75. E. T. Walters and J. Byrne, *Soc. Neurosci. Abstr.*, in press.
76. T. Abrams, R. D. Hawkins, T. J. Carew, E. R. Kandel, *Soc. Neurosci. Abstr.*, in press.
77. Y. Dudai and W. G. Quinn, *Trends Neurosci.* **3**, 28 (1980); Y. Dudai, Y. N. Jan, D. Byers, W. G. Quinn, S. Benzer, *Proc. Natl. Acad. Sci. U.S.A.* **73**, 1683 (1976).
78. D. Byers, R. L. Davis, J. A. Kiger, Jr., *Nature (London)* **289**, 79 (1981).
79. J. Duerr and W. G. Quinn, *Proc. Natl. Acad. Sci. U.S.A.*, in press.
80. A. N. Epstein, *Neurosci. Res. Program Bull.* **17**, 634 (1979).
81. E. T. Walters, T. J. Carew, E. R. Kandel, *Proc. Natl. Acad. Sci. U.S.A.* **76**, 6675 (1979); T. J. Carew, E. T. Walters, E. R. Kandel, *Science* **211**, 501 (1981).
82. A. Gelperin and D. Forsythe, in *Simpler Networks and Behavior*, J. C. Fentress, Ed. (Sinauer, Sunderland, Mass., 1976), p. 239.
83. G. J. Mpitsos and W. J. Davis, *Science* **180**, 317 (1973); G. J. Mpitsos and S. D. Collins, *ibid.* **188**, 954 (1975).
84. T. J. Crow and D. L. Alkon, *ibid.* **201**, 1239 (1978); D. L. Alkon, I. Lederhendler, J. J. Shoukimas, *ibid.* **215**, 693 (1982).
85. G. Hoyle, in *Cellular Pacemakers*, D. O. Carpenter, Ed. (Wiley, New York, 1982), vol. 12, pp. 3–26.
86. F. Belardetti, C. Biondi, L. Colombaioni, M. Brunelli, A. Trevisani, *Brain Res.* **246**, 89 (1982).
87. Supported by NIMH grant MH 26212, by NIH grants GM 23540 and NS 15834, and by an award from the McKnight Foundation.

Plant Productivity and Environment

J. S. Boyer

Summary. An analysis of major U.S. crops shows that there is a large genetic potential for yield that is unrealized because of the need for better adaptation of the plants to the environments in which they are grown. Evidence from native populations suggests that high productivity can occur in these environments and that opportunities for improving production in unfavorable environments are substantial. Genotypic selection for adaptation to such environments has already played an important role in agriculture, but the fundamental mechanisms are poorly understood. Recent scientific advances make exploration of these mechanisms more feasible and could result in large gains in productivity.

Most plants grow in environments that are, to a considerable degree, unfavorable for plant growth. In consequence, they have developed numerous sophisticated adaptations, some of which are unique in the biological world. Roots and stems gather and distribute sparse water and nutrients, surface tissues and stomata conserve water, and leaves intercept solar radiation. Because these features make plants nonmobile and because reproduction in most plants depends on genetic recombination, evolution has selected for floral structures that take advantage of agents that move in the environment: wind, water, and animals.

Plants growing under natural conditions have as the ultimate criterion for productivity the ability to reproduce. If reproduction is unsuccessful, all other criteria of productivity become meaningless because the individuals disappear from subsequent populations. In agriculture the criteria are similar, since reproductive structures are often the economically valuable parts of the plant. However, in agriculture reproductive success is gauged not only by the ability to leave descendants in subsequent growing seasons but also by the productivity of a unit of land. Also, reproductive success bears little relation to the composition of the succeeding plant community. Thus the forces of evolution are coupled differently to productivity in agriculture than to productivity in nature, and this has provided opportunities to use man-made selection pressures to change plants to types successful in agriculture. The techniques involve plant breeding and cultural practices that favor high economic yields. Although the specific techniques are numerous, there appear to be certain ones that have not been widely used but which have much promise for further increasing productivity. These techniques are the subject of this article.

Impact of Environment

Plants growing in natural environments are often prevented from expressing their full genetic potential for reproduction and are considered "stressed." The best way of assessing this potential is by determining plant productivity under conditions that are nonlimiting. One method is to identify the highest yields attained by crops. Table 1 shows the average yields and record yields of eight major crops as of 1975 (*1*). Record yields were three to seven times greater than the average yields. Corn, for example, yielded 4600 kilograms per hectare on average but had a record yield of 19,300 kilograms per hectare (Table 1). For all the crops with economically valuable reproductive structures (corn, wheat, soybeans, sorghum, oats, and barley), the discrepancy between average and record yields is at least as large as for corn. For the crops having marketable vegetative structures (potatoes and sugar beets), the discrepancy is smaller than for the other crops because the complexities of reproductive development are not involved. Nonetheless, record yields were still three times larger than average yields.

Two conclusions can be drawn from these data. First, the genetic potential for very high productivity is present in the crops of today. Second, productivity usually falls far short of the potential. Hence, improvements in plant productivity need not rest solely on increases in genetic potential but should also emphasize ways of bringing productivity closer to the existing genetic potential. Large increases in productivity should be possible with this approach.

Why is higher productivity not realized? Disease and insect losses, while often devastating to individual farmers, depress U.S. yields below the genetic potential by only 4.1 and 2.6 percent, respectively (Table 1) (*2*). The remainder must be attributed to unfavorable physicochemical environments caused by weedy competitors, inappropriate soils, and unfavorable climates. As shown in Table 1, unfavorable physicochemical environments depress yields 71.1 percent, of which 2.6 percent is attributable to weeds (*2*). Some of these losses can be attributed to inherently unfavorable environments and some to lack of use of

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Table 1. Record yields, average yields, and yield losses due to diseases, insects, and unfavorable physicochemical environments for major U.S. crops (1, 2). Values are kilograms per hectare.

Crop	Record yield	Average yield	Average losses			
			Diseases	Insects	Unfavorable environment*	
					Weeds	Other
Corn	19,300	4,600	750	691	511	12,700
Wheat	14,500	1,880	336	134	256	11,900
Soybeans	7,390	1,610	269	67	330	5,120
Sorghum	20,100	2,830	314	314	423	16,200
Oats	10,600	1,720	465	107	352	7,960
Barley	11,400	2,050	377	108	280	8,590
Potatoes	94,100	28,300	8,000	5,900	875	50,900
Sugar beets	121,000	42,600	6,700	6,700	3,700	61,300
Mean percentage of record yield		21.6	4.1	2.6	2.6	69.1

*Calculated as follows: record yield − (average yield + disease loss + insect loss).

known management practices by farmers, often for economic reasons.

The kinds of physicochemical environments that affect plants adversely can be quantified even though they overlap and are often sporadic in their impact. A classification of U.S. soils (3) indicates that those with low water availability occupy the largest fraction (44.9 percent) of the U.S. land surface (Table 2). Soils that are too wet or too cold cover 16.5 and 15.7 percent of the United States, respectively. Finally, saline soil, alkaline soil, and soilless areas account for 7.4 percent. Only 12.1 percent of the land surface is free from physicochemical problems, and this area, when supplied with plant nutrients to replace those removed when crops are harvested, is our most productive. Similar data apply to the soils of the world (4).

The effects of unfavorable climates are as pervasive as those of unfavorable soils. As shown in Table 3, of the total indemnification made to U.S. farmers for crop losses (5), drought, excessive water, and cold account for 71 percent.

Possible Technological Solutions

The major physicochemical resources of plants are water, soil nutrients, carbon dioxide, oxygen, and radiation. Water is the most limiting resource (Tables 2 and 3), so irrigation has been an important contributor to increased yields. About 83 percent of the water that is consumed (that is, not recycled) is devoted to irrigation (6), and runoff and ground water supplies can support about double this amount (6). About 5 percent of U.S. farmland is irrigated (5), and this area is growing, particularly in the Southeast (7) and in parts of the Great Plains.

Water that is usable for irrigation must increasingly be shared with municipal and industrial users, who offer larger economic returns (estimated at 50 to 1) than can be obtained from irrigation (8). Furthermore, irrigation brings with it problems of salinization. The accumulation of salts in agricultural soils is a problem that has plagued civilization for thousands of years. The persistence of this problem suggests that there are no easy solutions, although recent evidence (9) indicates that crops can be adapted to more saline conditions than previously thought possible. Considering competing needs and possible soil degradation, it is likely that no more than 10 percent of U.S. agricultural land will be irrigated. Therefore, irrigation can only be a partial solution to the water resource problem.

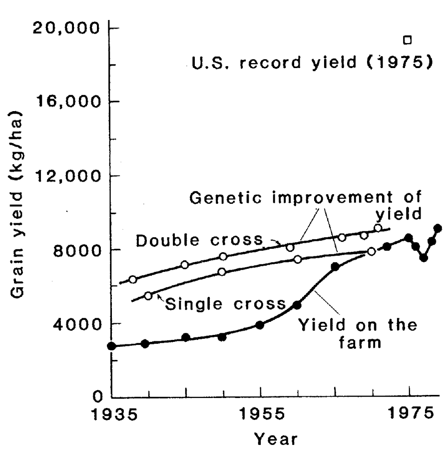

Fig. 1. Genetic improvement of yield, grain yield on the farm, and record yield for corn during a 40-year period. Genetic improvement of double-cross and single-cross hybrids was determined by growing introductions from the years indicated in a common field environment in Iowa; current planting densities and techniques were used (12). Grain yield on the farm was determined from records for Champaign County, Illinois. Increased yield due to genetic improvement was 50 and 53 percent of yield increase on the farm for single- and double-cross hybrids, respectively (12).

Plant nutrients will probably be more available than water in the future. World demand for nitrogen, phosphorus, and potassium is expected to quadruple during the next 30 to 40 years, and supplies are likely to remain adequate, although the most accessible sources of phosphorus and potassium may ultimately be depleted (10). The greatest problem is the energy used in the manufacture of ammonia, which is the largest energy input to the nonirrigated farm (11). Therefore, the cost of nutrients will be a major consideration in the future. Similarly, the cost of pesticides will increase as energy costs escalate.

The conclusions are inescapable: water and nutrient resources are often limited, and economic and environmental problems are likely to restrain their use.

Plant Adaptation to Existing Environments

Advances in agricultural production have relied on the availability and low cost of environmental resources. Energy for irrigation has been cheap, and plant nutrients have been abundant and inexpensive. This has allowed the use of increasingly dense plant populations adapted to high production in environments richly endowed with resources.

As an example, consider corn cultivation in Champaign County, Illinois. When drained, most of the soil in this area has no physicochemical limitations (Table 2), and irrigation is usually unnecessary. During the past 35 years, corn yields have more than tripled (Fig. 1). Increases between 1935 and 1955 were largely attributable to increased use of hybrid corn. From 1950 to the present, increased yields have been attributable to the increased use of plant nutrients, particularly nitrogen (ammonia). To determine how much of this increase is associated with genetic adaptation, old and new maize hybrids were planted at modern population densities in a fertile environment in Iowa (12). Hybrids released in recent years performed better than older hybrids, indicating that genetic adaptation has accounted for 50 percent (single cross) and 53 percent (double cross) of the increased yield on the farm (Fig. 1). Thus the adaptation of maize hybrids to fertile environments has accounted for about half the total increase in corn yields experienced by farmers (12), the remainder being attributable to improved fertilization, pest control, and other cultural practices.

The abundant resource approach to plant production has the advantage that the environment is reasonably predictable and that genotypes can be adapted to it. The approach is often justified as the only one giving a high economic return. However, as the scarcity of agricultural inputs increases, the cost of growing crops increases and alternatives will be sought. Already the cost of fuel, nutrients, pesticides, and loans is causing many farmers to reduce inputs. The feasibility of their approach is illustrated by a recent comparison of farms consuming large amounts of nutrients and pesticides with farms consuming smaller amounts (*13*). Both types of farms had similar incomes because somewhat lower yields associated with the lower inputs were balanced by lower costs.

The costs of agriculture also include longer term environmental costs such as soil erosion. As immediate costs increase there is a tendency for longer term costs to increase, because one method of maintaining farm income is to abandon expensive conservation practices such as the use of cover crops and contour tillage (*14*). The trend toward continuous cropping of corn and other row crops has caused severe erosion by wind and water in many productive regions of the United States (*14*). These losses will inevitably limit yields as the area of soil with no physicochemical problems shrinks and problem soils become ever more prevalent.

Responding effectively to mounting world food demands, economic pressures, and the need for conservation are dilemmas for farmers and legislators alike. If present cropping practices continue in the United States, lower yields due to unfavorable soil environments will be forced upon us (*14*). A greater emphasis on conservation would render production more sustainable but would necessitate alterations in many farming methods. The most likely incentive will be economic; we can therefore expect that cost pressures will determine the course of agricultural practice. In this situation, plant types that are productive with lower inputs should be readily accepted by farmers.

An important question is whether plants experiencing low inputs can be highly productive. By comparing the productivity of plants in natural communities, where resoures are limited, with productivity in agricultural communities, it should be possible to determine whether natural selection has provided plants with effective ways of dealing with limited resources.

One natural community that allows this comparison is a pure stand of giant ragweed (*Ambrosia trifida*) in Champaign County (*15*). The aboveground biomass of the ragweed community was similar to that of corn and greater than that of soybeans (Fig. 2) even though no attempt was made to manage the ragweed community, whereas corn (*16*) and soybeans (*17*) required intensive management. Seed biomass in the ragweed was less than in corn or soybeans (Fig. 2), probably because selection pressures have not favored seed production per unit of land area under natural conditions. Even so, the production of ragweed seed was equal to the average soybean grain yield per hectare in the United States in 1975 (Table 1). Ragweed is unlikely to be used as a food crop, but its productivity illustrates that mechanisms in native vegetation allow high production even though inputs are low. Methods of selecting for these characteristics in our crops could have beneficial effects on yields as inputs decrease.

Table 2. Area of the United States with soils subject to environmental limitations of various types (*3*).

Environmental limitation	Area of U.S. soil affected (%)
Drought	25.3
Shallowness	19.6
Cold	16.5
Wet	15.7
Alkaline salts	2.9
Saline or no soil	4.5
Other	3.4
None	12.1

Table 3. Distribution of insurance indemnities for crop losses in the United States from 1939 to 1978 (*5*).

Cause of crop loss	Proportion of payments (%)
Drought	40.8
Excess water	16.4
Cold	13.8
Hail	11.3
Wind	7.0
Insect	4.5
Disease	2.7
Flood	2.1
Other	1.5

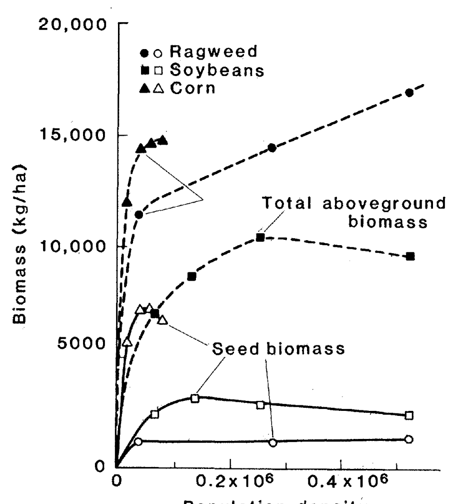

Fig. 2. Aboveground biomass and seed biomass at various population densities (plants per hectare) in a native plant community of giant ragweed (*Ambrosia trifida*) (*15*) and in managed crops of soybeans (*17*) and corn (*16*).

This is not to imply that native plants require fewer soil nutrients and other resources. There are genetic differences in the ability of plants to accumulate nutrients from a given soil (*18*). Particularly large effects are observed with iron, nitrogen, phosphorus, and certain micronutrients (*18*). Thus, selection for efficient nutrient acquisition and avoidance of ion toxicities may be one approach to adapting plants to unfavorable environments.

Is there evidence that such selection improves yield? Epstein *et al.* (*9*) showed that the ability of conventional crops to tolerate saline conditions can be improved by imposing appropriate selection pressures. Salt-tolerant tomato genotypes were grown with irrigation water having 70 percent of the salinity of seawater. Their yields were 20 percent of those of control tomatoes grown with fresh water. The domestic cultivar died under the saline conditions. Also, wheat biomass production was significantly increased by selection of salt-tolerant lines (*9*). It may be surprising that, with the impact of salinity on agriculture in past civilizations—which lost vast areas of production because of improper irrigation techniques—salinity tolerance is not at its maximum in present-day crops. However, selection has been sporadic, and sufficient genotypic variation still exists to provide an opportunity for improved yields under saline conditions.

Similar success has been achieved with iron utilization by plants. Different cultivars within a species differ in their ability to utilize iron, which usually is present in soils in large amounts. The difference is attributable to the ability of roots to solubilize iron in the soil and maintain it in the appropriate redox state in the plant (*18*).

It appears that considerable success can be expected if plant improvement includes selection under conditions that are often unfavorable for growth. The key is to make the selections under the adverse conditions likely to be encountered rather than solely in favorable environments, so that genotypes capable of exploiting limited resources can be identified. With these genotypes, large-scale modification of the environment is less necessary.

Mechanisms of Plant Adaptation to Stress

The mechanisms by which plants cope with adverse environments, while undoubtedly highly evolved, have only begun to be understood. There is increasing awareness that understanding these mechanisms might increase the rate at which crop species can be improved. In addition, such knowledge might suggest entirely different ways of increasing productivity in these environments.

Soybean productivity is lower than that of some other crops (Table 1). Figure 3 shows that there has been a steady increase in the grain yield of this crop in Champaign County. In 1935 yields were about 1500 kg/ha, but by 1975 they had reached 3000 kg/ha. Measurements of the yield of old and new genotypes in a common field environment (Fig. 3) showed that 47 percent of the improvement was due to genetic changes (*19*).

However, this improvement was also associated with changes in the ability of the plants to cope with the Champaign County environment. The genetic improvement of yield in newer cultivars was correlated with an improvement in the average afternoon water potential observed in these cultivars (*19*) when growing in soil containing adequate water (Fig. 4). Water potentials below a threshold of about -11 bars cause inhibition of photosynthesis, transpiration, and nitrogen fixation in soybeans (*20*), and the afternoon water potentials of -12 to -14 bars found in these cultivars (Fig. 4) could inhibit these processes or other similarly sensitive ones. Figure 5 shows that the steep response of photosynthesis to water potentials below -11 bars in soybeans can translate into a large inhibition of activity. It therefore appears that the midday water deficit is a physiological attribute that has been altered by plant breeders in the pursuit of higher yields. This alteration gave the plants a more favorable water status under the atmospheric evaporative conditions prevailing in Champaign County. It seems that, if plant breeders had known that water deficits were prevalent in the cultivars of the day and had bred selectively against this factor, genetic progress might have been more rapid than is indicated in Fig. 4.

That this kind of information can materially increase the effectiveness of breeding programs was illustrated in 1972. My laboratory (*21*) and an Australian group (*22*) showed that plants can compensate osmotically for the onset of dryness in soils, and the growth-maintaining effect of this behavior was also demonstrated (*21*). Morgan (*23*) subsequently found that the capability for osmotic adjustment differs between wheat genotypes, and, in collaboration with Ray Hare, showed that a cultivar selected for this character outyielded conventionally grown cultivars by 100 percent under dry conditions (*24*). Conditions of adequate soil water gave yields comparable to those of the conventional high-yield genotypes, so the adaptation was only called into play under adverse conditions.

This type of selection could not have been made before 1972 because then it was not known that osmotic adjustment occurs in plants growing in dry soil. In this situation, the new knowledge had a rapid impact on productivity.

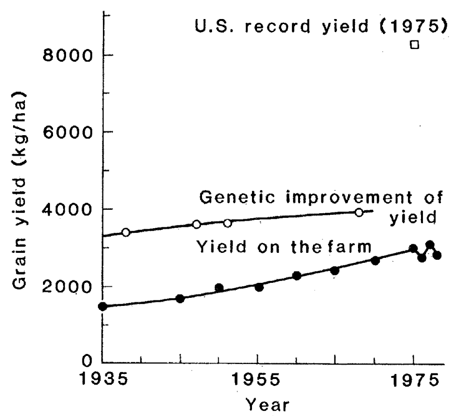

Fig. 3. Genetic improvement of yield, grain yield on the farm, and record yield for soybeans during a 40-year period. Genetic improvement was determined by growing cultivars released during the years indicated in a common field environment in Champaign County; current planting densities and techniques were used (*19*). Grain yield on the farm was determined from records for Champaign County. Increased yield due to genetic improvement was 47 percent of the yield increase on the farm.

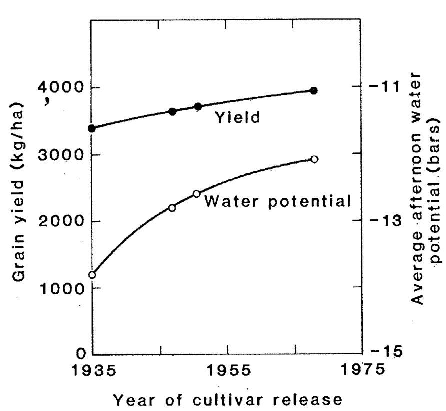

Fig. 4. Grain yield and afternoon water potential of soybean cultivars released during a 40-year period (*19*). Grain yield is the average for 3 years in a common field environment. Leaf water potentials were measured in the same plots and are averaged for the same 3 years. During these years, rainfall was sufficient to support high yields. The low water potentials of old cultivars were caused by poor ability of the plants to extract water from the soil. Water potentials that are more negative represent leaves that are more water-deficient.

Others have also observed a correlation between some aspect of productivity and specific biochemical or physiological phenomena. Pearcy *et al.* (*25*) and Björkman and Badger (*26*) demonstrated that plants in Death Valley, California, lose photosynthetic activity in hot weather because the heat has deleterious effects on chloroplasts. The inhibition is localized in photosystem II and appears to involve an alteration in the lipid membranes of the chloroplasts. Some of these species are capable of acclimating to heat; recent evidence (*26*) suggests that the acclimation can occur in a matter of days. In an extreme environment such as Death Valley, plant success is likely to be tied closely to photosynthetic output. This suggests a means for adapting plants to hot conditions.

It has also been found that some of the effects of water deficits can be attributed to alterations in chloroplast activities, particularly photophosphorylation and photosystem II (*27*). Water potentials low enough to cause an inhibition of photosynthesis in intact leaves cause alterations in chloroplast activity that are equally severe. In addition, the stomata begin to close. The losses in photosynthate cause losses in grain yield (*28*). However, there is evidence that photosynthetic behavior can be altered by prior exposure of the plant to low leaf water potentials (*29*). The plant responds in such a way that the photosynthetic inhibition is delayed during the onset of drought.

Others have shown that mycorrhizae protect plants against phosphorus stress in soils low in phosphorus (*30*) and that plant susceptibility to chill injury is often associated with the fatty acid composition of phospholipids in cell membranes (*31*).

Future Research

Taken together, these findings suggest that, with sufficient understanding of the response of plants to the environment, considerable improvements in plant productivity are possible. Investigations of plant response mechanisms show that specific processes are affected and that the plant has evolved ways to change these processes, leading to adaptation. More important, these changes can be transmitted genetically.

However, much additional research is needed. Only a few studies have been made in which closely related species or lines were compared for their response to a given environmental condition. Comparative studies could provide much more rapid progress in understanding metabolic and genetic aspects of the response of plants to adverse environments. In addition, more needs to be learned about the transfer from one genotype to another of those characters giving advantages in adverse environments. Frequently, this transfer has occurred during selection for yield without the investigators being aware of the physiological attributes of the plant that were responsible for the improvements in yield.

At present, scientific efforts to improve plant productivity fall into two broad categories: (i) selection for superior yield in fertile environments and (ii) basic research emphasizing dramatic alterations in genetic potential for yield by modifying physiological processes, hybridizing different species, and so forth. Although these efforts are worthwhile, the potential for large gains in plant performance in unfavorable environments has, by comparison, been neglected. Plant breeders and geneticists are aware of the contribution of plant adaptation to increased yield but generally have been forced to rely on yield criteria for selection because of the paucity of information showing how environment affects yield.

Despite what has been learned about the responses of plants to unfavorable environments, relatively little has been done to probe the genetic and physiological mechanisms of these responses. There have been only sporadic efforts to demonstrate that a particular physiological system actually regulates the response to a particular environment. Even less has been done to take what information we have and apply it to agricultural species. Exploitation of the available diversity in plants to select and breed for desirable traits is a method of proven effectiveness. In principle, this method could be used to develop environmentally tolerant crops. However, it is necessary to know the traits for which selection is desirable.

A literature survey shows that relatively little research is being done on the mechanisms of plant growth in unfavorable environments (Table 4). Journals dealing exclusively with plant physiology or agronomy devote only about 4 percent of their space to articles that address these fundamental mechanisms.

Table 4. Number of articles devoted to fundamental mechanisms of plant growth in unfavorable environments in 1977. Journals surveyed were *Plant Physiology*, *Planta*, *Physiologia Plantarum*, *Journal of Experimental Botany*, *Australian Journal of Plant Physiology*, *Crop Science*, and *Agronomy Journal*. Numbers in parentheses are percentages.

Journal type	Total articles	Articles devoted to mechanisms of plant growth in unfavorable environments	
		U.S. laboratories	Foreign laboratories
International plant physiology journals	943	46 (4.9)	43 (4.7)
U.S. agronomy journals	490	10 (2.4)	1 (0.2)
Total	1433	56 (3.9)	44 (3.7)

Why has this area of plant science been ignored? One possible reason is the increasingly urban nature of the U.S. population. The comparative isolation of urban dwellers from the factors that affect plant performance causes a tacit feeling that those factors are not important. Individuals who become scientists often carry this impression with them.

A second reason is the lack of suitable scientific tools until recent years. Advances in biochemical techniques, environmental control, and transducer technology now permit many measurements to be easily made that required great effort only a few years ago.

Finally, there have been few identifiable programs to support scientific research in this area. Without such support, scientists are unable to undertake the studies that are necessary and many young people are discouraged from entering the field.

The usual approach to improving agricultural productivity has been to improve the growth environment and select for genotypes that are successful in that environment. The approach has been a good one, and it will continue to be central to agriculture. However, we also need to develop plants to withstand adverse conditions. These environments are everyday phenomena rather than occasional events occurring in faraway places. The study of mechanisms by which adverse environments alter plant behavior represents an area of fundamental regulatory biology that is unique to plants.

To improve the response of plants to adverse environments, more must be learned about desirable traits, the amount of genetic variation of these traits, and the selection procedures for desirable genotypes. The identification of desirable traits is essential for the successful use of genetic diversity in the selection of plant types. In addition, the germ plasm already available as a source of diversity needs to be augmented by the collection of wild relatives. Finally, there is a need for controlled-environment research combined with field testing to identify factors that may have importance in the field environment. Controlled environments permit the behavior of plants to be understood most rapidly without the complicating effects of environmental variability.

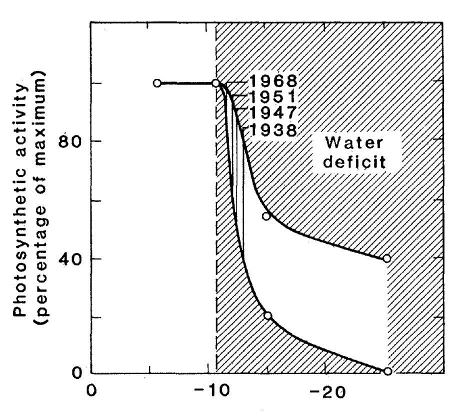

Fig. 5. Response of leaf photosynthetic activity to low leaf water potential in soybeans (*20*). The expected rate of photosynthesis is shown for four cultivars (represented in Fig. 4) according to the year of release of each cultivar. The range of response (*20*) is shown by the open space between the curves.

Conclusions

Improvements in the adaptation of plants to adverse environments can make major contributions to agricultural production in the United States. Progress has already been made by selecting plants for improved yield, but faster progress will occur if the fundamental mechanisms of adaptation are understood. The lack of extensive knowledge of this kind often limits the use of advanced genetic techniques and selection procedures.

The adaptation approach would conserve resources because enhanced nutrient acquisition, drought resistance, ion toxicity avoidance, temperature tolerance, and so forth would be achieved without large-scale modification of the environment. Since agricultural inputs are becoming more costly and scarce, plants having genetic adaptations for improved performance in adverse environments are likely to be readily accepted.

In the evolutionary struggle of native vegetation, certain traits provide an advantage over the competition. When these are understood, we will be in a position to markedly improve plant types and hence to bring about major increases in plant productivity.

References and Notes

1. S. H. Wittwer, *Science* **188**, 579 (1975).
2. Calculated from U.S. Department of Agriculture, *Agric. Handb. No. 291* (1965). The calculated losses are percentages of the record yields.
3. Calculated from U.S. Department of Agriculture, Soil Conservation Service, *Soil Taxonomy* (Government Printing Office, Washington, D.C., 1975).
4. R. Dudal, in *Plant Adaptation to Mineral Stress in Problem Soils*, M. J. Wright, Ed. (Cornell University Agricultural Experiment Station, Ithaca, N.Y., 1976), p. 3.
5. U.S. Department of Agriculture, *Agricultural Statistics* (Government Printing Office, Washington, D.C., 1979).
6. U.S. Department of the Interior, *U.S. Geol. Surv. Circ. No. 765* (1977).
7. R. R. Bruce, J. L. Chesness, T. C. Keisling, J. E. Pallas, Jr., D. A. Smittle, J. R. Stansell, A. W. Thomas, *Irrigation of Crops in the Southeastern United States* (Agricultural Review and Manual No. 9) U.S. Department of Agriculture, Science and Education Administration, New Orleans, La., 1980).
8. M. L. Peterson, *Am. Soc. Agron. Spec. Bull. No. 19* (1971), p. 43.
9. E. Epstein, J. D. Norlyn, D. W. Rush, R. W. Kingsbury, D. B. Kelley, G. A. Cunningham, A. F. Wrona, *Science* **210**, 399 (1980).
10. P. J. Stangel, in *Plant Adaptation to Mineral Stress in Problem Soils*, M. J. Wright, Ed. (Cornell University Agricultural Experiment Station, Ithaca, N.Y., 1976), p. 31.
11. D. Pimentel, L. E. Hurd, A. C. Bellotti, M. J. Forster, I. N. Oka, O. D. Sholes, R. J. Whitman, *Science* **182**, 443 (1973).
12. D. N. Duvick, *Maydica* **22**, 187 (1977).
13. W. Lockeretz, G. Shearer, D. H. Kohl, *Science* **211**, 540 (1981).
14. L. R. Brown, *ibid.* **214**, 995 (1981).
15. H. A. Abul-Fatih, F. A. Bazzaz, R. Hunt, *New Phytol.* **83**, 829 (1979).
16. D. E. Termunde, D. B. Shank, V. A. Dirks, *Agron. J.* **55**, 551 (1963).
17. C. R. Weber, R. M. Shibles, D. E. Byth, *ibid.* **58**, 99 (1966).
18. R. A. Olsen, R. B. Clark, J. H. Bennett, *Am. Sci.* **69**, 378 (1981).
19. J. S. Boyer, R. R. Johnson, S. G. Saupe, *Agron. J.* **72**, 981 (1980).
20. J. S. Boyer, *Plant Physiol.* **46**, 236 (1970); R. Ghorashy, J. W. Pendleton, D. B. Peters, J. S. Boyer, J. E. Beuerlein, *Agron. J.* **63**, 674 (1971); C. Y. Huang, J. S. Boyer, L. N. Vanderhoef, *Plant Physiol.* **56**, 222 (1975).
21. R. F. Meyer and J. S. Boyer, *Planta* **108**, 77 (1972).
22. E. L. Greacen and J. S. Oh, *Nature (London) New Biol.* **235**, 24 (1972).
23. J. M. Morgan, *Nature (London)* **270**, 234 (1977); ——, *J. Exp. Bot.* **31**, 655 (1980).
24. ——, private communication. The new line was selected under greenhouse conditions for ability to compensate osmotically for dry soils. During seasons with adequate water supply, the line gives yields in the field equivalent to those of wheat cultivars grown in Australia (3000 kg/ha). Field tests in dry soil showed yields of 1000 kg/ha whereas local cultivars yielded 500 to 600 kg/ha. The new line is expected to be released next year subject to its passing a commercial milling test.
25. R. W. Pearcy, J. A. Berry, D. C. Fork, *Plant Physiol.* **59**, 873 (1977).
26. O. Björkman and M. Badger, *Carnegie Inst. Washington Yearb. No. 78* (1978), p. 145.
27. J. S. Boyer, in *Water Deficits and Plant Growth*, T. T. Kozlowski, Ed. (Academic Press, New York, 1976), vol. 4, p. 153.
28. H. G. McPherson and J. S. Boyer, *Agron. J.* **69**, 714 (1977).
29. R. C. Ackerson and R. R. Hebert, *Plant Physiol.* **67**, 484 (1981).
30. L. H. Rhodes and J. W. Gerdemann, *New Phytol.* **75**, 555 (1975).
31. J. M. Lyons, *Annu. Rev. Plant Physiol.* **24**, 445 (1973).

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Declaration on Prevention of Nuclear War

On 24 September 1982, this statement was presented to His Holiness, Pope John Paul II, by an assembly of presidents of scientific academies and other scientists from all over the world convened by the Pontifical Academy of Sciences to consider the issue of nuclear warfare.

I. Preamble. Throughout its history, humankind has been confronted with war, but since 1945 the nature of warfare has changed so profoundly that the future of the human race, of generations yet unborn, is imperilled. At the same time, mutual contacts and means of understanding between peoples of the world have been increasing. This is why the yearning for peace is now stronger than ever. Mankind is confronted today with a threat unprecedented in history, arising from the massive and competitive accumulation of nuclear weapons. The existing arsenals, if employed in a major war, could result in the immediate deaths of many hundreds of millions of people, and of untold millions more later through a variety of aftereffects. For the first time, it is possible to cause damage on such a catastrophic scale as to wipe out a large part of civilization and to endanger its very survival. The large-scale use of such weapons could trigger major and irreversible ecological and genetic changes, whose limits cannot be predicted.

Science can offer the world no real defense against the consequences of nuclear war. There is no prospect of making defenses sufficiently effective to protect cities since even a single penetrating nuclear weapon can cause massive destruction. There is no prospect that the mass of the population could be protected against a major nuclear attack or that devastation of the cultural, economic, and industrial base of society could be prevented. The breakdown of social organization, and the magnitude of casualties, will be so large that no medical system can be expected to cope with more than a minute fraction of the victims.

There are now some 50,000 nuclear weapons, some of which have yields a thousand times greater than the bomb that destroyed Hiroshima. The total explosive content of these weapons is equivalent to a million Hiroshima bombs, which corresponds to a yield of some 3 tons of TNT for every person on earth. Yet these stockpiles continue to grow. Moreover, we face the increasing danger that many additional countries will acquire nuclear weapons or develop the capability of producing them.

There is today an almost continuous range of explosive power from the smallest battlefield nuclear weapons to the

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