part of the plant's leaf area must be below the ear. If we outline the silhouette of the leaf pattern of tropical varieties, we get an oval which is widest near the base. In the Corn Belt of the United States where cultural methods are more efficient than in the humid tropics and competition with aggressive weeds is less severe, the ear is usually borne in the middle position of the stalk, and about half of the leaf area, being below the ear, is primarily concerned with nourishing the root system; the other half, above the ear, with nourishing the ear. The silhouette of the leaves of a typical Corn Belt corn outlined diagrammatically is, like that of tropical corn, an oval but one which is widest in the middle.

Now that the use of herbicides can virtually eliminate competition with weeds and the use of nitrogen fertilizer tends to develop a deeper and more efficient root system, perhaps we should be breeding corn plants which have a larger proportion of their leaf area above the ear. A diagrammatic outline of the leaf pattern of such a plant is an oval widest at the top. Corn breeders may already be working empirically in this direction without knowing why they are doing so. Some of the inbred strains used in the most productive hybrids now being grown have up to 60 per cent of their leaf area above the ear.

There are many other questions of this general nature for which we are not likely to have answers until we begin to study the corn plant as a species *sui generis* and indispensable to the welfare of mankind. And what I have said about corn applies to the other principal food plants, some of which, from the standpoint of the number of people which they feed, are even more important than corn. It applies also to our principal domestic animals.

As we are now exploiting the products of basic research in agriculture done 40 and 50 years ago, so we should also be doing now the basic research that will provide the new techniques for producing the food needed to feed the world's population in the year 2000. And at least a part of that research might well be devoted to gaining a better understanding of our principal food plants and animals as unique biological systems.