We can detect several types of relationships between the structure of animal communication signals and the function that they serve. The almost ubiquitous requirement for aid in or hindering of the localization of signals has led to the evolution of many distinctive properties of both auditory and olfactory signals. The ease of localization of visual stimuli is one of several factors that make vision peculiarly suitable as a means of social communication when circumstances permit.

The diversity of signal structure in animals must exist partly to maintain species specificity, partly to permit a signaler to elicit different responses from another animal, and partly to select among the various classes of respondents that are available. With the evolution of a complex society, in which different animals have different roles to play, the specification by different signalers of appropriate respondents may require a considerable increase in the number of signal types used by a species, irrespective of any increase in the number of response patterns that may occur.

There is still no plausible explanation for the emergence of the cultural transmission of patterns of sound production in man. The change must somehow have been related to the advantage of an increased repertoire and flexibility of sound patterns, not necessarily related to sex or age class. The use of tools obviously played a vital role (*20, 15*). Increase in the subdivision of labor in early human society, such that members of the same sex and age class might assume many different roles, and the need for a signaler to select respondents among the array of possibilities, would create a need for dramatic increase in signal diversity. Perhaps this contributed to a switch from genetic to environmental control of variation in patterns of sound production in a population. Once established, albeit for the satisfaction of a relatively simple linguistic requirement, the increased flexibility of the patterns of sound production would pave the way for the more remarkable changes in the processes of communication that ultimately made human language a unique phenomenon in the animal kingdom (*21*).

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Agricultural Production in the Developing Countries

G. F. Sprague

At least half the world's population endures some degree of malnutrition. The gap between food production and world population is constantly widening. It has been estimated that by 1985 this situation could become catastrophic. Two approaches appear obligatory: (i) a substantial decrease in the rate of population growth, and (ii) full utilization of our biological technology to increase food production on all economically arable lands. The utilization of microorganisms, algae, or petrochemicals to produce protein has been suggested by many. These and other possibilities should be actively explored and, where feasible, utilized. However, the total impact of such possible developments cannot greatly lessen the need for an expanded agriculture limited only by the ecological potential.

This article is concerned primarily with the possibilities for increasing agricultural production in the developing countries through improvement in varieties, in fertilization, and in management practices. As background, a brief review of selected examples of progress achieved in the developed countries with the three most important food crops—rice, wheat, and corn—during the past 35 years seems desirable.

Rice Production in Japan

Japan has the highest acre yields of paddy rice among the major rice-producing countries. There is evidence that rice was cultivated in Japan as early as 300 B.C. Through the centuries there

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has been a gradual expansion in acreage, improvement in varieties, and modification of cultural and production practices.

The major developments, however, have occurred since about 1885, when the national average yield was approximately 1800 kilograms per hectare. Average yields had increased to approximately 4000 kilograms per hectare by 1963. Somewhat greater percentage gains have been achieved in the cool northeast portions of Honshu and in Hokkaido.

As is typically the case, this increase in yield is the result of many factors: improvement in varieties, increased use of fertilizer, modification of cultural and production practices, and better control of disease, insect pests, and weeds.

In the earlier days varietal improvement was limited to selection among the various land-race populations. Later, intensive selection for pure lines was practiced by the National and Prefectural Experiment Stations. Since about 1927 breeding efforts have been centered on crossing of selected parents, followed by the isolation and evaluation of true-breeding types from among the resulting progeny. All the varieties now in use have resulted from this breeding method. In the development of new varieties major attention has been given to short, stiff-strawed types able to make effective use of large quantities of fertilizer.

The first artificial fertilizers to be used extensively were fish-scrap and soybean cake. These were replaced by ammonium sulfate, superphosphate, and other chemical fertilizers. Attention has also been given to soil-dressing, deep plowing, and a more liberal use of iron and other minor elements. Current rates of application of nitrogen, phosphorus, and potassium are higher for Japan than for any other rice-producing country.

With the expansion and intensification of rice production, both disease and insect infestation became increasingly important. Efforts toward disease control have been continuing, use having been made of resistant varieties and of fungicides ranging from Bordeaux mixture to the new mercury and phosphorus compounds. The earlier measures for controlling stem borer and leafhoppers ranged from the burning of refuse to applications of whale oil. Extensive use is now being made of the many organic insecticides.

Wheat Production in the United States

Wheat is the world's second most important food crop. Approximately 15 percent of the total supply is produced within the United States, where five main types are grown: soft red winter, hard red winter, hard red spring, white, and durum. Each of these types has its maximum concentration in a different geographical area, each fills a special commercial need, and each presents unique problems with respect to quality evaluation, resistance to disease and to insect infestation, and hazards of production.

Wheat is not native to the United States. The varieties grown during the colonial period and the era of expansion were direct importations from abroad or selections of deviant types within the imported strains. The scientific approach to the improvement of wheat dates from about 1900. The first efforts were directed toward selection of pure lines within the better adapted strains. The possibilities of improvement under this method were soon exhausted. Increased genetic variability was obtained through hybridization, followed by intensive selection within the segregating populations. This breeding method is responsible for all of our modern varieties of wheat.

Average per-acre yields have doubled in the past 30 years. The impact on the economy has been greater than this rate of increase would suggest. Severe losses from stem rust were experienced in 6 of the 20 years between 1920 and 1940, and measurable losses occurred in many of the remaining years. Rust-resistant types in a continuous succession have been developed, and used extensively for a time, only to be replaced by newer strains in the continuing battle to cope with the ever-changing biotypes of the pathogen. In comparisons involving old and new varieties, in the absence of rust epiphytotics the newer varieties exhibit only moderate superiority, suggesting that the greater selective pressure has been for resistivity to disease.

This situation has been drastically changed in the Pacific Northwest in recent years with the development of new semi-dwarf varieties. These types have a tremendous capacity to respond to improved cultural practices, particularly to increased levels of nitrogen fertilization. Yields of 200 bushels per acre (13,450 kilograms per hectare) have been recorded. Comparative yields for the area and for the nation were 38 and 23 bushels, respectively. Northwestern Europe provides a more favorable climate for wheat, and average yields for the same period would approximate 60 bushels per acre. Unfortunately the semi-dwarf types adapted to the Pacific Northwest do not appear to have the same yield potential in other major wheat-producing areas of the United States. Work is progressing, however, on the development of semi-dwarf types adapted to other geographical areas.

Corn Production in the United States

The development and utilization of hybrid corn has had an important impact on our agricultural economy. In the early 1930's, before hybrid corn was used, the United States produced approximately 2.5 billion bushels of corn per year on roughly 100 million acres. In 1963 we produced over 4 billion bushels on 60 million acres—that is, 70 percent more corn on 40 percent fewer acres. In other words, the average per-acre yield of corn has nearly tripled in the past 30 years. In this same period the percentage of our corn acreage planted to hybrids has increased from 0.1 to more than 95 percent. The pertinent data are presented in Table 1.

I do not mean to imply that the increases in production, just detailed, have resulted solely from genetic improvements. Genetic improvements, however, have been one of the components of what may be described as an agricultural revolution. Other components include the use of increasing quantities of fertilizer; an increase in plant populations; improved means of controlling weeds, insects, and disease; and better timing of all farming operations, made possible by the availability of more efficient machinery. It would be extremely difficult to assign realistic weights to these individual components, inasmuch as their relative importance would vary for different crops.

In the case of corn, however, the development and adoption of hybrids in the major production areas preceded and made economically feasible the utilization or improvement of the other components. Only limited quantities of fertilizer were used on open-pollinated varieties because yield response from such applications was limited. The open-pollinated varieties were susceptible to root-lodging and stalk-breaking, thus mechanical harvesting was both costly and inefficient. Population densities were low, by current standards, because the varieties could not tolerate heavier planting without reductions in yield.

Many farmers felt that the public research agencies had little real knowledge of agricultural problems and were slow to accept new recommendations. This general attitude accounts for the initial reluctance to accept hybrid corn. The superiority of this product was readily apparent, however, and after the first few years the rate of utilization was limited only by the availability of seed. In the Corn Belt the transition from open-pollinated varieties to hybrids was essentially completed in a 10-year period. Hybrid corn and the many other more recent innovations have resulted in a drastic change in the farmer's viewpoint.

Farmers now recognize the value of research, do a considerable amount of experimentation on their own initiative, and tend to adopt new practices before their value has been adequately established. This historical sequence must be kept in mind in any attempt to extrapolate from our highly developed agricultural economy to the agricultural economy of the developing countries.

Most of the developing countries lie outside the latitudes of the United States. Although basic principles know no geographical boundaries, the practices flowing from such research have strong ecological limitations. In general the improved crop varieties grown in the United States are unsuited to the requirements of the developing countries. When grown in Kenya, a hybrid from the Corn Belt may be inferior to a local unimproved variety. A fertilizer regime suited to the southeastern United States may be quite inappropriate in Nigeria. Improved crop varieties and management and cultural practices suitable for the developing countries must be developed through locally conducted research.

Table 1. Corn acreage, production, average yields per acre, and percentage of acreage planted to hybrids for selected years during the period 1933 to 1964. [*Agricultural Statistics* (U.S. Department of Agriculture)]

Year	Acreage harvested (1000 acres)	Total production (1000 bushels)	Average yield (bushels/acre)	Percent of acreage planted to hybrids
1933	105,918	2,397,593	22.6	0.1
1938	92,160	2,548,753	27.7	14.9
1943	92,060	2,965,980	32.2	52.4
1948	83,778	3,605,078	42.5	76.0
1953	80,459	3,209,896	39.9	86.5
1958	63,549	3,356,205	52.8	93.9
1963	60,549	4,091,785	67.6	95.0+

International Rice Research Institute

The International Rice Research Institute was established at Los Baños, the Philippines, in 1961. The research program organized possibly represents the most extensive effort yet made, within a developing country, to study all factors affecting production of a single crop. The institute is jointly sponsored by the Ford and Rockefeller foundations and has a senior staff of approximately 20 scientists, representing all the major areas which affect production capabilities. These areas include genetics and breeding, physiology, pathology, soil science, agricultural engineering, entomology, crop production, management and rotations, economics, and extension. It became apparent almost immediately that neither the technology nor the varieties developed in Japan or the United States were suited to tropical regions.

Marked progress has been achieved in several areas. Information has been accumulated on growth form, on efficient utilization of sunlight, on short-statured types with erect leaves, and on the minimizing of shading effects. Through the use of insecticides and insect-resistant plant varieties, damage caused by the major insect pests has been materially reduced. In some experimental plantings, control of the stem borer through the use of the insecticide gamma BHC has given yield increases of 150 percent. Extensive screening within the world rice collection, maintained at Los Baños, has revealed types resistant to some virus diseases, to leaf blight, to certain strains of rice blast, and to other important diseases. Resistance is being incorporated into high-yielding types. Striking increases in yield have been achieved through nitrogen fertilization. In some instances the return on investment in fertilizer has been as high as 600 percent, as calculated on the assumption that nitrogen costs about four times as much as paddy rice.

The opportunities for growing two or more crops of rice per year depend upon the availability of water and the growth requirements of the varieties used. The early short-statured varieties are well suited for this purpose. Where water is limiting, sorghum, mung beans, and other short-season crops may follow rice. Some form of multiple cropping appears to offer great promise for increasing total production.

Perhaps the most striking of the short-term developments has been development of the variety IR-8. This short-statured type has many of the characteristics desired, and has given yields of over 10 metric tons of rough rice under conditions in which the tall *Oryza indica* types produced less than 6 tons. Yields of IR-8 have also been high in experimental tests in Pakistan, Thailand, Malaysia, and India. In some cases yields of IR-8 have been double those of local varieties. Production of seed of IR-8 has been increased, so that additional comparative trials may be made and planting of IR-8 may be started in these countries. At the same time, work on breeding is going forward in an effort to incorporate greater resistance to disease, improved milling characteristics, and improved quality of the rice.

Rockefeller Agricultural Program in Mexico

A research program involving the Rockefeller Foundation and the Mexican Ministry of Agriculture was initiated in 1943. This was a broad-based program, designed to improve the agriculture of Mexico and to provide opportunity for the training of Mexican scientists who would eventually assume leadership of all phases of research. The operation has been so successful that it has served as a model for other assistance programs. Although work was initiated with several crops, here I consider only one phase—wheat research.

In 1943, when the program was initiated, Mexico imported half of the wheat consumed. At present, in spite of the high rate of population increase during the past 20 years, Mexico is a wheat-exporting nation. The progress achieved is shown in Table 2.

This increase in production has been achieved through a combination of research developments in several disciplines: genetics and breeding, soil fertility, irrigation management, plant pathology, entomology, and cereal technology. Stem rust (*Puccinia graminis* var. *tritici*) and stripe rust (*P. glumarum*) were the diseases of primary importance. Extensive use was made of known sources of resistance, and new sources were identified. The first of many improved varieties was released in 1947. A continuing succession of new varieties followed, each superior in productive capacity to those it replaced. The most spectacular developments have been achieved in recent years with the release and rapid adoption of several semi-dwarf varieties.

As is often the case with new varieties, the maximum utilization of genetic potential can be achieved only through a complete reevaluation of production practices. The new semi-dwarf types could make effective use of up to 140 to 160 pounds of nitrogen per acre. Similarly, under the heavy cropping practices followed, applications of 40 pounds of phosphoric acid became profitable. Four irrigations were required where two had previously been adequate. With this combination of improved varieties and modified management practices, yields of 80 to 100 bushels per acre were achieved. This is in contrast to the 7- to 10-bushel yields that were common with the varieties and cultural practices used in 1943.

In addition to the increase in total production which has been achieved in Mexico, this program has made other outstanding contributions.

The new varieties developed in this program are relatively insensitive to day length and therefore exhibit wide adaptability. One strain, designated Mexipak, is currently being grown extensively in Pakistan.

Where stem rust is a serious problem, new resistant varieties resist rust for approximately 5 years, after which time a new race of rust, to which the variety is susceptible, becomes predominant. The concept of controlled backcross derivatives (multilineal varieties) was developed, in which each component of the mixture would possess resistance to a different race or constellation of races of rust. Practical results with the method have been satisfactory. Recently, the concept has been extended to include hybrid seed production, when this becomes feasible in wheat.

Techniques for early-generation testing of gluten quality, which should simplify the evaluation of quality, have been developed.

Table 2. The impact of research on wheat production in Mexico. [N. E. Borlaug, *Phytopathol.* **55**, 1088 (1965)]

Year	Cultivated area (1000 hectares)	Yield (kg/hectare)	Production (1000 metric tons)
1945	500	750	330
1950	625	900	600
1955	790	1,100	850
1960	840	1,417	1,200
1964	846	2,600	2,200

Important as these developments have been, they are probably overshadowed by the extensive training aspects which have been an integral part of the program. In the 20 years from 1943 to 1963, more than 700 young men and women, representing many different countries, received in-service training. Many of these received advanced degrees and are now contributing to agricultural progress in their respective countries.

Maize Improvement in Kenya

The maize-improvement program of Kenya (*maize* is the common term for corn outside the United States) provides a striking illustration of the genetic improvement that is possible when other technological requirements are met. Support for this program is provided by the Kenya Government, the Kenya Maize and Produce Marketing Board, the Ministry of Overseas Development (Great Britain), the Rockefeller Foundation, and the United States AID-ARS Major Cereals in Africa Project. The research staff includes both geneticists and agronomists. Excellent and widespread extension support has been provided by the Kenya Ministry of Agriculture.

This maize-breeding program was initiated in 1958 as a conventional inbreeding-hybridization program based on use of the local variety, Kenya Flat White. By 1963 a double-cross hybrid which gave yield increases of 25 percent had been developed; the percentage increase was roughly equivalent to that achieved in the United States with the first hybrids produced commercially.

Table 3. Acreages of hybrid maize grown in Kenya. ["Major Cereals in Africa Project Third Annual Report"]

Year	Large-scale farms (acres)	Small-scale farms (acres)
1963	300	10
1964	27,000	3,000
1965	52,000	18,000
1966	50,000	50,000
1967*	100,000	350,000

* This projection is based on seed produced and seed orders currently in hand.

During the early stages of this program it became apparent that lack of genetic diversity was limiting progress. Extensive introductions were made from the United States, from Central America, and from northern South America. The great bulk of this introduced material was unadapted and was discarded. A few of the high-altitude types from Central and South America appeared worthy of further evaluation. This exotic material was crossed with the local variety, and the resulting hybrids were evaluated in yield trials. One of these, Kenya Flat White × Ecuador 573, gave yields equal or superior to those of the double-cross hybrid, depending upon altitude and fertility level. As the varietal hybrid possessed the greater potential for yield enhancement, breeding efforts were increasingly directed toward improvement of the two base populations.

Agronomic research had established optimum planting densities and planting dates, as well as efficient fertilization practices. The Ministry of Agriculture established an effective demonstration program, showing the advantages of hybrids over the local variety of maize and the relative importance of the major management practices. The Kenya Seed Company, which had specialized in grass-seed production, was induced to undertake large-scale production and distribution of hybrid maize.

Hybrid seed was first offered under a package plan. Each purchaser of seed was obliged to buy fertilizer of the recommended formulation and amount, and each agreed to follow certain minimum cultural recommendations. The utilization of hybrid seed which has been attained is shown in Table 3.

Each year the acreage of hybrid grown has been limited by shortage of seed rather than by lack of demand. After an initial lag, acceptance by the small-scale native farmer has been as great as acceptance by the large-scale farmer. Because of the procedures followed, the farmers consider hybrid maize to be a new crop, and the saving of seed from the hybrid planting, F_2 seed, has not been a problem.

This program involving use of hybrid seed, proper fertilization, and improved cultural practices has already had an important impact on total production. Further increases appear to be quite feasible. The genetic variance of the two parental varieties has been found to be primarily additive. Simple selection schemes have resulted in yield increases of 10 percent in the parental populations, and this improvement is retained in their F_1 hybrids.

Breeding programs such as the one in Kenya are admirably designed to fulfill both short- and long-range needs. Short-term needs are met by the rapid development and utilization of improved hybrids. Substantial improvement of the parental types is possible through simple selection schemes which pose minimum demands for trained manpower, financial support, or operational facilities. The improvement achieved in the base parental populations increases their potential value as sources of inbred lines, should a conventional inbreeding-hybridization program later become desirable.

Similar programs are feasible in many of the developing countries. Varietal hybrids, superior to the best available double crosses, have been identified in Mexico, India, and Thailand, but, outside of Kenya, little commercial use is being made of such material. This appears to be largely a problem of seed-production capabilities and of status. Because single and double crosses constitute the hybrids of commerce within the United States and other developed countries, the developing countries feel that commercial utilization of heterosis should be deferred until they can market hybrids of similar types. Thus substantial, immediate, and potential progress is being sacrificed to prestige.

These examples of success need not be unique. The improved varieties of rice, wheat, and maize, developed in the programs cited, are being extensively used outside the area of their development. Similar programs could develop new types of these or other crops to satisfy different ecological requirements. A total increase in food production of 50 percent in the developing countries appears to be a completely realistic goal. An increase in wheat yields of this magnitude in India would represent over 6.5 million metric tons.

Requirements for an Effective Assistance Program

A consideration of programs exhibiting varying degrees of success suggests that significant progress requires the fulfillment of certain minimum conditions. (i) A realistic system of research priorities must be developed. Under food-deficit conditions emphasis should be given to one or two of the major food crops of the area. (ii) The program must be broadly based. Staffing must include research scientists representing several disciplines (genetics, agronomy, plant pathology, entomology, and so on) if the program is to achieve continuing success. The concept of "critical mass" in nuclear physics provides a useful analogy. A vigorous extension program must complement research activities. (iii) The scientific staff must actively participate in the research. Consultative and advisory functions have their place, but an adequate program cannot be developed on the basis of these alone. (iv) Adequate financial support must be provided, and operations in a foreign country are always expensive. (v) Provision must be made for the training of nationals. Such persons must be assigned responsibility as rapidly as their training and aptitude will permit. (vi) Governmental policies must be favorable to agricultural development. Provision must be made for satisfying a wide variety of needs—adequate supplies of fertilizers and other agricultural chemicals, a realistic pricing policy for agricultural produce to make the adoption of improved techniques attractive to farmers, and policies which will permit the development of an effective seed production and distribution industry responsive to local needs, to name only a few.

The importance of the first five requirements is generally recognized. The necessity for the sixth is often overlooked. The achievement of increased agricultural productivity in the developing countries requires more than the improvement of crop plants and associated management practices. Favorable economic, political, and social conditions and policies also are essential.

The food shortage in India has been much in the news and may thus serve as a useful illustration. It should be stressed that the situation in India is not unique. Detailed consideration of governmental policies and priorities lies outside the scope of this article and of my capabilities. It is readily apparent, however, that, had agriculture received a higher priority, the current situation would be much less critical than it is.

India uses about 4 pounds of fertilizer per acre (4½ kilograms per hectare). Local varieties of wheat, rice, and corn have a limited capacity to respond to high levels of fertilization. The new varieties of wheat introduced from Mexico, however, are much more responsive to application of fertilizer. Yield increases of at least 50 percent are possible, under adequate management. If all the fertilizer currently available in India were used on such varieties, only a fraction of the wheat acreage could be fertilized at the optimum rate. Similar situations prevail for the new varieties of rice and for corn hybrids. Thus, potential gain in food production has not been realized because of inadequate supplies and the high cost of fertilizers.

India produces some nitrogenous fertilizer and imports more. Importation costs represent a serious drain on the supply of hard currency. Nitrogenous fertilizers could be produced locally from either naphtha or natural gas. The need for a major expansion of this industry has been recognized in the successive 5-year plans, but the goals established fall short of the need, and no decision has yet been reached on the production process to be used.

An effective seed industry is essential to agricultural progress. Historically, government-controlled operations have been unsatisfactory. The quality of seed produced is often inferior, distribution is inadequate, and seed-production goals are relatively insensitive to local needs.

Other instances could be cited, in India and other developing countries, of the effects of low priorities for agricultural development on food-production capabilities.

Conclusion

The following general conclusions appear valid. The developed countries cannot feed the world. On a short-term basis, food must be supplied to developing countries as needs exist. A long-continuing policy of supplying food grains, through donation or by sale, may be self-defeating if this practice tends to limit expansion of local food-production capabilities.

Tremendous possibilities exist for an expansion of food production within the developing countries. The extent to which this potential is realized will depend upon the scope of assistance programs undertaken, and upon the priorities assigned to agriculture by the developing nations. Even though capabilities are fully utilized, the result may still be inadequate if population growth remains unchecked.