COMMERCIAL STRATEGIES FOR EXPLOITATION OF HETEROSIS[1]

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INTRODUCTION

Private firms are attracted to the hybrid seed business because of the built-in plant variety protection of hybrids. Customers need to buy new seed for every planting season. But the breeding, production, and sale of hybrid seed — the "commercialization of heterosis" — can be successful only if it meets the following criteria: 1) The hybrids must satisfy the needs of the customer for all important traits. Simply to be "hybrid", or simply to exhibit "heterosis", is not enough. 2) The price of hybrid seed must be low enough to enable the customer to make substantial profits from annually recurring investments in expensive hybrid seed. A rule of thumb is that a first time use of hybrid seed should enable the farmer to earn an extra profit equal to at least three times the added cost of the seed. 3) The price of hybrid seed must be high enough to enable the seed company to make substantial profits from its investments in research, production, and sales. A successful seed company needs to realize a 10-15% return on equity. Its investments in research — one of the essential business expenditures for a research-based seed company — should be equivalent to 5-10% of sales income.

Two other criteria underpin all other requirements for success in the hybrid seed business: 1) Farmers will risk investment in improved seed only when they have some assurance of a fair price — a dependable market — for their crop. 2) Government regulations, formal and informal, must give minimal hindrance to honest and prudent business operations. These two requirements apply to all seed firms, not just hybrid seed companies. They have particular significance in many developing countries.

DISCUSSION

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To satisfy the three primary criteria for success in the hybrid seed business, companies must integrate a host of variables such as: 1) the pollinating system of the crop, 2) options for manipulation of the pollinating system, 3) supply and cost of labor for emasculation or other requirements for hybridization, 4) the yield of the crop in the farmer's field, 5) the commercial value of the crop per unit of land area, 6) the seeding rate of the crop, 7) the seed yield in the seed production field, 8) the extra yield to be expected from heterosis, 9) the implications of hybrid uniformity, 10) the most important traits to improve in the crop, and their genetics, 11) the ease of demonstrating improvements in new hybrids, 12) availability of inbred parents and other breeding materials in either public or private institutions. The following examples illustrate, for three different crop species, some of the many ways in which these twelve variables can be integrated.

Hybrid Maize

Hybrid maize was introduced in the USA in the late 1920s and early 1930s. Hybrids were well received by the farmers and they rapidly replaced open pollinated maize varieties in the major maize growing areas of the country. The first maize hybrids yielded only about 15% more than the better open pollinated varieties (OPVs), but they had much better resistance to root and stalk lodging. USA farmers were beginning to use mechanical corn pickers in the 1930s. The mechanical pickers were inefficient at gathering lodged corn, and so farmers often chose to plant hybrids because the hybrids lodged less, and, therefore, were better adapted to machine harvest. Some of the pioneering corn breeders have said that the very first hybrids might not have been accepted so readily if their higher yield had not also been accompanied by superior resistance to lodging. Superior drought tolerance of hybrids compared to OPVs also helped sell the next generation of hybrids; they were introduced just at the time of two exceptionally severe drought seasons (1934 and 1936) in the USA Corn Belt.

Maize is a naturally outcrossing species. The complete separation of male and female flowers ensures ease of emasculation (called detasseling), and the plant sheds copious amounts of pollen for hybridization, as a byproduct of its natural adaptation for outcrossing. Although hand detasseling is relatively easy and gives precise results, cytoplasmic male sterility eventually was developed (starting in the 1950s) as an option for hand detasseling. It reduced dependence on expensive hand labor and lessened the problem of interruptions of detasseling by rainy weather. Despite failure of one cytoplasmic system (Texas cytoplasm) due to disease susceptibility, other systems are available and in use. Machinery also has been developed to mechanically remove tassels. Thus, three options are available for emasculating the maize plants in the crossing fields. Each has its limitations but seed producers can choose an optimal mix of the three. (Several variations of a fourth option, involving genetically engineered male sterility, also are in process of development.)

When hybrid maize was introduced in the USA, the commercial value of the maize crop per unit of land was not particularly high, compared to high value crops such as tomato, but seeding rates were low for a field crop (one seed gave about 300 seeds in return), and seed yields in the hybridization field (to make double cross hybrids) were relatively high. Therefore, seed companies could set prices at a level low enough to be attractive to farmers but high enough to allow comfortable profit margins for the seed companies.

Yield and standability were the prime traits in need of improvement in maize. Both traits were susceptible to improvement by use of the inbred/hybrid method, and improvements in both traits (especially standability) could be demonstrated to the farmer with relative ease. Both traits were inherited in quantitative fashion, and were governed by many genes, but genetic variability for both traits was high, and replicated yield trials at a few locations easily differentiated the poorest from the best hybrids. To identify the most superior hybrids for yield and standability required several years of performance trials at multiple locations, but this requirement was not onerous, once a well-organized maize breeding program was in operation. Minimal application of scientific method, and rudimentary statistical design and analysis, ensured reliable decisions about hybrid performance.

Breeders had some difficulty in making further improvements in hybrid yield and standability, once the first cycle of selfing in OPVs was completed. Inbreds derived from a second round of selfing OPVs did not give improved hybrids. But breeders soon found that progress could be made by developing new inbreds from crosses of the best first cycle inbreds (Hallauer and Miranda, 1988). Although exact inheritance of yield and standability was not known, and still is not known, breeders were able to establish, through trial and error, the procedures and population sizes that were needed to ensure satisfactory breeding progress.

The uniformity of hybrids, as compared to heterogeneous OPVs, allowed farmers to distinguish hybrids from OPVs, and made it easier for them to make critical comparisons between the two classes. Uniformity of hybrids helped the maize breeders also, in their efforts to develop cultivars with specific product qualities, or to fit unique ecological niches. Differences among uniform hybrids were more clear-cut than among heterogeneous OPVs.

But hybrid uniformity increased the dangers of susceptibility to unforeseen disease or insect problems. Widespread use of a few hybrids, or of hybrids based on a small number of inbred lines, gave opportunity for explosive multiplication of specifically adapted disease or insect pests. In the early days, only a few hybrids were available, and farmers tended to concentrate on an even smaller number, those they judged to be the best of the lot. In the 1940s, a severe outbreak of Northern Corn Leaf Blight (*Exserohilum turcicum)* occurred in the eastern Corn Belt of the USA, largely because of over-dependence on a few inbreds that had been developed in the western Corn Belt, where climatic conditions are less conducive to development of the disease. Breeders responded rapidly. They replaced susceptible hybrids with tolerant ones, and initiated new breeding programs to develop blight resistant inbreds for use in future hybrids.

This cycle of: (1) concentration on a few hybrids, (2) pest epidemic, and (3) introduction of new hybrids, was only the first of many. These cycles continue to occur in various regions of the country, and with various pest organisms. None have been catastrophic, except for the anomalous epidemic involving T cytoplasm in 1970. Hybrid choices within and among the various seed companies are numerous enough that farmers can switch to more resistant hybrids from one season to the next, if necessary, and breeders have sufficient strength in their breeding pools to bring out new resistant hybrids in a relatively short time. Collectively, the hybrid maize seed industry provides the farmers with "genetic diversity in time" (Duvick, 1984).

In the critical early years of development of the hybrid maize seed industry in the USA, inbreds were bred and supplied by public breeding institutions at the universities and in the USDA (Duvick, 1997). Commercial seed companies combined the inbreds into hybrids which they produced and sold. Sometimes public institutions produced single cross seed for use as parents of double cross hybrids. The commercial seed companies needed to make only the final double crosses, in hybrid combinations recommended by the public institution. Some of the public institutions multiplied and sold the parent seed that they had developed. This practice continued for a decade or two but gradually was dropped by all public institutions.

Private firms produced their own inbred lines also, but in the early years they could not produce enough to fill their needs. For many years they depended on public breeders for most or all of their inbred lines. The large seed companies became relatively self-sufficient in inbred lines by about the 1950s, although they continued to use public inbreds whenever they gave superior hybrids. The smaller seed companies depended on public inbred lines until about the 1970s and 1980s, when private foundation seed companies began to lease out their own privately developed inbreds, on large scale. Their proprietary inbreds were available to all seed companies but the primary targets were the small companies that had few or no proprietary lines of their own.

Most of the public institutions reduced or completely stopped efforts to develop commercially useful inbred lines in the 1980s, and devoted their maize research programs to investigation of maize genetics and breeding techniques. A small number of public programs still develop and release new inbred lines for use in commercial hybrids, but most public germplasm releases now are of basic breeding materials and genetic stocks, rather than finished inbred lines.

The record shows, therefore, that hybrid maize in the USA was commercialized successfully as a joint public/private enterprise, and that the roles of public and private entities have undergone continuous evolution over the years. The contribution of public breeders was absolutely essential in the start-up years, but as the seed industry matured, the seed companies gradually assumed responsibility for all functions of research and development, except for long-range fundamental studies in genetics and breeding.

Changes continue. Use of intellectual property rights for plants has stimulated public entities such as the USDA and land grant universities to encourage their researchers to patent or obtain plant variety protection for their inventive products or processes. In the universities, royalties from the protected materials and processes typically are divided between the researcher and the parent institution. Thus public maize research in the USA has gone from partly commercial, to non-commercial, and then back to partly commercial practices, in the course of the past 70 years.

Hybrid maize was introduced in Canada shortly after its introduction in the USA, and was adopted at about the same rate and intensity as in the USA.

Hybrid maize was successfully introduced in Europe in the 1950s, following World War II. Use of hybrids started in the southern countries, those best able to use germplasm from the USA Corn Belt. Hybrids gradually moved north as new inbreds and hybrids were developed with adaptation to needs and growing practices of the northern parts of Europe. Subsidized prices for maize grain stimulated farmers to make annual investments in high yielding hybrid maize seed, once adapted hybrids were available. Public breeding played an important role in establishing maize hybrids in Europe, but, as in the USA, private seed companies gradually assumed dominant roles in breeding as well as in seed production and sales.

Hybrid maize was introduced on a limited scale in the tropics and sub-tropical regions (mostly developing countries) in about the 1960s. Progress in utilizing hybrids was slow at first in most of the developing countries, with a few exceptions. During the past decade, however, interest and planting of hybrid maize has increased, perhaps due to an increased market demand for feed grain to produce meat and eggs demanded by the rapidly urbanizing populations of many developing countries. A second change in many developing countries is encouragement of the development of a private seed industry, in contrast to earlier emphasis on development of public seed enterprises, sometimes known as “parastatals”.

The country of Zimbabwe was an outstanding early exception to the rule of slow progress in adoption of hybrid maize in developing countries. Hybrid maize was introduced in the late 1940s and its area expanded rapidly, reaching nearly 100% concentration in about 25 years’ time. Single cross hybrids were successful, and semi-subsistent smallholders as well as large scale commercial farmers adopted hybrid maize (CIMMYT, 1994). Hybrid success was due in part to the fact that the hybrids were purposely bred to fit a new niche in dryland farming; they were early flowering and drought tolerant, traits not found in the existing OPVs.

In each of these examples of establishment and growth of a hybrid maize seed industry, success has depended on strong farmer demand for hybrid maize. Farmer demand in turn was predicated on a strong and reasonably dependable commercial market for maize grain, and on financial and technical capability of the farmers themselves to supply extra inputs to allow hybrids to reach their yield potential. Farmers bought hybrid maize seed from the private seed companies because of proven ability of the companies to deliver quality products on time, in needed amounts, and at affordable prices. Also, in these examples, the public sector has led the way in research and development, but in time the private sector has taken over most of the applied aspects of research and development, in addition to performing its original function of production, sales, and delivery of hybrid seed.

Apomictic Maize Hybrids

A notably different approach to utilization of heterosis and hybrids has been advocated by researchers who propose use of apomixis to generate self-reproducing maize hybrids. Farmers who cannot afford to buy hybrid maize seed could plant apomictic hybrids and save part of their grain production as replant seed (Anonymous, 1996; Jefferson, 1994). Such farmers typically might be poor semi-subsistent smallholders in developing countries. Two parallel systems have been proposed for making apomictic plant hybrids; each has potential pluses and minuses; neither of them is ready to use.

Simply to develop genetic systems for production of apomictic hybrids will not be the end of the task, however. As smallholders replace their heterogeneous OPVs with homogeneous apomictic hybrids, they will be confronted with the potential dangers of genetic uniformity. The familiar cycle of narrow genetic base, pest epidemics, and hybrid replacement could easily be instituted for the poor smallholders, just as has happened with farmers in other parts of the world, when they adopted conventional maize hybrids. Maize breeders will need to ensure that "genetic diversity in time" and "genetic diversity in place" are available for poor smallholders using apomictic maize hybrids, in the same manner as they have done, successfully, for commercial farmers who adopted conventional maize hybrids in temperate regions of the world.

Some important differences should be noted, however. Disease and insect pressure is greater in the tropics than in the temperate zones, and hybrid lifetimes may be shorter; replacements may be needed more frequently. (This will be a problem for conventional as well as for apomictic hybrids.) The poorest smallholders are heavily dependent on genetic diversity within and among their crop varieties, for security against problems with disease and insects, unfavorable weather, or variability in soil type. Unlike larger scale commercial maize farmers, they cannot purchase chemical or mechanical aids to control insects and diseases, or to correct nutrient imbalance.

Maize breeders, therefore, must be prepared to provide the needed kinds of genetic diversity to smallholders who plant apomictic hybrids. They can do so by bringing out replacement apomictic hybrids at frequent intervals ("diversity in time"), and they can release large numbers of genetically dissimilar apomictic hybrids for each adaptation zone, and encourage farmers to plant all of them ("diversity in place"), rather than to concentrate on planting one or two favorites.

Alternatively, the farmers themselves, rather than professional maize breeders, might take responsibility for providing necessary amounts and kinds of genetic diversity in place and in time, much as they have done through the millennia with their own farmer varieties. Genetically heterogeneous populations of apomictic hybrids, or heterogeneous facultative apomictic populations, could be furnished to the smallholders; they could select desired apomictic hybrids and grow them in mixtures that seemed best to them. But professional breeders still would have the ultimate responsibility of furnishing base populations to smallholders in needed amounts, at suitable intervals, and with appropriate kinds of pest resistance and environmental adaptation. Explanation and instructions for use probably should accompany the releases, and a reliable system of delivering them would be needed. Thus, even though they selected and saved seed of their own hybrids, smallholders would not be self-sufficient; they would depend on the professionals.

One need not assume that only poor smallholders would appreciate the potential savings from saving seed of apomictic maize hybrids. Commercial maize farmers may wish to save money, also, by growing publicly available apomictic hybrids and replanting their own seed. Whether or not they do so will depend primarily on whether the apomictic hybrids are competitive with standard hybrids. For example, in the USA Corn Belt, a yield reduction of about 5% would cancel out any savings from not buying hybrid seed.

A second financial consideration might influence the more specialized commercial farmers, as they consider whether or not to plant apomictic maize hybrids. Maize seed harvest and conditioning — harvesting with special equipment, drying, shelling, sizing, treating with insecticide and fungicide, packaging, and labeling — is a highly technical operation. If done improperly, it can severely damage the yielding ability of hybrids with good genetic potential. Some commercial producers might prefer to leave this specialized and important operation to the seed companies. But less specialized growers might decide that it was worth their time to save and prepare seed for planting.

Seed companies some day may produce and sell apomictic maize hybrids. An easily manipulated apomictic system might improve opportunities to develop new hybrids. The method might make it possible to bypass multi-generation selfing for inbred development, and it could eliminate the need for large-scale and expensive cross-pollination blocks to produce hybrid seed. Intellectual property rights would be used to ensure that the companies, as well as the farmers, could profit from the results of the companies' self-financed research and development.

Such an outcome, of course, would not provide products for farmers who are too poor to buy seed; it primarily would serve commercial maize farmers. Public breeding programs would have the major and continuing responsibility to provide apomictic hybrids and breeding materials to the poor smallholders. One can expect that farmers would abandon their own OPVs once they converted to use of apomictic hybrids, just as has happened wherever farmers have switched to new, professionally bred varieties such as the Green Revolution wheat and rice varieties. The trade-off for improved incomes has been dependence on professional plant breeders.

Time will tell just what niches can be filled by apomictic maize hybrids. One can be certain that, as skill develops in manipulating apomixis in maize, new uses for apomictic hybrids will be devised. As with all plant breeding, the breeding of apomictic maize hybrids will be an evolutionary art and science.

Hybrid Wheat

Wheat hybrids can yield up to 30% more than their parents, but hybrids with heterosis at these levels usually are the product of crosses between different classes of wheat, such as a cross of hard red winter wheat by soft red winter wheat. Commercially useful wheat hybrids must be made within a class, to maintain milling and baking quality. Crosses within a quality class typically have less heterosis, only about 5-15% more than their parents. The lower amount of heterosis may be because of relationship among members of a relatively closed gene pool.

Wheat is a self-pollinated crop. It has perfect florets, limited supplies of pollen, and a relatively brief period of stigma receptivity. Hand emasculation is impractical for commercial production of hybrid seed, but cytoplasmic male sterility allows production of hybrid wheat seed on a field scale. Limited pollen production by male lines (in comparison to maize, for example) means that the ratio of male rows to female rows must be relatively high, and seed yield per hectare is reduced correspondingly.

Value of the wheat crop per unit of land is similar to that for maize. (Both crops are commodities; wheat yields less than maize but it commands a higher price.) Seed yield in the crossing field is low and seeding rates for commercial grain production are high for wheat, relative to maize. One kg of wheat seed will produce 30 to 50 kg of grain, compared to the maize ratio of 1 to 300 or more. Therefore, if a seed company prices its hybrid wheat seed safely above cost of production, the seed cost from the farmer's point of view could be very high in relation to the expected extra income from the hybrid. If a hybrid has only a small yield advantage over the best pure line cultivars, the expected gain in the farmer's income from increased yield of the hybrid could be less than the cost of the hybrid seed (assuming the company priced the seed to cover cost of research, production, and sales plus profit). Such a hybrid would be unacceptable, despite its yield advantage.

Yield, standability, and pest resistance are important traits for wheat varieties, just as with maize, but acceptable wheat varieties also must meet rigorous milling and baking standards. A cross with high heterosis for yield may be unusable if it lacks needed levels of milling and baking quality, or is out of bounds for protein percentage.

Wheat hybrids are not more uniform than standard inbred cultivars, thus they do not introduce new dangers due to genetic uniformity, nor do they introduce new opportunities based on an increase in uniformity. But wheat hybrids, although uniform from plant to plant, are heterozygous at many loci, in contrast to homozygous inbred cultivars. Therefore, wheat hybrids can carry useful combinations of dominant disease or insect resistance genes in heterozygous form. Two inbred parents, neither of which has all needed genes for resistance, can be crossed to make a hybrid with acceptable resistance. Further, by crossing new combinations of inbred parents, one can quickly produce new hybrids with needed new forms of resistance. This process can be much faster than the usual backcrossing or selfing process for placing pest resistance genes into a new inbred variety.

In the early years of hybrid wheat breeding, widely used elite wheat cultivars could be used as female parents with no change in their nuclear genotypes, since they nearly always lacked fertility restoration genes. This fact allowed rapid access to the high general combining ability of these varieties. Through simple backcrossing, their nuclear genomes were placed in sterility-inducing cytoplasm, and they then could be used as the female parent of a hybrid.

But because of this same circumstance, breeders had to develop entirely new male lines, by inserting nuclear genes for fertility restoration into non-restorer genotypes. Restorer lines usually were made by introgressing dominant fertility restorer genes from widely divergent germplasm into elite wheat lines. Typically, the strongest and most useful restorer genes came from different species, sometimes weedy or wild species. This introduced problems of linkage to undesirable traits from the alien species. Breeders devoted years of time and energy to backcrossing with selection for strong fertility restoration, and, as a consequence, they spent less time on breeding for increased yield and general performance. Also, in contrast to the early years of hybrid maize development, publicly employed wheat breeders gave very little input to hybrid wheat breeding. This led to under-investment in development of germplasm and breeding methods (particularly for restorer males) in the important start-up period. The private sector had to carry the load.

Breeding work with hybrid wheat in especially the 1970s coincided with a period of rapid improvement in yielding ability of standard inbred wheat cultivars, as high yielding semi-dwarf germplasm came to dominate the USA wheat germplasm pool. The rapid increase in yield and performance of standard inbred cultivars meant that hybrids, in spite of a yield advantage from heterosis, could not compete with standard cultivars. The hybrid parents lagged behind, in improvement of non-heterotic traits for yield and general performance.

Several research-based seed companies in the USA invested heavily in research to develop hybrid wheat, starting in the 1960s (Knudson and Ruttan, 1988). A few wheat hybrids were developed and released, but most of them did not succeed in the marketplace, primarily because farmers decided that the hybrids' performance did not justify the increased cost of the hybrid seed. Seed companies gradually dropped their hybrid wheat programs, and by the end of the 1980s only a few programs were still in operation.

Interest in hybrid wheat is still present, however, particularly in regions where wheat yields and commercial value of the crop are relatively high (Edwards, 1997). Two companies are marketing wheat hybrids in France. Both companies use chemical hybridizing agents (CHAs) to produce the hybrids. (CHAs, applied at appropriate stages of development, prevent pollen development.) Several wheat hybrids, both hard red winter and soft red winter, are bred and sold at the present time by a seed company in the USA. Four wheat hybrids are marketed in Australia by a private company. The University of Sydney is a shareholder in the company. A cooperative in South Africa is selling wheat hybrids. The American, Australian, and South African hybrids are made with the cytoplasmic male sterile method.

The French and also the Australian hybrids are targeted for high yield production areas, where the farmers use high levels of management. Such producers, it is expected, can make best use of added investment in hybrid seed. In sharp contrast, the South African hybrids are sold in dryland production areas with low yield expectation. However, the hybrids are planted at very low seeding rates, thus keeping seed cost in line with expected return.

Research is in progress in several seed companies, on new ways to produce hybrid wheat seed, using new sterility systems, some of which are introduced into wheat via genetic transformation. The goal is to build systems that are reliable, easy to manipulate, and that interfere as little as possible with routine wheat breeding programs aimed at making improvements in yield and general performance.

These examples show that seed companies and breeders still believe that hybrid wheat can succeed on large scale, and perhaps more importantly they show that there are numerous ways to produce the hybrids, and then to manage them for profit in the farmers' fields. The examples also demonstrate that small companies as well as large can participate in the hybrid wheat seed business.

Hybrid Tomato

Tomatoes are a self-pollinating inbred crop with perfect flowers. Although genetic sterility is available in tomato, hand emasculation and hand pollination are preferred for making hybrids. Crossing is performed in countries where labor costs are low. Seed number per pollination is high. Tomatoes are a high value crop, grown for fresh market or for processing, and seeding rates are very low compared to the value of the commercial crop. In the USA, 100% of fresh market and 80% of processing tomatoes are F_1 hybrids.

Although tomato hybrids can exhibit heterosis for yield, the amount of yield increase in absence of stress is small or even non-existent. The unique utility and attraction of hybrid tomatoes is that they allow breeders to assemble, in one cultivar, complementary genes for disease resistance as well as for traits affecting product quality such as shelf life. Breeders of hybrid tomatoes do not need to place all desirable resistance genes in one inbred cultivar, which accentuates problems with linkage drag; they instead can hybridize two complementary inbred lines to produce a hybrid with the desired full set of resistance genes. Hybrids are essential for expression of the slow ripening trait governed by the gene *nor*. The homozygous wild type, +/+, ripens too fast; homozygous *nor/nor* does not ripen at all, but the heterozygote *nor*/+ ripens slowly, as desired by the market. Tomato hybrids also exhibit increased yield stability, perhaps because they have a better balance of genes for disease resistance (Janick, 1996).

The success of hybrid tomatoes shows that hybrids can be commercially successful in an inbred crop. Expensive means of seed production, such as hand pollination, are feasible with tomatoes because of the high value of the commercial crop, the relatively low seed requirement, and the large number of seeds produced per pollination. This example also points up the fact that heterosis for yield need not be the major factor in determining whether hybrids will be successful. Hybrids can provide many advantages over non-hybrid cultivars, in addition to heterosis for yield.

Large vs. Small Seed Companies

In recent years, the size of many seed companies has increased, and total numbers have been reduced, due to consolidations and buyouts. This phenomenon has been true for seed companies of all kinds, not just those specializing in hybrids. In part this may be because of the growing need to incorporate expensive biotechnology research into the seed breeding process, which means that only large companies can support biotechnology research on a meaningful scale. The consolidations and buyouts also may be just one more part of the current global trend of corporate enlargement.

For whatever reason, to an outsider it may seem that opportunities no longer exist, for small hybrid seed companies. In actuality, small seed companies are still numerous in all parts of the world, and they account for a large amount of the seed business, including the hybrid seed business. In the USA, for example, small firms account for about 25-30% of hybrid maize seed sales (Duvick, 1997). Small hybrid seed firms tend to depend heavily on parental lines developed by public institutions. They often sell seed in niches not conveniently reached by large firms, or perform specialized contract services. They fill a vital role in the hybrid seed economy, and will continue to do so, especially in countries where the hybrid seed industry is in early stages of development. As time goes by, some small firms become large firms, and in their place new small companies arise. This cyclic phenomenon has been documented for hybrid maize in the USA (Norskog, 1995), and general observation indicates that it occurs in other crops in other countries, as well.

The three criteria for success in the hybrid seed business: selling good hybrids, providing profit for farmers, and providing profit for seed companies, can be met by small companies as well as by large ones.

COMMENTARY AND CONCLUSIONS

Demonstration of heterosis for yield and other traits in many crops has prompted efforts to commercialize the breeding, production, and sale of hybrids of cross-pollinated field crops, self-pollinated field crops, and numerous vegetable and bedding floral crops. As a general rule, hybridization has been commercially successful with cross-pollinated field crops, relatively unsuccessful with self-pollinated field crops, with the exception of sorghum and rice (Doggett, 1988, Virmani, 1994), and successful with many kinds of high value vegetable and bedding crops (Janick, 1996). Heterosis is only one of several determinants to the success of hybridization.

Cytoplasmic male sterility has been the method of choice for hybridizing field crops. (Maize also can be detasseled.) Vegetable and ornamental crops are hybridized in a variety of ways, including cytoplasmic male sterility, hand emasculation, genetic male sterility, self incompatibility, and production of gynoecious or highly pistillate monoecious plants. For all crops, research is in progress on use of chemical male sterilants, or new ways of manipulating pollen sterility with genetic engineering, to produce new systems for hybridization. And finally, new knowledge about the genetics and manipulation of apomixis someday may open up entirely new ways for commercial exploitation of heterosis and hybrids, in many crops.

Commercial development of the hybrid seed business has been most successful when public breeders led the way, providing not only breeding technology and genetic knowledge, but also the breeding materials needed to make hybrids. Private firms, in the early years, primarily produce and deliver hybrid seed of materials developed by the public sector. They then begin to develop their own proprietary germplasm and proprietary hybrids, and gradually take over much or even all of the public sector’s responsibility for applied research and development. The rate of change and the amount of change varies with the crop species, as well as with the economy and organization of agriculture in a particular country.

In recent years, reduction in public funding for plant breeding research has impelled public researchers to seek funds from private industry, and to produce products to be marketed to private industry. Industry-oriented research naturally tends to be pointed towards short-term goals that can help industry fulfill its function of producing improved seeds. Over-concentration on such goals by the public sector may lead to neglect of pioneering research for the long term, and neglect of research for the public good, i.e., research on needed food production practices that cannot be commercialized. Underfunding of such long-range and “public good” research eventually will hamper success of commercial seed companies as well as limit progress in improving vital non-commercial aspects of sustainable food production.

When farmers and seed companies simultaneously can profit from production and use of hybrid varieties, a hybrid seed industry can flourish. But the industry as a whole is based on a complex interweaving of public research, private research, small local seed companies, and large national or international companies. Each crop species calls for a slightly different mix of ingredients. And farmers — those who grow the crop — are at the base of it all.

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