HETEROSIS: FEEDING PEOPLE AND PROTECTING NATURAL RESOURCES[1]

Donald N. Duvick

INTRODUCTION

Hybrid vigor, or heterosis, usually refers to the increase in size or rate of growth of offspring over parents; for example, hybrid vigor in crop plants can be observed as in increase in yield of grain, or reduction in number of days to flower. Heterosis in plants has been utilized on large scale for the past 75 years, as carefully selected and reproduced hybrid cultivars. Field crops such as maize, sorghum and sunflower are produced as hybrids in all of the industrialized world; they also are grown as hybrids in increasing amounts in the developing world. Hybrid rice is grown extensively in China, and increasingly in India (Virmani, 1994). Many commercial vegetable and flower crops are grown almost entirely as hybrids. Heterosis is credited for large increases in production per unit area, thus sparing large amounts of land for other uses such as environmentally benign nature preserves.

Examination of the historical record suggests that the major gift of heterosis was its stimulation of interest in the entire system of breeding and use of hybrid crops, rather than a simple exploitation of hybrid vigor *per se*. Development and use of hybrid seeds can enhance crop yields and performance in ways that are different from and not necessarily dependent on heterosis by itself. This essay will examine the historical record on utilization of hybrids to exploit heterosis in some of the major field crops, discuss the present use of heterosis and hybrids, and attempt to predict how heterosis and hybrids may be used in the future. The purpose of this analysis will be to show how hybrids and heterosis can help to supply food for burgeoning populations and also help to improve environmental health of the global food production system.

[1] For presentation to CIMMYT symposium, “The Genetics and Exploitation of Heterosis is Crops”, 17-22 August 1997, Mexico City, Mexico. Published as Duvick, D. N. 1999. Heterosis: Feeding People and Protecting Natural Resources. p. 19-29. *In* J. G. Coors and S. Pandey (ed.) *The Genetics and Exploitation of Heterosis in Crops*. American Society of Agronomy, Inc., Crop Science Society of America, Inc., Soil Science Society of America, Inc., Madison, WI.

Hybrid Maize

Hybrid maize (*Zea mays* L.) was first bred and produced in the USA. The first hybrids, in the 1920s, yielded about 15% more than the better open pollinated varieties (OPVs) (Iowa, 1934). Starting in the mid-1930s, the area planted to hybrid maize began to increase rapidly and after 15 years 95% of the land in the USA Corn Belt was planted to hybrid maize (USDA, 1953). Concomitantly with the rise in plantings of hybrid maize, on-farm maize yields began to climb. They continued to climb after USA maize plantings were essentially 100% hybrid (about 1965) and they are still rising (Fig. 1). Several studies have shown that about 40-50% of USA maize yield gain since the 1930s is due to changes in management such as increases in nitrogen fertilizer and higher plant densities, while the other 50-60% is due to changes in maize genotype (Duvick, 1992, Russell, 1991).

Table 1. Estimates of the current annual global contributions of hybridization to production of maize, sorghum, sunflower. and rice.

Crop	Area planted to hybrids[1]	Hybrid yield advantage[2]	Annual added yield	Annual added yield	Annual land savings
	%	%	%	Mil. MT	Mil. Ha
Maize	65	15	10	55	13
Sorghum	48	40	19	13	9
Sunflower	60	50	30	7	6
Rice	12	30	4	15	6

[1] Production data from USDA National Agricultural Statistics Service.

[2] Estimated gain in yield of hybrids over superior open pollinated varieties at time of hybrid introduction.

If one assumes that present-day maize hybrids will yield on average 15% more than OPVs, as they did in the USA in the 1920s, one can conclude that use of hybrids to produce a given quantity of grain requires only 85% as much land as if the production were made with OPVs (Table 1). One can say, further, that present-day maize yields, as a worldwide average, are about 10% higher than they would be if all maize were open pollinated. Assumptions are as follows: 65% of maize area, worldwide, is planted to hybrids; 65% of the maize area times the hybrid yield advantage of 15% gives an estimated worldwide average yield increase of 10%.

Similar assumptions can be used to support claims that (a) the hybrid yield advantage can be credited for 55 million of the current total world maize production of about 550 million metric tons (MMT), and (b) use of hybrids has spared cultivation of about 13 million hectares of land for maize production.

These exercises in arithmetic indicate that use of hybrids no doubt saves land by increasing yield per unit area, but one should not give large credence to the precision of these numbers. For example, if as much effort had been put into improvement of OPVs as has been devoted to hybrid improvement over the years, the gap between the best hybrids and the best OPVs might be less than 15%, or it might be more than 15%, depending on relative effectiveness of breeding methods to produce the two kinds of product. Some authors say that OPVs would be superior to hybrids if as much effort had been expended on OPVs as went into hybrid development (Lewontin and Berlan, 1990), but their assumption is not backed up by data. No experiments have been designed and conducted to test the theory that OPVs could be improved at the same rate as hybrids (or at a higher rate), if equal effort were expended on each kind of breeding.

Minimal data indicate, however, that some improved populations (they are more or less equivalent to elite OPVs) were improved in yield at rates equivalent to those achieved in a time series of commercial hybrids (Duvick, 1992). The populations, however, were not subjected to selection for the full panoply of traits that were improved in the hybrids, thus stronger selection could be made for yield in the populations than in the hybrids, other things being equal. The question remains unanswered, as to whether or not OPVs can be improved in all needed traits at the same rate as hybrids, given equal effort to both kinds of breeding.

More to the point, any advantage of hybrids over OPVs is not necessarily due to an increase in heterosis *per se*. OPVs are themselves a collection of hybrid plants, each one exhibiting heterosis and other yield traits to a greater or lesser degree. The yield of the OPV is an average of the yield of all its hybrid combinations. The highest-yielding hybrid genotype in an OPV by definition will outyield the OPV as a whole.

The goal of hybrid breeding is to identify and then reliably reproduce superior hybrid genotypes. Virtually all commercial maize hybrids are made from crosses of inbred lines. The inbreds are low yielding but their hybrids exhibit a high degree of heterosis for yield as well as for other traits such as maturity and plant height. Maize hybrids typically yield two to three times as much as their inbred parents.

But superior hybrid genotypes, from the farmer's point of view, are not necessarily genotypes with high heterosis. A cross of two extremely low yielding inbreds can give a hybrid with high heterosis but comparatively low yield, whereas a cross of two high yielding inbreds might exhibit less heterosis but nevertheless produce a high yielding hybrid. High yielding hybrids owe their yield not only to heterosis but also to other heritable factors that are not necessarily influenced by heterosis. One needs to know the relative importance of each genetic contribution — of heterosis and "non-heterosis" — in individual hybrids.

Furthermore, when examining yield trends in a time series of successively released hybrids, breeders need to know what portion of the genetic yield gains (if gains are made) is due to increases in heterosis, and what portion to increases in "non-heterosis". This knowledge can help them as they plan future breeding operations.

The record shows clearly that the yielding ability of maize hybrids worldwide has improved steadily over the years (Castleberry, et al., 1983, Derieux, et al., 1987, Duvick, 1992, Eyhérabide, et al., 1994, Ivanovic and Kojic, 1990, Russell, 1991). Rates of improvement in the USA have averaged about 100 kg ha^{-1} yr^{-1}. Although maize breeders informally often credit the steady increase in genetic yielding ability of maize hybrids to improvements in heterosis, they also know that hybrids continually are improved in yield limiting traits (often called "defensive traits") such as disease and insect resistance, stronger roots, resistance to stalk lodging, tolerance to heat and drought, and tolerance to abnormally cool and wet growing conditions. Many of the defensive traits exhibit little or no heterosis. Inheritance of most of these traits is quantitative, their interaction with environment is high, and so they are not easily subjected to genetic analysis. Perhaps for this reason, few studies have attempted to sort out the relative importance of defensive traits for provision of high and reliable yields. Even fewer studies have been designed and carried out to compare the importance of sequential improvements in defensive traits, relative to sequential improvements in heterosis, over the years.

Fifty years ago, Frederick Richey (Richey, 1946) observed that, "there seem to be no comprehensive data showing a negative relation between parents and hybrids. On the contrary, the higher yielding inbreds have consistently tended to produce the higher yielding hybrids."

But early attempts to correlate inbred yields with yields of their hybrids showed disappointingly low positive correlations, and subsequent studies have confirmed the early findings (Hallauer, et al., 1988). However, when some of the early analyses compared correlations of (a) inbreds with their specific single cross hybrids, and (b) inbreds with the mean of all their hybrid progeny, the correlations for method "b" were appreciably higher than those for method "a" (Sprague, 1964). The results showed that inbred yields predicted general combining ability more accurately than they predicted specific combining ability. But the correlations still were not high enough to warrant selecting inbreds on the basis of their yield *per se*; performance in crosses was and still is essential for evaluating the worth of an inbred for yield in hybrids, as well as for other traits affected by yield, such as standability.

Despite their low values, the inbred-hybrid yield correlations were positive. They indicated a tendency for high yielding inbreds to produce high yielding hybrids. The question was still open: how important is heterosis, as a cause of increases in yielding ability of maize hybrids over the years? Does heterosis account for all of the increase, part of it, or none of it?

To answer this question one must compare a time series of inbred lines with their single cross hybrids. If heterosis has increased over time, single crosses will yield increasingly more than the mean of their parents. But the question still can be asked, "Has the proportionate contribution of heterosis to hybrid yield changed over the years?". Thus, two methods of analysis are needed: (1) calculation of heterosis as grain yield per unit area (i.e., yield of a single cross minus average yield of its inbred parents), and (2) calculation of heterosis as proportion of hybrid yield (i.e., yield of single cross minus yield of midparents, divided by yield of single cross). Alternatively, one can calculate rate of genetic gain for single cross yield and compare it to rate of gain for heterosis.

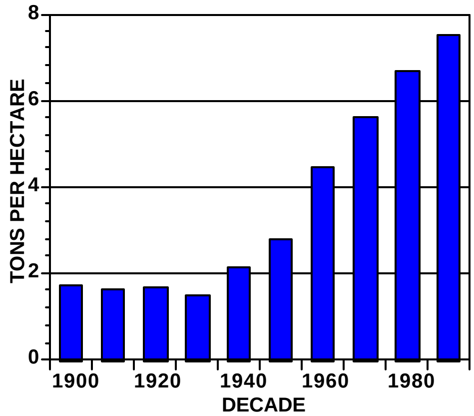

Figure 1. USA maize yields 1900 - 1996, decade means. Hybrid maize was introduced in about 1930 and was used on 100% of USA maize plantings by about 1965. (USDA NASS, "Agricultural Statistics")

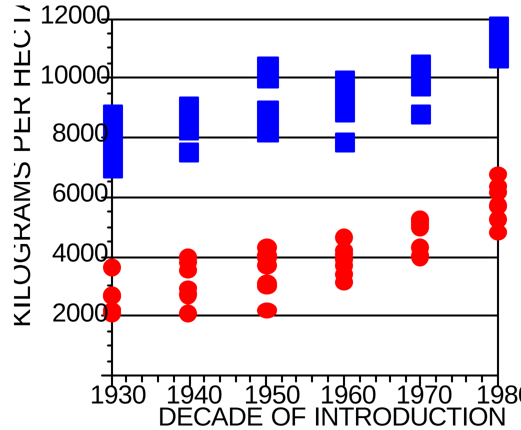

Figure 2. Yields of maize single crosses (SX) and means of their parent inbreds (MP). Widely used pedigrees in Iowa (USA), 7 SX per decade, 1930s through 1980s. Means of 3 densities, 2 years. (Duvick, unpublished data)

A few experiments have been designed to compare yields of a time series of important inbreds with yields of their single crosses. Two are reported in the literature (Duvick, 1984, Meghi, et al., 1984), and unpublished data are available for a third experiment (Duvick, unpublished data). All experiments were conducted in the USA Corn Belt, with inbreds that were highly successful in the Corn Belt at some period of time during the past 60 years. Some of the results of the three experiments are summarized in figure 2, and tables 2 and 3. All three experiments show that:

(1) Yields of inbreds, and of their single crosses, have risen continually since the 1930s.

(2) Rates of yield gain were higher for single crosses than for their midparents in all experiments except at the low density (typical of the 1930s) in experiment 3.

(3) Heterosis, calculated as yield of single cross minus yield of midparent, rose continually in all experiments, except at the lowest density in experiment 3.

(4) Heterosis, calculated as percent of single cross yield, ranged from about 50% to 65%. Heterosis as percent of single cross yield increased in the most recent decade (1970s) in experiment 1, but it declined in the most recent decades (1960s through 1980s), in experiments 2 and 3.

(5) Gains in heterosis did not account for all of the gains in hybrid yield over time; gains in "non-heterosis" (measured as midparent yield) made important contributions, also. Presumably this means that improvements in the contribution of additive genes was an important factor in improvement of hybrid yield.

Further study of these three experiments shows that yield gains in the hybrids always were accompanied by improvements in tolerance to abiotic and biotic stress, and that the improvements occurred in parental inbreds as well as in their hybrid progeny. Numerous additional comparisons of commercially important maize hybrids also show that all important defensive traits have shown strong improvement over the years

(Cardwell, 1982, Castleberry, et al., 1983, Derieux, et al., 1987, Duvick, 1992, Eyhérabide, et al., 1994, Russell, 1991). Most of these defensive traits do not exhibit heterosis.

Table 2. Yields of single crosses (SX) and midparents (MP), and values for SX minus MP (Het) and for heterosis as percent of single cross yield (Het÷SX (%)). Data from three experiments[1]. *b* = rate of gain for yield category, in kg ha^{-1} yr^{-1}

Expt.	Yield Category	1930s	1940s	1950s	1960s	1970s	1980s	*b*
		-------------- kg ha^{-1}						
1	SX	7097		7407		9538		61
	MP	2985		2969		3400		10
	Het	4112		4438		6138		51
	Het÷SX (%)	(58)		(60)		(64)		
2	SX	4600	5300	6900	7000	7900		83
	MP	1900	2100	2800	3400	3600		47
	Het	2700	3200	4100	3600	4300		36
	Het÷SX (%)	(59)	(60)	(59)	(51)	(54)		
3	SX	5941	6371	6865	7174	7929	9164	60
	MP	2154	2618	2722	2985	3827	4506	45
	Het	3787	3754	4143	4188	4102	4658	16
	Het÷SX (%)	(64)	(59)	(60)	(58)	(52)	(51)	

[1] Expt. 1: Recalculated data, (Meghi, et al., 1984), means of two densities, 31,500 and 58,800 plants ha^{-1}. Expt. 2: (Duvick, 1984), means of three densities, 30,000, 47,000, and 64,000 plants ha^{-1}. Expt. 3: (Duvick, unpublished data), means of three densities, 30,000, 54,000 and 79,000 plants ha^{-1}

One can conclude, therefore, that:

(1) Heterosis plays an important role in maize hybrid yields.

(2) Heterosis has increased in absolute amounts (e.g., kg ha^{-1}) over the years.

(3) Heterosis probably will contribute increasingly smaller proportions to total yield gains in years to come, because of proportionately higher rates of improvement in inbred yield. (An interesting observation: table 3 shows that modern inbreds, grown at today's high densities, can yield nearly as much as hybrids of the 1930s.)

This proportionate lack of increase in heterosis, as hybrid yields increase, was foretold quite clearly in a summary of data from experiments designed for other purposes but which included yields for inbreds and their single cross hybrids (Schnell, 1974). Schnell summarized his analysis by saying, "there was only a modest increase in heterosis as compared to the large simultaneous increase in the yields of inbreds,...the...non-heterotic part of the yields of corresponding hybrids."

Table 3. Yields of single crosses (SX) and midparents (MP), and values for SX minus MP (Het) and for heterosis as percent of single cross yield (Het÷SX (%)), in experiment 3. Means of 7 SX per decade at 3 densities: L = 30,000 plants ha^{-1}, M = 54,000 plants ha^{-1}, H = 79,000 plants ha^{-1}. *b* = rate of gain for yield category, in kg ha^{-1} yr^{-1}.

Density	Yield category	1930s	1940s	1950s	1960s	1970s	1980s	*b*
		kg ha^{-1}						
L	SX	6717	6703	7099	7387	7187	8174	26
	MP	2062	2373	2395	2658	3309	3875	35
	Het	4655	4330	4703	4730	3877	4298	-8
	Het÷SX (%)	(69)	(65)	(66)	(64)	(54)	(52)	
M	SX	6569	7033	7960	8171	8747	10024	64
	MP	2337	3065	3174	3493	4352	4969	50
	Het	4232	3968	4786	4679	4396	5055	15
	Het÷SX (%)	(64)	(56)	(59)	(57)	(50)	(50)	
H	SX	5708	6648	6823	7192	9098	10492	90
	MP	2308	3003	3063	3390	4463	5476	59
	Het	3400	3645	3760	3802	4635	5016	32
	Het÷SX (%)	(59)	(55)	(53)	(53)	(51)	(48)	

Hybrid Sorghum

Grain sorghum (*Sorghum bicolor* (L.) Moench) has been grown as hybrids for about 40 years, starting in the USA (Doggett, 1988). About 48% of grain sorghum plantings, worldwide, are now hybrid (Table 1). The first hybrids yielded at least 40% more than the local varieties; the advantage was much higher under severe drought stress. Grain sorghum varieties naturally are quite highly inbred and presumably have low numbers of deleterious recessive genes. Perhaps for this reason, sorghum hybrids exhibit much less heterosis for yield than is typical for crosses of maize inbreds. Using assumptions similar to those for the maize calculations, one can state that (a) worldwide sorghum yields are about 19% higher than they would be without use of hybrids, (b) the hybrid yield advantage accounts for 13 MMT of the total annual worldwide production of about 66 MMT, and (c) use of hybrids spares about 9 million hectares of land that otherwise would be planted to grain sorghum. These figures are no more reliable than those for the maize calculations, since they, too, depend on specific assumptions about the advantage of current hybrids over hypothetical improved varieties.

Grain sorghum yields have risen over the years, but it is not a simple matter to calculate the genetic contribution to yield gains, even in the USA with 100% hybrids. In part, this is because the relative amounts of land planted to irrigated and rain-fed sorghum have varied widely over the years. The area planted to irrigated sorghum increased for several years after hybrids were introduced, then declined as water supplies declined, and pumping costs increased (Miller and Kebede, 1984). Onsets of severe insect and disease problems also have caused high variability in yields, despite breeders' success in countering new problems. Furthermore, yield increases sometimes are stepwise, as superior new breeding lines come into use. Breeders have estimated, nonetheless, that genetic gains have been made over the years, at rates of about 1% per year. They estimate that genetic contributions have provided 35-40% of the total yield gains in grain sorghum in the USA, since the advent of hybrids. Improvements in cultural practices, such as added nitrogen fertilizer and irrigation, are responsible for 60-65% of the gains in yield.

Measurements of sequential changes in heterosis for yield have not been made for sorghum, but it seems likely that heterosis is greater in present-day hybrids than in the first hybrids. Breeders say that inbred yields *per se* are not useful indicators of hybrid yields, and they also say that inbred yields have not improved over the years to any large degree, certainly not at rates comparable to those for maize inbreds. Major yield gains have come from discovery of well-balanced heterotic combinations of superior new germplasm families. Nevertheless, new inbreds do tend to be more vigorous than their predecessors (Doggett, 1988). In particular, they are better equipped with defensive traits such as disease and insect resistance, and tolerance to abiotic stresses such as heat and drought or mineral imbalance. It seems likely, therefore, that increased yield in grain sorghum hybrids gradually will depend less on heterosis *per se* and more on other kinds of gene action, particularly for defensive traits that confer yield stability. As any breeder knows, high average yield depends on stability of performance year in and year out under all expected stresses, as well as on ability to make top yields in highly favorable environments. Selection for specific combining ability often means balancing non-heterotic defensive traits as much as or more than balancing theoretical dominant or epistatic gene combinations for "yield".

Hybrid Sunflower

Oil sunflower (*Helianthus annuus* L.) has been grown as hybrids for about 20 years (Miller, 1987), starting in the USA. Sunflower hybrids now are planted in all parts of the world where sunflower is grown commercially as an oil crop. About 60% of the crop is now hybrid, worldwide (USDA, 1995). Sunflower hybrids yield about 50% more than the better OPVs (Miller, 1987). Sunflower is cross-pollinated, and OPVs, like those of maize, are themselves a collection of hybrid plants, each exhibiting heterosis to some degree. However, most commercial sunflower OPVs are somewhat inbred, as a consequence of strong selection for uniformity for desired traits; thus, oil sunflower hybrids show a relatively high yield advantage compared to OPVs. (The estimated sunflower hybrid yield advantage over OPVs is more than three times as large as that for maize.) Making assumptions like those already described for maize and sorghum, one can say that (a) worldwide sunflower yields are 30% higher than they would be if all were OPVs, (b) the hybrid yield advantage is responsible for about 7 MMT of the total global production of 24 MMT, and (c) about 6 million hectares of land are spared from planting to sunflower, because of the hybrid yield advantage. And as with maize and grain sorghum, these calculations are based on unproved assumptions about advantage of hybrids over OPVs.

Experiments designed to measure genetic contribution to yield gains in hybrid sunflower have not been made, nor have experiments been conducted to measure changes in amount of heterosis. New heterotic groups involving new germplasm lines show promise of giving hybrids with even higher yield, but no data are on hand, to show whether or not the higher yields are due to gains in heterosis. As with both maize and sorghum, inbred yield *per se* is not a good predictor of hybrid yield (Miller, 1987). However, as with sorghum and maize, some of the best new inbred parents (at least the females) are clearly more vigorous and higher yielding than their predecessors. Demands of low cost seed production also dictate that female seed yields be increased if at all possible, so it seems likely that yields *per se* of female inbreds gradually will increase in years to come. Breeders will not try directly to increase yields of male inbreds, however. Sunflower is unique among the hybrid crops in that females are single-headed but males have multiple heads, a recessive trait. Presence of multiple heads in the male ensures a long period of pollen availability, and better seed yields on the female, but it also hinders visual estimates of yield of the line *per se*.

Performance gains in hybrid sunflower primarily are due to improvements in traits that confer stability of performance, e.g., in disease and insect resistance, and resistance to lodging. High oil percentage of course is also important in this oil crop. Parents as well as hybrids have acquired these improvements; they are not the unique product of heterosis. Thus, changes in non-heterotic traits that could just as well have been improved in the OPVs (but with more difficulty) are responsible for much of the improved hybrid performance in sunflower, as with maize and sorghum. It seems likely, therefore, that increased yield in oil sunflower gradually will depend less on heterosis *per se* and more on non-heterotic traits, for gains in yield and yield stability. In this regard, sunflower will be like maize and sorghum — gains in average yield (across years and in many locations) are more important than high yield under ideal conditions, and gains in average yield owe much to improvements in defensive traits, many of which do not exhibit heterosis *per se*.

DISCUSSION

Heterosis is an important cause of the increasingly high yields of maize, grain sorghum, and oil sunflower but it is not the only cause. Improvements in general combining ability as well as in specific combining ability, in additive genes as well as in dominant, over-dominant or epistatic gene combinations, have been crucial to improvement of hybrids in all three crops. For each of these crops, one can theorize that similar gains in yield and performance might have been made if more attention had been devoted to improvement of OPVs, starting with the then existing superior varieties. The facts are, however, that impressive gains in yield and performance have been made since hybrid breeding began for each crop, but minimal or even no breeding progress had been made before the advent of hybrids to those crops. Why did this happen? What was the unique contribution of heterosis? And what can one say about the future importance of hybrid breeding in these crops, or in other crops?

Perhaps the greatest gift of heterosis has been its indirect effect, in forcing attention on hybrids as the medium for genetic improvement of the crop. The hybrid seed industry has made several important contributions to crop improvement that are not due directly to heterosis. Some of the beneficial indirect effects of hybrids are:

(1) Precise genotype identification and multiplication. Instead of a random collection of hybrid and/or inbred plants in an OPV, the most superior hybrid combinations can be identified and reproduced at will, in unlimited quantity. Despite concerns about dangers of genetic uniformity, experience shows that stability in performance can be most easily identified and utilized in uniform genotypes, including hybrids.

(2) Breeders of hybrid crops can react faster and with more options to meet changing times and changing demands, as compared to breeders of either inbred crops or OPVs. New hybrids with needed new traits can be made and put out to test within one or two seasons, given a broad-based pool of inbred lines.

(3) Hybrids facilitate combination of multiple traits into one cultivar, e.g., one hybrid can carry several dominant genes for disease resistance, some coming from one parent, some from the other, or one hybrid may derive its drought tolerance from one parent and its lodging resistance from the other parent.

(4) Farmers can easily identify hybrids as a class, and in some cases they can identify specific hybrids. They expect more from hybrids, they are more likely to provide extra agronomic inputs to hybrids, and they are more likely to press breeders to make continuing and rapid improvements in hybrids. Commercial breeders are especially vulnerable to this farmer pressure for continuing improvement.

(5) The prospect of annual seed sales at profitable prices attracts private capital to hybrid breeding and sales. Hybrid breeding, and the associated seed production and distribution technologies, are doubly supported, by both public and private funds.

Within limits, it seems likely that some of the benefits of the inbred/hybrid method also can be applied to improvement of highly self-pollinated crops such as rice and wheat, but the likelihood of high seeding rates in these crops introduces an economic problem: seed production costs must be low enough and yield of hybrids in the farmers' fields must be high enough that farmers can profit from purchase and use of hybrid seed and companies can profit from production and sale of hybrid seed. Hybrids have been successful with sorghum, an inbred crop, but seed yields are high, and seeding rates are low, compared to those for wheat and direct-seeded rice. For some parts of the world, this seed-yield/seeding-rate problem may be insurmountable. But one should never discount the ability of farmers and breeders to come up with ingenious solutions to the problem.

CONCLUSIONS

Gains in yield and yield stability offered by heterosis have prompted use of hybrids in several crops. As a result, substantially increased amounts of breeding effort have been devoted to these crops. Genetic yielding ability has been increased greatly, and thus total production has been increased, with minimal dependence on chemical inputs and maximum use of biological power. Enthusiasm and funds have been directed to hybrid breeding, in part because of the proven efficiency of the inbred/hybrid method for producing products that farmers need and want, and in part because private capital was attracted to the profit potential of hybrid breeding and sales. The inbred/hybrid method has given breeders greater precision in developing, identifying, and multiplying the best hybrid genotypes in cross-pollinated crops. The pace of genetic improvement in these crops has been greatly accelerated thereby, and shows no sign of slackening. Inbred crops have benefited from use of the inbred/hybrid method as well. Initial improvements in the inbred crops were in yield gains caused by heterosis, but continuing gains will depend on breeders' facility in using the inbred/hybrid method to make superior new hybrid genotypes with greater speed and precision than is possible with homozygous inbred varieties.

Evidence to date indicates that improvements in inbreds *per se* will play an increasingly large role in improving the performance of hybrids. Improvements in non-heterotic traits that confer stability of performance ("defensive" traits) will enhance hybrid yields as well as their overall performance.

But heterosis itself will continue to be a highly important cause of hybrid superiority in yield and yield stability. Specific combining ability — specific combinations of inbred lines with good general combining ability — will remain as the final and always essential requirement for production of superior new hybrids.

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