

Genetic Diversity in Major Farm Crops on the Farm and in Reserve¹

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Genetic vulnerability does not at this time present a major threat to production of United States field crops, according to a 1981 survey of U.S. crop breeding directors. But plant breeders do regard genetic vulnerability as an important and potentially dangerous problem. The 1981 survey indicated that although the genetic base of U.S. field crop production is not as narrow as in 1970, it still is concentrated on a relatively small number of favored cultivars. Genetic diversity is provided, nevertheless, in other and less obvious ways. Survey responses indicated that the genetic base of the elite germplasm pool is wider and provides more useful diversity than is usually supposed. However, breeders also value the national germplasm repositories as indispensable sources of needed diversity.

IN THE BEGINNING

Sheeder Prairie, in central Iowa, is a 10 ha remnant of the millions of hectares of native prairie that once covered the American midwest. In this living museum hundreds of species of plants and animals live in stable and harmonious coexistence. Pocket gophers plow the prairie, turning over the top soil in a 5–10 yr cycle. Legumes add nitrogen; big bluestem and other grasses add organic matter. In drought years, wet years, short seasons, long seasons, the prairie persists, only changing its plant growth habits to accommodate to each new season.

Surrounding Sheeder Prairie—in the state of Iowa—6 mill ha are planted solidly to uniform rows of single-cross hybrid maize. Checkerboarded among the maize plantings are 3 mill ha of equally uniform soybeans. Aside from maize and soybeans very few species of plants now grow anywhere in the entire state, except for a few thousand hectares of oats, alfalfa and wheat and an unstable mixed flora along roadsides, railroads, and watercourses. The prairie is gone.

In 1780, Sheeder Prairie and the rest of Iowa's 12 mill ha of native prairie supported a human population of perhaps 5,000 native Americans, the first Iowans (Blaine, 1979; Smith, 1981).

In 1980, Iowa's 10 mill ha of maize, soybeans and other crops supported 3,000,000 Iowans and, in addition, its crops were exported annually to the rest of the United States and to the world in quantities sufficient to feed upwards of 300,000,000 people (Iowa Crop and Livestock Reporting Service, 1980; Gavan and Dixon, 1975).

As botanists, we mourn the passing of the virgin prairies and we yearn for their return. As realists, we know that a world population of 4 bill people, moving in 20 yr to 6 bill, will not let that happen. Population pressure demands production of food and feed, dependably and in ever increasing amounts and efficiencies. As botanists, how can we reconcile this demand with the laws of nature, as we

¹ Received 23 September 1983; accepted 10 November 1983. Presented to the Thirteenth International Congress of Botany, Sydney, Australia, 28 August 1981.

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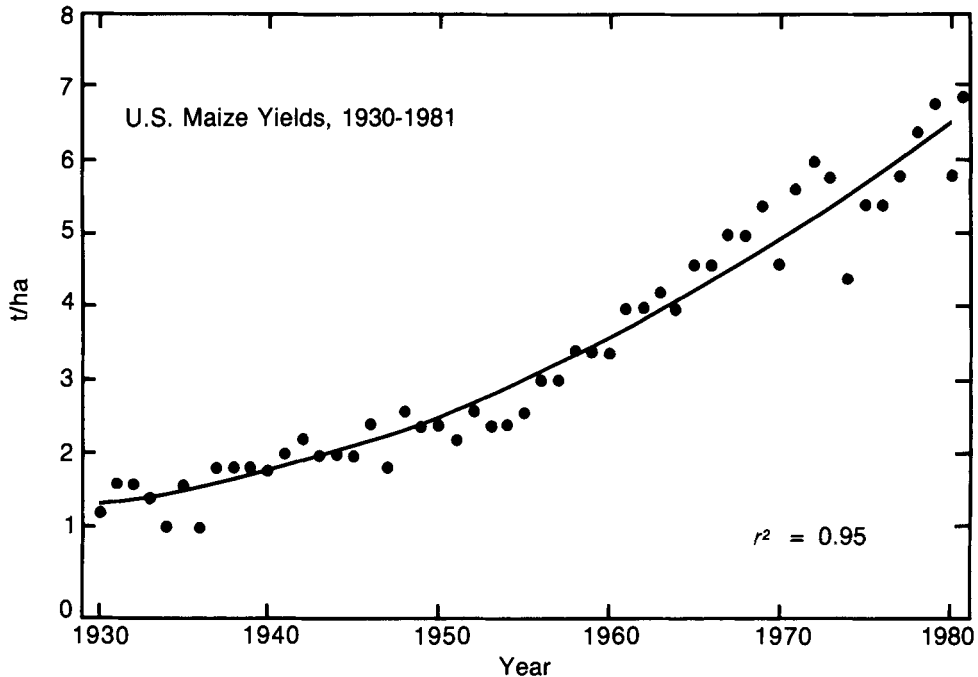


Fig. 1. U.S. maize grain yields, 1930–1981. Each point represents the mean yield for the indicated year. Regression calculated on the basis of 1930–1980 data, using the formula $Y = a + bX + cX^2$. r^2 = coefficient of determination. (Data obtained from various volumes of USDA's *Agricultural Statistics*.)

understand them? Specifically, how can we reconcile the imperatives of maximum yield and efficiency—which call for uniform, intensely managed monocultures—with the imperative of stability, which biologists often equate with diversity?

We in agriculture know that we have been successful in continually increasing the yields and stability of yields of our major farm crops (Newman, 1978). Maize in the United States, for example, has increased in productivity at an average rate of 3%/yr for the past 50 yr (USDA, 1981). This rate of gain has not decreased and shows no signs of doing so (Fig. 1). We are proud of these gains, the result of collaborative efforts of breeders, agronomists and, most important of all, U.S. farmers.

GENETIC VULNERABILITY

But we also know that these gains have been accompanied by an apparent increasing risk of genetic vulnerability, due to narrowing of the genetic base of our farm crops. Much of our production depends on a very small number of crop cultivars. For example, a special Committee on Genetic Vulnerability, appointed by the National Academy of Sciences, noted that in 1970 6 cultivars of cotton accounted for 68% of the cultivated surface area planted to cotton in the United States, 6 cultivars of soybeans planted 56% of the soybean area, 6 cultivars of wheat planted 41% of the wheat area and 6 inbred lines of maize were used in

TABLE 1. NUMBER OF QUESTIONNAIRES RETURNED.

Crop	Public programs	Private programs	Total	% returned
Cotton	12	5	17	74
Soybean	21	12	33	79
Wheat	15	5	20	80
Sorghum	4	4	8	73
Maize	<u>15</u>	<u>8</u>	<u>23</u>	<u>85</u>
Total	67	34	101	81

hybrids planting 71% of the area devoted to hybrid maize in the United States (National Academy of Sciences, 1972).

The committee concluded that farm crop production in the United States was indeed genetically vulnerable. They recommended that we increase the number of widely-grown cultivars per crop, that breeders increase the genetic diversity among released cultivars and within source breeding materials, and that government increase its activity in collecting, storing and describing the world's rapidly disappearing diverse germplasm stocks.

A SURVEY—1981

More than 10 yr have passed since the Academy report was published. What has been done in this brief time? As a plant breeder, I am especially concerned with what we breeders have done and will do to alleviate the problem of genetic vulnerability, or speaking positively, to increase the genetic diversity in our crop plants.

I, therefore, have asked the breeders of 5 major U.S. farm crops to quantify for me the numbers and quality of diverse genotypes now on hand on the farm and in reserve. Questionnaires were sent in 1981 to the leaders of 125 breeding programs. I received a total of 101 replies, a return of 81% (Table 1). I think the replies can be accepted as giving a representative picture of the state of genetic diversity and genetic reserves in U.S. plant breeding in 1980. The results of the survey are reviewed in the following section. They will give a background of information for further exposition (in the "Discussion" section) of my personal opinions about genetic diversity in our major farm crops.

TABLE 2. PERCENT OF TOTAL CROP PLANTED TO THE 6 MOST POPULAR CULTIVARS.

Crop	1970 (%)	1980 (%)
Cotton	68	38
Soybean	56	42
Wheat	41	38 ^b
Maize ^a	71	43

^a Inbreds, used as one parent of a hybrid.

^b 1979 crop.

TABLE 3. PERCENT OF TOTAL CROP PLANTED TO LEADING COTTON CULTIVARS.

Cultivar	1970 (%)	1980 (%)
Deltapine 16	26	1
Stoneville 213	16	8
Acala SJ-1	11	—
Acala SJ-2	0	8
GSA 71	0	7
Stoneville 825	0	7

REPORT OF SURVEY

Cultivar concentration

A first concern is to compare the concentration of leading cultivars in 1980 with that in 1970, the approximate year of the Academy survey. (Data for 1980 were obtained from USDA Agricultural Marketing Service, 1980; Crop Reporting Board, ESS, USDA, 1980; Briggie et al., 1982; Harvey, 1977; and Zuber and Darrah, 1979.) It appears that for cotton, soybeans and maize the concentration of the leading cultivars had decreased, but concentration of the 6 leading cultivars of wheat was about as great in 1980 as in 1970 (Table 2).

Diversity in time

An important observation is that by 1980 nearly all the leading cultivars of 1970 had been replaced by new leading cultivars. Deltapine 16 cotton had dropped from 26% to 1% of surface area (Table 3). Only Lee and Amsoy soybeans were still widely grown in 1980 (Table 4). Chris wheat was replaced by Olaf and Era (Table 5). B37 maize inbred had ceded first place to B73 (Table 6). Sometimes new cultivars were closely related to those they replaced, sometimes they were not. But they always were different in some important trait, for otherwise they could not have forced their way to the top. This kind of cultivar replacement, a continual and evolutionary process, can be called *genetic diversity in time* (Simmonds, 1962). It is important. It usually is unrecognized except by farmers and breeders.

Breeders were asked to estimate the average lifetime of a successful cultivar, based on their observations. Estimates averaged from 7 yr for maize hybrids up

TABLE 4. CHANGES IN LEADING SOYBEAN CULTIVARS.

1970	1980	
Wayne	Williams	Essex
Amsoy	Forrest	Davis
Corsoy	Centennial	"Amsoy" ^a
"Clark" ^a	Bedford	Ransom
Lee	Lee	
<u>Bragg</u>		
56% of acres	56% of acres	

^a Name includes related backcross versions.

TABLE 5. PERCENT OF TOTAL CROP PLANTED TO LEADING WHEAT CULTIVARS.

Class	Cultivar	1969 (%)	1979 (%)
Hard Red Spring	Chris	4	—
Hard Red Spring	Olaf	0	4
Hard Red Winter	Era	0	3
Soft Red Winter	Monon	4	—
Soft Red Winter	“Arthur” ^a	0	8
Hard Red Winter	“Scout” ^a	14	8
Hard Red Winter	“Triumph” ^a	11	6
Hard Red Winter	TAM101	0	5
Hard Red Winter	Centurk	0	6

* Name includes closely-related backcross versions.

to 9 yr for soybean and wheat cultivars (Table 7). The breeders further said that cultivar lifetimes would be even shorter in the future (Table 8). They indicated that this would be due largely to the marked increase in breeding activity of the private sector and the resulting increased number of superior new cultivars appearing each year.

Therefore, genetic diversity in time is real, according to the breeders who have seen it happen. Perhaps more diversity in time is furnished now than in earlier days when farmer cultivars were handed down from father to son to grandson.

Genetic reserves

Genetic reserves were listed by the crop breeders in several categories. First-line reserves are those now on the farm. They are proven, released cultivars and hybrids. Many of them may not now be grown in large amounts (as compared to the favored few), but they could be increased very quickly if the need arose. First-line reserve cultivars of cotton, soybeans, and wheat numbered about 30 per crop in 1980. The released hybrids of sorghum and maize were 134 and 454, respectively (Table 9).

Cultivars in advanced yield trials, the second line of genetic reserves, always are much more numerous than the released cultivars. In 1980 they numbered in the thousands (Table 10). Many of these partially tested cultivars are discarded or put into long term storage once it is established they are not superior to the current leading cultivars; but in case of a special need, as for example a new type of disease resistance, almost any of these cultivars would be acceptable to the

TABLE 6. CHANGES IN MAIZE INBRED USE.

Inbred	1970 (%) ^a	1979 (%) ^a
B37	26	2
Oh43	12	0
B14	9	0
A632	7	10
Mo17	0	12
B73	0	16

* Percent of total crop planted to maize hybrids using indicated inbred lines as one parent.

TABLE 7. ESTIMATED AVERAGE LIFE SPAN OF CULTIVARS.

Crop	Yr
Cotton	8
Soybean	9
Wheat	9
Sorghum	8
Maize	7

TABLE 8. PERCENT OF RESPONDENTS REPLYING "SHORTER," IN RESPONSE TO QUESTION: WILL THE LIFE SPAN OF CULTIVARS GROW LONGER OR SHORTER?

Crop	%
Cotton	73
Soybean	90
Wheat	63
Sorghum	100
Maize	76

TABLE 9. FIRST-LINE RESERVES (CULTIVARS AND HYBRIDS PLANTED FOR COMMERCIAL PRODUCTION), 1980.

Crop	No. cultivars
Cotton ^a	36
Soybean ^a	25
Wheat ^a	32
Sorghum ^b	134
Maize ^b	454

^a Cultivars planted on 1% or more of crop area.

^b All released hybrids.

TABLE 10. SECOND-LINE RESERVES (CULTIVARS AND HYBRIDS IN ADVANCED YIELD TRIALS), 1980.

Crop	No. cultivars
Cotton	981
Soybean	6,382
Wheat	4,061
Sorghum	3,683
Maize	7,642

TABLE 11. THIRD-LINE RESERVES (CULTIVARS AND HYBRIDS IN PRELIMINARY TRIALS), 1980.

Crop	No. cultivars
Cotton	2,410
Soybean	46,271
Wheat	15,114
Sorghum	15,862
Maize	60,625

TABLE 12. PRIMARY BREEDING POOLS, 1980.

Crop	No. F ₂ populations
Cotton	642
Soybean	3,719
Wheat	15,429
Sorghum	1,880
Maize	8,561

TABLE 13. SECONDARY BREEDING POOLS, 1980.

Crop	No. active synthetic populations	No. broadly-based, synthetic populations
Sorghum	45	22
Maize	550	620

TABLE 14. INBRED LINES OF SORGHUM AND MAIZE, 1980.

Crop	No. proven inbred lines	No. inbreds in topcross
Sorghum	1,826	5,787
Maize	2,799	22,525

farmers if they fortuitously carried the desired new disease resistance. And indeed, numerous examples can be cited in which searches were made, resistance was found, and useful replacement cultivars were put into use in a minimum amount of time (Duvick, 1975; Kehr et al., 1968; Kuhn and Jellum, 1970; McVey, 1980; McVey and Roelfs, 1978; Bernard and Shannon, 1980).

Cultivars in preliminary trials, the third-line reserves, are even more numerous and are counted by the tens of thousands per crop (Table 11).

The breeding systems can be followed to their sources, such as F₂ populations (Table 12) and synthetic populations (Table 13), to give infinitely larger numbers of genetically diverse selections, but the point that should be understood is that a very large number of genetically diverse strains at several levels of selection are on hand in U.S. breeders' programs today, ready to use as needed.

An interesting mathematical exercise illustrates the instant diversity available to hybrid crops, as compared to the self-pollinated crop plants. The response to my survey indicated that at least 2,800 well-tested, acceptable inbred lines of maize are on hand today (Table 14). If from this total 500 inbred lines were crossed in all combinations with a second set of 500 inbred lines, 124,750 genetically different maize hybrids could be produced, all of which would be reasonably acceptable for yield and standard agronomic traits. They would be worth sorting over in case a new type of pest resistance or stress tolerance were needed. And, indeed, something approaching this procedure is done from time to time as the need arises, usually with successful results. For example, see ahead in the section entitled "Examples of hidden genetic diversity."

The data summaries also point out that private plant breeding stocks in 1980 were about three times as numerous, in total, as public materials (Table 15). This ratio held, approximately, in all levels of selection and in all crops except wheat. In wheat, the numbers of public selections at the nursery and preliminary trial levels exceeded the private stocks in 1980.

Diversity in breeding pools

A large majority of respondents in all crops said the breeding base of their program had been broadened considerably during the past 10 yr (Table 16). Sources of broadening germplasm listed by the breeders were diverse and tended to vary according to crop (Table 17). Landraces—farmer-selected cultivars—were the most frequently used source. Several breeders noted that an informal worldwide breeder-to-breeder germplasm exchange program has developed in the past 10–15 yr and said that it has become an important aid to broadening their programs.

It was my expectation that breeders only rarely would find useful pest resistance in elite-adapted lines. I thought that for pest resistance they nearly always would need to cross out to exotics such as landraces or related species. But I was surprised to find that for all 5 crops included in my survey, elite adapted lines were said to be one of the most important and widely used sources of useful pest resistance (Table 18). This response shows that breeders very often find sufficient genetic diversity for pest resistance among highly-selected, adapted breeding lines. Their experience directly contradicts commonly-heard statements to the effect that gene pools of elite materials have been so narrowed by successive generations of selection for yield that they no longer contain the diversity needed to counter new disease and insect problems.

Examples of hidden genetic diversity

I should not have been surprised at this discovery—I know that in my own field, maize breeding, much hidden diversity is on hand in our superficially uniform Corn Belt breeding stocks. Thus, when a new virus disease (maize chlorotic-dwarf virus) arose in the southern Corn Belt several years ago, we found the resistance we needed in adapted, elite inbred lines that, although largely Corn Belt in phenotype and performance, nevertheless traced part of their ancestry to a Cuban open-pollinated corn, the source of the virus resistance. (The pedigree of one of these lines, B37CZ, is shown in Table 19.) And in a second search, resistance to another new virus disease (corn lethal necrosis) was found in a pair of adapted, elite inbred lines of Corn Belt phenotype that traced part of their ancestry back to an Argentinian open-pollinated cultivar. (The pedigree of one of these lines, B64, is shown in Table 19.)

Sometimes, useful genetic diversity is present with no record of exotic parentage at all. Sorghum downy mildew (*Peronosclerospora sorghi* (Weston) C. G. Shaw) appeared in south Texas about 10 yr ago as a new disease in maize. A survey of standard elite Corn Belt inbred lines revealed that several lines of purely Corn Belt pedigree gave completely satisfactory resistance to the new disease (Table 19 illustrates one such line, B37AY). And on the other hand, a series of exotic lines

TABLE 15. COMPARATIVE AMOUNTS OF BREEDING EFFORT IN PRIVATE AND PUBLIC PROGRAMS, 1980.

	Advanced trials		Preliminary trials		Nursery selections	
	Private (no. cv.) ^a	Public (no. cv.)	Private (no. cv.)	Public (no. cv.)	Private (no. sel.) ^b	Public (no. sel.)
Cotton	745	236	1,453	957	59,985	17,454
Soybean	5,185	1,197	34,740	11,531	413,500	104,850
Wheat	2,510	1,551	5,478	9,636	205,106	335,140
Sorghum	3,468	215	15,317	545	31,031	2,400
Maize	<u>6,042</u>	<u>1,600</u>	<u>54,010</u>	<u>6,615</u>	<u>745,950</u>	<u>23,585</u>
All crops	17,950	4,799	110,998	29,284	1,455,572	483,429

^a Number of cultivars.

^b Number of selections.

TABLE 16. PERCENT OF RESPONDENTS REPLYING "BROADER" IN RESPONSE TO QUESTION: IS THE BREEDING BASE IN YOUR PROGRAM BROADER OR NARROWER THAN IN 1970?

Crop	%
Cotton	87
Soybean	78
Wheat	85
Sorghum	100
Maize	77

TABLE 17. MAJOR SOURCES OF BROADENING GERmplasm; PERCENT OF RESPONDENTS USING EACH SOURCE.

Crop	Elite unadapted (%)	Landraces (%)	Related species (%)
Cotton	59	76	24
Soybean	9	85	0
Wheat	100	25	15
Sorghum	13	88	0
Maize	<u>48</u>	<u>70</u>	<u>4</u>
All crops	34	71	8

TABLE 18. MAJOR SOURCES OF NEEDED PEST RESISTANCE; PERCENT OF RESPONDENTS USING EACH SOURCE.

Crop	Elite adapted (%)	Elite unadapted (%)	Landraces (%)	Related species (%)
Cotton	41	65	35	35
Soybean	79	70	33	24
Wheat	95	95	50	50
Sorghum	63	75	38	38
Maize	<u>83</u>	<u>61</u>	<u>39</u>	<u>17</u>
All crops	76	72	39	17

TABLE 19. USEFUL GENETIC DIVERSITY IN 2 "NARROW-BASE" MAIZE FAMILIES

Inbred	Pedigree	CLNV ^a	MCDV ^b	SDM ^c
B37	Stiff-Stalk Syn.	S ^f	S	S
B37CZ ^d	B37 (C103 × CUBA O.P.)	S	R	R
B37AY ^d	B37 (B14 × C103)	S	S	R
B14	Stiff-Stalk Syn.	S	S	S
B64	41.2504B ^e × B143	R	S	S
Oh514	B14 (B14 × GT059-272-1-7)	S	R	S

^a CLNV—Corn lethal necrosis virus.

^b MCDV—Maize chlorotic dwarf virus.

^c SDM—Sorghum downy mildew.

^d Privately developed inbred line.

^e 41.2504B—Selection from Argentinian landrace.

^f S—Susceptible, R—Resistant.

derived directly from several different Caribbean and Central American landraces had absolutely no resistance to the disease (Table 20).

Sources of resistance to environmental stress

In addition to disease and insect resistance, crop cultivars must be reasonably stable in their performance under a wide range of environments, including those with excessive heat, drought, low soil fertility, cool temperatures, or rapid fluctuation from one environmental extreme to another. When questioned about the best sources of breeding for stability of performance (breeders often call this trait "stress tolerance"), the breeders of all crops overwhelmingly stated that elite-adapted breeding materials were the best sources of stress tolerance (Table 21). In their experience, the old farmer cultivars are not good sources of genes for stress tolerance, despite often-heard claims to the contrary. For example, in soils with low levels of nitrogen, the highest yields come from the newest, most elite cultivars and hybrids, the same ones that also are top yielders on soils with high levels of nitrogen (Austin et al., 1980; Duvick, 1984).

Use of gene banks

Despite their high degree of success with elite-adapted breeding materials as sources of pest and stress resistance nearly all breeders reported that they also

TABLE 20. UNIFORM SUSCEPTIBILITY IN DIVERSE MAIZE GENOTYPES.

Inbred	Varietal source	SDM ^a
TA2	Antigua Comp. (Mexico)	S ^b
TB11	Tiquisate (Guatemala)	S
TC11	Coastal Tropical Flint	S
TC53	Chandelle (Cuba)	S
TM11	Tuxpeño (Mexico)	S
TP54	Mayorbella (Puerto Rico)	S

^a Sorghum downy mildew.

^b S—Susceptible.

need and do make good use of germplasm collections (Table 22). In every crop, serious disease, insect or nematode pests can arise, with virulence that overcomes all current adapted lines. Breeders then must search in the nooks and crannies of the species, or in related species, for new sources of resistance. Therefore, the germplasm collections are absolutely essential to continued success in modern plant breeding.

When asked if they were satisfied with the U.S. germplasm collections and services, fewer than half of the respondents said they were completely satisfied, although only 13% were clearly dissatisfied (Table 23). Criticisms of the collections fell into 3 categories: Breeders said that 1) collections were not large enough, and the work of collecting was too poorly supported; 2) items in the collections were being lost due to insufficient funds for proper reproduction and storage; 3) the collections on hand need to be described more completely in regard to agronomically-useful traits.

Genetic vulnerability today: breeders' assessment

The final question put to the U.S. crop breeders was: "How serious is the problem of genetic vulnerability in your crop?" The response to this question was rather complicated, in that breeders tended to qualify their remarks quite carefully. However, in the end very few breeding program directors said without qualification, "Yes, genetic vulnerability is a serious problem in my crop" (Table 24). I think it may be significant that wheat breeders had the highest percent of "yes" replies. Wide-ranging epidemics of stem and leaf rust, following race change in the pathogens, have repeatedly decimated U.S. wheat fields during the past 75 yr.

Subdivision of replies according to public versus private sectors showed decidedly more concern in the public sector (Table 25). This perhaps represents a longer-term view on the part of public breeders, who often are charged with development of basic breeding stocks as well as of finished cultivars. On the other hand, the private breeders are in the front line whenever disease or insect epidemics strike, and their replies must reflect successful experience in countering problems to date.

In the course of answering this final question about genetic vulnerability, many of the breeders (public and private) told me with considerable emphasis that the public needs to be better informed about plant breeders' proven ability to move quickly, efficiently and successfully in utilization of breeding techniques and deployment of germplasm resources to deal with disease and insect problems. They cited numerous examples of cases in which they had forestalled, or corrected in acceptably short times, potential disease, insect or nematode problems. (For examples, see Froberg et al., 1977; Hartwig and Epps, 1978; Gallun, 1977; Fredericksen et al., 1977.) Most of the breeding successes are not described or published as such in scientific journals because they are regarded as routine breeding accomplishments. Breeders also cited records of annually-increased yield and stability of yield of their crops, along with experimental data showing that breeding is responsible for 30–70% of these gains, as proof of the soundness of their accomplishments (Russell, 1974; Duvick, 1976; Sims and Araji, 1981; Leudders, 1977; Maunder, 1972).

Summing up the response to the survey question about genetic vulnerability: only a few of the respondents thought that we were in immediate, serious danger;

TABLE 21. MAJOR SOURCES OF STRESS TOLERANCE; PERCENT OF RESPONDENTS USING EACH SOURCE.

Crop	Elite adapted (%)	Elite unadapted (%)	Landraces (%)	Related species (%)
Cotton	65	29	0	0
Soybean	88	27	9	0
Wheat	100	35	20	5
Sorghum	75	50	13	0
Maize	<u>83</u>	<u>26</u>	<u>0</u>	<u>0</u>
All crops	84	31	8	1

TABLE 22. RESPONSE TO QUESTION: DO YOU USE GENE BANK COLLECTIONS?

Crop	Yes (%)	Rarely (%)	No (%)
Cotton	60	20	20
Soybean	78	15	6
Wheat	75	20	5
Sorghum	63	38	0
Maize	<u>45</u>	<u>41</u>	<u>14</u>
All crops	65	24	9

TABLE 23. RESPONSE TO QUESTION: ARE THE GENE BANK COLLECTIONS SATISFACTORY?

Crop	Yes (%)	Partly (%)	No (%)
Cotton	50	43	7
Soybean	41	45	14
Wheat	37	42	21
Sorghum	29	71	0
Maize	<u>50</u>	<u>39</u>	<u>11</u>
All crops	43	45	13

TABLE 24. RESPONSE TO QUESTION: HOW SERIOUS IS THE PROBLEM OF GENETIC VULNERABILITY IN YOUR CROP?

Crop	Serious (%)	Some concern (%)	Not serious (%)
Cotton	7	33	60
Soybean	10	48	42
Wheat	25	50	25
Sorghum	0	62	38
Maize	<u>5</u>	<u>32</u>	<u>64</u>
All crops	10	44	46

TABLE 25. PUBLIC VERSUS PRIVATE BREEDING DIRECTORS, PERCENT OF EACH GROUP REPLYING "SERIOUS" IN RESPONSE TO QUESTION: HOW SERIOUS IS THE PROBLEM OF GENETIC VULNERABILITY IN YOUR CROP?

Crop	Public (%)	Private (%)
Cotton	10	0
Soybean	16	0
Wheat	33	0
Sorghum	0	0
Maize	7	0

46% thought there was no danger at all; but an impressive number of respondents (44% over all crops) fell between these two extremes and said that although they thought the problem was manageable, we must not be complacent, we should be on guard, we should continue to improve our speed and flexibility of response to new pest and environmental problems, and we should continue to increase the genetic diversity of our breeding pools and cultivar releases.

DISCUSSION

Future diversity of U.S. farm crops

I now would like to present my own comments on the charge given to American agriculture and to American plant breeders by the Committee on Genetic Vulnerability in their 1972 report (National Academy of Sciences, 1972). I will make some predictions, relative to the committee's recommendations.

First, I expect that individual cultivars and hybrids will continue to be highly uniform. Farmer and processor needs will dictate phenotypic uniformity within cultivars, and experimental data and farmer experience continue to indicate that with few exceptions genetic diversity within cultivars adds no useful amount of protection proportionate to its disadvantages (Walker and Fehr, 1978; Eberhart and Russell, 1969).

Second, I expect that farmers will continue to plant a relatively small number of favored cultivars or hybrids per crop. Farmers, especially today, very quickly learn which cultivars are most profitable—and safe—and insist on planting those cultivars. They also drop a cultivar very quickly when it gets into trouble or when a better one comes along. I do expect to see a larger number of widely-grown cultivars in the near future, because the U.S. Plant Variety Protection Act has encouraged a significant increase in private plant breeding activity in the self-pollinated crops, such as cotton, soybeans, and wheat. Farmers will be able to choose among a much larger number of superior cultivars with a wider range of genetic backgrounds. But the total number of highly popular cultivars still will seem small in comparison to the total area planted to the crop.

Third, I expect that the several cultivars of each crop will continue to be phenotypically similar to each other within a cultural zone (although they may not look alike to breeders, who know their own children). Farmer preference—and need—for a particular plant type acts as a powerful brake on rapid change in

phenotype. For example, farmers in the High Plains of Texas may choose a particular head type and grain color of sorghum because of local style preferences; or, harvesting machinery limitations may require that all cotton plants have bolls of a special conformation at maturity.

Fourth, I expect that cultivars within an adaptation zone will continue to have a high degree of pedigree relationship to each other. Only a few highly efficient gene combinations—often in apparently tight linkage blocks—ever give maximum performance for yield and stability in a given growing region. Such combinations, usually tracing back to certain key parents, inevitably rise to the top in any efficient selection program. This phenomenon, conservation of successful linkage blocks, is also common in evolving natural populations as was demonstrated by Dobzhansky and others (1977) in numerous experimental studies. I do expect that the new cultivars, even though closely related, will also have a very broad array of added traits and ancestors, and that, therefore, they will have increased amounts of useful but usually invisible genetic diversity. Examples were pointed out in the section on hidden genetic diversity.

So in these 4 ways—uniformity within cultivars, number of widely grown cultivars, phenotypic similarity among cultivars and relationships among cultivars—I see little chance of obvious change toward much more diversity. Are we, therefore, inevitably pointed toward disaster? I think not, for the following reasons.

Conventionally recognized genetic diversity is not enough

I think we must remind ourselves that genetic diversity does not infallibly prevent epidemics, nor does it always give protection against environmentally-induced crop failures. As examples, one can cite Dutch elm disease, American chestnut blight or even wheat rust and ensuing famine in ancient Rome and medieval England (National Academy of Sciences, 1972; Large, 1940). In every case, genetic heterogeneity was massively large but failed to give the needed protection. Simple genetic diversity is not enough. It must be supplemented by additional inputs, and it must be provided in additional, special ways that may not be obvious to observers outside the field of plant breeding. In the next section I will list a few of the extra kinds of diversity available to today's U.S. farmers and plant breeders.

Extra kinds of diversity available to present-day plant breeding and crop production

I have already pointed out that modern plant breeding provides “genetic diversity in time” (that is to say, cultivar replacements) at a faster pace than ever before.

I also have pointed out the multilayered series of “genetic reserves” available to today's breeders of each crop species, with available genetic diversity growing successively greater in each layer of breeding materials until the ultimate base (the landrace collections, or the wild progenitor species) is reached. These extremely broadly-based genetic reserves are used by breeders in much the same way that wild species draw on their genetic reserves in times of reproductive emergency.

Today's plant breeders have an advantage neither given to primitive farmers nor to a wild species. They have an information network, worldwide, that lets them know of disease or insect pests elsewhere that might become a problem in their own region. This advance warning allows them to do "breeding in anticipation"—something evolution sometimes does accidentally, but not with foreknowledge.

One more kind of diversity is also available, but rarely recognized. Today's U.S. farmer, thanks to modern transportation and communication, has access to the genetic variability of the entire nation, or even of the world. An example: in the spring of 1981, heavy and continual rains prevented farmers of southern Ohio and Indiana from planting maize until many weeks past the usual planting dates. Hybrids normally grown in these regions could never have matured before frost if planted at such a late date. But the farm-seed supply companies moved short-season hybrids down to the rain-delayed areas, and farmers were able to plant hybrids capable of producing a sound crop before the first killing frost. This example illustrates a fourth kind of hidden genetic diversity: "transportable genetic diversity."

So in at least 4 extra ways—diversity in time, diversity in reserves, diversity through anticipation, and transportable genetic diversity—modern plant breeding and the farm-seeds industry supply additional genetic diversity not ordinarily seen or understood by nonbreeders.

A comment on lessons of the past

At this point I would like to comment on our enthusiasm for the lessons of the past: for primitive agricultural societies and their genetically diverse crops, for pristine natural ecosystems and their stability and wealth of inter- and intra-specific genetic diversity. I think that sometimes we are imputing a uniformity of success to the early agricultural systems that never existed (Simmonds, 1979), that we are choosing as exemplary ecosystems only those that fit our preconceived notions (Pimm, 1984), and that we are failing to study thoroughly and to understand the biological complexity and constructive ecological potentials of our present-day agriculture. I suspect that some of the criticisms of modern plant breeding and modern agricultural practices represent a wish to retreat to the simpler days of the past, born out of fear, fear of being unable to understand the complexities of the present agricultural systems, fear of being unable to formulate them into a new synthesis, a new biology, comprising yesterday's fundamentals and today's new facts. Perhaps we need a brave new Darwin.

CONCLUSIONS AND RECOMMENDATIONS

I have pointed out that we do have a large amount of genetic diversity on the farm and in reserve in our major U.S. crops, that the diversity is greater and more subtle than is usually recognized, and I have intimated that we may have more usable diversity on hand today than was available to equivalent working units of yesterday's subsistence farmers.

But this should not be construed as saying that I am satisfied with the margin

of safety we now have achieved through breeding. On the contrary, I am dissatisfied. We can and must increase our margin of safety.

We must do everything possible to increase the number of cultivars in each crop and to increase the useful genetic diversity among these cultivars. Breeders must do more to point out to farmers the amount of genetic diversity (or genetic similarity) among cultivars, so that U.S. farmers, who are increasingly sophisticated, can use their own good judgment to balance their needs for profitability and safety of performance.

I think our soybean and wheat breeders must work harder to get away from dependence on all-or-none types of vertical resistance to disease, insect and nematode pests. I think cotton breeders need to find and incorporate more and better genetic resistance to insects in order to reduce cotton farmers' dependence on massive amounts of chemical protection. I think maize breeders need urgently to incorporate more useful germplasm from the wealth of diversity available to them. The sorghum breeders depend more than I think they should on a few basic breeding families. They, like the maize breeders, can and should be adding to their stock of key breeding-line combinations. (However, in recent years sorghum breeders have been very successful in introducing exotic germplasm into commercial cultivars.)

I have serious misgivings about a new trend in our state universities and agricultural experiment stations. Some of them are starting to increase their emphasis on cultivar development at the expense of more basic breeding activities such as developing broad-based germplasm pools, finding and incorporating new kinds of pest resistance, and learning about the genetics and physiology of stress resistance. Universities are running short on funds for agricultural research. Therefore, some universities are hoping, with expanded cultivar release programs, to influence state legislators to vote more funds for agricultural research. A few universities even plan to earn money from royalties on their new cultivars, plowing their profits back into more end-product breeding, essentially like private seed firms (but using tax-supported buildings and scientific staff). Unfortunately, the universities' short term gains in cultivar development cannot long continue if their more basic breeding efforts are cut back. Further, the increased pace of cultivar development in the private sector reduces the need for cultivar development at universities and state experiment stations while at the same time it increases the need for the background breeding work that the universities are uniquely equipped to perform.

I reserve my most severe condemnation for those government agencies ultimately responsible for funding of our germplasm collections. Our national stinginess in collecting, storing, renewing and describing the collections is inexcusable, not only in regard to our national obligations, but also in regard to our responsibility to the entire world.

But in the end, I return to this theme—our plant breeders are doing a remarkably good job of protecting our food and fiber crops from disaster. They are doing a much better job than they are given credit for. They are likely doing a better job than has ever been done before. And I want them, using modern technology, more imagination, and better funding, to do even better; for I know they can, and I think they must.

LITERATURE CITED

- Austin, R. B., J. Bingham, R. D. Blackwell, L. T. Evans, M. A. Ford, C. L. Morgan, and M. Taylor. 1980. Genetic improvements in winter wheat yields since 1900 and associated physiological changes. *J. Agric. Sci. (Cambridge)* 94: 675-689.
- Bernard, R. L., and J. G. Shannon. 1980. Registration of Franklin soybean. *Crop Sci.* 20: 825.
- Blaine, M. R. 1979. *The Ioway Indians*. Univ. Oklahoma Press, Norman, OK.
- Briggle, L. W., S. L. Strauss, D. E. Hamilton, and G. H. Howse. 1982. Distribution of the varieties and classes of wheat in the United States in 1979. USDA-ARS Statistical Bulletin No. 676, Washington, DC.
- Crop Reporting Board, Economics and Statistics Service, USDA. 1980. Soybeans: regional distribution of major varieties. *In* Crop Production, November, 1980. Crop Reporting Board, ESS, USDA, Washington, DC.
- Dobzhansky, T., F. J. Ayala, G. L. Stebbins, and J. W. Valentine. 1977. Polymorphism and balancing natural selection. p. 107-117. Postzygotic isolating mechanisms in animals and plants. p. 210-218. *In* Evolution. Freeman, San Francisco, CA.
- Duvick, D. N. 1975. Using host resistance to manage pathogen populations. *Iowa State J. Res.* 49: 505-512.
- . 1976. Genetic rates of gain in hybrid maize during the past 40 years. *Maydica* 22: 187-196.
- . 1984. Genetic contributions to yield gains of U.S. hybrid maize, 1930 to 1980. *In* Genetic Contributions to Yield Gains of Five Major Crop Plants. W. R. Fehr, ed., Crop Sci. Soc. Amer. Special Publication No. 7, Madison, WI (In press).
- Eberhart, S. A., and W. A. Russell. 1969. Yield and stability for a 10-line diallel of single-cross and double-cross maize hybrids. *Crop Sci.* 9: 357-361.
- Frohberg, R. C., L. D. Sibbett, R. H. Busch, and J. D. Miller. 1977. Butte, an early high yielding, hard red spring wheat. *North Dakota Farm Res.* 35: 1-7.
- Fredericksen, R. A., A. J. Bockholt, L. E. Clark, J. W. Cosper, J. Craig, J. W. Johnson, B. L. Jones, P. Matocha, F. R. Miller, L. Reyes, D. T. Rosenow, D. Tuleen, and H. J. Walker. 1977. Sorghum downy mildew, a disease of maize and sorghum. *Texas Agric. Exp. Sta., Texas A & M Univ., College Station, TX.*
- Gallun, R. L. 1977. Genetic basis of Hessian fly epidemics. *In* The Genetic Basis of Epidemics in Agriculture, P. R. Day, ed. Ann. New York Acad. Sci. 287: 223-224.
- Gavan, J. D., and J. A. Dixon. 1975. India: a perspective on the food situation. *Science* 188: 541-549. (I used their figures for annual per capita grain and pulse consumption in India in 1974 to calculate the food potential of Iowa's maize and soybean production.)
- Hartwig, E. E., and J. M. Epps. 1978. Bedford, a new soybean resistant to cyst nematodes. Information Sheet 1280, Mississippi Agric. and Forestry Exp. Sta., Mississippi State Univ., Mississippi State, MS.
- Harvey, H. P. 1977. Sorghum germplasm base in the United States. *Proc. 32nd Annual Corn and Sorghum Res. Conf.* 32: 186-198.
- Iowa Crop and Livestock Reporting Service. 1980. Iowa Agriculture Statistics, 1980. Iowa Dept. Agric. and USDA, Des Moines, IA, and Washington, DC.
- Kehr, W. R., G. R. Mauglitz, and R. L. Ogden. 1968. Dawson alfalfa—a new variety resistant to aphids and bacterial wilt. *Nebraska Agric. Exp. Sta. Bull.* 497.
- Kuhn, C. W., and M. D. Jellum. 1970. Evaluations for resistance to corn stunt and maize dwarf mosaic diseases in corn. *Georgia Agric. Exp. Sta. Res. Bull.* 82.
- Large, E. C. 1940 (reprinted by Dover, New York, 1962). The barberry and the wheat. *In* The Advance of the Fungi, p. 121-122. Jonathan Cape, London.
- Leudders, V. D. 1977. Genetic improvement in yield of soybeans. *Crop Sci.* 17: 971-972.
- Maunder, A. B. 1972. Objectives and approaches to grain and forage sorghum improvement in the Americas. *In* Sorghum in Seventies, N. G. P. Ras and L. R. House, ed, p. 60-99. Oxford and IBH, New Delhi.
- McVey, D. V. 1980. Postulation of genes for stem rust resistance in the International Wheat Performance Nursery I through XI. *In* Third Int. Wheat Conf. Proc., Madrid, Spain, 22 May-3 June 1980 p. 466-476. Agric. Exp. Sta., Univ. Nebraska-Lincoln, Lincoln, NE.

- , and A. P. Roelfs. 1978. Stem rust resistance of the cultivar "Waldron." *In Proc. Fifth Int. Wheat Genetics Symp.*, p. 1061–1065. New Delhi.
- National Academy of Sciences. 1972. Genetic Vulnerability of Major Crops. Committee on Genetic Vulnerability of Major Crops, Agricultural Board, National Research Council, National Academy of Sciences, Washington, DC.
- Newman, J. E. 1978. Drought impacts on American agricultural productivity. *In North American Droughts*, ed. N. J. Rosenberg, ed, p. 43–62. Westview Press, Boulder, CO.
- Pimm, S. L. 1984. The complexity and stability of ecosystems. *Nature* 307: 321–326.
- Russell, W. A. 1974. Comparative performance for maize hybrids representing different eras of maize breeding. *Proc. 29th Annual Corn and Sorghum Res. Conf.* 29: 81–101.
- Simmonds, N. W. 1962. Variability in crop plants, its use and conservation. *Biol. Rev.* 37: 422–465.
- . 1979. Epidemics, populations and the genetic base. *In Principles of Crop Improvement*, p. 262–269. Longman, London and New York.
- Sims, R. J. R., and A. A. Araji. 1981. The economic impact of public investment in wheat research in the Western Region. *Idaho Agric. Exp. Sta. Res. Bull.* 116.
- Smith, D. D. 1981. Iowa prairie—an endangered ecosystem. *Proc. Iowa Acad. Sci.* 88: 7–10.
- United States Department of Agriculture. 1981 (and previous volumes). *Agricultural Statistics*, 1981. U.S. Gov. Printing Office, Washington, DC.
- USDA Agricultural Marketing Service. 1980. Cotton varieties planted, 1980 crop. USDA Agric. Marketing Service, Cotton Division, Memphis, TN.
- Walker, A. K., and W. R. Fehr. 1978. Yield and stability of soybean mixtures and multiple pure stands. *Crop Sci.* 18: 719–723. (This paper gives a brief review of the advantages of heterogeneity versus homogeneity. The subject needs—but does not have—a full-length, up-to-date review for full exposition and evaluation.)
- Zuber, M. S., and L. L. Darrah. 1979. 1979 U.S. corn germplasm base. *Proc. 35th Annual Corn and Sorghum Res. Conf.* 35: 234–249.

Book Review

Cellular and Subcellular Localization in Plant Metabolism. Edited by Leroy L. Creasy and Geza Hrazdina. 277 pp. illus. Plenum Press, New York, 1982. \$37.50.

This book is a collection of eight chapters prepared by different persons who participated in a symposium on cellular and subcellular specialization in plant metabolism conducted during the 1981 annual meeting of the Photochemical Society of North America. Two chapters dealing with the vacuole and the peroxisome are comprehensive discussions of the metabolic events currently recognized to occur in these organelles. In three other chapters a specific metabolic feature of a cell structure is treated in depth. These include a discussion of the cyanide-resistant pathway in mitochondria, the role of microtubules in cell-wall growth, and photosynthetic carbon metabolism in chloroplasts. The remaining three chapters deal with metabolic events associated with certain types of cells: carbon metabolism in guard cells, C_4 leaf metabolism, and the metabolism of cyanogenic glycosides.

The eight chapters do not cover all aspects of metabolic compartmentation, nor is there a cohesiveness to the book that would make it a desirable textbook. The book's merit is the thorough and current treatment given to eight active areas of plant research. Each chapter is well written, including an extensive list of references, and several chapters focus attention on major unanswered questions. The book is a useful update for individuals with an interest in any of the eight covered topics.

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