ECONOMICS

Working Paper 99-07

Genetic Change in Farmer-Recycled Maize Seed: A Review of the Evidence

**Michael L. Morris, Jean Risopoulos,
and David Beck**

CIMMYT

ECONOMICS

Working Paper 99-07

Genetic Change in Farmer-Recycled Maize Seed: A Review of the Evidence

**Michael L. Morris,[a] Jean Risopoulos,[a]
and David Beck[b]**

---

[a] Economics Program, International Maize and Wheat Improvement Center (CIMMYT).

[b] Maize Program, International Maize and Wheat Improvement Center (CIMMYT).

CIMMYT (www.cimmyt.mx or www.cimmyt.cgiar.org) is an internationally funded, nonprofit scientific research and training organization. Headquartered in Mexico, the Center works with agricultural research institutions worldwide to improve the productivity, profitability, and sustainability of maize and wheat systems for poor farmers in developing countries. It is one of 16 similar centers supported by the Consultative Group on International Agricultural Research (CGIAR). The CGIAR comprises over 55 partner countries, international and regional organizations, and private foundations. It is co-sponsored by the Food and Agriculture Organization (FAO) of the United Nations, the International Bank for Reconstruction and Development (World Bank), the United Nations Development Programme (UNDP), and the United Nations Environment Programme (UNEP). Financial support for CIMMYT's research agenda also comes from many other sources, including foundations, development banks, and public and private agencies.

CIMMYT supports Future Harvest, a public awareness campaign that builds understanding about the importance of agricultural issues and international agricultural research. Future Harvest links respected research institutions, influential public figures, and leading agricultural scientists to underscore the wider social benefits of improved agriculture—peace, prosperity, environmental renewal, health, and the alleviation of human suffering (www.futureharvest.org).

Printed in Mexico.

Correct citation: Morris, M.L., J. Risopoulos, and D. Beck. 1999. *Genetic Change in Farmer-Recycled Maize Seed: A Review of the Evidence.* CIMMYT Economics Working Paper No. 99-07. Mexico, D.F.: CIMMYT.

ISSN: 0258-8587
AGROVOC descriptors: Developing countries; Maize; Zea mays; Crop performance; Performance testing; Seed characteristics; Seed testing; Innovation adoption; Crop management; Farming systems; Yield factors; Genetic parameters; Selection; Segregation; Natural selection; Mutation; Yields; Productivity; Economic analysis
AGRIS category codes: E14 Development Economics and Policies
F30 Plant Genetics and Breeding
Dewey decimal classification: 338.16

Contents

Page

Executive Summary

This paper summarizes what is known about farm-level maize seed management practices and reviews the theoretical and empirical evidence regarding the relationship between farmers' seed recycling practices and the genetic composition (and agronomic performance) of maize cultivars. The focus is on farmers in developing countries, many of whom do not replace their seed annually with newly purchased commercial seed but rely instead on recycled seed saved from their own harvest or obtained from other farmers.

Why is it important to know about the genetic composition of maize plants found in farmers' fields? Although there are many possible reasons, for research organizations such as CIMMYT that carry out plant breeding activities one of the most important is to be able to calculate the value of improved germplasm. Modern varieties of maize (MVs) have been a major source of productivity growth in the past and are likely to be an increasingly important source in the future. In order to calculate the economic value of MVs (which is needed to determine the optimal level of investment in maize breeding research), it is necessary to estimate the productivity gains associated with adoption of improved germplasm. These productivity gains cannot be estimated unless it is possible to identify unequivocally the materials growing in farmers' fields.

Many empirical studies make clear that maize farmers in developing countries frequently save seed from their own production to replant the following season. By far the most common seed selection practice is post-harvest selection. Although there are a number of obvious advantages associated with selecting kernels from harvested ears, the practice does not always result in the production of genetically pure seed. Largely for this reason, recycling is often associated with changes in the genetic composition of maize cultivars.

What happens, genetically speaking, when farmers save maize seed from their own harvest and replant it the following cropping cycle? Based on what is known about the reproductive biology of maize, as well as farmers' varietal management practices and seed selection strategies, there are strong reasons to expect that the genetic composition of farmer-maintained cultivars will change over time. Seven potential sources of genetic change in recycled maize can be distinguished: (1) farmers' seed selection practices, (2) unintentional seed mixing, (3) contamination, (4) genetic drift, (5) mutation, (6) natural selection, and (7) segregation. Each of these is discussed, and published studies are reviewed to determine whether theoretical predictions about the amount of genetic change attributable to each source are supported by empirical evidence.

Our review of the literature suggests that landraces, improved open-pollinated varieties (OPVs) and hybrids all undergo changes in genetic composition as a result of seed recycling. The sources of these changes vary in importance by type of material.

In landraces and improved OPVs, genetic changes result from a combination of intentional and unintentional selection pressure. Landraces and OPVs evolve not only because farmers deliberately select for desired characteristics, but also because of environmental influences,

accidental cross-pollination, random mutation, and gene segregation. Since both types of selection pressure are highly variable, it is difficult to generalize about the rate of genetic change; depending on the circumstances, the genotype of a landrace or improved OPV can change significantly from one generation of plants to the next, or it can remain essentially unchanged across many generations of plants.

In hybrids, by far the most important source of genetic changes is segregation — random recombination of alleles that occurs when seed is recycled. Key results of a simulation exercise designed to show the likely effects of inbreeding in maize hybrids appear to be supported by findings published in the empirical literature on seed recycling:

- When maize hybrids are recycled, yield usually decreases significantly from the F1 to the F2 generation. Yield tends to stabilize in subsequent generations, however, and may eventually begin to increase again if farmers are exerting selection pressure.
- When maize hybrids are recycled, the size of the yield decrease observed between the F1 and F2 generations depends in large part on the level of inbreeding of the original parents. Generally speaking, the greater the degree of inbreeding in the parents, the greater the degree of heterosis in the F1 generation, and the greater the yield decline observed between the F1 and F2 generations. This relationship may be confounded by environmental factors, however.
- The degree of inbreeding of the parents affects not only the size of the expected yield decrease but also its variability. The greater the level of heterozygosity in F1 plants, the greater the variability in inbreeding depression expected in F2 and F3 plants.
- Whether or not advanced-generation hybrids outyield landraces and improved OPVs depends on the original difference in yield and on the magnitude of the decline in yield caused by recycling. In some instances, recycled hybrids continue to outyield the other types of materials, which explains why hybrid recycling may make sense.
- Recycling of hybrids may have little effect on qualitative traits such as kernel size and shape, grain texture, and pounding quality.

The finding that seed recycling often leads to significant genetic changes in farmer-maintained cultivars suggests that there may be a need to reassess the categories traditionally used to classify maize varieties (e.g., landraces, improved OPVs, hybrids). In addition, the rapid rate of genetic change observed to take place in farmers' fields has important implications for research impacts assessment studies. Practical guidelines for use in estimating the returns to maize breeding research are presented in the appendix.

Acknowledgments

Any report that is based on a comprehensive review of the literature owes a great deal to previously published work, and this one is no exception. We would like to recognize the contributions of the many researchers whose findings we have liberally cited; without their efforts, this synthesis would not have been possible. We especially acknowledge the pioneering work on farmers' varietal and seed management practices carried out by our CIMMYT colleagues Dominique Louette, Melinda Smale, and Mauricio Bellon.

Drafts of this paper were reviewed by Gregory Edmeades, Melinda Smale, and Miguel López-Pereira, all of whom provided useful comments. In addition, many CIMMYT colleagues and national program collaborators took the time to go through their files in search of studies of potential relevance. The manuscript was copyedited by Kelly Cassaday of the CIMMYT Publications Unit.

Genetic Change in Farmer-Recycled Maize Seed: A Review of the Evidence

Michael L. Morris, Jean Risopoulos, and David Beck

Introduction

Objectives of the paper

This paper summarizes what is known about farm-level maize seed management practices and reviews the theoretical and empirical evidence regarding the relationship between farmers' seed recycling practices and the germplasm content (and agronomic performance) of maize cultivars. The focus is on farmers in developing countries, many of whom do not replace their seed annually with newly purchased commercial seed but rely instead on recycled seed saved from their own harvest or obtained from other farmers.

The paper is divided into four parts. The remainder of this introductory section explains why the issue of seed recycling in maize merits attention. The second section reviews the literature on farmers' varietal and seed management practices in an effort to determine whether maize seed recycling is widespread. The third section examines the relationship between farmers' seed management practices and the agronomic performance of maize cultivars, taking into account both the predictions of quantitative genetics theory, as well as empirical evidence collected in farmers' fields. The fourth and final section summarizes the main findings. Implications for research impacts evaluation are spelled out in the appendix.

Maize in the developing world

Maize is the world's most widely grown cereal and is the primary food staple in many developing countries. In 1990, of 58 million hectares planted to maize in non-temperate regions of the developing world, approximately 25 million hectares (43%) were planted to modern varieties (MVs), including both improved open-pollinated varieties (OPVs) and hybrids (López-Pereira and Morris, 1994).[1] The widespread diffusion of maize MVs attests to the success of the many organizations that are engaged in crop improvement and technology delivery, including national maize breeding programs, government agricultural extension services, and public and private seed companies.

While there is reason to be encouraged by the fact that half of the developing world's non-temperate maize area is planted to MVs, concerns can justifiably be raised by the fact that the other half is still planted to local varieties (also known as landraces) that have not benefited from formal plant breeding efforts. Looking back over the global history of changes in the kinds of crop varieties that farmers grow, it is apparent that maize has

---

[1] The term *modern varieties* (MVs) as used here refers to cultivars developed since 1960. For maize, this includes both improved open-pollinated varieties (OPVs) and hybrids. For rice and wheat, it includes mainly semidwarf varieties. *Traditional varieties* (TVs) refers to landraces (also known as local varieties) that have never been worked on by a formal plant breeding program, as well as older improved OPVs and hybrids. As Byerlee (1994) has pointed out, the term *modern variety* is something of a misnomer, since some MVs are now more than 30 years old. It is preserved here, however, to maintain consistency with other publications. The term *high-yielding varieties* (HYVs), which is often used to refer to the same varieties, is equally inaccurate, since many MVs were bred for characteristics other than yield potential.

followed a very different path compared to other leading crops. The green revolutions in rice and wheat are by now well known. During the late 1960s and early 1970s, improved semidwarf varieties of rice and wheat were introduced into some of the developing world's most populated countries. When grown with increased levels of fertilizer and an assured water supply, these MVs performed significantly better than the traditional varieties (TVs) they replaced, leading to substantial production increases, higher incomes for millions of farmers who adopted the technology, and lower food prices for consumers. Following their introduction, modern rice and wheat varieties spread rapidly throughout many of the irrigated zones where rice and wheat cultivation was concentrated; later, they gradually disseminated into less favorable environments, including many non-irrigated areas of modest production potential. By the early 1990s, roughly three-quarters of the developing world's wheat area and two-thirds of the developing world's rice area were planted to MVs (Byerlee and Moya, 1993).

One reason why maize MVs have spread relatively slowly compared to wheat and rice MVs relates to the biological properties of the three species. Rice and wheat are self-pollinating crops, so when they reproduce each generation of plants retains the genetic and physiological identity of the preceding generation. This means that farmers can set aside part of their harvest for use as seed in future cropping seasons, as long as they are careful to avoid mixing seed of different varieties. If they wish, they can also distribute seed to other farmers. This is precisely what happened during the green revolutions in rice and wheat: after small quantities of seed were released by public breeding programs, rice and wheat MVs quickly spread though farmer-to-farmer seed exchanges.

Maize presents a different story, however. Maize is a cross-pollinating species, so when maize plants reproduce, the pollen used to fertilize a given seed (kernel) may come from the same plant or from another plant growing nearby. If the pollen comes from another plant, the pollen parent may be genetically similar or genetically distinct from the seed parent. What this means is that in maize the potential is far greater than in wheat and rice for genetic changes to occur in successive generations of plants. When farmers replant maize seed harvested from their own fields or from the fields of other farmers (a practice known as *seed recycling*), each generation of plants may or may not retain the essential genetic and physiological identity of the preceding generation. Consequently, whenever maize seed is being recycled, it is difficult to be certain about the genetic composition of the cultivars growing in farmers' fields.

Why is it important to know about the genetic composition of maize plants found in farmers' fields? In fact there are many reasons — reasons that vary widely, depending on whether one is interested in biodiversity issues, farmers' crop and varietal management strategies, technological innovation and diffusion processes, the performance of the seed industry, or any one of many other subjects. For research organizations such as CIMMYT that carry out plant breeding activities, however, one of the most important reasons is to be able to measure the value of improved germplasm. Modern maize varieties have been a major source of productivity growth in the past and are likely to be an increasingly important source in the future as agricultural land becomes more scarce. To calculate the economic value of MVs (which is needed to determine the optimal level of investment in maize breeding research), it is necessary to estimate the productivity gains associated with adoption of improved germplasm. These productivity gains cannot be estimated unless it is possible to identify unequivocally the materials growing in farmers' fields.

Definition of key terms

Before proceeding, it is necessary to clarify a number of key terms. By convention, the products of scientific maize breeding programs, whether OPVs or hybrids, are referred to as *improved materials*, reflecting the fact that their characteristics have systematically been altered in ways that bring economic benefits to those who grow them. Although use of the term *improved* is appropriate in this context, an unfortunate consequence of the convention is that the traditional varieties grown by farmers (referred to interchangeably in this paper as *landraces* or *local varieties*) often end up being considered *unimproved*. This is clearly incorrect. Landraces have been subjected to numerous cycles of improvement at the hands of farmers, many of whom are skilled at identifying superior germplasm and expert at selecting individual plants that embody desired traits. Farmers' selection procedures in many ways resemble the selection procedures used in formal plant breeding programs, and although scientific breeding methods may allow progress to be achieved more rapidly in breeders' plots than in farmers' fields, the gains made by farmers over thousands of years have been enormous.

In addition to implying that local varieties are unimproved, use of the term *improved germplasm* to refer only to materials produced by formal breeding programs can have another unfortunate consequence. As we shall see, varieties and hybrids undergo continual genetic change in farmers' fields. In the case of varieties and hybrids developed by formal breeding programs, this phenomenon is often referred to as "genetic deterioration" or "genetic depreciation," and the process is frequently described as one in which improved materials become "contaminated" by exposure to external sources of pollen. Use of such negative terms is misleading and may in fact incorrectly characterize what is actually happening. Although genetic change is undesirable when farmers would prefer to preserve the characteristics of the original germplasm, in many instances genetic change occurs as cultivars become better adapted to local production conditions and/or consumption preferences. In other words, what plant breeders sometimes refer to with the pejorative term "genetic deterioration" may be quite desirable from farmers' point of view. For this reason, some authors use the more positive term "rustication" to describe the process by which materials produced by formal breeding programs change in the hands of farmers (see Wood and Lenné, 1997).

In this paper, we use the term *improved materials* to refer to the varieties and hybrids produced by formal breeding programs. We do so with the caveat, however, that this does not imply that local varieties are in any sense unimproved. Similarly, we try to avoid use of terms such as "contamination" and "genetic depreciation" in describing the genetic changes observed in farmers' fields.

Farmers' Management of Maize Varieties and Seed

Before attempting to determine what happens to the genetic composition of maize seed when it is recycled, it is useful to examine farmers' seed management practices. If the number of farmers who regularly recycle maize seed is small, then the area planted to recycled seed is likely to be limited, and it can probably be ignored in calculating the impacts of maize improvement research. But if the number of farmers who regularly recycle seed is large, then the area planted to recycled seed is likely to be extensive, and calculations of research impacts should attempt to account for any productivity gains associated with recycled seed.

This section of the paper reviews what is known about farm-level maize seed management practices in developing countries, with the goal of answering the following questions: How many maize farmers recycle their seed? Among farmers who recycle their seed, how often do they do so? What factors influence the decision to recycle? Does the incidence of seed recycling vary according to the type of material being grown (i.e., landraces vs. improved OPVs vs. hybrids)? Of the total area planted to maize in developing countries, approximately what proportion is affected by seed recycling?

Reasons for using improved seed

Analysis of what is frequently referred to as "adoption of improved seed" is often muddled by a failure to distinguish properly between the different reasons that motivate farmers to seek out and plant seed of improved crop varieties. When farmers acquire seed of an improved variety or hybrid (e.g., through purchase, loan, gift, or theft) and plant that seed, they may be doing one of several things. It is important to distinguish between three different activities: (1) MV adoption, (2) MV replacement, and (3) seed replacement.

MV adoption. A modern variety is "adopted" when a farmer who previously has grown only local varieties plants an improved OPV or hybrid for the first time. MV adoption usually is motivated by the belief that planting the MV will bring greater benefits than those which would have been realized by continued use of the local variety. MV adoption is thus motivated by the desire to gain access to the genetic material contained in seed. In most cases, MV adoption is associated with a substantial one-time yield increase representing the difference in genetic potential between a local variety and an MV.

MV replacement. A modern variety is "replaced" when a farmer who is already growing MVs stops planting one and starts planting another. Like MV adoption, MV replacement is motivated by the belief that switching to the new MV will bring greater benefits than those which would have been realized through continued use of the old MV. MV replacement is thus also motivated primarily by the desire to gain access to the genetic material contained in seed. Since the cultivar being replaced was itself developed by a formal plant breeding program, in most cases MV replacement is associated with a fairly modest yield increase. Since MV replacement may occur regularly at relatively frequent intervals, however, the cumulative effect can be quite large.

Seed replacement. Seed replacement is what happens whenever a farmer acquires new seed from an external source (as opposed to saving a portion of his or her own harvest for replanting the following season). The adoption and replacement of MVs are always associated with seed replacement, since it is impossible to change varieties without changing seed. The converse is not true, however, in the sense that it is possible to replace seed without changing varieties. The latter practice is in fact very common; many farmers regularly replace seed without changing varieties. Typically this happens because they are satisfied with the performance of the variety and see no need to change their choice of germplasm, but for one reason or another they wish to replace their seed. Unlike MV adoption and MV replacement, seed replacement has nothing to do with gaining access to new genetic material contained in seed. Rather, the seed replacement decision is driven by the desire to avoid losses in performance associated with planting seed that has become old, diseased, genetically impure, or mixed with seed of other cultivars or weeds.

To help clarify the distinction between varietal replacement and seed replacement, it is useful at this point to introduce the concept of a seed lot. According to Louette et al. (1997:24), "…a seed lot consists of all kernels of a specific type of maize selected by a farmer and sown during a cropping season to reproduce that particular maize type. A 'variety' or 'cultivar' is defined as all seed lots held by farmers that bear the same name and are considered by them to form a homogeneous set… A seed lot therefore refers to a physical unit of kernels associated with the farmer who grows it, whereas a variety is associated with a name."

Since technical change in agriculture is often led by varietal change, MV adoption and diffusion processes have attracted considerable attention from researchers. No attempt will be made here to review the vast literature on MV adoption and diffusion. In this paper, we are concerned primarily with seed replacement, which as we have explained may or may not be associated with MV adoption or MV replacement.

Varietal management strategies in traditional farming systems

Before examining farmers' seed management practices and discussing the genetic changes that may result from seed recycling, it is important to clear up some common misconceptions about varietal management practices in traditional farming systems. Until quite recently, the conventional wisdom held that subsistence-oriented farming systems are internally focused and static, in contrast to commercial farming systems, which are externally focused and dynamic. According to this view, which continues to prevail in some circles, subsistence-oriented farmers are close-minded and conservative, lacking knowledge of improved technologies and clinging stubbornly to time-honored production practices that keep them trapped in poverty. Their lack of innovation supposedly extends to their choice of varieties, so that year after year they continue to cultivate their traditional landraces of low genetic potential. In contrast, commercial producers are seen as dynamic innovators who actively seek out new sources of productivity growth; their drive to experiment extends to their choice of varieties, leading them regularly to replace their cultivars with new and better ones.

In recent years, new evidence has emerged to suggest that this stylized view is at least partly incorrect. While the dynamic nature of commercial farming systems has not been seriously questioned, the notion that subsistence-oriented agriculture is static and unchanging has come under increasing attack. Nowhere is this more evident than in the case of varietal management practices, which have been the subject of a number of detailed household- and community-level studies. Some of the most important of these studies have been those carried out among maize producers in Mexico. These studies have shown that the varietal choices made by subsistence-oriented households are both complex and sophisticated. Maize varieties are carefully selected according to their suitability to local ecological conditions, their compatibility with the prevailing farming system, and their responsiveness to expected crop management practices. Farmers' varietal choices depend also on consumption criteria, because a large proportion of production is consumed within the household or fed to animals. Important consumption-related criteria typically include color, taste, processing quality, suitability for the preparation of local dishes, storability, and palatability for animals (Aguirre, 1997; Rice et al., 1997; Bellon and Bush, 1994). Selection criteria thus tend to be very diverse, and many households regularly grow a number of different maize landraces to meet the full range of household consumption requirements and at the same time accommodate multiple production constraints.

Belying the notion that traditional farming systems are closed and static, several recent studies have shown that the germplasm used by subsistence-oriented farmers is often extraordinarily diverse. For example, of the 26 named maize varieties grown in the Cuzalapa Valley in the Mexican state of Jalisco, only six can be considered local; the remaining 20 varieties must be considered foreign in the sense that they have been introduced recently from outside the community (Louette, 1994). Although varieties defined by Louette as local occupy most of the cultivated maize area, maize production depends not only on local varieties, but also on a diverse and constantly changing group of foreign varieties introduced through farmer-to-farmer seed exchanges.

Perhaps not surprisingly in view of the constant inflows of foreign germplasm, most farmers in the Cuzalapa Valley define maize varieties in terms of morphologic and phenotypic criteria, rather than in terms of geographic origin (Louette, 1997). This finding that the farmer's concept of a variety corresponds closely to the breeder's concept of a phenotype seems to reflect the reality in most traditional farming systems. Indeed, a definition based on morphologic and phenotypic criteria makes sense, given the magnitude and frequency of seed exchange. In the Cuzalapa Valley, randomly collected seed lots of what was supposedly a single variety were found to vary greatly in terms of the numbers, origin, and genetic composition of the parental seed lots from which they had been derived. Local varieties thus constitute genetically open systems to which seed lots of external origin are regularly being added.

Independently of the constant infusions of foreign germplasm, gene exchange among maize landraces is encouraged in many traditional farming system by the common practice of cultivating different varieties on contiguous areas. This can lead to important modifications in the allelic frequencies and morpho-phenological characteristics of different landraces.

Despite the constant intermingling of genetic material, however, farmers select materials to maintain essential differences between varieties. In the Cuzalapa Valley, for example, local and foreign varieties appear to be complementary from a morpho-phenological point of view (Louette et al., 1998). Most local varieties feature short growing cycles, low plant height, and large kernels, and many are grown in the dry season. Most foreign varieties have long growing cycles, tall plant height, and small kernels, and most are grown in the rainy season.

Louette's work shows not only that landraces are dynamic, but also that the process of genetic change is hardly haphazard. The Cuzalapa farmers have demonstrated an impressive ability to manage their varieties in ways that avoid the two undesirable extremes of too much gene flow (which leads to uniformity in subpopulations) and too little gene flow (which leads to inbreeding). Rather than replacing local varieties, foreign varieties occupy only a small proportion of the total maize area in Cuzalapa; instead of competing with local varieties, foreign varieties are taken up only if they satisfy a need that local varieties do not meet. Thus, foreign varieties are more a source of phenotypic diversity than a cause of genetic erosion. Although the Cuzalapa example does not involve MVs (since Louette's "foreign varieties" are simply landraces that have been introduced from outside the community), this finding should help to allay the concern expressed in some circles that the introduction of MVs will lead to the displacement of landraces, resulting in an overall reduction in genetic diversity at the farm level.

In Cuzalapa, farmers have deliberately increased overall levels of genetic diversity in their maize populations by encouraging inflows of foreign germplasm. These inflows are clearly valued, so much so that farmers often lose interest in conserving stable and distinct varieties (Louette and Smale, 1998). Similar findings have been reported elsewhere in Central America. For example in Costa Rica and Honduras, Almekinders et al. (1994) found that hybridization between local and improved maize is highly valued by farmers, to the extent that when seed is being recycled, the distinction between local and improved varieties eventually loses its significance.

These studies contradict the assumption that traditional systems are closed and isolated with respect to gene flows. A small group of local varieties (landraces) are continuously cultivated, while another group of morphologically distinct "foreign" varieties are cultivated for limited periods, being replaced periodically by newer varieties obtained from outside the community.[2] New foreign varieties are constantly being introduced for testing; if they perform well, they may be retained long enough that they eventually come to be recognized as local varieties (Louette, 1994).

Similar results have been reported by others working in different regions of Mexico. Bellon and Brush (1994) conclude that in the southern state of Chiapas, potential genetic erosion from the widespread adoption of introduced varieties is frequently offset by farmers' seed selection practices, heterogeneous farming conditions, and the outcrossing nature of maize. Aguirre (1997) documents the prevalence of farmer-to-farmer seed exchanges in the central

---

[2] Louette (1998) defines as "foreign" those varieties whose seed lots have been recently introduced into the community, as well as varieties that are sown episodically.

state of Guanajuato and discusses the effects of these exchanges on the genetic composition of maize landraces. Interestingly, although Bellon and Brush indicate that farmers in Chiapas do not manage their planting patterns so as to minimize gene flow between plots, Aguirre reports that many farmers deliberately refrain from planting colored maize near fields where white maize is being grown because the price for multicolored ears is lower.

Although introgression of foreign germplasm may be highly appreciated, deliberate preservation of valued local varieties is also common. Farmers often go to great lengths to maintain the genetic purity of favorite varieties. For example, farmers in Honduras grow hybrids in valleys and local varieties on hillsides; the purpose of growing the varieties on the hillsides is to maintain their genetic purity (Almekinders et al., 1994). Deliberate isolation of valued varieties can result in their preservation for extended periods. For example, in Zimbabwe farmers still grow an improved OPV released in 1975 under the name Salisbury White, even though the seed industry has not produced or sold any seed of the variety for well over a decade (Friis-Hansen, 1995).

Seed replacement

Farmers replace their seed for different reasons. Most obviously, seed must be replaced whenever there is a change in variety. Varietal changes can result from deliberate decisions on the part of farmers, for example when the current variety is abandoned in favor of another variety with higher yield potential, better resistance to stresses, a shorter growth cycle, or improved consumption qualities. Varietal changes also can be forced on farmers, for example when seed of a particular variety becomes unavailable. Highly appreciated varieties sometimes disappear from farmers' fields following extremely poor production years in which little grain is harvested, as a result of seed storage problems, or even because households may have been driven by hunger to eat their seed (Sperling et al., 1993; Rice et al., 1997; Almekinders et al., 1994).

When farmers change varieties, obviously they must acquire fresh seed. But seed replacement is not necessarily associated with varietal change. Even when they have no intention of changing varieties, farmers may decide to replace seed from the variety they are currently growing with "fresh" seed of the same variety if they notice undesirable changes in the variety's performance, such as decreased yield, loss of height uniformity, or increased susceptibility to diseases (Ortega Sequeira et al., 1993; Louette et al., 1997; Louette and Smale, 1998). Farmers do notice these types of changes and frequently take actions to offset them (Seeley, 1988; Ortega Sequeira et al., 1993; Louette et al., 1997). In such cases, the farmers may say that the variety has become "tired," indicating that they attribute the changes in performance to genetic changes in the variety itself, rather than to changes in environmental conditions or in crop management practices.

References to the concept of reviving "tired" varieties abound in the literature, although the way this is accomplished can vary. One common strategy is to combine seed lots. Wierema et al. (1993) describe farmers in highland regions of Costa Rica, Honduras, and Nicaragua who renew tired varieties by obtaining fresh seed from cooler, more fertile lowland areas. Deliberate mixing of seed lots for the purpose of re-invigorating tired varieties has also been reported in the Mexican state of Guanajuato by Aguirre (1997). Another common strategy is to subject a variety to beneficial environmental selection pressure. Bellon and Brush (1994) report that Mexican farmers in the southern state of Chiapas deliberately plant landraces in different environments (e.g., highlands, valleys) to fight off tiredness. Castillo (personal communication) indicates that in central Mexico, one benefit of informal seed exchange systems is that they allow landraces to be returned to their (assumed) place of origin every few years, where they can be grown for a few seasons in a different environment before they are sent back to the community. In all of these examples, farmers recognize that varietal performance declines through time, and they understand that the seed must regularly be changed if the productivity of the variety is to be maintained.

Frequency of seed replacement

It is difficult to generalize about the frequency of seed replacement, which can vary widely even within the same community. Seed replacement rates depend on many factors, including the type of cultivar, the physical environment, the cropping system, and the degree of market integration (Aguirre, 1997). Popular landraces are often grown by many farmers within the same community, so individual farmers who are growing landraces generally find it easy to replace their seed periodically. In the case of MVs, seed replacement rates will depend in part on the availability of alternative seed sources. If MV seed is not always available, farmers may have difficulty finding seed of the variety they are currently growing, so replacement rates may be low. But if MV seed is readily available, renewing seed will be quite easy, and seed replacement rates may be high.

In a survey conducted in 1992-93, only 27% of Nicaraguan farmers reported having purchased fresh maize seed in that year. Those who had not purchased fresh seed indicated that their seed selection practices were sufficient to maintain acceptable levels of seed quality, although many added that they had only recently started sowing their current variety and that it was still too early to observe changes in varietal performance. Most of the respondents said that they make a conscious effort to ensure the quality of their seed by regularly replacing seed, periodically changing varieties, and pursuing good seed selection and crop management practices (Ortega Sequeira et al., 1993).

In a series of surveys carried out in 1991 in Costa Rica, Honduras, and Nicaragua, only 3% of farmers were found to be replacing their seed every year. Most farmers reported that they replace their seed every 2-4 years on average, with a significant number (up to 25% in some zones) indicating that they replace their seed only every 4-6 years (Almekinders et al., 1994). The rate of seed replacement was found to be much higher in areas where farmers were growing MVs.

In a survey conducted in 1994-95 in the department of Jutiapa, Guatemala, Sain et al. (1996) found that over 24% of farmers replace their improved seed after only one season, 36% after two seasons, 26% after three seasons, and the remaining 14% after four or more seasons (Sain et al., 1996).

Based on the results of a survey conducted in 1995-96 in six states of India, Singh and Morris (1997) documented the rate at which Indian maize farmers replace their seed (Table 1). Seed replacement rates were found to vary dramatically: 42% of the farmers reported that they replace their seed annually, while 38% indicated that they never replace their seed. Seed replacement practices depended on the type of farmer and on the nature of the maize production system. In the states of Andhra Pradesh, Karnataka, and Bihar, where maize is grown as a commercial crop and adoption of MVs has been extensive, most farmers replace their seed annually. In contrast, in Madhya Pradesh, Rajasthan, and Uttar Pradesh, where maize is grown mainly for home consumption and adoption of MVs has been limited, the vast majority of farmers rarely or never replace their seed.

Sources of replacement seed

When farmers change their variety, intentionally or not, replacement seed may be obtained from various sources. These sources differ depending on the type of material, the proximity of the formal seed system, and the personal circumstances of the farmer. Subsistence-oriented farmers who grow local varieties in marginal environments mainly for home consumption will generally rely on different sources of maize seed than commercial farmers who grow MVs in favorable environments mainly as a cash crop.

In remote areas featuring mainly subsistence-oriented agriculture, when farmers change varieties, the change often involves replacement of one landrace by another. Landraces tend to be replaced with other landraces, with seed usually being obtained from relatives, friends, or neighbors within the same community. The popularity of this farmer-produced seed stems from the fact that it tends to be inexpensive, of known quality, and well adapted to local conditions (Almekinders et al., 1994).

Farmer-to-farmer seed exchange mechanisms for landraces are frequently based on traditional social networks and family relations. Despite their apparently informal nature, local seed systems are often very efficient in providing a diverse, flexible and readily available seed supply (Almekinders et al., 1994). They can also encompass surprisingly large areas; in central Mexico, maize seed circulates between communities located as far as 200 km apart (Castillo, personal communication).

Table 1. Frequency of replacement of improved maize seed, India (% of farmers)

	Frequency of maize seed replacement			
State	Replace annually	Replace every 2-3 years	Replace every 4 years or more	Never replace
Andhra Pradesh	79	10	3	8
Bihar	74	13	3	10
Karnataka	85	7	3	6
Madya Pradesh	4	14	14	68
Rajasthan	4	13	13	71
Uttar Pradesh	6	17	17	60
Total (six states)	42	12	12	38

Source: Singh and Morris (1997).

The extensive reliance by subsistence-oriented maize farmers on local seed exchange systems has been documented through numerous case studies. Selected examples are briefly summarized below.

In Nicaragua, many small-scale farmers prefer to recycle maize seed from their own harvest because it is the most reliable and cheapest way of obtaining good quality seed. Based on a 1991 survey, Ortega Sequeira et al. (1993) reported that among farmers who were growing landraces, 89% were using recycled seed, while 11% were using seed acquired from family and friends. Among farmers who were growing improved OPVs or hybrids, 85% were using recycled seed (either saved from their own production or obtained from family members), while 15% were using seed that had been purchased from a commercial source.

Sain et al. (1996) identified three major methods of acquiring maize seed among farmers who were participating in a seed project in Guatemala. Farmers either saved seed from the previous harvest (66% of farmers), purchased seed (26%), or traded for seed (8%) (Table 2). Three-quarters of the farmers surveyed reported using only one form of seed acquisition, while the rest reported engaging in two or more forms. Among those who were growing local varieties, the only reported source of seed was other farmers. Among farmers who were growing improved OPVs and hybrids, other farmers were still the major source of seed, although there was also some reliance on the formal seed market (i.e., local shops). Farmers who were growing hybrids exhibited a greater tendency to purchase seed than those who were growing improved OPVs, but in both cases, the greatest proportion of seed is farmer-produced (recycled or traded), rather than purchased.

Table 2. Method of seed acquisition, Guatemala (% of farmers)

	Method of acquisition	
Type of cultivar	Purchase	Recycle or trade
Hybrids	46	54
Improved OPVs	35	65
Landraces	0	100

Source: Sain et al. (1996).

Surveys carried out in 1991 and 1992 in Costa Rica, Honduras, and Nicaragua revealed that maize seed management practices were similar in all three countries. When acquiring fresh seed (as opposed to recycling), farmers who were growing landraces relied primarily on the informal seed sector; on average, over four-fifths of the farmers who were growing landraces indicated that the original source of their seed was neighbors or relatives (Table 3). In contrast, farmers who were growing MVs

Table 3. Sources of maize seed, by type of cultivar, Central America

	Costa Rica, Honduras		Nicaragua	
Type of cultivar	Informal seed source	Formal seed source	Informal seed source	Formal seed source
Landrace	83	17	75	25
Improved OPVs and hybrids	45	55	19	54

Source: For Costa Rica and Honduras, Almekinders et al. (1994) and Wierema et al. (1993);
Nicaragua, Ortega Sequeira et al. (1993).

relied with greater frequency on the formal seed sector; on average, over one-half of the farmers who were growing MVs reported that they had originally obtained their seed from a government agency or from a local shop. Despite the differences in seed acquisition practices, seed recycling practices were found to be similar whether farmers were growing landraces or MVs. On average, the main source of replacement seed was own seed; about 80% of the recycled seed was own seed, while only 20% had been obtained from local sources, including family, friends, and neighbors (Wierema et al., 1993; Ortega Sequeira et al., 1993; Almekinders et al., 1994; De Bruijn et al., 1994).

In the Cuzalapa Valley, farmers grow no commercial cultivars, although many of the local varieties grown in Cuzalapa include in their parentage a changing and diverse group of foreign varieties introduced through farmer-to-farmer exchanges (Louette, 1994, 1997). On average, Cuzalapa farmers select slightly over 50% of their seed from their own harvest; about 36% is obtained from other farmers in the valley, and 11% is brought in from other regions. The Cuzalapa Valley findings are interesting because they reveal that different seed lots of the same local variety can vary greatly in origin and genetic composition. Louette argues that local varieties are best thought of as genetically dynamic, since seed lots of external origin are regularly added to local seed lots.

Citing data from a 1995 survey of maize producers in Malawi, Smale et al. (1998) report that while seed of F1 hybrids was mainly purchased from government-run retail outlets, seed of landraces and advanced-generation hybrids was mainly saved from the farmer's own production (Table 4).

In 1994, approximately 85% of farmers in two districts in eastern and northern Tanzania reported having planted recycled seed saved from their own harvest or obtained from friends or neighbors (Akulumuka et al., 1997). Only about 15% of the farmers said that they had planted commercial seed; these farmers accounted for approximately 7% of the total area planted to maize in the two districts. The commercial seed was purchased from local shops, from the government seed agency, or from non-governmental organizations (NGOs).

Table 4. Sources of maize seed, Malawi (% of farmers)

	Local varieties	F1 hybrids	Advanced-generation hybrids
Informal sector	100	50[b]	98
On farm storage	87	0	80
Purchase from local market	2	15[a]	0
Purchase from other farmers	7	5	11
Gift	4	30	7
Formal sector	0	74[b]	0
Purchase from parastatal	0	59	0
Purchase from local retailer	0	15[a]	0

Source: Smale et al. (1998).

[a] 30% purchased from local retailers or local market.

[b] Total adds up to more than 100% because farmers grow more than one type of hybrid.

In a survey carried out in 1995 among 150 households in northern Zimbabwe, 15% of the respondents reported using seed saved from their own production. Often this seed is used in small garden plots, late-planted fields, or re-planted fields (Chikwati and Mariga, quoted in Waddington et al., 1997).

Maize seed procurement practices in India were documented through a 1995-96 survey conducted in six important maize-producing states (Singh and Morris, 1997). Among farmers growing MVs, 45% reported having bought their seed from a private trader, and an additional 13% said they had bought their seed from a government agency (Table 5). Only 38% reported having used recycled seed saved from their own production, and a minuscule 4% indicated that they had acquired seed from other farmers. In states where maize is commercially produced, more than three-quarters of farmers purchase their seed from outside sources, usually private traders. In states where maize is grown primarily for home consumption, two-thirds of farmers save their seed from last season's harvest.

In summary, these studies suggest that subsistence-oriented farmers tend to use recycled seed saved from their own harvest, acquired from other farmers, or purchased in local grain markets—although on occasion they may also resort to the formal seed sector. In contrast, commercial farmers tend to replace their maize seed on a regular basis, buying commercial seed from local input distributors or from government seed agencies.

Seed recycling

While it is hardly surprising to find that seed recycling is common, especially in many developing countries in which farmers lack access to reliable sources of commercial seed, what is unexpected is to discover that seed recycling apparently extends in many cases to hybrids. Mainly because of the phenomenon of inbreeding depression, progeny of F1 hybrids tend to underperform their parents. For this reason, hybrid seed is generally sold with the recommendation that it not be recycled.

In recent years as maize hybrids have gradually spread throughout many regions of the developing world, evidence has begun to accumulate that some farmers are choosing to ignore the recommendation that hybrid seed be replaced at each planting. Instead of purchasing fresh seed for each new cropping cycle, these farmers plant advanced-generation

Table 5. Sources of maize seed, selected states, India (% of seed)

	Maize seed procured from:			
State	**Own harvest**	**Other farmers**	**Private trader**	**Government agency**
Andhra Pradesh	8	1	84	7
Bihar	15	2	77	6
Karnataka	5	1	73	20
Madhya Pradesh	64	3	14	19
Rajasthan	69	6	13	12
Uttar Pradesh	67	10	9	14
Total	38	4	45	13

Source: Singh and Morris (1997).

hybrid seed. Initially, it was generally believed that farmers recycled hybrids only when they could not obtain fresh seed and thus had no other option but to replant seed saved from their own harvest. Over time, however, evidence began to suggest that some farmers were deliberately choosing to plant advanced-generation hybrid seed even when F1 seed was available.

Frequency of hybrid seed recycling

As the following case studies suggest, the practice of recycling hybrids is much more prevalent than is generally believed.

In El Salvador, where most maize farmers grow hybrids, seed recycling is widespread. According to Choto et al. (1996), of the maize farmers who grew hybrids in 1994, 84% reported that they planted commercial F1 seed, while 16% reported that they had planted advanced-generation seed saved from their own production or from that of other farmers.

Recycling of hybrid seed is also reported to be common in the highlands of Mexico, although no reliable estimates exist of the area affected (Perales, 1998; Perales et al., 1999). In this area, use of advanced-generation seed up to the F4 generation has been reported by Espinosa Calderón et al. (1990, 1993).

Recycling of hybrid seed appears to be extensive throughout most of Malawi. Based on survey data, Smale et al. (1998) estimate that in 1997 the ratio of the area sown to commercial (F1) hybrid seed to the area sown to advanced-generation hybrid seed was approximately 1:3. This finding is consistent with the difference observed between commercial seed sales data and official estimates of the area planted to hybrids. In a different study, Zambezi et al. (1997) report that while 15% of Malawi's maize area was planted to commercial hybrid seed, an additional 40% was sown with recycled hybrids (Zambezi et al., 1997). These results are important, because national crop reporting statistics apparently understate the true extent of hybrid use. In official crop estimates, recycled hybrids are not considered improved material, and the area planted to recycled hybrids is reported along with the area planted to landraces.

In addition to documenting the extent of hybrid seed recycling, the Malawi studies are noteworthy because they show that use of recycled seed varies greatly from year to year. According to Smale et al. (1998), between 1990 and 1997 (excluding years in which seed was distributed free), the proportion of farmers growing commercial (F1) hybrid seed fluctuated between 22% and 39%; during the same period, the proportion of farmers growing advanced-generation hybrids also varied noticeably (Table 6). In 1997, among the 54% of

Table 6. Use of different types of maize seed, Malawi, 1990-97 (% of farmers)[a]

	1990	1991	1992[b]	1993	1994	1995	1996	1997	Avg.
F1 hybrid	27	36	96	24	23	34	39	22	30
Advanced-generation hybrid	6	14	0	63	47	38	37	54	37
OPV	4	1	0	1	0	0	1	2	1
Local maize	98	97	73	72	70	68	67	69	77

Source: Smale et al. (1998).

[a] Columns sum to more than 100% because farmers may plant more than one type of seed.

[b] In 1992, many farmers received 5 kg of hybrid maize seed from the government. In 1994 and 1995, some farmers received free hybrid seed from the government or from an NGO.

farmers growing advanced-generation hybrids, seed of the two most popular hybrids (MH18 and NSCM41) had been recycled for 2.6 seasons on average, with some farmers reporting that they had recycled seed of one or the other hybrid for as many as six consecutive cropping seasons (Smale et al., 1998).

In Zimbabwe, recycling of hybrid seed is apparently common among some small-scale farmers. According to Waddington et al. (1997), farmers who recycle seed generally purchase commercial hybrid seed every 2-3 years and then replant F2 and F3 seed in the intervening years. Although this practice is widespread, the area planted to recycled hybrid seed is relatively small; a survey carried out in 1990 in two communal areas of northwestern Zimbabwe by Chiduza et al. (1994) revealed that 84% of the maize area was planted to commercial hybrid seed, with most of the rest (16%) planted to advanced-generation seed.

In India, seed recycling practices depend at least partly on the type of material being grown. Farmers who grow OPVs tend to replace their seed infrequently, preferring instead to save seed from their own harvest to replant in the following season. In contrast, most farmers who have adopted hybrids understand the importance of regularly replacing seed. In states where hybrid use is extensive, the majority of farmers replace their seed for each cropping cycle. However, there is evidence that the practice of replanting F2 and more advanced generations of hybrid seed is widespread. In a 1994 survey covering the six most important maize-growing states, 21% of farmers indicated that they planted recycled F2 hybrid seed (Singh and Morris, 1997). Unfortunately no information was collected as to the area sown to recycled hybrids.

Farmers' seed selection practices

These case studies provide compelling evidence suggesting that: (1) large numbers of maize farmers in developing countries regularly recycle their seed, and (2) recycled seed accounts for a considerable proportion of maize area. Before taking up the question of how seed recycling may affect varietal performance, it is useful to review farmer's seed selection practices, since these can greatly influence the genetic composition of the resulting seed lot.

Seed selection can take place at different times (e.g., prior to the harvest, at the time of harvest, after the harvest), at different places (e.g., in the field, at a drying or storage facility, in the home), and by different people (e.g., the farmer, the farmer's spouse or children, hired laborers). The following examples from recent case studies illustrate the wide range of common seed selection practices.

Numerous studies from Latin America, Africa, and Asia have revealed that in areas where farmers grow mainly landraces, seed is usually selected at home following the harvest, not in the field (for example, see Louette et al., 1998; Rice et al., 1997; Singh and Morris, 1997; Smale et al., 1997; Bellon and Brush, 1994; SEP, 1982). Harvested ears are brought home and segregated by variety, and the largest ears with good husk cover are opened and examined for characteristics such as kernel color, kernel size, cob length, number of rows, and number of seeds per row. After ears that do not meet the selection criteria have been discarded, those remaining are shelled, and the grain is stored in plastic bags along with insecticide. In some cases, seed grain is selected from the middle of the cob; kernels located at either end of the cob (tip or base) are not used.

In Veracruz State, Mexico, where mostly landraces are grown, men and women play different roles in the seed selection process (Rice et al., 1997). After the maize crop is harvested and brought home, an initial selection is performed by the male head of household, with the selected ears being set aside for storage. During subsequent months, women of the household make additional selections when taking ears for cooking. The practice of selecting ears just prior to cooking appears to be a continuous process and not a single event. Unlike other selection practices, which are primarily conducted by men, this last selection practice is the responsibility of women. At the beginning of the next planting season, household members together select ears from the two piles. Interestingly, seed selection practices frequently differ according to the type of material. Seed of improved OPVs tends to be selected earlier, often in the field immediately following the harvest, and it is usually shelled, treated with insecticide, and bagged. Seed of landraces tends to be selected later, particularly during food preparation.

In Central America, maize seed selection practices often resemble those observed in Mexico. Seed is usually selected following the harvest, in most cases after the ears have been transported from the field back to the farmer's house. Ears are selected for their size and healthy aspect, taking into account grain color and husk cover. Only grain from the center of each ear is used for seed. Selection of ears prior to harvest is uncommon; only 25% of farmers surveyed in Costa Rica, 15% of the farmers surveyed in Honduras, and none of the farmers surveyed in Nicaragua select ears in the field (Wierema et al., 1993).

In a study of maize-millet relay cropping systems in Nepal, Khadka et al. (1993) report that maize seed is rarely selected in the field; rather, seed is usually saved from whatever healthy and large cobs are left following the harvest. Although most farmers prefer to select seed from the largest ears, not all farmers select seed from the same part of the ear: 54% use grain from the middle of the ear, 25% use grain taken from the bottom of the ear, and 17% use all grain (Leslie, 1986).

Longmire et al. (unpublished) studied seed selection practices in the Swat Valley of northern Pakistan, an area in which both landraces and improved OPVs are grown. Although virtually all maize seed in the Swat Valley is selected some time after the harvest has been completed, selection methods differ by type of material (Table 7). In the case of landraces, over 70% of farmers reported selecting seed from unshelled ears; only around 20% reported selecting seed after shelling. In the case of improved OPVs, on the other hand, equal numbers of farmers reported using each of these two selection practices.

In the Indian states of Madhya Pradesh, Rajasthan, and Uttar Pradesh, where maize is grown mainly for home consumption, the majority of households that recycle maize seed make their selections following the harvest (Singh and Morris, 1997). Seed selection takes place directly in the field (35% of cases), or, more commonly, at the farmer's house (55% of cases) (Table 8).

Table 7. Seed selection methods, Swat Valley, Pakistan, 1992

Seed selection method	Local varieties	Improved varieties
From cobs on plant	6	0
From cobs before shelling	74	56
From shelled grain	20	44

Source: Longmire et al. (1994).

In Egypt, 72% of the maize farmers surveyed by Fitch (1983) reported using specialized practices to select and store seed. Of those, 86% reported making selections at home, rather than in the field, and 81% reported storing seed separately from regular grain destined for consumption. Maize seed is usually stored on the cob; very few farmers shell their seed prior to storage. Important seed selection criteria include large ear size, large kernel size, resistance to diseases, and resistance to storage pests (Fitch, 1983).

In the southern highlands of Tanzania, 84% of farmers surveyed in 1995 reported recycling seed. Of those who recycle, 60% said they selected seed by choosing "good ears" immediately following the harvest, while the remaining 40% said they selected ears from their granaries at planting time (Bisanda et al., 1998).

Factors influencing replacement vs. recycling

At the beginning of every planting season, farmers must decide what seed to use. Assuming they have saved a portion of the previous harvest, the choice they face is between recycling seed (i.e., planting seed saved from the previous harvest) or replacing seed (i.e., acquiring new seed). When the farmer wants to change variety (adoption or replacement), the choice is obvious: a change in variety necessarily entails seed replacement. But when the farmer wants to continue growing the same variety, the choice is not obvious, because seed recycling and seed replacement are both feasible options.

What factors determine whether farmers decide to recycle seed, as opposed to replacing seed? In most cases, the decision is basically an economic one driven by considerations of expected profitability (Heisey et al., 1997). Replacing seed is usually more costly than recycling seed, so farmers will replace seed only when they expect that the marginal benefits of replacement will exceed the marginal costs. The marginal benefits of seed replacement are related to the expected yield gains associated with planting high-quality seed (i.e., seed that is genetically pure, healthy, and viable). The marginal costs of seed replacement are related most directly to acquisition costs, which may simply be the price (in the case of purchased seed), although other transactions costs may also be involved (e.g., the cost of traveling to a seed distributor, the cost of credit).

Table 8. Farm-level seed selection practices in six states, India, 1994-95

	Maize seed selection practice			
State	Prior to harvest	After harvest, in field	After harvest, in house	Other
Andhra Pradesh	4	12	14	70
Bihar	4	12	23	61
Karnataka	5	6	12	77
Madhya Pradesh	7	34	56	3
Rajasthan	6	40	51	3
Uttar Pradesh	3	31	63	3
Total	5	23	36	36

Source: Singh and Morris (1997).

Recent work in the highlands of Mexico illustrates why many farmers choose to recycle hybrid seed. Espinosa Calderón et al. (1990, 1993) show that under high levels of management, the most profitable option is to buy new seed every year, but under the levels of management provided by most farmers, seed prices are often too high to make hybrid use profitable. The authors conclude that lowering seed prices would increase hybrid seed sales and discourage farmers from recycling.

High seed prices have also been blamed for discouraging regular seed replacement in Tanzania, where most farmers recycle their hybrid seed for an average of three years. Following the removal of input subsidies in 1995, the seed-to-grain price ratio increased from 10:1 to 30:1 in just one year (Akulumuka et al., 1997).

Evidence from Malawi suggests that a number of factors influence the choice between recycling or replacing hybrid seed. Yield is clearly an important consideration. Wright and Tylor (1994) report that many small-scale farmers in Malawi who recycle hybrid seed indicate they are generally satisfied with yields derived from F2 generation seed. Yield trials conducted by Zambezi et al. (1997) help explain this attitude: Zambezi et al. found that advanced-generation hybrids often yield as well as or better than most landraces and even some improved OPVs. While yield is usually a very important factor influencing the decision to recycle or replace hybrid seed, it is not the only factor. Smale et al. (1998) report that Malawian farmers perceive clear differences in the effects of recycling on characteristics such as germination rate, storability, and grain quality, which suggests that recycling behavior is also influenced by factors other than yield.

In India, farmers who were observed recycling hybrid seed gave a number of reasons to explain this behavior (Singh and Morris, 1997). In some areas, farmers indicated that they often are forced to recycle hybrid seed because the input supply system is unreliable and replacement seed is unavailable. But even when replacement seed is available, many farmers choose not to purchase F1 seed because they do not expect the investment to be profitable. These farmers were able to discuss the profitability issue in extremely sophisticated terms, relating the cost of purchasing F1 seed to the expected incremental benefits associated with its use. The incremental benefits stem mostly from the expected yield difference between F1 seed and advanced-generation seed (which may have suffered a loss in genetic purity and/or a loss of viability), although another important factor is the risk of weather-induced crop failure. In states where two crops per year are grown (an irrigated crop in the *rabi* season and a rainfed crop in the *kharif* season), this probably explains why many farmers choose to plant F1 seed during the (secure) *rabi* season and F2 seed during the (risky) *kharif* season. Since most of the hybrids grown in India are double-cross and three-way-cross hybrids that suffer relatively modest yield declines between the F1 and F2 generations, and taking into account the possibility of weather-induced crop failure, farmers may be acting rationally in planting F2 hybrids.

Discussion

Maize farmers in developing countries often save seed from their own production to plant in the following season. By far the most common seed selection practice is post-harvest selection, usually from ears that have been transported to the farmer’s home. Superior ears are selected based on physical characteristics, such as ear size, ear shape, grain color, husk cover, number of kernels per row, and number of rows per ear. Seed is collected from a particular part of the cob, usually the center or the base.

Although there are obvious advantages to selecting seed after the harvest is over, post-harvest selection does not necessarily produce genetically pure seed. When a farmer selects seed ears from a pile of ears located on the porch of the home or in the storehouse, there is no way to ensure that the ears came from plants located in the middle of the field (which minimizes the risk of cross-pollination). Mainly for this reason, recycling is often associated with genetic drift, or gradual changes in the composition of varieties.

When farmers recycle their maize seed, sooner or later they begin to notice changes in performance, such as a decline in yield, a change in height, or a loss of uniformity. As mentioned earlier, in Meso-America when this happens farmers say their varieties are "tired." These changes in performance are not always attributed to seed recycling practices and in fact are often blamed on environmental factors, such as changes in soil fertility or climatic variability. Farmers commonly attempt to revive "tired" seed by exchanging seed with other farmers and/or by mixing seed lots of the same variety obtained from inside or even outside their community. In some places, farmers refresh tired seed by periodically growing it in a different environment or on different soils, where it presumably comes into contact with and cross-pollinates with exotic germplasm.

Most maize farmers periodically choose to replace their seed. Although seed replacement is frequently associated with the decision to change varieties (MV adoption or MV replacement), it is also observed among farmers who are satisfied with the variety they are growing and who have every intention of continuing to grow the same variety (seed replacement). For this latter group of farmers, the decision to replace seed is usually motivated by an observed decline in the performance of their current seed lot.

Replacing and recycling are opposite sides of the same coin. By definition, if farmers do not replace their seed, they must recycle. Table 9 summarizes the information presented earlier on rates of seed recycling and seed replacement in selected developing countries.

Farmers who wish to replace their seed can look to various sources of fresh seed. Farmers who are growing landraces (many of whom are small-scale, subsistence-oriented

Table 9. Frequency of maize seed replacement, selected countries (% of farmers)

	India	Nicaragua	Guatemala	Central America	Malawi
Replace seed:	62	27	—	25	—
Annually	42	—	24	3	—
Every 2-3 years	12	—	62	—	—
Every 4+ years	8	—	14	—	—
Never replace seed	38	73	—	75	52
Recycle hybrids	21	—	—	—	54

Source: For India, Singh and Morris (1997); Nicaragua, Ortega Sequeira et al. (1993); Guatemala, Sain et al. (1996); Central America, Almekinders et al. (1994); Malawi, Smale et al. (1998).

producers) tend to rely on family, friends, or neighbors for replacement seed, partly because these familiar sources offer a readily accessible supply of inexpensive seed of known quality, and partly because seed of landraces is rarely available through formal seed supply channels. In contrast, farmers who are growing improved OPVs and hybrids (many of whom are large-scale, commercially oriented farmers) tend to rely on the formal seed sector for replacement seed. Table 10 provides an overview of the relative importance of the formal and informal seed sectors in selected developing countries.

In summary, many studies present convincing evidence that maize-based cropping systems in developing countries are often very dynamic. Whether farmers are growing landraces and relying mainly on recycled seed, or whether they are growing MVs and using mainly commercial seed acquired from external sources, crop and seed management practices generally leave plenty of room for genetic changes to occur. But just how significant are these genetic changes? In order to answer this question, it is necessary to determine how seed recycling practices affect the genetic composition of maize cultivars. This issue is addressed in the next section.

Genetic Effects of Seed Recycling

What happens, genetically speaking, when farmers save maize seed from their own harvest and plant it in the following cropping cycle? Based on what is known about the reproductive biology of maize, as well as farmers' varietal management practices and seed selection strategies, there are strong reasons to expect that the genetic composition of farmer-maintained cultivars will change over time. To track the diffusion of MVs in farmers' fields, it is important to understand the nature of the genetic changes attributable to seed recycling, as well as the rate at which they occur.

Table 10. Sources of maize seed, selected countries (% of farmers)

Country	Study	Type of material	Informal sector	Formal sector
Central America	Almekinders et al. (1994)	Landraces, OPVs, and hybrids	100	0
Nicaragua	Ortega Sequeira et al. (1993)	Landraces	100	0
		OPVs and hybrids	85	15
Mexico	Rice et al. (1997)	Landraces	65	?
		OPVs and hybrids	60	22
Guatemala	Sain et al. (1996)	Landraces	100	0
		OPVs	65	35
		Hybrids	54	46
India	Singh and Morris (1997)	OPVs and hybrids	42	58
Malawi	Smale et al. (1998)	Landraces	91	7
		Hybrids	50	74[a]

[a] Sums to more than 100% because farmers grow more than one hybrid.

Seven potential sources of genetic change in recycled maize can be distinguished: (1) farmers' seed selection practices, (2) unintentional seed mixing, (3) contamination, (4) genetic drift, (5) mutation, (6) natural selection, and (7) segregation. Each of these sources of genetic change is briefly described in the sections that follow, and published studies are reviewed in an attempt to determine whether theoretical predictions about the genetic effects of seed recycling are supported by empirical evidence.

Farmers' seed selection practices

Farmers' seed selection practices can exert an important influence on the genetic content of maize cultivars. As we have seen, seed may be selected at different times (before, during, or after the harvest), at different stages in the production cycle (from growing plants, from harvested cobs, from shelled grain), at different places (field, storeroom, home), by different people (the farmer, a paid laborer, the farmer's spouse, the farmer's children), and according to different criteria (physical aspect, agronomic characteristics, consumption qualities). This variability is important, because the *who*, *when*, *where*, *how*, and *why* of seed selection clearly can influence genetic content.

Many studies have documented farmers' seed selection practices, but relatively few have tried to measure the relationship between seed selection practices and the rate of genetic change in maize varieties. The very existence of thousands of distinct maize landraces attests to the effectiveness of farmers' seed selection practices in bringing about genetic changes; for purposes of estimating the impacts of maize breeding programs, the important issue is how quickly these genetic changes occur. The question is actually rather complicated, because in attempting to generalize about the rate of genetic changes attributable to farmer's seed selection practices, it is necessary to distinguish between situations in which farmers are consciously attempting to alter the characteristics of a variety by applying deliberate selection pressure and situations in which they are not trying to alter the characteristics of a variety but may be doing so inadvertently.

As part of their Cuzalapa study, Louette and Smale (1998) examined morphological characteristics and isoenzymatic loci of a set of maize varieties in an attempt to assess the effects of farmer seed selection practices at the phenotypic and genotypic levels. They concluded that farmers exert two distinct types of selection pressure. The first involves selection for production criteria (e.g., well-developed ears with healthy kernels), while the second protects ideotypes by preserving the characteristics of the variety as perceived by the farmer. Since the study involved only three cycles of selection, however, it is not clear how the changes that were detected can be extrapolated over a longer time frame.

In another study in Mexico, Vega (1973) compared samples of well-known maize landraces collected between 1940 and 1950 in the states of Mexico, Puebla, and Tlaxcala with samples of the same landraces collected in 1971. On average, the more recent collections yielded 0.7t/ha mor e than the original collections, equivalent to an increase of 25-33% achieved over a period of 20 to 30 years. The genetic changes observed may have resulted in part from natural selection pressure, as well as from the introgression of foreign germplasm, but most of the observed yield gains apparently were attributable to farmers' selection practices (Castillo-González et al., 1995).

Unintentional seed mixing

Unintentional mixing of grain or seed is another potential source of genetic change in maize. Unintentional mixing can occur during harvest, while ears are being dried, when grain is being shelled, during storage, or during seed selection.

Judging by the dearth of published studies on the topic, unintentional mixing of maize seed apparently has not been the focus of much research attention. *A priori*, one would expect that unintentional seed mixing is probably less common in maize than in small-grained cereals such as wheat and rice, since seed of different maize varieties and hybrids often can be distinguished visually based on differences in grain size, shape, or color. Also, because maize is an open-pollinating species, farmers presumably are more careful to avoid seed mixtures in maize than in the self-pollinating cereals, in which the risk of unwanted gene flows between varieties is small. In the absence of empirical studies on the incidence and consequences of unintentional mixing, however, it is difficult to confirm or deny these hypotheses.

Contamination

Contamination, or the unwanted pollination of one or more plants in a field by genetically distinct plants, is one of the most common sources of genetic change in maize, both in farmers' fields and in commercial seed production plots. The risk of contamination depends most critically on two factors: (1) the physical proximity of foreign sources of pollen, and (2)the degr ee to which the foreign sources of pollen flower at the same time. In addition, weather (especially wind) can play an important role in facilitating contamination. Because the question of genetic purity is so important to commercial seed producers, considerable research has focused on exploring the relationship between genetic purity and the two principal factors that directly influence the risk of contamination: distance and timing.

Distance. Maize produces a lot of pollen, which because it is very light can be dispersed by wind over considerable distances. The extent to which pollen moves across maize fields has been well documented (Airy, 1950; Sprague, 1977; Jugenheimer, 1985). Based on pollen weight and movement, and taking into account flower morphology, standards governing minimum isolation distances have been developed for commercial seed producers. Although these standards vary from country to country, it is generally accepted that an isolation distance of 200 m effectively prevents contamination (Jugenheimer, 1985; Beck, 1991).

Timing. For one maize plant to be contaminated by another, the two plants must not only be located close enough for pollen to travel between them, but they must flower at about the same time. Whether their flowering stages coincide depends on the date when each plant was sown, the amount of time each plant takes to reach the flowering stage, and the length of the inflorescence period of each plant. The length of the inflorescence period depends, among other things, on the genetic uniformity of the plant. Because of their greater degree of genetic diversity, most landraces flower over a longer period than improved OPVs, and most improved OPVs in turn flower over a longer period than hybrids (Longmire et al., unpublished; D. Beck, personal communication).

Numerous studies have been carried out to determine how distance and timing are likely to affect the degree of contamination in maize, both separately and in combination. Many of these studies have been conducted by seed companies in an attempt to establish spatial and temporal isolation standards for commercial seed production operations.[3]

Seed production specialists from the Seed Coop of Zimbabwe (1987) conducted an experiment to determine how time isolation influences the degree of contamination in the single-cross hybrid SR52. The experiment was designed to measure the amount of contamination that occurs when planting of the female line is delayed by different periods. Since the field in which the experiment was conducted was surrounded by a yellow pollen source, the degree of contamination could be determined by measuring the percentage of (white) female parent seed that was fertilized by yellow pollen. When the male and female parent lines were planted simultaneously, 95% of the pollen shed coincided with 5% of the silking. Time isolation was adequate when the difference between 95% of the pollen shed and 5% of the silking was 12 days or more. This was obtained when planting of the female parent was delayed by at least three weeks (Havazvidi et al, 1987). No information was given on the relationship between the degree of contamination and yield change.

Also in Zimbabwe, Kok et al. (1985) conducted a spatial isolation trial at Rattray Arnold Research Station. A seed production field containing the white-grained, single-cross hybrid SR52 was surrounded by a contaminating source of yellow-grained commercial maize. The contaminating maize was planted in three belts on three separate sowing dates to ensure that yellow pollen would be available in large quantities throughout the silking period of SR52. The degree of contamination in the field of SR52 was measured at various distances from the contaminating source. Over three cropping cycles, the largest penetration distance was 122 m. Again, no information was given on the relationship between the degree of contamination and yield change.

In a related trial involving a double-cross and a three-way-cross hybrid, researchers working for the Seed Coop of Zimbabwe (1987) measured the yield depression attributable to contamination caused by incomplete detasseling and poor isolation (Havazvidi et al., 1987). Incomplete detasseling results in self-fertilization of some female parents and/or fertilization of some female parents by genetically similar plants located nearby. Poor isolation results in fertilization of some female parents by genetically different plants located in nearby fields. Interestingly, the degree of yield depression was determined to vary by type of hybrid and by source of contamination. Yield depression was greater in the case of the double-cross hybrid than in the case of the three-way-cross hybrid, and yield depression caused by incomplete detasseling was greater than yield depression caused by poor isolation (Table 11). Irrespective of the type of hybrid or the cause of contamination, yields declined progressively as the degree of contamination increased.

Twumasi-Afriye (personal communication) describes an experiment carried out in Ghana to measure the rate of contamination in fields of quality protein maize (QPM). Since the high-quality-protein trait is coded by a single recessive gene, researchers are interested in

---

[3] Many studies on contamination in maize are based on the so-called *xenia effect*, which has to do with kernel color. In cases in which kernel color is coded by a dominant allele associated with pollen, after fertilization the pollen source can be determined by simple visual inspection of the ripening kernels. Thus, if a white-grained test plant is exposed to pollen from a yellow-grained plant, the degree of contamination can be determined by counting the number of yellow kernels that develop on the test plant.

Table 11. Yield depression resulting from bad detasseling or poor isolation, Zimbabwe

Percent of seed fertilized by by alien pollen	Double-cross hybrids: Poor detasseling: Yield (kg/ha)	Double-cross hybrids: Poor detasseling: Decline (%)	Double-cross hybrids: Poor isolation: Yield (kg/ha)	Double-cross hybrids: Poor isolation: Decline (%)
0	7,604	0	7,394	0
10	7,271	5	7,202	3
20	7,137	7	7,240	2
30	6,171	20	6,919	6
40	5,720	26	6,818	8
100	2,566	67	5,149	30

Percent of seed fertilized by by alien pollen	Three-way-cross hybrids: Poor detasseling: Yield (kg/ha)	Three-way-cross hybrids: Poor detasseling: Decline (%)	Three-way-cross hybrids: Poor isolation: Yield (kg/ha)	Three-way-cross hybrids: Poor isolation: Decline (%)
0	6,825	0	6,496	0
10	6,392	6	6,234	4
20	5,915	13	5,948	8
30	5,574	18	5,764	11
40	5,454	20	5,586	14
100	4,866	29	5,200	20

Source: Havazvidi et al. (1987).

determining whether QPM varieties released by the national program are likely to lose the trait as the result of contamination by local varieties. In the trial, a field of white-grained QPM was surrounded by several rows of yellow-grained local maize. The rate of contamination was measured at various stages of the crop's growth cycle at 6 m intervals along eight radial axes leading toward the center of the field. The mean level of contamination throughout the field was found to be around 11%. However, contaminated kernels were not distributed evenly; prevailing winds had increased contamination in the southeastern part of the field, and the level of contamination was greater nearer the edge of the field.

Farm-level studies suggest that many farmers are unable to maintain the distances and time isolation needed to prevent unwanted contamination.

Bellon and Brush (1994) conclude that maize farmers in Chiapas, Mexico, are generally unable to manage the physical location of their fields and/or the timing of their planting dates to prevent unwanted contamination. These farmers' management options are severely restricted by the need to cultivate many maize landraces (adapted to different ecological niches or grown to meet different consumption requirements), combined with extreme fragmentation of their landholdings (fostered by the *ejido* system, which equitably distributes different land types and soil qualities). The small size and physical proximity of fields greatly increases the chances of cross-pollination, especially since farmers have no control over what their neighbors grow. Because farmers do not attempt to coordinate their planting dates, varieties that have different growing cycles frequently have overlapping flowering dates. Although research has shown that the flowering dates of different landraces must be staggered by at least 21 days to prevent unwanted cross-fertilization, virtually all of the landraces grown by the farmers in the study area flowered within 21 days of each other.

Louette (1994) reaches similar conclusions in her study of maize landraces in Cuzalapa, Mexico. In Cuzalapa, farmers do not attempt to isolate varieties, either spatially or temporally. As a result, nearly one-quarter of all of the fields monitored by Louette featured overlapping flowering periods between long- and short-cycle varieties (overlapping flowering periods were even more common among varieties of similar cycles). While differences in flowering dates do not necessarily guarantee reproductive isolation between varieties, the risk of unwanted gene flow is obviously much greater when flowering dates overlap.[4] The rate of contamination between two randomly selected adjacent plots averaged around 2%, which was surely an underestimate because contamination was measured by the xenia effect, even though plants were not homozygous for kernel color. Based on this evidence, Louette concludes that farmers' management practices create favorable conditions for gene flow between varieties and probably explain the high level of intra-seed-lot diversity observed in local varieties.

Studies on gene flows between improved OPVs and landraces in various regions of Mexico have been carried out by researchers from the Colegio de Postgraduados (Ortiz Torres, 1993; Murillo Navarette, 1978; Vega, 1973). Generally speaking, these studies confirm that the rate of contamination can be very high (10-60%) at adjacent edges of neighboring plots when flowering is simultaneous. The rate of contamination drops considerably (to as little as 2-3%) when measured 15 m away from the plot borders, however. This latter finding is consistent with the results reported by Louette (1995) for gene flows between landraces.

The studies cited previously focused either on gene flows between landraces or between landraces and improved OPVs. Similar results have been reported by researchers investigating gene flows between improved OPVs. For example, in a study carried out in the state of Guerrero, Mexico, Murillo Navarette (1978) observed 8-23% contamination in border rows of plots planted with two improved OPVs, but less than 1% contamination 14 m away from the plot borders.

Although most contamination emanates from wind-borne pollen coming in from adjacent fields, contamination can also be caused by volunteer plants (also known as rogue plants). These are genetically dissimilar plants that have grown from seed inadvertently left in the field following the previous harvest. Very little research has been published on genetic changes attributable to volunteer plants. In what may be the only study of its kind, researchers from the Seed Coop of Zimbabwe conducted an experiment to determine how much contamination might be caused by a single volunteer when it is allowed to shed its pollen freely. The greatest amount of contamination occurred when between 5% and 50% of the ears on the surrounding female seed parents were silking. Most contamination was confined to a radius of 5 m from the volunteer, so destroying female plants found silking within a distance of 5 m from a volunteer was determined to be very effective for avoiding contamination (Havazvidi et al., 1987).

---

[4] Basseti and Westgate (1993) estimate that there is a 38% probability of gene flow between varieties when masculine flowering of one variety and female flowering of the other variety differ by less than five days.

Genetic drift

When farmers select ears of maize from their harvest to save as seed, they rarely use a statistically defensible sampling strategy. Often they select too few ears, or they select non-randomly by picking ears from the same field or from the same region within a field. These selection practices can lead to a phenomenon known as genetic drift. In small or non-representative samples, randomly distributed rare alleles may be lost. In the case of open-pollinated maize populations, a randomly selected sample of 100 ears will preserve (with a probability of 95%) rare alleles that occur with frequencies of only 5%, but alleles present with a frequency of 3% or less are likely to be lost. Genetic drift is linked to losses in variability and to decreases in the proportion of heterozygous individuals within populations (Crossa, 1989).

In her study of gene flows among maize landraces in Cuzalapa, Mexico, Louette (1994, 1995) determined that 32% of the seed lots in the study area were constituted by shelling fewer than 40 ears. According to Crossa (1989, 1994), 40 ears is the minimum number needed to avoid problems of genetic drift associated with non-representative sampling, so it seems likely that these seed lots regularly suffer losses of rare alleles. Many of the seed lots constituted from less than 40 ears involved colored landraces, which tend to be grown in extremely small plots for specialized purposes. Quite unexpectedly, the level of genetic diversity of colored landraces (measured by enzymatic polymorphism parameters) was found to be comparable to the level of genetic diversity of other landraces whose seed lots were constituted from much larger numbers of ears. This suggests that whatever rare alleles are lost because of farmers' non-representative seed selection practices are being replaced by alleles introduced as a result of gene flows between landraces planted in adjacent plots (Louette, 1995).

Mutation

Mutation can occur during meiosis when chromosomes become separated and are later reassembled in different combinations bearing new collections of alleles. Essentially a random event, mutation allows recombination of genetic material at each generation.

No studies were found in the literature reporting specifically on the effect of mutation on the rate of genetic change in maize. Mutation and random variation were implicated, however, in an interesting case study on seed production practices in Zambia. In the late 1980s, agricultural officials in Zambia became concerned that seed of the highly popular single-cross hybrid SR52 had become highly contaminated. A trial conducted to compare seed lots obtained from different commercial producers confirmed that there was a high level of variability not only between seed lots of different producers, but even within seed lots from the same producer (Ristanovic et al., 1985). Across six locations, yields ranged from 5.7 t/ha to 6.9 t/ha, a difference of more than 21%. Further investigation revealed that the inbred lines used to produce SR52 had become highly contaminated. This contamination was thought to have resulted from residual variation and mutation, rather than from accidental outcrossing.

Natural selection

Because of genotype by environment (G*x*E) interactions, every environment will favor some maize plants more than others. Deliberate selection pressure imposed by farmers or plant breeders thus always takes place against a background of natural selection, the direction of which will depend on the environment.

Our literature search failed to turn up any studies designed to measure the rate and/or direction of genetic change in maize attributable to natural selection. To the extent that deliberate selection pressure (whether imposed by farmers or by scientifically trained plant breeders) necessarily takes place against a background of environmental factors, natural selection pressure is always present when plant breeding is conducted. To isolate the effects of natural selection from other sources of genetic change, however, it would be necessary to grow out carefully isolated trials in a number of locations over many years. This would be a rather pointless exercise, which presumably explains why it has never been attempted.

Segregation

Segregation is often the major cause of deleterious genetic change (and hence yield reductions) when farmers recycle maize seed. Although segregation occurs in all open-pollinated materials, the effects of segregation are most apparent in the case of recycled hybrids. Each of the parents used in making a hybrid contributes genes that interact in specific combinations to produce hybrid vigor. When hybrids are recycled, because of gene segregation the resulting seed no longer contains the specific gene combinations responsible for hybrid vigor. As a result, plants grown from advanced-generation hybrid seed (F2 or later) will not resemble plants grown from first-generation (F1) hybrid seed.

The following discussion relates to hybrids, on which the greatest amount of theoretical work has been done. To provide an adequate context for the discussion that follows, it is necessary to begin with a brief overview of some basic maize breeding principles.

Development of hybrid maize

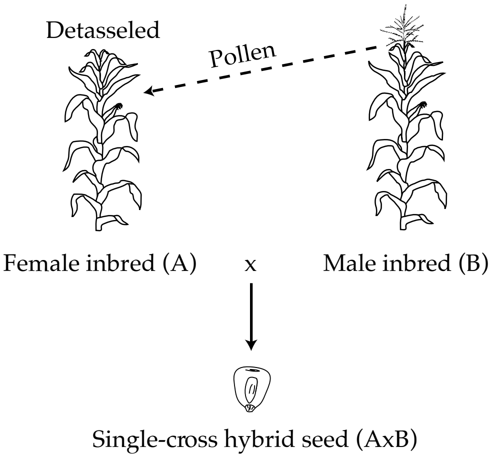
Maize hybrids are produced by crossing some combination of genetically distinct parents. *Conventional hybrids* are produced using two or more inbred lines as parents, while *non-conventional hybrids* are produced from parents at least one of which is not an inbred line (Table 12, Figure 1). Conventional hybrids include single crosses formed by crossing two inbred lines (A x B), three-way crosses formed by crossing an inbred line with a single cross [(A x B) x C], and double crosses formed by crossing two single crosses [(A x B) x (C x D)]. Examples of non-conventional hybrids include varietal crosses formed by crossing two OPVs and top crosses formed by crossing an inbred line with an OPV.

Table 12. Types of maize hybrids, showing genetic composition of parents

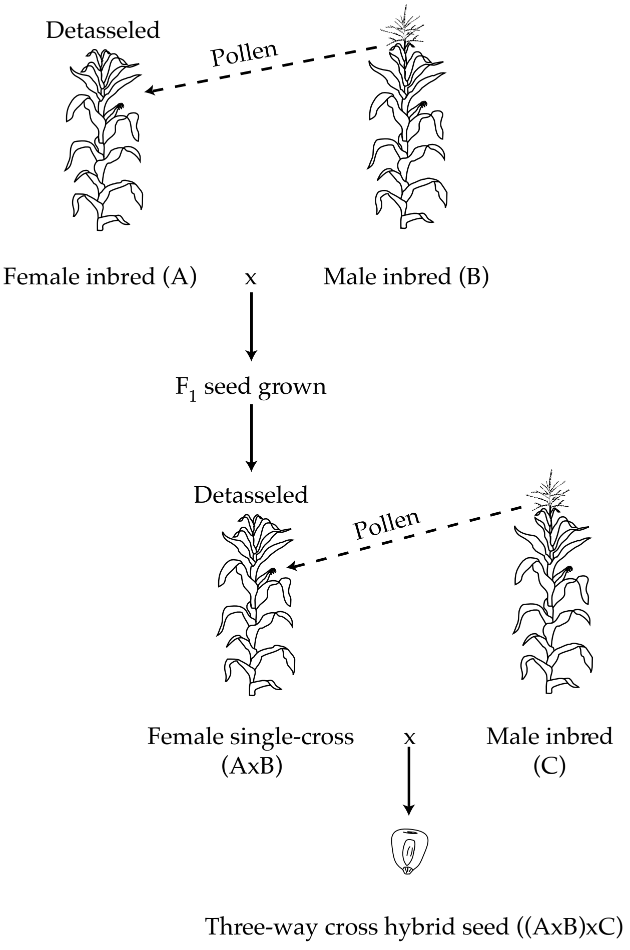
Type of hybrid	Genetic composition of parents
Conventional hybrids	
Single cross	Inbred line *x* inbred line
Three-way cross	Single-cross hybrid *x* inbred line
Double cross	Single-cross hybrid *x* single-cross hybrid
Nonconventional hybrids	
Top cross	Open-pollinated variety *x* inbred line
Double top cross	Single-cross hybrid *x* open-pollinated variety
Varietal cross	Open-pollinated variety *x* open-pollinated variety

Source: Compiled by the authors.

(a) Production of a single-cross hybrid



(b) Production of a three-way cross hybrid



(c) Production of a double-cross hybrid

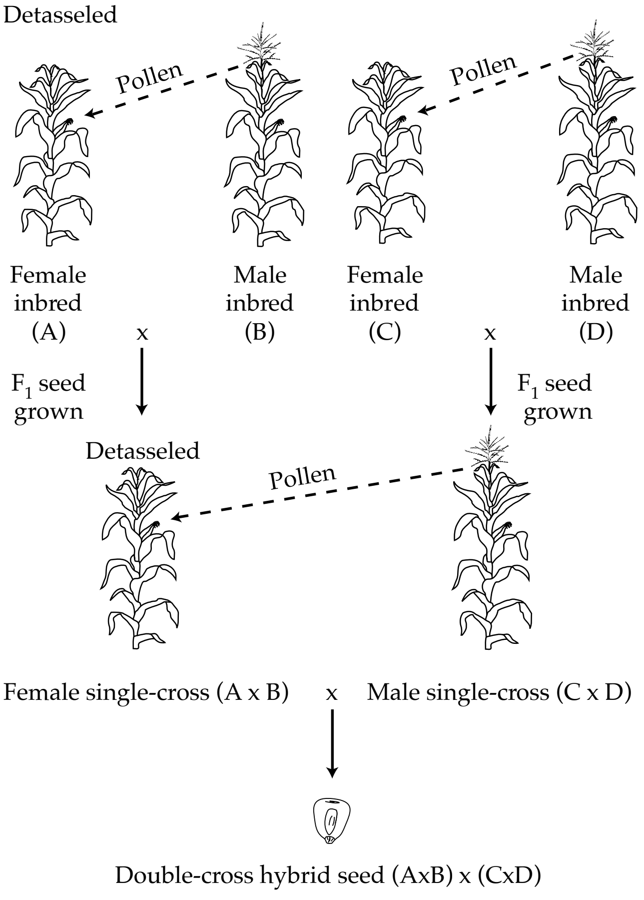
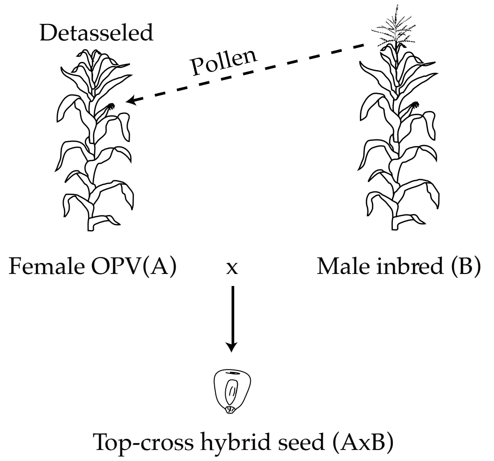
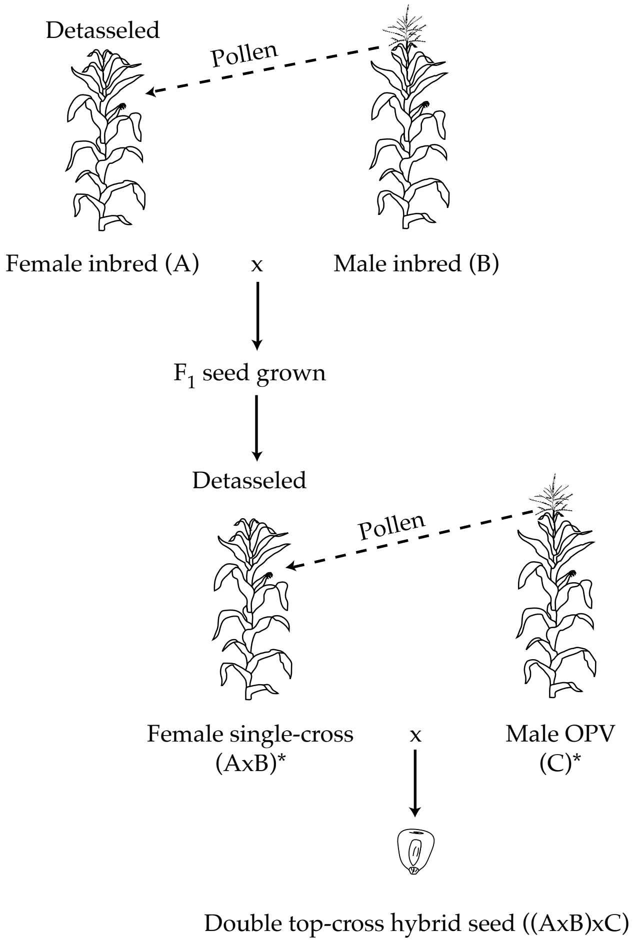


Figure 1. Production of different types of maize hybrids.

(d) Production of a top-cross hybrid



(e) Production of a double top-cross hybrid



* Parentage may be reversed

(f) Production of a varietal cross hybrid

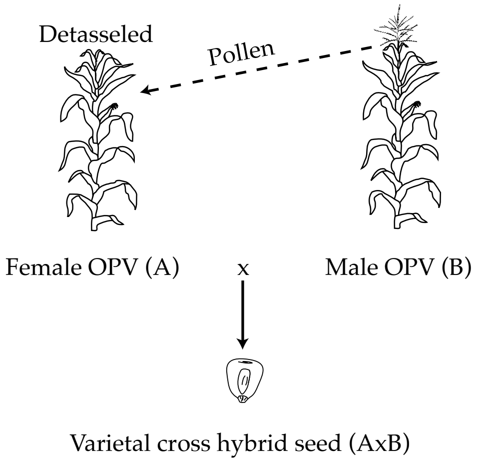


Figure 1 (Continued). Production of different types of maize hybrids.

Breeding hybrid maize begins with the development of suitable parental material. Inbred lines are typically developed through repeated cycles of controlled self-pollination in which the silks on a given plant are fertilized using pollen from the same plant. Inbred lines may also be developed through sib-pollinations in which the silks on a given plant are fertilized using pollen from a sibling plant. The inbred lines (as well as the varieties being used as parents, in the case of non-conventional hybrids) then must be evaluated for their ability to make productive crosses. The final step is to produce the best crosses in large quantities for commercialization.

To understand the importance of inbred lines, it is necessary to know a little bit about the genetic basis of inheritance. Genes are basic units of inheritance, passed on from one generation to another and made up of sequences of paired bases (nucleotides) located at particular loci on chromosomes inside the cell nucleus. Most genes can have several forms, known as alleles, that provide different alternatives for inheritance. For example, kernel color in maize can vary widely; this characteristic is coded by one major gene having various alleles (expression of the major gene may be modified by other genes, however). Generally one allele is dominant and the other(s) recessive. When all copies of a gene found within one plant are identical, i.e., when they consist of the same allele, the plant is said to be homozygous. When the copies of a gene found within one plant are different, i.e., when they consist of different alleles, the plant is said to be heterozygous.

The main purpose of inbreeding is to fix desirable characters in a homozygous condition in such a way that the genotype can be maintained with limited genetic change. Inbred lines are commonly developed by self (and in rare cases sib) pollination. Heterozygosity is reduced by one-half with each successive self-fertilization. With self-fertilization, heterozygous allele pairs (Aa or aA) will segregate into the genotypes 1 AA : 2 Aa : 1 aa. Homozygous allele pairs (AA or aa) will remain homozygous. Five to seven generations of selfing are usually required to obtain uniformity and homozygosity.

The inbreeding process is characterized by two important phenomena: (1) reduction in vigor and (2) segregation. Typically, reduction in vigor of up to 50% is observed in the first selfing generation, followed by smaller declines in subsequent generations. Segregation results in the exposure of deleterious characteristics, such as chlorophyll-deficiency, disease susceptibilities, lodging, etc. The reduction in vigor and the exposure of deleterious characters as a result of segregation make most inbred lines unusable. In most commercial breeding programs, undesirable plants are simply discarded, and the most vigorous plants retained for further selfing in succeeding generations.

Once superior inbred lines have been developed, they must be evaluated for their ability to make productive hybrids. This involves testing them for what is known as “combining ability.” A major practical problem in applied maize breeding involves the identification of favorable combinations of inbred lines from among the large number of possible combinations that can be formed using a given set of lines. The task is complicated by the fact that the number of favorable combinations is often low. Hallauer and Miranda (1989) estimate that for every 10,000 twice-selfed (S2) or thrice-selfed (S3) lines tested, on average only one is eventually used to produce commercial hybrids. To facilitate the task, groups of inbreds are often crossed with one or more common testers selected from among the materials that are known to combine well with the inbreds being evaluated (known as "heterotic partners"). The top-cross test may be done as early as the S1 generation or as late as the S7 or S8 generation. Most commonly it is first done at some intermediate stage, such as S3. Lines showing good combining ability are further inbred and then evaluated again in additional hybrid combinations.

After a superior hybrid has been identified, the final step involves the production of commercial seed. This is accomplished by planting both parents in the same field. A proportionally greater area is planted to the female parent (or seed parent) which will produce hybrid seed. Enough plants of the male parent are sown to ensure that sufficient pollen is produced to cross-pollinate the female parents. The female parents are detasseled to eliminate any possibility of self-pollination.

The profitability of hybrid maize seed production depends critically on the seed yield of the female parent, which tends to vary greatly between hybrid types. Seed of single-cross hybrids is usually expensive to produce, because it is harvested from female parent lines that are often low in productivity. Seed of three-way-cross and double-cross hybrids tends to be less expensive to produce, because it is harvested from more productive female parent lines. Seed of non-conventional hybrids tends to be cheapest of all to produce, because it is harvested from female parents that are always full-vigor (non-inbred) plants.

Theories of hybrid vigor and inbreeding depression

The term *hybrid vigor* refers to the increase in performance of a hybrid compared to the mean performance of its parents (with performance expressed in terms of one or more measurable characteristics, such as size, vigor, and/or yield). George Shull (1908, 1909, 1952) coined the term *heterosis* – actually a contraction of "stimulus of heterozygosis" – to denote this increase in performance. Today, the terms *hybrid vigor* and *heterosis* are considered synonyms and are used interchangeably.

Most geneticists view heterosis and inbreeding depression as opposite manifestations of the same phenomenon. In his classic text *Introduction to Quantitative Genetics*, Falconer (1989) states that "complementary to the phenomenon of inbreeding depression is its opposite, 'hybrid vigor' or 'heterosis'…. That the phenomenon of heterosis is simply inbreeding depression in reverse can be seen by considering how the population mean depends on the coefficient of inbreeding."

Two major theories and several minor theories have been advanced to explain heterosis (and, by implication, inbreeding depression). Although several of these theories have gained large numbers of adherents, none offers a complete explanation of this complex phenomenon (Crow, 1997).

The most widely accepted theory of heterosis (known as the *dominant theory*) is based on the assumption that hybrid vigor results from bringing together favorable dominant genes.

According to this theory, genes that promote vigor and growth are dominant, while genes that discourage vigor and growth are recessive. When a hybrid is formed by crossing two genetically distinct parents, dominant genes contributed by one parent may complement dominant genes contributed by the other parent, so that the resulting progeny will have a more favorable combination of dominant genes than either parent.

The dominant theory can be illustrated using a simple empirical example. Let us assume that the dominant alleles A, B, C, D, and E are favorable for high yield and that inbred A has the genotype AAbbCCDDee (A, C, and D are dominant) and that inbred B has the genotype aaBBCCddEE (B, C, and E are dominant). If these two inbreds are used as parents to form a single-cross hybrid (A x B), the hybrid would have the genotype AaBbCCDdEe. In the F1 generation, this hybrid would contain dominant alleles at all five loci and would therefore outperform both parent inbred lines, each of which has dominant alleles at only three loci.

If this explanation is correct, it should theoretically be possible to concentrate a sufficient number of favorable dominant alleles in a homozygous condition within the same inbred line – which would make the inbred line as productive as the hybrid cross. Unfortunately, practical considerations get in the way. So-called quantitative characteristics such as yield are controlled by such a large number of genes that it is for all intents and purposes impossible to recover all of them in a homozygous state within an individual plant. Furthermore, cross-pollinating species such as maize contain significant numbers of deleterious recessive alleles. In the presence of cross-pollination, the effects of deleterious recessive alleles are often masked by the presence of favorable dominant alleles, but after repeated cycles of self-pollination, many of the deleterious recessive alleles become homozygous, leading to loss of vigor in inbred lines.

The second major theory explaining heterosis (known as the *overdominance theory*) assumes that heterozygosity is often superior to homozygosity, so that better performing plants tend to have higher numbers of heterozygous loci (Crow, 1997; Hallauer and Miranda, 1989). This theory is based on the supposition that when there are different alleles (a1 and a2) for a single locus, each allele produces favorable yet different effects in the plant. In a heterozygous plant (a1a2), a combined effect is produced that is more favorable to the plant than the effect produced by either one of the alleles acting alone in a homozygous state (a1a1 or a2a2).

A third theory explaining heterosis (known as the *epistasis theory*) focuses on epistatic gene interactions. Whereas the dominant and overdominance theories concentrate on intra-allelic gene action, the epistasis theory explains heterosis in terms of inter-allelic gene actions, i.e., it posits that a gene found at one locus can affect the expression of genes found at other loci. Examples of epistasis include gene complementarity, gene silencing, and duplicate gene interactions. The interaction of non-allelic genes to influence plant characteristics is a well-known genetic phenomenon, although limited evidence can be cited to show that the interaction leads to a heterotic effect (Goodnight, 1997; Hallauer and Miranda, 1989).

Recent developments in biotechnology have shed important new light (at the molecular level) on the twin phenomena of heterosis and inbreeding depression (Lee, 1997; Tsaftaris et al., 1997), but a complete understanding remains elusive. Hallauer (1997) has speculated that "the exact genetic basis of heterosis may never be fully understood because of interactions: interactions of alleles at a locus, interactions of alleles at different loci, interactions of the nucleus and cytoplasm, and interactions of the genotypes and environment. Because of the complexity of interactions within genotypes and between genotypes and environments, only general explanations may be feasible. But heterosis will continue to have a major role in the future of plant improvement even though our knowledge of its genetic basis is limited."

The existence of competing theories merely serves to emphasize that heterosis and inbreeding depression are complex phenomena that defy simple explanation. In discussing what we expect to happen when farmers recycle hybrid seed, we will rely to a certain extent on the most widely accepted theories of heterosis and inbreeding, however incomplete they may be.

Expected yield reductions in recycled seed

Superior hybrids – i.e., hybrids that exhibit high levels of heterosis – are produced by combining genetically distinct parents in ways that result in specific favorable combinations of alleles. The first time a hybrid is recycled, the seed saved by the farmers is produced on F1 plants that for the most part received pollen from other genetically similar F1 plants in the same field. Because of segregation, this seed (known as F2 seed) will have fewer of the favorable gene combinations responsible for hybrid vigor in the F1 generation, resulting in inbreeding depression. As a result, plants grown from F2 seed will tend to under-perform their F1 parents.

If hybrid seed is recycled two or more times (resulting in F3 hybrids, F4 hybrids, F5 hybrids, etc.), segregation will continue, but the deleterious effects of inbreeding depression may be offset partly or wholly by random recombination of favorable alleles as a result of random cross-pollination.

To what extent will the performance of maize hybrids change as a result of seed recycling? The following discussion focuses on one measure of performance that is of widespread interest – yield.

The theoretical basis for predicting yield changes in F2 maize hybrids comes from Wright's (1922) investigations of heterosis and inbreeding depression in guinea pigs. Based on experimental evidence, Wright concluded that changes in vigor are directly proportional to the change in heterozygosity of the population. Wright summarized his findings as follows: "A random-bred stock derived from n inbred families will have $(1/n)^{\text{th}}$ less superiority over its inbred ancestry than the first cross or a random-bred stock from which the inbred families might have been derived without selection."

Wright's finding, which is based on the assumption of additive gene action, can be expressed mathematically as follows:

$$\text{F2} = \text{F1} - (\text{F1} - P) \;/\; n \qquad (1)$$

where:

F2 = the mean of all possible F2 double crosses among a set of F1 single crosses,
F1 = the mean of all possible F1 single crosses among a set of inbred parents,
P = the mean of all the parents, and
n = the number of inbred parents.

Kiesselbach (1933) reports results that support Wright's conclusion. Yield data from F1 hybrids with 2, 4, 8, and 16 inbred parents and their F2 generations confirm that yield is highly correlated with heterozygosity. Although yield data of the inbred parents are not reported, Kiesselbach summarizes his findings by stating that the decrease in yield observed among F2 generation hybrids can be attributed to a reduction in the number of favorable growth factors as a consequence of close breeding. He further concludes that for any hybrid in which the parents are composed of equal numbers of parent inbreds, the reduction in yield tends to be inversely proportional to the number of lines involved.

Neal (1935) used Wright's formula to predict the performance of advanced-generation maize hybrids. Ten single crosses, four three-way crosses, and ten double crosses, their F2 progeny, and F3 progeny of six of the single crosses were used to validate Wright's formula with maize. Neal reports that the single crosses, three-way crosses, and double crosses decreased in vigor by 29.5%, 23.4%, and 15.8%, respectively, between the F1 and F2 generations, which was in close agreement with the predicted losses of 31.0%, 21.0%, and 15.3%. Neal concludes that the observed decreases in vigor were very consistent with Wright's formula. Powers (1941) reanalyzed Neal's data using both arithmetic and geometric models and found that the best agreement between observed and predicted values was obtained with the arithmetic model.

Martin and Hallauer (1976) examined the relationship between different levels of heterozygosity in four sets of inbred lines. Each set of 21 materials included the F1, F2, and F3 generations of seven different inbred lines. Data were generated in replicated trials grown in five environments. Sums of squares for levels of heterozygosity were partitioned into linear, quadratic, and lack-of-fit components. Some evidence of epistatic effects was detected in all four sets of materials, although the frequency of detectable epistatic effects was significantly lower than that of linear effects. Among all four sets of materials, the authors detected 84 instances of linear, 3 instances of quadratic, and 1 instance of lack-of-fit components affecting grain yield. The presence of linear components indicates that individual loci contribute their effects independently of all other loci, while the presence of quadratic and lack-of-fit mean squares show evidence of epistatic effects – so on the whole these results suggest that net epistatic effects did not greatly affect grain yield.

Other researchers have developed empirical evidence in support of Wright's formula (Hallauer and Miranda, 1989). Although the arithmetic model has been shown to be the best in most studies, it may be dangerous to conclude that traits such as vigor and yield are expressed only in additive fashion. Cancellation of inter-locus interactions (epistasis) may prevent detection of non-additive variation.

Unlike most previous researchers who had focused on crosses made among inbred lines, Pollak et al. (1957) studied heterosis and inbreeding depression in crosses made among three OPVs. In their study, the F1, F2, and backcross populations of the OPVs were used to establish different levels of heterozygosity. After determining that the mean yield of the F2 plants lay in between the mean yield of the parents and the mean yield of the F1 plants, Pollak et al. concluded that their results were consistent with an additive genetic model (with dominance) and that epistatic effects were minimal.

Shehata and Dhawan (1975) evaluated inbreeding depression among three sets of diallel crosses; each set included 10 parents that were either OPVs or synthetics. In comparing the yields of F1 and F2 plants, the average inbreeding depression for each of the three diallels was estimated to be 10.2%, 11.4%, and 11.2%. The deviation in yield performance of the F2 plants from the mean performance of the parental varieties and the F1 variety crosses was small in all instances, suggesting largely additive effects among loci, with limited net epistaticef fects.

Most studies in the plant breeding literature confirm that the arithmetic model best predicts the decline in yield performance observed between F1 and F2 plants. In a comprehensive review, Hallauer and Miranda (1989) conclude that the yield decreases observed when F1 plants are self-pollinated (inbred) to produce F2 plants generally are smaller when the F1 plants are OPVs, rather than inbred lines. While epistatic effects are generally minimal, they tend to be greater in line-based crosses compared to variety-based crosses. Hallauer and Miranda remark, “This difference seems reasonable because of the nature of the material included in the crosses. For varieties this would involve an array of genotypes included in the crosses, whereas crosses of inbred lines would involve the expression of two specific genotypes.” Extrapolating from this observation, one would expect that the inbreeding depression observed in three-way crosses, double crosses, and non-conventional hybrids formed using one inbred line to fall somewhere in between that observed in single crosses and variety crosses.

Mather and Jinks (1971) propose equations derived from Wright’s original equation to predict the performance of F2, F3, F4, and subsequent generations of plants in self-pollinated crops.

For quantitative traits, the mean of F2 generation plants (obtained by selfing or sib-mating F1 plants) can be calculated as follows:

$$F2 = (1/4)(P1 + P2 + 2F1) \qquad (2)$$

where:

F2 = the mean of F2 generation plants,
F1 = the cross-mean F1 generation plants,
P1 = the mean of the first parent line (assumed to be completely homozygous), and
P2 = the mean of the second parent line (assumed to be completely homozygous).

Similarly, the mean of F3 generation plants can be calculated as follows:

$$F3 = (1/8)(3P1 + 3P2 + 2F1) \qquad (3)$$

where:

F3 = the mean of F3 generation plants,
F1 = the cross-mean F1 generation plants,
P1 = the mean of the first parent line (assumed to be completely homozygous), and
P2 = the mean of the second parent line (assumed to be completely homozygous).

It is important to recall that these equations were developed for use with self-pollinated crops, such as wheat or rice. With maize, an open-pollinated crop, the incidence of self-pollination is typically very small. Kiesselbach (1922) reports only 0.7 % self-pollination in a white-grained OPV grown in a field amidst a yellow-grained OPV. The physical separation of the flowers, pollen dispersal by wind, and the protandrous nature of maize (where pollen is typically shed several days prior to silk emergence on the same plant) all promote cross-pollination.

To deal with the cross-pollinated nature of maize, equation (3) proposed by Mathers and Jinks can be divided by six, since six generations of half-sib matings theoretically equal one generation of self-fertilization (Hallauer and Miranda, 1989).

$$F3^* = [(1/8)(3P1 + 3P2 + 2F1)]/6 \qquad (4)$$

where:

F3 = the mean of F3 generation plants,
F1 = the cross-mean F1 generation plants,
P1 = the mean of the first parent, and
P2 = the mean of the second parent.

In a simple simulation exercise, equations (2) through (4) were used to predict the mean yield performance of the F2 and F3 generations of various types of maize hybrids. The yields assumed for the F1 parents used in the simulation appear in Table 13. These assumed

Table 13. Assumed yields (t/ha) of parents used in inbreeding simulation exercise

Varieties		Inbred lines		Single crosses		Three-way crosses		Double crosses		Top crosses		Varietal crosses	
Variety	(t/ha)	Line	(t/ha)	Cross	(t/ha)	Cross	(t/ha)	Cross	(t/ha)	Cross	(t/ha)	Cross	(t/ha)
V1	2.0	L1	4.5	L1 x L2	6.5	(L1 x L2) x L3	7.5	(L1 x L2) x (L3 x L4)	7.0	V1 x L1	5.5	V1 x V2	6.0
V2	2.5	L2	5.5	L1 x L3	9.5	(L1 x L3) x L4	8.0	(L1 x L3) x (L2 x L4)	7.0	V1 x L3	6.0	V1 x V3	5.5
V3	3.0	L3	5.0	L1 x L4	7.0	(L1 x L4) x L1	6.5	(L1 x L4) x (L2 x L3)	6.5	V2 x L2	6.0	V2 x V3	6.5
	2.5	L4		L2 x L3	7.5	(L2 x L3) x L3	6.5					V2 x L4	7.0
				L2 x L4	7.0	(L2 x L4) x L1	7.5					V3 x L1	6.0
				L3 x L4	8.0	(L3 x L4) x L2	7.0					V3 x L4	7.0

Source: Compiled by the authors.

yields may be considered typical for each class of material, i.e., the highest mean yields among F1 generation hybrid plants occurs among single crosses, followed by three-way crosses, double crosses, top crosses, and varietal crosses.

The results of the simulation exercise appear in Table 14.

The simulation exercise generated the following noteworthy results:

1. The highest mean yields among F2 and F3 generation plants can be expected to occur among double-cross hybrids, followed by three-way crosses, varietal crosses, single crosses and top crosses.

Table 14. Predicted yield changes resulting from inbreeding depression for various maize hybrid types (simulation results)

Cross	Type of hybrid	Yield (t/ha)			Inbreeding depression (%)		
		F1	F2	F3	F1 - F2	F2 - F3	F1 - F3
L1 x L2	Single cross	6.5	4.4	4.2	32.7	4.0	35.4
L1 x L3	Single cross	9.5	6.0	5.7	36.8	4.8	39.9
L1 x L4	Single cross	7.0	4.6	4.4	33.9	4.2	36.7
L2 x L3	Single cross	7.5	5.1	4.9	31.7	3.8	34.3
L2 x L4	Single cross	7.0	4.8	4.6	32.1	4.0	34.9
L3 x L4	Single cross	8.0	5.4	5.2	32.8	4.0	35.5
	Mean value (single crosses)	**7.6**	**5.0**	**4.8**	**33.5**	**4.2**	**36.3**
(L1 x L2) x L3	Three-way cross	7.5	6.1	5.7	19.3	5.8	24.0
(L1 x L2) x L4	Three-way cross	8.0	5.3	5.0	33.4	5.6	37.1
(L2 x L3) x L1	Three-way cross	6.5	6.1	5.7	6.9	6.5	12.9
(L2 x L4) x L3	Three-way cross	6.5	5.9	5.6	9.4	5.6	14.5
(L3 x L4) x L1	Three-way cross	7.5	6.3	5.9	16.3	5.6	20.9
(L3 x L4) x L2	Three-way cross	7.0	5.9	5.6	15.9	5.3	20.3
	Mean value (three-way crosses)	**7.2**	**5.9**	**5.6**	**17.4**	**5.7**	**22.2**
(L1 x L2) x (L3 x L4)	Double cross	7.0	6.3	5.8	10.7	6.6	16.6
(L1 x L3) x (L2 x L4)	Double cross	7.0	6.1	5.7	13.4	6.3	18.9
(L1 x L4) x (L2 x L3)	Double cross	6.5	6.4	6.0	0.9	6.8	7.7
	Mean value (double crosses)	**6.8**	**6.3**	**5.8**	**8.4**	**6.6**	**14.5**
V1 x L1	Top cross	5.5	4.4	4.3	20.5	2.2	22.2
V1 x L3	Top cross	6.0	4.9	4.8	18.8	1.9	20.3
V2 x L2	Top cross	6.0	5.0	4.9	16.7	1.6	18.0
V2 x L4	Top cross	7.0	5.5	5.4	21.4	2.4	23.3
V3 x L1	Top cross	6.0	4.8	4.7	20.8	2.1	22.5
V3 x L4	Top cross	7.0	5.4	5.2	23.2	2.5	25.1
	Mean value (top crosses)	**6.3**	**5.0**	**4.9**	**20.3**	**2.1**	**22.0**
V1 x V2	Varietal cross	6.0	5.5	5.3	8.3	4.5	12.5
V1 x V3	Varietal cross	5.5	5.1	4.9	6.8	3.6	10.2
V2 x V3	Varietal cross	6.5	5.9	5.4	9.6	7.9	16.8
	Mean value (varietal crosses)	**6.0**	**5.5**	**5.2**	**8.3**	**5.5**	**13.3**

2. Between the F1 and F2 generations, single-cross hybrids can be expected show the greatest amount of inbreeding depression (33.5% on average), followed by top-cross hybrids (20.3%) and three-way-cross hybrids (17.4%). Double-cross hybrids and varietal hybrids can be expected to show the least amount of inbreeding depression, approximately 8% on average in both cases.

4. Between the F2 and F3 generations, all hybrid types can be expected to show small amounts of inbreeding depression. The greatest amount of inbreeding depression is expected among double crosses (6.6%), and the least amount is expected among top-cross hybrids (2.1%).

5. The greater the level of heterozygosity in F1 plants, the greater the variability in inbreeding depression expected in F2 and F3 generations of plants. Thus, inbreeding depression is expected to be more highly variable in double crosses and three-way crosses than in single crosses.

If these simulated results are used to predict inbreeding depression in maize hybrids under actual farmers' conditions, several possible limitations must be noted.

First, the simulation implicitly assumes the use of highly homozygous lines (S6 lines or beyond). Many commercial hybrids are based on lines that have undergone fewer cycles of inbreeding (for example, S2 or S3 lines). Theoretically, an S6 line is 98.5% homozygous (or 1.5% heterozygous), while an S2 line is 75.0% homozygous (or 25.0% heterozygous). The amount of heterosis seen in top-yielding combinations formed using highly inbred lines is usually much greater than the amount of heterosis seen in crosses formed using early-generation lines. Similarly, the amount of inbreeding depression seen in F2 plants formed from hybrids based on highly inbred lines is likely be much greater than the amount of inbreeding depression seen in F2 plants formed from hybrids based on early-generation lines. The simulation results show the expected performance of hybrids formed using highly inbred lines; expected levels of inbreeding depression would not be as great with hybrids formed using early-generation lines.

Second, with maize hybrids the observed levels of inbreeding depression will depend partly on the amount of self-pollination that occurs. The only exception to this is when a single-cross hybrid formed using highly inbred parents goes from the F1 to the F2 generation; in this case, all F1 plants are genetically identical, so inbreeding depression in the F2 generation will be similar regardless of whether the seed parent is self- or sib-pollinated. With all other hybrid types, however (including single crosses based on early-generation lines), inbreeding depression will be greater when the seed parent is self- vs. sib-pollinated (Kiesselbach, 1960). Under normal production conditions, more than 95% of the silks on a given maize plant are cross-pollinated, but exceptional circumstances can increase the amount of self-pollination that occurs (Kiesselbach, 1922). Two factors in particular can increase the amount of inbreeding that occurs in a population of randomly mating maize plants: (1) small effective population size and

(2)envir onmental conditions likely to impede the physical dispersal of pollen, e.g., lack of wind, heavy rainfall, and high relative humidity. [5]

Third, deviations from the simulation results would be expected when epistatic effects are significant. Although experimental evidence suggests that epistatic effects are often inconsequential, they appear to be more important in hybrids (and especially single-cross hybrids) formed using highly inbred lines (Hallauer and Miranda, 1989).

Fourth, deviations from the simulation results could also result from strong G x E effects. Experimental evidence shows that because of buffering effects associated with heterozygosity, maize hybrids typically show smaller G x E interactions than inbred lines (Shank and Adams, 1960). For this reason, the performance of heterozygotic materials tends not only to be superior to that of homozygous materials, but in the presence of high levels of environmental variability, it also tends to be more stable. The longer farmers recycle maize seed, the more inbred their material is likely to become – and hence the more unstable. To the extent that recycled conventional hybrids based on highly inbred lines show greater interactions with environmental factors than recycled non-conventional hybrids based on more heterozygous parents, the simulation results could diverge from the performance observed in farmers' fields.

Empirical evidence on the effects of segregation in farmers' fields

To what extent are the predicted levels of inbreeding depression in different types of maize hybrids (calculated on the basis of quantitative genetics theory) borne out by empirical evidence? A considerable amount of research has focused on genetic changes in advanced-generation hybrids. The topic is of obvious practical interest, given the rising popularity of hybrids around the world. Evidence from a number of developing countries is presented below. An effort has been made to distinguish between results obtained from on-farm trials involving farmers' management and results obtained from on-station trials conducted under controlled conditions. For simplicity, we have chosen to concentrate on yield effects, although results are frequently reported for other characteristics as well.

---

[5] The amount of unavoidable inbreeding that occurs in a randomly mating population of maize plants is determined by the number (N) of unrelated individuals in the population whose gametes unite at random in every generation. Li (1974) shows that the probability that a given gamete will unite with a gamete from the same individual is $1 / N$, while the probability that it will unite with a gamete from a different individual is $(N-1) / N$. Building on Li's formula, Sprague and Eberhart (1977) propose the following formula for effective population size:

$$Ne = 2N / (1 + Fp) \qquad (6)$$

where:

Ne = effective population size
N = number of plants
Fp = the inbreeding coefficient of parent plants (empirical investigation revealed that Fp ranges from 0 for non-inbred parents to 1 for highly inbred lines).

Thus, the greater the number of individual plants and the lower the levels of inbreeding in those plants, the larger the effective population size. Hallauer and Miranda (1981) use this formula to show the effect of population size on inbreeding and resulting performance. For our application, smaller effective population sizes would be more likely with conventional hybrids, which tend to be based on highly inbred lines and typically have a narrower genetic base than non-conventional hybrids.

In a series of on-station trials conducted in the highlands of central Mexico, Espinosa Calderón et al. (1990) examined the effects of seed recycling on the performance of two popular commercial hybrids, one single cross and one double cross. Three generations of the single cross and two generations of the double cross were grown and compared to equivalent generations of an improved OPV. As expected, the yields of both hybrids declined significantly between generations (Table 15). The yield of the single cross decreased by 25% from the F1 to the F2 generation and by an additional 5% from the F2 to the F3 generation. Contrary to expectations, the yield decline experienced by the double cross was more severe; the yield fell 42% from the F1 to the F2 generation. Interestingly, although the F1 hybrids significantly outyielded the OPV, plots of the OPV (grown from recycled seed) consistently outyielded plots of the advanced-generation hybrids (Figure 2).

Espinosa Calderón et al. (1993) later conducted a similar trial using three single-cross hybrids (H-34, H-36, H-68) and one double-cross hybrid (H-33). As expected, all of the hybrids suffered a drop in yield between the F1 and F2 generations, although the size of the yield decline was highly variable, ranging from 6% to 51% (Table 16). Once again, the yield decline

Table 15. Inbreeding depression observed in two hybrids, Mexico

	Yield (kg/ha)			Inbreeding depression (%)	
Cultivar	F1	F2	F3	F1 F2	F2 F3
Single-cross hybrid (H-34)	7,595	5,719	5,431	25	5
Double-cross hybrid (H-30)	6,933	4,005		42	
Improved OPV (V-23)	6,445				

Source: Espinosa Calderón et al. (1990).

Table 16. Inbreeding depression, selected hybrids, Mexico

Cultivar	Generation	Yield (kg/ha)	Inbreeding depression (%)	Yield (% of F1 yield)
Single-cross hybrid (H-34)	F1	8,892	51	100
	F2	4,327	-10	49
	F3	4,748	-20	53
	F4	5,678		64
Double-cross hybrid (H-33)	F1	8,887	27	100
	F2	6,513		73
Double-cross hybrid (H-68)	F1	6,404	6	100
	F2	6,050		95
Double-cross hybrid (H-36)	F1	9,133	29	100
	F2	6,481		71
Improved OPV (V-23)	F1	7,488		

Source: Espinosa Calderón (1993).

observed in the double cross unexpectedly exceeded the yield decline observed in some of the single crosses. Also once again, the yield of an OPV planted as a check was always superior to advanced generations of hybrids. But a noteworthy new result of the second trial was the finding that yields do not necessarily continue to decline after the second generation; in the case of the single cross H-34, yield actually increased in the F3 and F4 generations (Figure 3).

In another on-station trial conducted in a tropical lowland region of Mexico, Ramírez Vallejo et al. (1986) evaluated the effects of seed recycling on the performance of three double-cross hybrids (H-503, H-507, H-510). With all three hybrids, F1 plants yielded better than advanced-generation progeny and better than a check OPV, V-522 (Table 17). After five cycles of inbreeding, the yield decline averaged 16%. Virtually the entire yield decline occurred between the F1 and F2 generations; an equilibrium was reached in subsequent generations, as no statistically significant changes in yield were observed between the F2 and F5/F6 generations. Ramírez Vallejo et al. (1986) emphasize, however, that no selection pressure was applied during the trial, and they speculate that had selection pressure been applied (e.g., to simulate farmers' selection practices), then the advanced-generation progeny might well have outyielded the F2 plants.

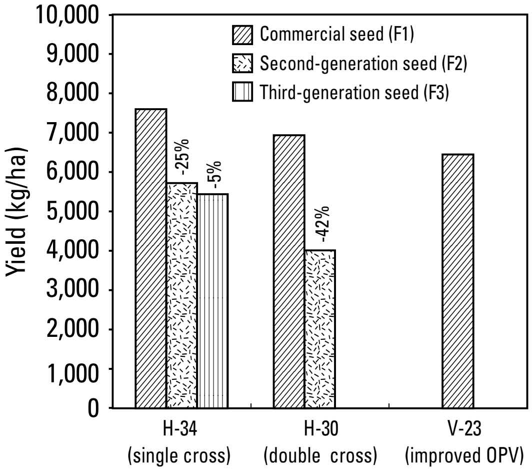


Figure 2. Effects of seed recycling on yields of two commercial maize hybrids, Mexico.
Source: Espinosa Calderón et al. (1990)

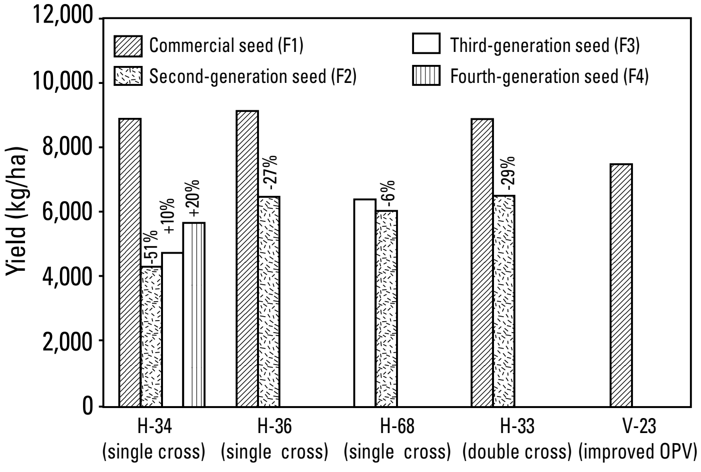


Figure 3. Effects of seed recycling on yields of selected maize hybrids, Mexico.
Source: Espinosa Calderón et al. (1993)

Table 17. Yield decline in advanced generations of hybrids, Mexico

	Generation of inbreeding					
	F1	F1′	F2′	F3′	F4′	F5′
H-503	4,194	3,577	3,213	2,586	3,097	3,160
H-507	3,964	3,393	3,014	2,937	3,122	3,092
H-510	4,239	3,473	2,781	3,302	2,710	3,216
Mean	4,132	3,481	3,002	2,942	2,976	3,156
Inbreeding depression (%)	n.a.	16	27	29	28	24

Source: Ramírez Vallejo et al. (1986).

As part of the same trial, Ramírez Vallejo et al. (1986) also tested the yields of double-cross hybrids formed by crossing advanced-generation plants (F1 to F5) of the single-cross hybrid parents used to form the original double-cross hybrids. They found that many of the double-cross hybrids produced using progressively more inbred single-cross parents yielded about the same as the check OPV and better than local varieties. They concluded that this finding helps explain why farmers in lowland tropical Mexico are often observed recycling their hybrids: by repeatedly recycling commercial hybrids and re-crossing the progeny, farmers in effect conduct their own breeding programs, and in many cases the superior genetic potential of commercial hybrids allows them to produce new "home-made" hybrids that outyield local landraces.

In the tropical lowlands of Guatemala, Pérez Rodas (1997) evaluated the effects of seed recycling on nine hybrids (seven double crosses and two three-way crosses) and three OPVs. As expected, F1 plants always significantly outperformed advanced-generation plants (Table 18, Figure 4). With all nine hybrids, the largest drop in yield was observed between the F1 and F2 generations; this initial yield decline observed between the F1 and F2 generations ranged from 8% to 28%. Yield performance in subsequent generations varied. In cases in which there had been a large yield decline between the F1 and F2 generations, the yield decline observed in the following generation was often negative – meaning F3 plants outyielded F2 plants. But in cases in which there had been a relatively small yield decline between the F1 and F2 generations, yield usually continued to fall in the following generation. In all cases, however, the yield change between the F2 and F3 generations was small – and often statistically insignificant. According to Pérez Rodas (1997), these results lend support to the hypothesis that after a single generation of cross pollination, a genetic equilibrium is achieved and expressed as yield stability (assuming no further addition of genetic material, no selection, and no mutation occur).

Table 18. Inbreeding depression in nine hybrids and three OPVs, Guatemala

	Type of material	Yield (t/ha)			Inbreeding depression (%)		
		F1	F2	F3	F1 → F2	F2 → F3	F1 → F3
HE-9103	DC	6,930	5,374	5,641	22	-5	19
HE-9101	DC	6,918	5,364	5,518	22	-3	20
HE-9122	DC	6,718	4,851	4,982	28	-3	26
HB-85	DC	6,601	5,100	5,083	23	0	23
HA-46	TWC	6,427	5,058	5,014	21	1	22
HB-83	DC	6,411	5,560	5,240	13	6	18
HE-9126	DC	6,359	5,494	5,270	14	4	17
HE-9124	DC	6,348	5,154	5,153	19	0	19
HA-28	TWC	5,710	5,227	4,974	8	5	13
Hybrid mean	—	6,491	5,242	5,208			
ICTA B1	OPV	5,775					
LM-7843	OPV	5,379					
LM-7442	OPV	5,656					

Source: Adapted from Pérez Rodas (1997).
Note: DC = double-cross hybrid, TWC = three-way-cross hybrid, and OPV = open-pollinated variety.

In the same trial, no statistically significant difference was detected between the performance of the advanced-generation hybrids and the three OPVs. Based on this finding, Pérez Rodas (1997) concludes that in cases in which F1 hybrid seed is unavailable or unaffordable, recycling of hybrids would be rational.

Zambezi et al. (1997) and Kumwenda et al. (1996, 1997) describe a series of on-farm trials carried out in Malawi with the objective of evaluating the effects of seed recycling on two single-cross hybrids (MH12 and MH16), one three-way-cross hybrid (NSCM41), and two top-cross hybrids (MH17 and MH18). One landrace (LFM) and one improved OPV (Chitedze Composite C, or CCC) were also included for comparative purposes. Between the F1 and F2 generations, recycled hybrids suffered marked declines in yield (Table 19). Averaged across three levels of fertilization, inbreeding depression was greater in the single-cross hybrids (24-33%) than in the three-way crosses (22%) or in the top crosses (16-21%). A much greater degree of inbreeding depression was observed in the unfertilized treatments. An additional generation of recycling (from F2 to F3) produced less inbreeding depression in both the single-cross and the top-cross hybrids; in several cases, F3 plants outyielded F2 plants, especially in unfertilized treatments.

In this trial, many of the advanced-generation hybrids maintained their yield advantage over the improved OPV and the landrace. In general the top-cross hybrids tolerated recycling better than the other types of hybrids, although one of the recycled single crosses also yielded well, particularly in the F3 generation (Figure 5). After one year of recycling, the recycled top crosses significantly outperformed the landrace, and after two years of recycling, they outperformed both the OPV and the landrace. In addition to showing that

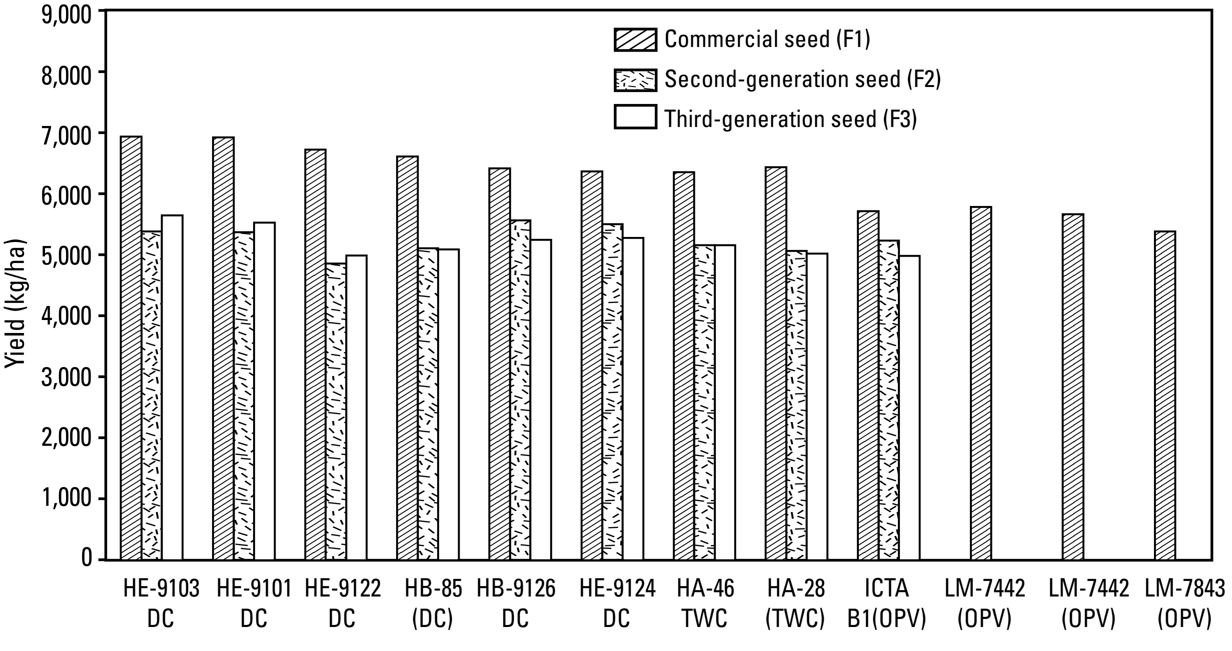


Figure 4. Effects of seed recycling on yields of selected maize cultivars, Guatemala.
Source: Pérez Rodas (1997).
Note: DC = double-cross hybrid, TWC = three-way-cross hybrid, and OPV = open-pollinated variety

Table 19. Inbreeding depression observed in selected maize hybrids, Malawi

Cultivar	Generation	Yield (kg/ha)	Inbreeding depression (%)	Cultivar	Generation	Yield (kg/ha)	Inbreeding depression (%)
MH12 [a]	F1	3,647		MH12 [a]	F1	4,429	
MH12 [a]	F2	2,762	24	MH12 [a]	F2	2,978	33
MH16 [a]	F1	3,945		MH12 [a]	F3	2,992	-1
MH16 [a]	F2	2,799	29	MH17 [b]	F1	5,027	
MH17 [b]	F1	4,405		MH17 [b]	F2	4,013	20
MH17 [b]	F2	3,711	16	MH17 [b]	F3	4,053	-1
MH18 [b]	F1	4,263		MH18 [b]	F1	4,449	
MH18 [b]	F2	3,448	19	MH18 [b]	F2	3,515	21
NSCM41 [c]	F1	3,997		MH18 [b]	F3	3,275	7
NSCM41 [c]	F2	3,135	22	CCC [d]		2,947	
LFM [e]		2,721		LFM [e]		2,609	

Source: Zambezi (1997); Kumwenda (1996, 1997).

[a] Single-cross hybrid.

[b] Top-cross hybrid.

[c] Three-way-cross hybrid.

[d] Open-pollinated variety.

[e] Local variety.

recycled hybrids often compare favorably to improved OPVs and landraces, these results also show how use of fertilizer tends to reduce inbreeding depression in recycled hybrids. The important implication of this latter finding is that depending on the price of fertilizer, it may be economical for farmers to recycle their top-cross hybrids rather than planting landraces.

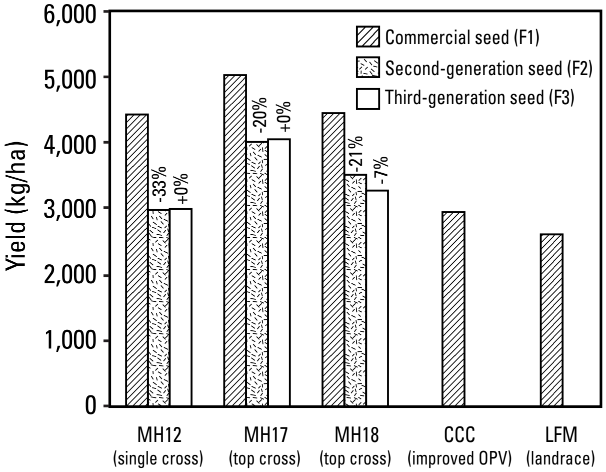


Figure 5. Effects of seed recycling on yields of three commercial maize hybrids, Malawi.
Source: Zambezi et al. (1997)

In a trial on an experiment station in Zimbabwe, Shumba (1990) evaluated the effects of seed recycling on the performance of two three-way cross hybrids (PNR473, R201) and one improved OPV (Kahalari Early Pearl). In both high-yielding and low-yielding environments, the hybrids outyielded the OPV. After one year of recycling, yields in F2 hybrid plants decreased by 7.4%; surprisingly, yields in recycled OPV plants decreased by about the same amount (7.8%) (Table 20, Figure 6). This unexpected result may have been attributable to management problems with the trial. The recycled seed was collected from extremely small experimental plots which may not have been sufficiently isolated; some outcrossing might have occurred with superior genotypes, thereby conserving some degree of heterosis in the recycled hybrids (Shumba, 1990; Waddington et al., 1997).

Table 20. Inbreeding depression observed in selected hybrids, Zimbabwe

		Location				
Cultivar	Generation	Makaholi	Mlezu	Matopos	Mean	Inbreeding depression (%)
R201[a]	F1	2,220	4,600	2,130	2,983	
R201[a]	F2	1,990	3,720	2,580	2,763	7
PNR 473[a]	F1	1,840	3,290	2,450	2,527	
PNR 473[a]	F2	1,890	3,370	2,860	2,707	-7
KEP[b]	F1	1,780	3,610	2,690	2,693	
KEP[b]	F2	1,300	3,290	2,860	2,483	8

Source: Shumba (1990).

[a] Three-way-cross hybrid.

[b] Open-pollinated variety.

In another trial carried out in Zimbabwe, Waddington et al. (1997) evaluated the effects of seed recycling on the performance of three three-way-cross hybrids (R215, R201, SC601), one single-cross hybrid (SR52), and two improved OPVs (Kalahari Early Pearl, ZM607). In this trial, recycled (F2) seed was collected from smallholder farmers; care was taken to ensure that the seed lots came from larger fields. As expected, F1 plants consistently outyielded F2 plants (Table 21). Yields of the recycled three-way crosses declined slightly less than the yields of the recycled single cross; inbreeding depression in the three-way crosses ranged from 26% to 41%, compared

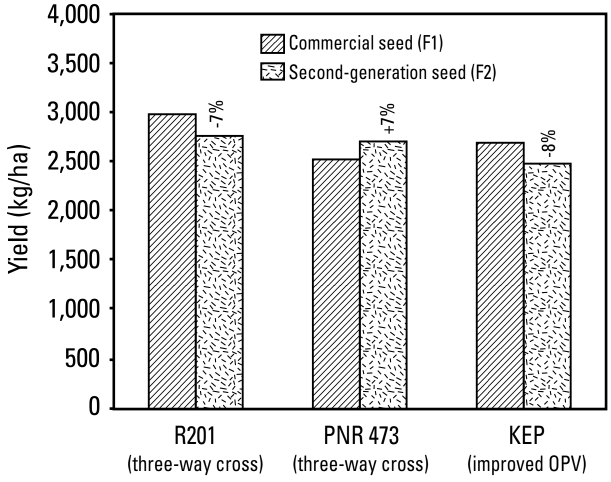


Figure 6. Effects of seed recycling on yields of two maize hybrids and one improved OPV (average across three semi-arid sites), Zimbabwe.
Source: Shumba (1990).

Table 21. Inbreeding depression observed in selected hybrids under two fertilizer application rates, Zimbabwe

	High fertilization rate				Low fertilization rate		
	Generation		Inbreeding		Generation		Inbreeding
Cultivar	F1	F2	depression (%)	Cultivar	F1	F2	depression (%)
SR52 [a]	4.98	2.92	41	SR52 [a]	3.55	2.09	41
SC601 [b]	5.15	3.04	41	SC601 [b]	4.23	2.53	40
R215 [b]	4.59	3.40	26	R215 [b]	3.09	2.06	33
R201 [b]	4.83	3.10	36	R201 [b]	3.64	2.47	32
KEP [c]	3.98			KEP [c]	3.12		
ZM607 [c]	3.94			ZM607 [c]	3.24		

Source: Waddington et al. (1997).

[a] Single-cross hybrid.

[b] Three-way-cross hybrid.

[c] Open-pollinated variety.

to 41% for the single cross (Figures 7 and 8). In percentage terms, the yield declines were similar under two different fertilizer application rates, a result that fails to support the findings of Zambezi et al. (1997) that fertilization reduces inbreeding depression in advanced-generation hybrids.

This trial produced unexpected results concerning the relative yield performance of recycled hybrids versus recycled OPVs. At the F1 generation, the hybrids tested by Waddington et al. outyielded the improved OPVs, but only under favorable conditions; under poor conditions, the yield advantage of the hybrids was negligible. At the F2 generation, the yield rankings were reversed: the improved OPVs outyielded the hybrids, with the yield advantage particularly pronounced under poor conditions. These findings suggest that in Zimbabwe, planting recycled hybrid seed under conditions of low rainfall and low soil fertility can be risky.

Combined effects

Most of the studies cited thus far involved trials that were specifically designed to isolate the effect of a particular source of genetic change. It is important to remember, however, that more than one source may be operating at the same time. Our search of the literature turned up several additional studies reporting on genetic changes in maize in which it was not possible to pinpoint the exact source of the change.

Perhaps the best example of how genetic changes can result from a combination of causes comes from a study carried out in northern Pakistan to assess the extent and rate of genetic change in Azam, an improved OPV (Longmire et al., unpublished). Following its release in 1985, Azam was widely adopted throughout the Swat Valley (Table 22). In an effort to assess the rate of genetic change in farmer-recycled Azam, seed samples of varying ages were collected from 50 farmers. These samples were grown out in on-station and on-farm trials,

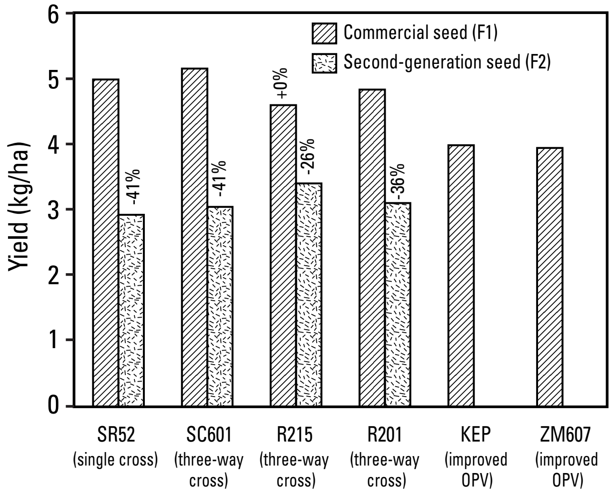


Figure 7. Effects of seed recycling on yields of four maize hybrids (high fertilizer treatment, Zimbabwe.
Source: Waddington et al. (1997).

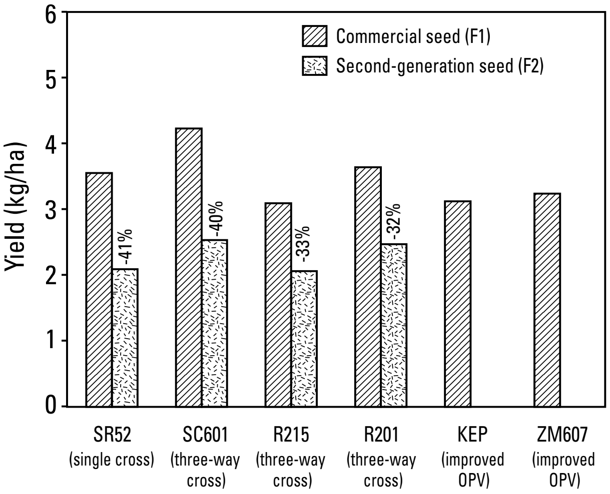


Figure 8. Effects of seed recycling on yields of four maize hybrids (low fertilizer treatment), Zimbabwe.
Source: Waddington et al. (1997)

Table 22. Maize production, variety, and seed use by environment, Swat District, Pakistan, 1989

	Irrigated valleys	Rainfed mountain zones	Swat District (total)
Maize area per farm (ha)	1.76	1.36	1.56
% area planted to improved maize	23	9	17
% area planted to Azam variety	16	4	13
% farmers growing local variety only	76	85	81
% farmers growing improved OPV only	18	8	13
% farmers growing local and improved	6	7	6
Age of local varieties (years)	16.7	14.1	15.5
Age of improved varieties (years)	3.4	2.1	3.2

Source: Longmire et al. (unpublished).

along with samples of commercial Azam seed. Data were recorded on grain yield, plant and ear height, and maturity (measured as days to 50% silking).

In the on-farm trials, plants grown from commercial seed yielded an average of 14% more than plants grown from recycled seed. Plant and ear height differed with a high degree of significance; plants grown from recycled seed were 10% taller on average, and ears on those plants were 12% higher on average. Small but significant differences were also observed in maturity, with plants grown from recycled seed showing shorter duration. In the on-station trials, the only significant differences detected involved plant and ear height, with plants grown from recycled seed again slightly taller, and ears on those plants again placed slightly higher. No difference was detected between plants grown from commercial versus recycled seed in terms of grain yield or maturity. The authors speculated that the lack of significance of these two characteristics in the on-station trials may have resulted from the relatively high levels of management, which might have reduced seed-related performance differences.

Contrary to expectations, no direct correlation was detected between the number of years the farmers had recycled Azam and the characteristics of interest (grain yield, plant and ear height, maturity). In other words, the observed genetic changes did not occur gradually through time. The authors concluded that this may have been due to the fact that successive generations of Azam grown in farmers' fields may have been exposed to different rates of contamination.

This example from Pakistan shows that it is not always possible to distinguish between the effects of multiple causes of genetic change that may be operating simultaneously. In the case of Azam, it is difficult to identify precisely the factor or factors responsible for genetic changes occurring through time. The increase in plant height resulted at least in part from farmer selection practices, but if these practices were consistent, the observed rate of genetic change should have been gradual. Since it was not gradual, unintentional contamination presumably was occurring as well.

Discussion

Every time a farmer recycles maize seed, as opposed to acquiring fresh seed whose genetic composition and degree of purity are reliably known, there is some risk that the latest generation of plants will differ from preceding generations in terms of its genetic composition. Various potential sources of genetic change have been discussed in this section, and evidence has been presented from studies that have sought to document the rate and extent of genetic change attributable to some of these sources.

Generally speaking, the empirical evidence suggests that throughout much of the developing world, maize cultivars are exposed to continual selection pressure. Genetic changes can be induced intentionally by farmers through varietal management and seed selection practices, or they can occur inadvertently as a result of environmental selection pressure, random mutation and gene segregation, unintentional contamination by foreign pollen, accidental seed mixing, and other factors. In the presence of seed recycling, intentional and unintentional selection pressure can lead to significant genetic changes, sometimes over relatively short periods.

Genetic change in maize is frequently mentioned in the context of the so-called "contamination" of MVs, but landraces also are subject to selection pressure. Although landraces are generally thought of as genetically stable and unchanging, we now know that even the most ancient landraces receive constant infusions of new genes and that their characteristics are constantly changing. Recent empirical work has shown that landraces may be subjected to several distinct types of intentional selection pressure. For example, Louette and Smale (1998) have shown that farmers in Cuzalapa, Mexico select seed for replanting on the basis of yield components (e.g., ear size, ear shape, kernel number, kernel size); selection based on these criteria tends to favor genotypes that are most productive under local conditions. At the same time, the Cuzalapa farmers also select seed based on characteristics of economic or cultural value in ways that protect perceived ideotypes. The presence of the second type of selection pressure helps explain how many different landraces can continue to coexist in conditions of heavy gene flow.

Landraces are not the only types of maize cultivars that undergo a continual process of genetic change, however. Improved OPVs and hybrids also undergo frequent changes in genetic composition as a result of seed recycling, which is much more common than is generally acknowledged.

In improved OPVs, as in landraces, genetic change results from a combination of intentional and unintentional selection pressure. Genetic change results not only from farmers' deliberate efforts to select for desired characteristics, but also from unintentional environmental pressures, accidental cross-pollination, random mutation, gene segregation, and so forth. Since both types of selection pressure are highly variable, it is difficult to generalize about the rate of change occurring in improved OPVs; depending on the circumstances, the genotype of an improved OPV can change significantly from one generation of plants to the next, or it can remain essentially the same across many generations of plants.

In hybrids, by far the most important source of genetic change is segregation — random recombination of alleles that occurs when seed is recycled. Several key results of our simulation exercise (designed to show the likely effects of inbreeding in maize hybrids) appear to be supported by findings published in the empirical literature on seed recycling:

- When maize hybrids are recycled, yield usually decreases significantly from the F1 to the F2 generation. Yield tends to stabilize in subsequent generations, however, and may eventually begin to increase again if farmers are exerting selection pressure.
- When maize hybrids are recycled, the size of the yield decrease observed between the F1 and F2 generations depends largely on the level of inbreeding of the original parents. In general, the greater the level of inbreeding in the parents, the greater the degree of heterosis in the F1 generation and the greater the yield decline between the F1 and F2 generations. This relationship may be confounded by environmental factors, however.
- The degree of inbreeding of the parents affects not only the size of the expected yield decrease but also its variability. The greater the level of heterozygosity in F1 plants, the greater the variability in inbreeding depression expected in F2 and F3 plants.
- Whether advanced-generation hybrids outperform landraces and improved OPVs depends on the original difference in yield and on the magnitude of the decline in yield caused by recycling. In some instances, recycled hybrids continue to outyield the other types of materials, which explains why hybrid recycling may make sense.
- Recycling of hybrids may have little effect on qualitative traits such as kernel size and shape, grain texture, pounding quality, etc.

Summary and Conclusion

This paper has reviewed the evidence on farmers' maize seed management practices and summarized what is known about the effects of seed recycling at the genotypic and phenotypic levels. Our goal in this final section is to summarize the findings of the empirical studies, identify recurring patterns, and if possible draw out implications for designing studies to measure the impacts of maize improvement research.

Many of the studies reviewed in this paper present convincing evidence that the practice of maize seed recycling is widespread. Although it is hardly surprising to learn that seed recycling is common among subsistence-oriented farmers (since many of these farmers grow landraces, and seed of landraces cannot be obtained through formal channels), it is interesting to learn that seed recycling is also quite common among many commercial farmers who regularly grow improved OPVs and hybrids.

The studies reviewed in this paper furthermore show that maize seed recycling is associated with a considerable amount of genetic change. Some of this change is intentional (resulting from seed selection practices, deliberate mixing of seed lots, and seed exchange), and some is unintentional (resulting from accidental contamination, random mutation, non-detectable environmental selection pressure, etc.).

The finding that genetic change in maize is ubiquitous and constant suggests that there may be a need to reassess the way we think about the traditional categories of maize cultivars – i.e., landraces, improved OPVs, and hybrids.

Landraces

Recent studies suggest that much of the conventional wisdom concerning maize landraces is incorrect. Despite the widespread belief that landraces are extremely stable, evidence is accumulating to show that landraces are often highly variable in terms of their origin and genetic composition. The magnitude of local seed exchange flows in fact raises questions as to whether the widely used concept of a landrace has any real genetic basis. Because seed of external origin is frequently added to local seed lots, and because farmers rarely succeed in maintaining complete isolation of their maize plots, even the most ancient of landraces frequently turn out to be genetically diverse and constantly changing (Louette, 1994). Many landraces apparently contain large amounts of improved germplasm, a fact that is generally overlooked in research impacts studies.

Improved OPVs

Improved OPVs are populations that have attained genetic equilibrium, so that random cross-pollination among plants of the same improved OPV should not affect the genic and genotypic frequencies. In theory, therefore, if an improved OPV is properly isolated, seed can be recycled for many years without undergoing visible changes. In practice, however, plant populations (and farmers' seed lots) are not infinitely large, so that rare alleles may be lost through time. Furthermore, farmers often cannot completely isolate their maize production plots, resulting in cross-pollination from other varieties growing in adjacent fields. Because these various sources of genetic change are difficult to control, most improved OPVs, like many landraces, turn out to be genetically diverse and constantly changing.

Hybrids

In the view of many professional maize breeders, hybrid maize constitutes "improved germplasm" only in the F1 generation; advanced-generation hybrids should not be considered improved because the genetic benefits of heterosis are greatly eroded when hybrid seed is recycled. Many research impacts studies implicitly support this view by including in the category "area planted to improved germplasm" only the area planted to F1 seed. But this restrictive view of what constitutes improved germplasm is likely to underestimate the impacts of maize breeding research. As many of the studies reviewed in this paper make clear, seed recycling practices frequently extend to maize hybrids, and planting of advanced-generation hybrids is common in many countries. While advanced-generation hybrids may not perform as well as crops grown from F1 seed, in many cases they significantly outperform the variety that the farmer was growing previously.

Implications for impacts studies

The finding that the categories traditionally used to classify maize germplasm are not nearly as discrete and well-defined as is commonly supposed has important implications for the practical business of estimating research impacts. Once we acknowledge that landraces, improved OPVs, and hybrids may be genetically diverse, and once we accept that materials in all three categories tend to change constantly, it becomes very difficult to define precisely what constitutes "improved germplasm" and to quantify the productivity gains associated with adoption. In order to make any progress in measuring research impacts, it may therefore be necessary to formulate workable criteria that can be used to distinguish between improved and unimproved germplasm. Only after such criteria have been defined will it be possible to estimate the area planted to improved cultivars and to quantify the productivity gains associated with their use.

We began this study hoping that a thorough review of the literature on seed recycling would allow us to formulate rigorous procedures for use in applied impacts assessment work. Our review of the theoretical and empirical evidence has indeed revealed many important insights about farmers' seed management practices and about the effects of those practices on the performance of maize varieties, but the enormous variability shown by the empirical evidence has complicated the task of formulating rigorous procedures for use in applied impacts assessment work. Answers to two key questions remain maddeningly elusive: What is the area planted to improved germplasm? What is the size of the productivity increase attributable to adoption of improved germplasm? Based on our review of the evidence on seed recycling, we can only conclude that in most cases, the only reasonable answer to both questions is, "It depends."

Unfortunately, "it depends" is not very useful for applied research impacts assessment work, because it implies that precise answers to the two key questions must be worked out empirically on a case-by-case basis. In cases in which this may not be feasible due to time and/or resource constraints, it may be necessary to formulate more workable rules of thumb to get on with the task (see the appendix). To a certain extent, these rules of thumb will have to be somewhat arbitrary, but arbitrariness is inevitable given the wide variability that this literature review has revealed.

References

Airy, J.M. 1950. "Current Problems of Detasseling," in American Seed Trade Association (ASTA), *Proceedings of the Fifth Hybrid Corn Industry Research Conference*, Chicago, Illinois, 28-29 November.

Aguirre, A. 1997. Analisis regional de la diversidad del maíz en el sureste de Guanajuato. Unpublished Ph.D. dissertation. Mexico, D.F.: Universidad Nacional Autonoma de Mexico, Facultad de Ciencias.

Akulumuka, V., Z. Mduruma, J. Kaswende, and E. Nkonya. 1997. Factors influencing maize seed recycling and their implications to hybrids. In: J.K. Ransom et al. (eds.), 1997. *Proceedings of the Fifth Eastern and Southern Africa Regional Maize Conference, 3-7 June, Arusha, Tanzania*. Nairobi: CIMMYT.

Allard, R.W. 1980. *Principios de la mejora genética de plantas* (traduccion L. Montoya). Barcelona: Omega.

Almekinders, C.J.M., N.P. Louwaars, and G.H. de Bruijn. 1994. Local seed systems and their importance for an improved seed supply in developing countries. *Euphytica 78*: 207-216.

Bassetti, P. and M.E. Westgate. 1993. Senescence and receptivity of maize silk. *Crop Science 33*: 275-278.

Beck, D. 1991. Management of maize seed production fields. Unpublished paper, CIMMYT, D.F., Mexico.

Bellon, M.R., and S.B. Brush. 1994. Keepers of maize in Chiapas, Mexico. *Economic Botany 48 (2)*: 196-209.

Bisanda, S., W. Mwangi, H. Verkuijl, A. Moshi, and P. Anandajayasekeram. 1998. *Adoption of Maize Production Technologies in the Southern Highlands of Tanzania*. Mexico, D.F.: CIMMYT, the Republic of Tanzania, and the Southern Africa Centre for Cooperation in Agricultural Research (SACCAR).

Brennan, J.P., and D. Byerlee. 1991. The rate of crop varietal replacement on farms: Measures and empirical results for wheat. *Plant Varieties and Seed 4*: 99-106

Byerlee, D., and P. Moya. 1993. *Impacts of International Wheat Breeding Research in the Developing World, 1966-1990*. Mexico, D.F.: CIMMYT.

Byerlee, D. 1994. *Modern varieties, productivity and sustainability. Recent experience and emerging challenges.* Mexico D.F.: CIMMYT.

Byerlee, D. and C.K. Eicher. 1997. *Africa's emerging maize revolution*. Boulder, Colorado: Lynne Rienner Publishers.

Castillo-González, F., and M. Goodman. 1995. Research on gene flow between improved maize and landraces. In: Serratos, J. A., M. C. Willcox, and F. Castillo-Gonzalez (eds). 1995. *Gene Flow among Maize Landraces, Improved Maize Varieties, and Teosinte: Implications for Transgenic Maize. Proceedings of a Forum.* Mexico, D.F.: INIFAP, CIMMYT, and CNBA.

Chiduza, C., S.R. Waddington, and I.K Mariga. 1994. Grain yield and economic performance of experimental open-pollinated varieties and released hybrids of maize in remote semi-arid areas of Zimbabwe. *Zimbabwe Journal of Agricultural Research 32 (1)*: 33-43.

Choto, C., G. Sain, and T. Montenegro. 1996. *Oferta y demanda de semilla mejorada de maíz en El Salvador.* Publicación Técnica de Difusión del Programa Colaborativo ICTA-PRM-CIMMYT.

Crossa, J., and R. Vencovsky. 1994. Implications of the variance effective population size on the genetic conservation of monoecious species. *Theoretical and Applied Genetics 89*: 936-942.

Crossa, J. 1989. Methodologies for estimating the sample size required for genetic conservation of outbreeding crops. *Theoretical and Applied Genetics 77*: 153-161.

Crow, J.F. 1997. Dominance and overdominance. In: CIMMYT, 1997. *Book of abstracts. The genetics and exploitation of heterosis in crops; An international symposium.* Mexico, D.F., Mexico.

De Bruijn, G., C. Almekinders and L. Keune. 1994. Farmers' knowledge and practices in smallholder seed production, with special reference to a case study in Central America. In: Hanson, J. (ed), 1994. *Seed production by smallholder farmers. Proceedings of the ILCA/ICARDA Research Planning Workshop held in ILCA, Addis Ababa, Ethiopia 13-15 June 1994.* Addis Ababa: ILCA.

Espinosa Calderón, A.E., M.A. López-Pereira, and M. Tadeo Robledo. 1993. Análisis agro-economico del uso de generaciones avanzadas de semilla mejorada de maíz en los valles altos de Mexico. Paper presented at the 40th Annual Meeting of the PCCMCA, 13-20 March, San José, Cost Rica.

Espinosa Calderón, A.E., M. Tadeo Robledo, and R. Valdivia Bernal. 1990. Capacidad productiva de semilla F1, F2 y F3 del hibrido simple de maíz H-34. *Proceedings of the12th National Congress of Phytogenetics, 3-7 September, Ciudad Juárez, Chihuahua, Mexico.*

Falconer, D.S. 1989. *Introduction to quantitative genetics.* London: Longman.

Fitch, J. 1983. Maize production practices and problems in Egypt: Results of three farmer surveys. CIMMYT Economics Program Working Paper 83/03. Mexico, D.F. CIMMYT.

Friis-Hansen, E. 1995. Seeds for African peasants, peasants' needs and agricultural research — The case of Zimbabwe. Uppsala, Sweden: Centre for Development Research.

Goodnight, C.J. 1997. Epistasis and heterosis. In: CIMMYT, 1997. *Book of abstracts. The genetics and exploitation of heterosis in crops; An international symposium.* Mexico, D.F., Mexico.

Granados, G., C. De Leon, and J. Lothrop (eds.). 1993. *Proceedings of the Fifth Regional Maize Workshop. Hanoi, Ho Chi Minh City: Vietnam, Nov. 15-21, 1993.*

Hallauer, A.R. 1997. Heterosis: What have we learned, what have we done, where are we headed? In: CIMMYT, 1997. *Book of abstracts. The genetics and exploitation of heterosis in crops; An international symposium.* Mexico, D.F., Mexico.

Hallauer, A. R., and J. B. Miranda. 1981. *Quantitative Genetics in Maize Breeding.* Ames: Iowa State University Press.

Hanson, J. (ed). 1994. Seed production by smallholder farmers. *Proceedings of the ILCA/ICARDA Research Planning Workshop held in ILCA, Addis Ababa, Ethiopia 13-15 June 1994.* Addis Ababa: ILCA.

Havazvidi, E. K., and M. J. Caulfield. 1987. Research on aspects of maize seed production in Zimbabwe. *Towards self-sufficiency. Proceedings of the Second Eastern, Central and Southern Africa Regional Maize Workshop, Zimbabwe, March 15-21, Harare.*

Heisey, P., M.L. Morris, D. Byerlee, and M.A. Lopez-Pereira. 1997. Economics of hybrid maize adoption. In: M.L. Morris (ed). 1997a. *Maize seed industries in developing countries.* Boulder, Colorado: Lynne Rienner Publishers.

Jugenheimer, R.W. 1981. *Variedades mejoradas, métodos de cultivo y producción de semillas.* (Traduccion Piña García). Mexico, D.F.: Limusa.

Khadka, R.J., G.B. Gurung, U.P. Rai, B.B. Kshetry, K. M. Syambu, and C.B. Karki. 1993. Report on a maize/millet Samuhik Bhraman in Dhankuta and Terhathum Districts. Pakhribas Agricultural Centre Working Paper No 38. Pakhribas Agricultural Centre, Dhankuta District, Koshi Zone, Nepal.

Kiesselbach, T.A. 1922. Corn investigations. *Nebraska Agricultural Experiment Station Research Bulletin 20*: 5-151.

Kiesselbach, T.A. 1933. The possibilities of modern corn breeding. *Proceedings of the World Grain Exhibitors' Conference (Canada), 2*:91-112.

Kiesselbach, T.A. 1960. Performance of advanced generation corn hybrids. *Agronomy Journal 52*:29-32.

Kumwenda, J.D. T., V.H. Kabambe, and W.D. Sakala. 1996. Edited by T.D. Benson. Maize commodity team annual report for the 1992/3 season, Chitedze Agricultural Research Station, Department of Agricultural Research, Ministry of Agriculture, Lilongwe, Malawi.

Kumwenda, J.D. T., V.H. Kabambe, and W.D. Sakala. 1997. Edited by T.D. Benson. Maize commodity team annual report for the 1993/4 season, Chitedze Agricultural Research Station, Department of Agricultural Research, Ministry of Agriculture, Lilongwe, Malawi.

Lee, M. 1997. Towards understanding and manipulating heterosis in crops – Can molecular genetics help? In: CIMMYT, 1997. *Book of abstracts. The genetics and exploitation of heterosis in crops; An international symposium.* Mexico, D.F., Mexico.

Leslie, J. 1986. The adoption of improved maize varieties in Pakhribas local target area: Results of a survey and their implications for further research. PAC Economic Planning Unit. Technical Paper No. 88, Pakhribas Agricultural Centre, Dhankuta District, Koshi Zone, Nepal.

Li, C.C. 1974. *Population genetics.* Pacific Grove, California: Boxwood Press.

Longmire, J.L., and M. Fida. No date. Unpublished manuscript. Assessing maize varietal deterioration using on-farm and on-station research: Azam maize in the Swat Valley, North West Frontier Province, Pakistan. Unpublished paper, CIMMYT Economics Program. Mexico, D.F.: CIMMYT.

López-Pereira, M.A., and A. Espinosa Calderón. 1993. Análisis economico de la producción y uso de la semilla mejorada de maíz: El caso de Mexico. Paper presented at the 39th Annual Meeting of the PCCMCA, 28 March - 3 April, Guatemala City, Guatemala.

López-Pereira, M.A., and M. Filippello. 1994. Maize seed industries revisited: Emerging roles of the public and private sectors. Part 1 of *CIMMYT 1993/4 World Maize Facts and Trends. Maize Seed Industries Revisited: Emerging Roles of the Public and Private Sectors.* Mexico, D.F.: CIMMYT.

López-Pereira, M.A., and M.L. Morris. 1994. *Impacts of international maize breeding research in the developing world, 1966-1990.* Mexico, D.F.: CIMMYT.

Louette, D. 1995. Seed exchange among farmers and gene flow among maize varieties in traditional agricultural systems. In: Serratos et al. (eds) (1994), *Gene Flow among Maize Landraces, Improved Maize Varieties, and Teosinte: Implications for Transgenic Maize. Proceedings of a Forum.* Mexico, D.F.: INIFAP, CIMMYT, and CNBA.

Louette, D. 1994. Gestion traditionnelle de variétés de maïs dans la réserve de la Biosphère Sierra de Manantlán (RBSM, états de Jalisco et Colima, Mexique) et conservation in situ des ressources génétiques des plantes cultivées. Thèse de doctorat, Ecole Nationale Supérieure Agronomique de Montpellier, Montpellier.

Louette, D., A. Charrier, and J. Berthaud. 1997. *In situ* conservation of maize in Mexico: Genetic diversity and maize seed management in a traditional community. *Economic Botany 51 (1)*: 20-38.

Louette, D., and M. Smale. 1998. Farmers' seed selection practices and maize variety characteristics in a traditionally-based Mexican community. CIMMYT Economics Program Working Paper. Mexico, D.F.: CIMMYT.

Martin, J.M., and A.R. Hallauer. 1976. Relation between heterozygosis and yield for four types of maize inbred lines. *Egyptian Journal of Genetics and Cytology 5*: 119-135.

Mather, K., and J.L. Jinks. 1971. *Biometrical genetics*. London: Chapman and Hall.

Morris, M.L. (ed). 1997a. *Maize seed industries in developing countries*. Boulder, Colorado: Lynne Rienner Publishers.

Morris, M.L. 1997b. Maize in the developing world: Waiting for a green revolution. In: M.L. Morris (ed.), 1997a. *Maize seed industries in developing countries*. Boulder, Colorado: Lynne Rienner Publishers.

Murillo Navarrete, P. 1978. Estimación del grado de cruzamiento en lotes de selección masal sin aislamiento. Tesis profesional. Universidad de Guadalajara, Colegio de Agricultura. Guadalajara, Jalisco, Mexico.

Neal, N.P. 1935. The decrease in yielding capacity in advanced generations of hybrid corn. *Journal of the American Society of Agronomy 27*: 666-670.

Ortega-Paczka, R.A. 1973. Variación en maíz y cambios socio-económicos en Chiapas, México 1946-1971. Tesis de especialidad Botánica. Colegio de Posgraduados, Chapingo, Mexico.

Ortega Sequeira, I., H. Bos, and J. Pasquier. 1993. Semillas, sistemas locales de provision de semillas de maíz y frijol. In: *Cuadernos del Centro para la Investigación, la promoción y el desarollo rural y social (CIPRES), No 16.* Managua, Nicaragua.

Ortiz Torres, E. 1993. Aislamiento y dispersión de polen en la producción de semilla de maíz. Tesis de M.C., Colegio de Postgraduados, Montecillo, Mexico.

Pandey, S. 1997. Varietal development: Conventional plant breeding. In M.L. Morris (ed.), 1997a. *Maize seed industries in developing countries*. Boulder, Colorado: Lynne Rienner Publishers.

Perales R., H. 1998. Conservation and evolution of maize in Amecameca and Cuautla valleys of Mexico. Unpublished Ph.D. dissertation. University of California at Davis.

Perales R., H., S.B. Brush, and C.O. Qualset. 1998. Agronomic and economic competitiveness of maize landraces and *in situ* conservation in Mexico. In: M. Smale et al. (eds), *Farmers, gene banks, and crop breeding: Economic analyses of diversity in wheat, maize, and rice.* Boston, Dordrecht, and London: Kluwer Academic Publishers.

Pérez Rodas, C. N. 1997. Evaluación de generaciones filiales de nueve hibridos de maíz *Zea mays L.* en tres localidades de la zona tropical baja de Guatemala. Tesis. Universidad Rafael Landivar, Facultad de Ciencias Agricolas y Ambientales, Guatemala.

Poehlman, J.M. 1979. *Breeding field crops.* AVI Publishing Co., Inc., Westport, Connecticut.

Pollak, E., H.F. Robinson, and R.E. Comstock. 1957. Interpopulation hybrids in open-pollinated varieties of maize. *American Naturalist 91*: 387-391.

Powers, L. 1941. Inheritance of quantitative characters in crosses involving two species of Lycopersicon. *Journal of Agricultural Research 63*:149-174.

Ransom, J.K., A. F.E. Palmer, B. T. Zambezi, Z.O. Mduruma, S.R. Waddington, K.V. Pixley, and D.C. Jewell (eds). 1997. *Maize productivity gains through research and technology dissemination. Proceedings of the Fifth Eastern and Southern Africa Regional Maize Conference. 3-7 June, Arusha, Tanzania.* Nairobi: CIMMYT.

Ramírez Vallejo, P., M.M. Balderas, and F. Gerón Xavier. 1986. Potencial productivo de las generaciones avanzadas de los híbridos tropicales de maíz H-503, H-507 y H-510. *Fitotecnia 8*: 20-34.

Rice, E., M. Smale, and J.L. Blanco. 1997. Farmers' use of improved seed selection practices in Mexican maize: Evidence and issues from the Sierra de Santa Marta. CIMMYT Economics Program Working Paper 97-03, Mexico, D.F.: CIMMYT.

Ristanovic, D., P. Gibson, and K.N. Rao. 1985. Development and evaluation of maize hybrids in Zambia. In: *Proceedings of the First Eastern, Central and Southern Africa Regional Maize Workshop, Lusaka, March 10-17, Zambia.* Nairobi: CIMMYT.

Sain, G., F. Herrera, and J. Martinez. 1996. Adopción y uso de semilla mejorada de maíz entre pequeños agricultores de Guatemala. Publicación Técnica de Difusión del Programa Colaborativo ICTA-PRM-CIMMYT.

Seed Coop Company of Zimbabwe, Ltd. 1987. Research Summary 1985-6. Rattray-Arnold Research Station Annual Report, agronomy section. Zimbabwe.

Seeley, J. 1988. Household maize variety selection in Lumle Agricultural Centre Extension Command Area. Technical Paper 88/24. Pokhara, Nepal: Lumle Agricultural Centre.

Serratos, J.A., M. C. Willcox, and F. Castillo-Gonzalez (eds). 1995. *Gene flow among Maize Landraces, Improved Maize Varieties and Teosinte: Implications for Transgenic Maize. Proceedings of a Forum.* Mexico, D.F. CIMMYT.

Sehgal, S. and J. Van Rompaey. 1993. Prospects for the hybrid seed industry in developing countries. In: G. Granados, C. De Leon, and J. Lothrop (eds.). 1993. *Proceedings of the Fifth Regional Maize Workshop. Hanoi, Ho Chi Minh City: Vietnam, Nov. 15-21, 1993.*

SEP (Secretaría de Educación Publica). 1982. *Nuestro maíz – Treinta monografias populares*. Consejo Naconal de Fomento Educativo, Secretaría de Educación Publica, Tomo 1 y 2, Mexico.

Shank, D.B. and M.W. Adams. 1960. Environmental variability within inbred lines and single crosses of maize. *Journal of Genetics 57*: 119-126.

Shehata, A.H. and N.L. Dhawan. 1975. Genetic analysis of grain yield in maize as manifested in genetically diverse varietal populations and their crosses. *Egyptian Journal of Genetics and Cytology 4*: 90-116.

Shull, G.H. 1908. The composition of a field of maize. *American Breeders Association Report 4*: 296.

Shull, G.H. 1909. A pure-line method of corn breeding. *American Breeders Association Report 5*: 51-59.

Shull, G.H. 1952. Beginnings of the heterosis concept. In: J.W. Gowen (ed.), *Heterosis.* Ames: Iowa State College Press.

Shumba, E.M. 1990. Yield comparison of first and second generation hybrid and open pollinated maize cultivars under similar growth conditions in semi-arid areas. *Zimbabwe Journal of Agricultural Research, 28*: 133-139.

Singh, R. P., and M.L. Morris. 1997. Adoption, management and impact of hybrid maize seed in India. CIMMYT Economics Program Working Paper 97-05. Mexico, D.F.: CIMMYT.

Smale, M., and A. Phiri, with contributions from G.A. Chikafa, P.W. Heisey, F. Mahatta, M.N.S. Msowoya, E.B.K. Mwanyango, H.G. Sagara, and H.A.C. Selemani. Institutional change and discontinuities in farmers' use of hybrid maize seed and fertilizer in Malawi: Findings from the 1996-97 CIMMYT/MoALD Survey. CIMMYT Economics Program Working Paper 98-01. Mexico, D.F.: CIMMYT.

Sperling, L., and M.E. Loevinsohn. 1993. The dynamics of adoption: Distribution and mortality of bean varieties among small farmers in Rwanda. *Agricultural Systems, 41*: 441-453.

Sperling, L., U. Scheidegger, and R. Buruchara. 1996. Designing seed systems with small farmers: Principles derived from bean research in the Great Lakes region of Africa. Agricultural Research and Extension Network Paper No 60 (January 1996). London: ODA.

Sprague, G.F. (ed). 1977. *Corn and Corn Improvement.* Madison, Wisconsin: American Society of Agronomy.

Tripp, R. 1996. Biodiversity and Modern Crop Varieties: Sharpening the debate. *Journal of the Agriculture, Food, and Human Values Society, 13 (4)*: 48-63.

Tripp, R., and W. van der Heide. 1996. The erosion of crop genetic diversity: Challenges, strategies and uncertainties. Natural Resource Perspectives, No 7, March 1996. London: ODI.

Tsaftaris, A.S., M. Kafka, A. Polidoros, and E. Tani,. 1997. Epigenetic changes in maize DNA and heterosis. In: CIMMYT, 1997. *Book of abstracts. The genetics and exploitation of heterosis in crops; An international symposium.* Mexico, D.F., Mexico.

Vega Zaragoza, G. 1973. Estudio de infiltración genética de los maices mejorados sobre los criollos de temporal de los estados de México, Puebla y Tlaxcala. Tesis de M.C. Colegio de Postgraduados de Chapingo, Mexico.

Waddington, S. R., J. Karigwindi, and J. Chifamba. 1997. CIMMYT maize soil fertility and agronomy research in Southern Africa. In: CIMMYT, 1997. *CIMMYT-Zimbabwe Annual Research Report, 1995/6.* Harare: CIMMYT.

Wierema, H., A. Almekinders, L. Keune, and R. Vermeer. 1993. La producción campesina en Centro-America: Los sistemas locales de semilla. Tilburg-IVO 204.

Wood, D. and J. Lenné. 1997. The conservation of agrobiodiversity on-farm: Questioning the emerging paradogm. *Biodiversity and Conservation 6*: 109-129.

Wright, S. 1922. The effects of inbreeding and crossbreeding on guinea pigs. III. Crosses between highly inbred families. USDA Bulletin No. 1121. Washinton, DC: United States Department of Agriculture.

Wright, M., and P. Tyler. 1994. Traditional seed saving practices in Northern Ghana and Central Malawi. R2102 (S), NRI: Chatham, U.K.

Zambezi, B.T., F.K. Nyondo, G. Nkhono, G.F. Mbingwani, and T.F. Chakhuta. 1997. Evaluation of recycled maize hybrids at three levels of nitrogen in Malawi. In: J.K. Ransom, A.F.E. Palmer, B.T. Zambezi, Z.O. Mduruma, S.R. Waddington, K.V. Pixley, and D.C. Jewell (eds), 1997. *Maize productivity gains through research and technology dissemination. Proceedings of the Fifth Eastern and Southern Africa Regional Maize Conference. 3-7 June, Arusha, Tanzania.* CIMMYT, Nairobi.

Appendix

Guidelines for Estimating the Returns to Maize Breeding Research

In order to measure the farm-level impacts of maize breeding research, it is necessary to estimate two key parameters: (1) the area planted to improved germplasm and (2) the productivity gains attributable to adoption of improved germplasm. Using a simple economic surplus model, these two parameters can be combined with the price of maize to calculate the gross benefits attributable to maize breeding research in a given period:

$$B_t = A_t * y_t * p_t \qquad (A1)$$

where:

B = gross economic benefits attributable to maize breeding research,
A = area planted to improved OPVs and hybrids,
y = yield gain attributable to maize breeding research,[6] and
p = price of maize.

Although the two key parameters (A and y) are conceptually straightforward, measuring them is often quite difficult in practice.

(1) *Area planted to improved germplasm*

Ideally, estimates of the area planted to improved germplasm should be based on farm-level survey data. Farm-level surveys tend to be costly, however, with the result that in many countries they are carried out infrequently if at all, and generally only in selected regions. Area estimates based on farm-level surveys can sometimes be cross-checked using data on commercial seed sales (assuming average seed rates are known), but this approach may be of limited use when seed recycling is extensive.

Estimates of the area planted to improved germplasm generally can be improved by taking into account the extent of seed recycling. Once seed recycling is considered, however, a new problem presents itself. Given the propensity of maize to cross-pollinate, at what point does recycling sufficiently alter the genetic composition of an improved variety or hybrid that it can no longer be considered “improved”? This is basically an empirical question, since the rate of genetic change from one generation of seed to the next depends on location-specific factors, including not only agroclimatic conditions, but also farmers’ crop and seed management practices.

Because of the difficulty of defining precisely what constitutes an “improved” cultivar, crop reporting authorities in many countries adopt a conservative approach under which only areas planted to commercial (F1) seed are considered to be planted to improved cultivars; areas planted to recycled seed are classified as being under “unimproved” or “local” varieties. Although conceptually defensible, the problem with this conservative approach is that it results in underestimation of the area planted to improved germplasm.

---

[6] The productivity gains associated with MV adoption are conventionally measured in terms of the yield increase per unit land area achieved when input costs are held constant. An alternative approach is to measure cost savings at a given yield level.

(2) *Productivity gains attributable to adoption of improved germplasm*

In theory, the productivity gains attributable to the adoption of improved germplasm are expressed as the difference between the yields obtained with the farmer's current variety (which depending on the circumstances may be a landrace, a local variety, or an older MV) and the MV developed by the breeding program, holding all other inputs constant. In practice, this difference is difficult to measure for at least two reasons. First, because the genetic potential of any cultivar interacts with environmental factors (GxE interaction), the yield difference tends to vary considerably across locations and between cropping seasons. Second, when farmers recycle seed, the genetic composition changes from one generation to the next, which may also affect the yield difference.

Practical approaches for estimating research impacts

Theoretical and empirical evidence reviewed in this paper make clear that because of seed recycling practices and other factors, genetic change in farmer-maintained maize cultivars is ubiquitous and constant. This finding has important implications for the practical business of estimating research impacts. Once we concede that landraces, improved OPVs, and hybrids may be genetically diverse, and once we accept that materials in all three categories tend to change constantly, it becomes very difficult to define precisely what constitutes "improved germplasm" and to quantify the productivity gains associated with adoption.

In order to make any progress in measuring the two key parameters described above, it is necessary to formulate workable criteria for distinguishing between improved and unimproved germplasm. Once such criteria have been defined, it may be possible to draw useful conclusions about the size of the productivity gains associated with the use of improved germplasm. The fact that the criteria to some extent must be arbitrary does not necessarily undermine their usefulness; what is important is that they be workable, defensible, and consistent.

Estimating the area planted to MVs

In estimating the area planted to MVs, what criteria can be used to distinguish between improved and unimproved germplasm?

Genotype-based criteria. From a technical point of view, the most rigorous way to define improved germplasm would be on the basis of genotypic information. For example, an improved cultivar might be defined as one whose genotype is identical to the genotype of an improved OPV or hybrid produced by a scientific plant breeding program. With the advent of genetic fingerprinting techniques, it should soon be possible to sequence individual plants rapidly and inexpensively, which would facilitate such comparisons.

While appealing in theory, genotype-based criteria may turn out to be tricky to define in practice. To begin with, exactly how similar would two (or more) plants have to be in order to be considered genetically identical? Because of their propensity to cross-pollinate, maize plants are by nature genetically heterogeneous, and even within a field of hybrids, individual plants will tend to differ at the genetic level. Thus, we would have to decide exactly how different the plants would have to be at the genetic level before they would be considered distinct. This decision would not be easy, especially considering that a large proportion of the maize genome consists of repetitive DNA sequences that code for no known function; this means that even if it could be established that two plants differ at the molecular level, these differences may or may not be reflected in differences that can be detected at the phenotypic level.

Ignoring for a moment these conceptual problems, a more serious limitation with genotype-based criteria is that often they would be impractical for applied impacts assessment. In attempting to estimate the area planted to a particular improved OPV or hybrid, for example, it would not be practical to sequence randomly selected plants to determine their genotype.

Performance-based criteria: If we concede that genotype-based criteria are likely to be conceptually elusive or impractical to implement, performance-based criteria may offer an alternative strategy for classifying maize cultivars. For example, a variety found growing in a farmer's field might be considered improved as long as certain key phenotypic and/or agronomic traits (e.g., yield, height, flowering date, insect or disease resistance) closely resemble those of a known MV (improved OPV or hybrid).

One big advantage of performance-based criteria is that they sidestep the complex issue of genotypic variability. The underlying philosophy is quite simple: If a plant looks like a particular MV and behaves like that MV, then for practical purposes it can be considered to be that MV, regardless of possible differences at the genotypic level. But while the use of performance-based criteria might solve one problem (i.e., the problem of having to sequence randomly selected plants to determine their genotype), it would not obviate the need for empirical measurement, because in many cases casual observation will not reveal whether a cultivar growing in a farmer's field does in fact resemble a known MV in terms of its phenotypic traits and/or agronomic performance.

Workable rules of thumb. While it would be convenient to be able to distinguish between improved and unimproved germplasm on the basis of genotype- or performance-based criteria, applied impacts assessment work requires criteria that are simple and workable. In this spirit, we propose the following rules of thumb that can be applied quickly and easily, using information that is relatively inexpensive to obtain and reasonably accurate.

The *area planted to unimproved germplasm* includes:
1. area planted to landraces or local varieties,
2. area planted to improved OPVs grown from seed that has been recycled four or more times, and
3. area planted to hybrids grown from seed that has been recycled two or more times (i.e., any advanced-generation seed).

The *area planted to improved germplasm* includes:
1. area planted to improved OPVs grown from commercial seed or from farmer-saved seed that has been recycled three times or less, and
2. area planted to hybrids grown from commercial seed (F1 seed).

It is important to understand that there is nothing magic about these proposed rules of thumb. Quite the opposite; they are in a sense rather arbitrary. But arbitrariness is inevitable, at least as long as farmers continue to recycle seed. Given that maize plants grown from recycled seed will tend to have diverse genetic backgrounds, "improved" and "unimproved" will rarely represent discrete, mutually exclusive categories; rather, "improved" and "unimproved' will almost always be matters of degree. Thus, it is unreasonable to expect to come up with objective criteria for defining improved and unimproved germplasm, and the best we can hope for is to establish some workable set of rules for distinguishing between the two. Based on the many empirical studies reviewed in this paper, we believe the rules we have proposed constitute such a set.

Two types of information are needed to implement these proposed rules of thumb: (1) information on the area planted to each type of cultivar (landraces, improved OPVs, hybrids) and (2) information on farmers' seed (particularly the source of the seed and, if it is recycled seed, the number of times it has been recycled). In many countries, the first type of information is regularly collected through periodic farm-level surveys and published in official crop reporting bulletins. Although the second type of information is rarely available in published form, it is relatively easy to obtain by interviewing farmers.

In cases when these two types of information are not available, it may be possible to implement the proposed rules of thumb indirectly by using a third type of information, namely, information about commercial seed sales. Although data on commercial seed sales are not always published, particularly in countries where the private sector is active in the seed industry, it is often easier to survey seed organizations than to conduct a large number of detailed farm-level adoption surveys.

Assuming data are available on commercial sales of hybrid seed within a given period, then the area planted to hybrids in that period can be calculated as follows:

$$A_{\text{hybrid}} = S_{\text{hybrid}} \,/\, r_{\text{hybrid}} \qquad \textit{(A2)}$$

where:

A_{hybrid} = area planted to hybrid maize,
S_{hybrid} = commercial sales of hybrid maize seed , and
r_{hybrid} = average hybrid maize seeding rate.

Similarly, assuming data are available on commercial sales of OPV seed within a given period, then the area planted to hybrids in that period can be calculated as follows:

$$A_{\text{OPV}} = (S_{\text{OPV}} \,/\, r_{\text{OPV}}) * c \qquad \textit{(A3)}$$

where:

A_{OPV} = area planted to improved OPVs,
S_{OPV} = commercial sales of improved OPV seed,
r_{OPV} = average seeding rate for improved OPVs, and
c = OPV recycling factor.

As a general rule, we propose that the OPV recycling factor (*c*) be assigned a value of 4. This implies that on average OPV seed will be recycled three times and that on average the area planted to recycled seed in the second, third, and fourth year will be equal to the area planted to commercial seed in the first year (i.e., no "multiplying up" effect). In some cases, these assumptions will result in an underestimation of the total area planted to improved OPVs, i.e., whenever the area planted to recycled seed in the second, third, and/or fourth years exceeds the area planted in the first year to commercial seed. However, in many cases this "multiplying up" effect will be offset at least in part by the fact that advanced-generation OPV seed does not perform as well as commercial seed.

Estimating productivity gains attributable to adoption of MVs

Estimating productivity gains associated with MV adoption is complicated by at least four factors:

(1) Productivity gains may be expressed in many different ways. Although productivity is often expressed in terms of grain yield per unit land area, this is not always an appropriate measure. In some instances, the benefits of improved germplasm are reflected in earlier maturity, enhanced grain quality, improved quantity or quality of fodder, or better tolerance of biotic or abiotic stresses (which may allow the crop to be grown in places or at times where it could not be grown before, even if the grain yield remains unchanged).

(2) Productivity gains will vary depending on the type of MV adoption that is taking place. For example, yield gains will differ greatly (both in absolute and relative terms) depending on whether farmers are replacing a landrace with an improved OPV, a landrace with a hybrid, an older improved OPV with a newer improved OPV, an improved OPV with a hybrid, an older hybrid with a newer hybrid, and so forth.

(3) Productivity gains will vary depending on environmental factors, including agroclimatic conditions and farmers' management practices. The same MV may deliver significant productivity gains in favorable production conditions and modest productivity gains in unfavorable production conditions.

(4) Productivity gains can change through time as a result of seed recycling. As we have seen, when farmers recycle their seed, grain yield and other productivity measures can change dramatically from one generation of plants to the next as a result of deliberate selection pressure or inadvertent genetic change.

Because of these four factors, the size of the productivity gains associated with the adoption of maize MVs can vary tremendously. In subsistence-oriented cropping systems where farmers are adopting MVs and improved crop management practices for the first time, it is not unheard of to witness yield increases of 100% or more. In modern commercial production systems in which farmers regularly replace high-yielding single-cross hybrids, a yield increase of only 2-3% might be considered satisfactory.

Given this variability, we are reluctant to suggest a single, universally applicable rule of thumb for use in applied research impacts work. Instead, we conclude that the productivity gains attributable to MV adoption are best estimated on a case-by-case basis, taking into account the specific circumstances, including the type of germplasm involved, the production environment, and farmers' seed and crop management practices. In the complete absence of location-specific data on incremental yield gains attributable to MV adoption, however, the following assumptions seem reasonable:

- improved OPV replacing a landrace: 25% average yield gain;
- improved OPV replacing an older improved OPV: 15% average yield gain;
- hybrid replacing a landrace: 50% average yield gain;
- hybrid replacing an improved OPV: 25% average yield gain;
- hybrid replacing an older hybrid: 15% average yield gain.

Recent Economics Working Papers

97-05 Organization and Performance of National Maize Seed Industries: A New Institutionalist Perspective
M.L. Morris and M. Smale

97-06 Adoption, Management, and Impact of Hybrid Maize Seed in India
R.P. Singh and M.L. Morris

98-01 Institutional Change and Discontinuities in Farmers' Use of Hybrid Maize Seed and Fertilizer in Malawi: Findings from the 1996-97 CIMMYT MoALD Survey
M. Smale, A.Phiri, and contributors

98-02 An Economic Analysis of the *Abonera* Maize Production System in the Atlantic Coast of Honduras
G. Sain and D.Buckles

98-03 Optimal Search in *Ex situ* Collections of Wheat Genetic Resources
D. Gollin, M. Smale, and B. Skovmand

98-04 Farmers' Seed Selection Practices and Maize Variety Characteristics in a Traditionally-Based Mexican Community
D. Louette and M. Smale

98-05 A Conceptual Framework for Valuing On-Farm Genetic Resources
M.R. Bellon and M. Smale

98-06 A Regional Analysis of Maize Biological Diversity in Southeastern Guanajuato, Mexico
J. A. Aguirre Gómez, M.R. Bellon, and M. Smale

99-01 Adoption of Maize Conservation Tillage in Azuero, Panama
A. Pereira de Herrera and G. Sain

99-02 Maize Production and Agricultural Policies in Central America and Mexico
G. Sain and M.A. López–Pereira

99-03 Cereal Crop Productivity in Developing Countries: Past Trends and Future Prospects
P. L. Pingali and P.W. Heisey

99-04 Adoption and Use of Improved Maize by Small-Scale Farmers in Southeast Guatemala
G. Saín and J. Martínez

99-05 Sources of Productivity Growth in Wheat: A Review of Recent Performance and Medium- to Long-Term Prospects
R.M. Rejesus, P.W. Heisey, and M. Smale

99-06 Changing Competitiveness of the Wheat Sector of Kazakstan and Sources of Future Productivity Growth
J. Longmire and A. Moldashev

CIMMYT Research Report

No. 4 Maize Technology in Malawi: A Green Revolution in the Making?
P.W. Heisey and M. Smale

CIMMYT World Facts and Trends

CIMMYT World Wheat Facts and Trends, 1995/96
Understanding Global Trends in the Use of Wheat Genetic Diversity and International Flows of Wheat Genetic Resources

CIMMYT World Maize Facts and Trends, 1997/98
Maize Production in Drought–stressed Environments: Technical Options and Research Resource Allocations